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Dynamics of Sudanian Savanna-Woodland Ecosystem in Response to Disturbances

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**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, Muluaem 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 Muluaem 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, Muluaem 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, Muluaem 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.

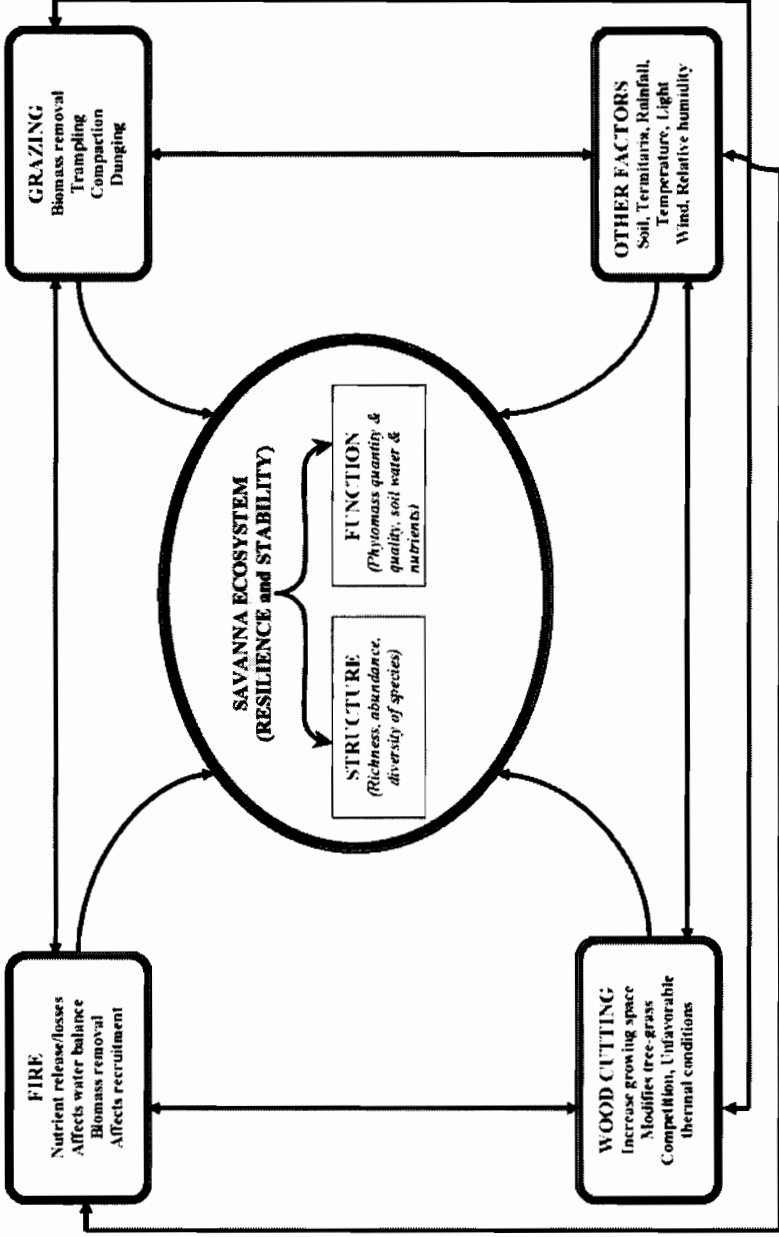


Fig. 1. A simplified conceptual framework of effects of disturbances and their interactions on structure and function of savanna-woodland ecosystem

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	Increased 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 (Myserud, 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, Mwangi & 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).

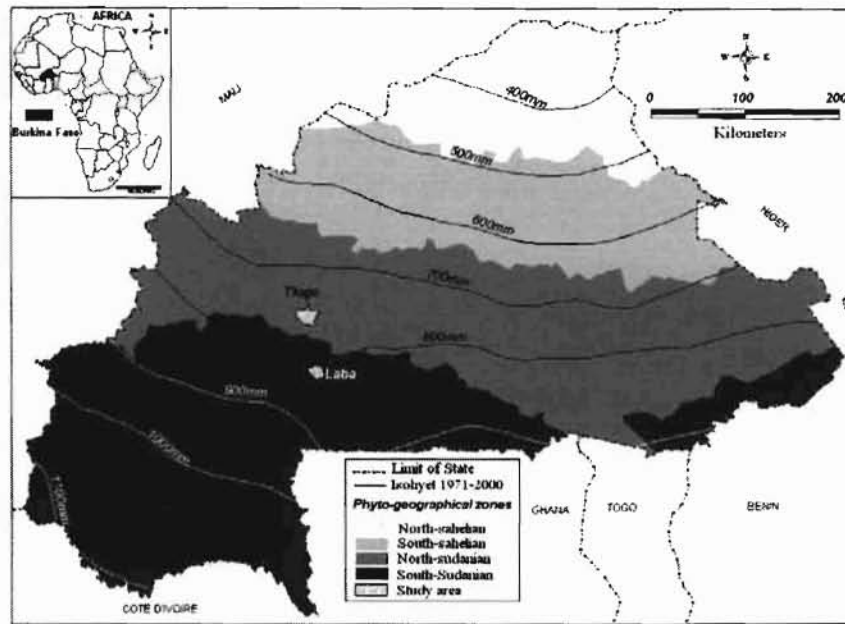


Fig. 2. Vegetation map of Burkina Faso with isohyets and location of the two study sites (Readapted April 2007 by CTIG/INERA/Burkina Faso after Fontes & Guinko 1995 and Direction of the National Meteorology).

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).

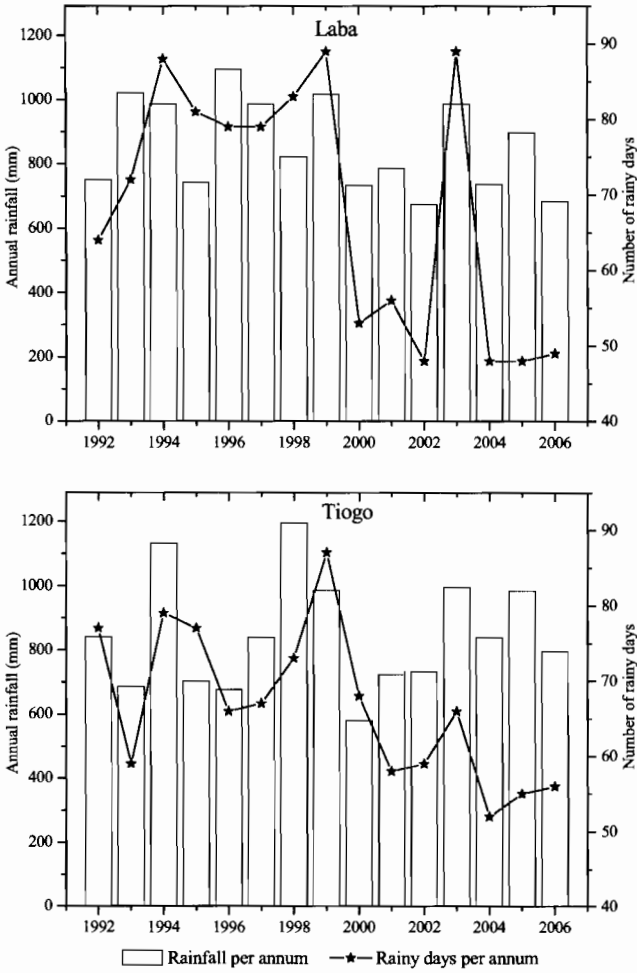


Fig. 3. Annual rainfall and number of rainy days for Tiogo and Laba across the study period.

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).

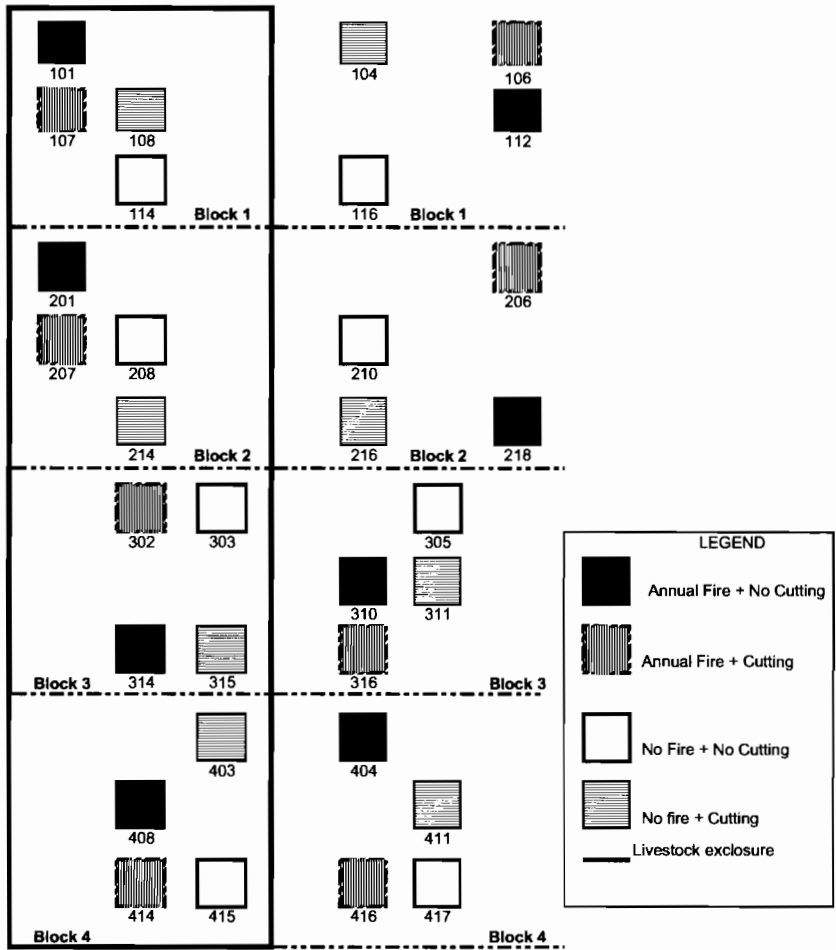


Fig. 4. Lay-out of the factorial experimental design employed.

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 ($^{\circ}\text{C} \pm$ standard error) and residence time (minutes \pm standard error) of temperature above 60°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 ($\text{Kj m}^{-1} \text{s}^{-1}$)	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.

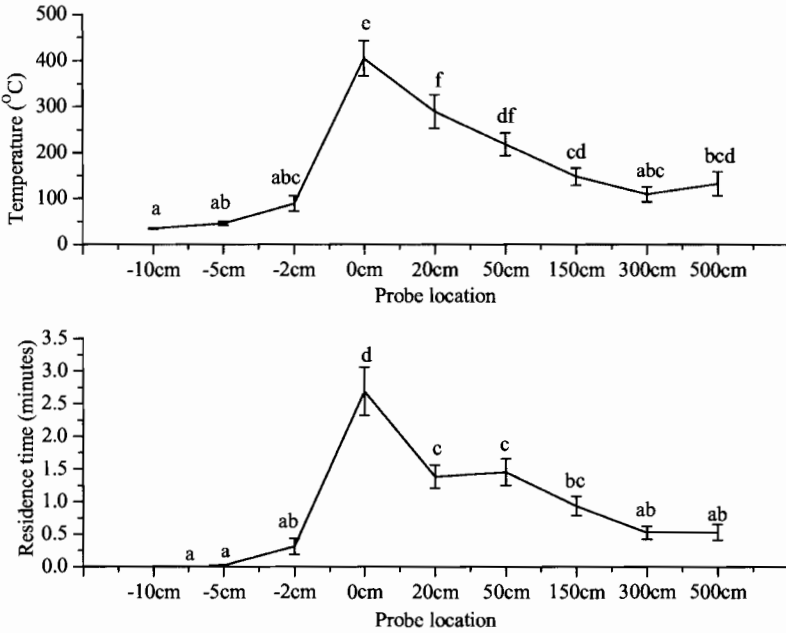


Fig. 5. Main effects of probe location on maximum fire temperature ($^{\circ}\text{C} \pm$ standard error) and residence time (minutes \pm standard error) of temperature above 60°C. Means with different letters are significantly different based on Tukey's HSD test.

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; Hérault & 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.

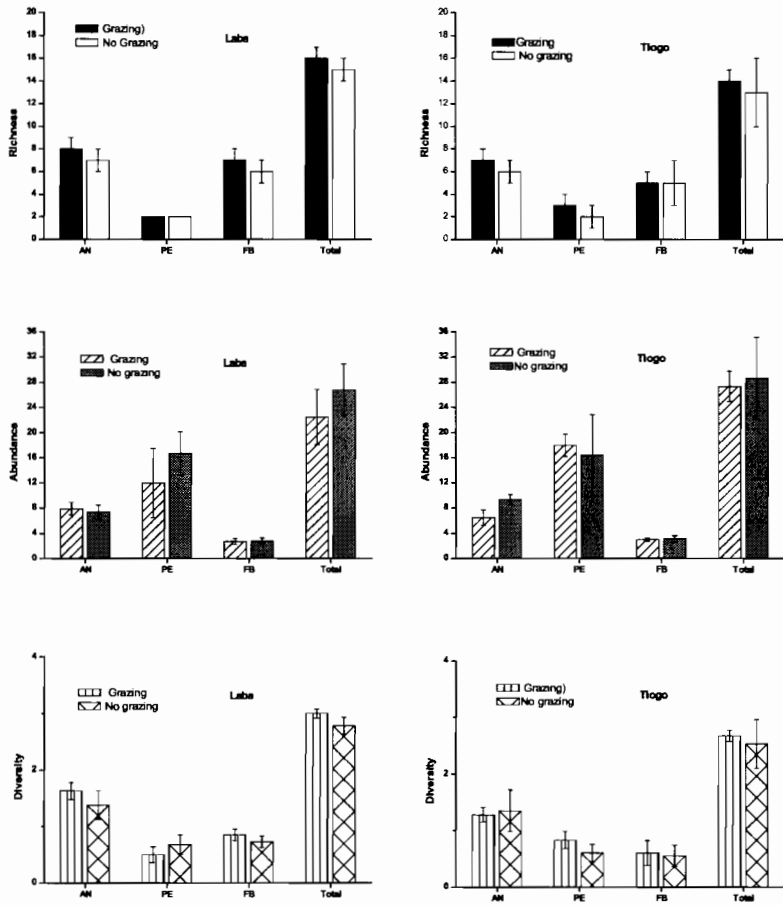


Fig. 6. The main effects of grazing on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna-woodlands at Laba and Tiogo (AN: annual grasses, PE: perennial grasses, FB: forbs).

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.

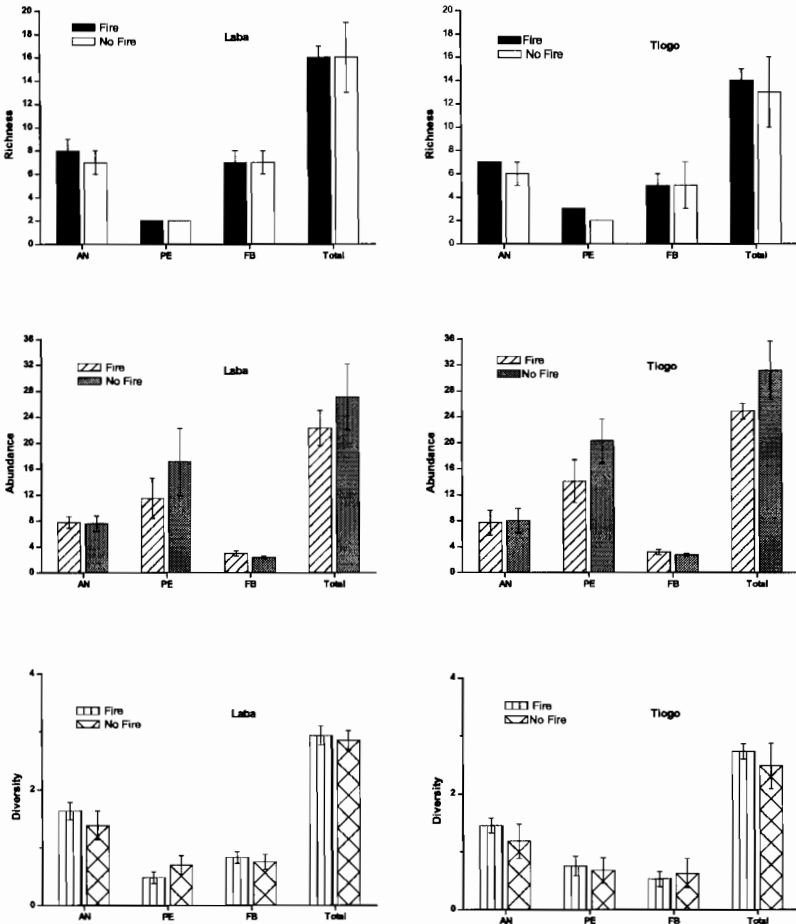


Fig. 7. The main effects of fire on species richness, abundance and diversity of herbaceous species in the Sudanian savanna-woodlands at Laba and Tiogo (AN: annual grasses, PE: perennial grasses, FB: forbs).

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 \times 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 \times grazing treatment significantly reduced the species richness of forbs at Tiogo ($p = 0.029$) compared to grazing treatment alone while fire \times 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 \times grazing \times 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*, *Chasmopodium 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.

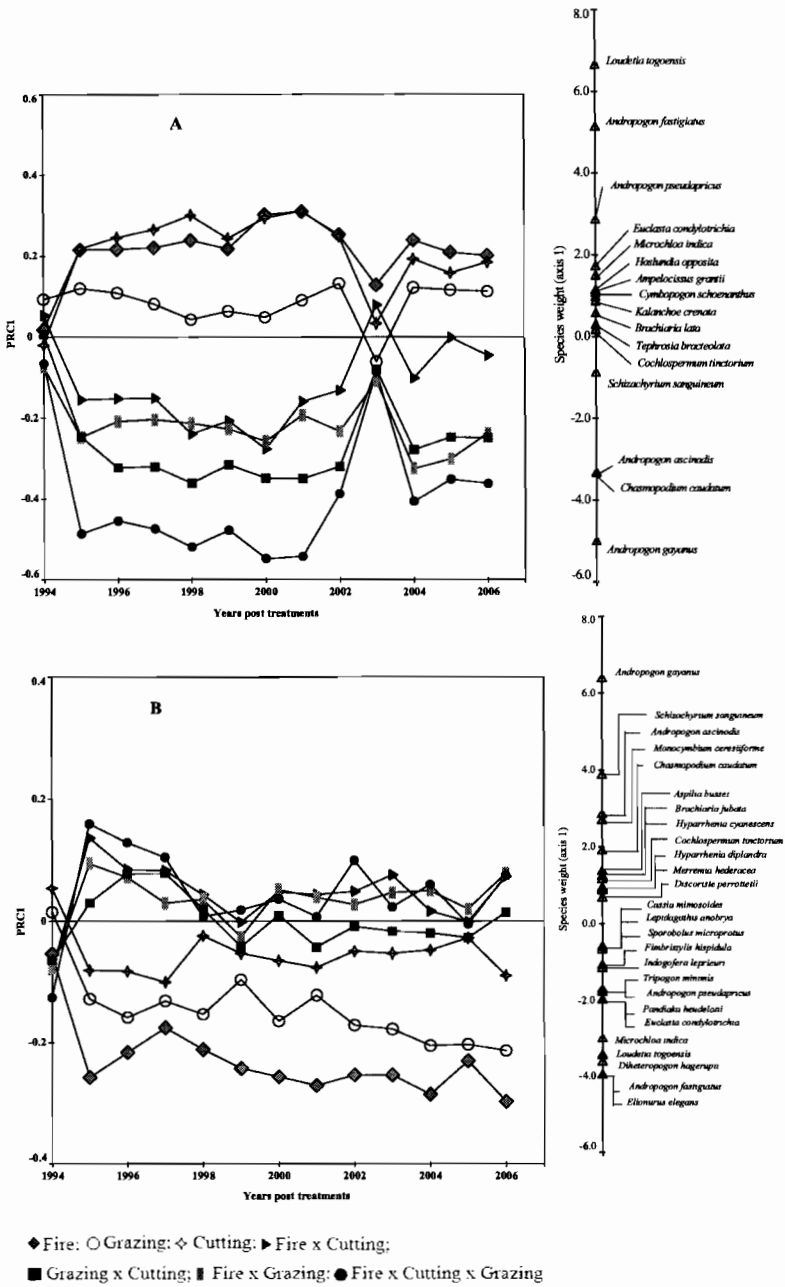


Fig. 8. Principal response curves (PRC) together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and interactions over 13 years at Tiogo (A) and Laba (B). Species with relatively strong weight are shown for clarity.

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

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 amplexens*, *Chasmopodium caudatum*, and *Rottboellia exaltata*) were investigated. The results indicated that post-fire regrowth produced lower above-ground dry matter than unburnt 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

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-Zoungrana (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 (Villocourt, 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-Zoungrana, 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-Zoungrana, 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.

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

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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 savanicoles. 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 savanicoles 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.

Fuel and fire characteristics in a savanna-woodland of West Africa in relation to grazing and dominant grass type

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Abstract

Fuel characteristics, fire behavior and temperature were studied in relation to grazing, dominant grass type and wind direction by lighting 32 prescribed early fires. Grazing significantly reduced the vegetation height, total fuel load, dead and live fuel fractions; plots dominated by perennial grasses had higher values for vegetation height, total fuel load and the quantity of live fuel load. While fire intensity remained insensitive ($p > 0.05$) to any of these factors, fuel consumption was significantly ($p = 0.021$) reduced by grazing, rate of spread was faster in head fire ($p = 0.012$), and flame length was shorter in head fire than back fire ($p = 0.044$). The average maximum temperature was higher ($p < 0.05$) on non-grazed plots, on plots dominated by annual grasses, on plots subjected to head fire, and at the soil surface. Lethal temperature residence time showed nearly similar trend as fire temperature. Wind speed and total fuel load were best predictors of fire behavior parameters (r^2 ranging from 0.557 to 0.862). In conclusion, grazing reduces fuel consumption during fire, maximum fire temperature and lethal temperature residence time, thus could be used as a potential management tool to modify fire behavior. From management viewpoint, back fire is recommended to lower fire severity. The fire behavior models can be employed to guide prescribed early fire in the study area.

Keywords: Burkina Faso; Fire temperature; Fire behavior prediction; Weather variables

1. Introduction

Fire has been an important ecological component of African savanna ecosystems for millennia (Goldammer 1990; Scholes and Walker 1993; van Langevelde *et al.* 2003). In the Sudanian savanna-woodland alone, an area stretching from Senegal in the west to the Ethiopian highlands in the east at 6° - 13° N (Menaut *et al.* 1995), between 25 and 50% of the savanna-woodland burns annually (Delmas *et al.* 1991), primarily due to anthropogenic causes. In most protected Sudanian savanna-woodlands, prescribed early fire (burning taking place between October

and December/January) has been adopted as an ecosystem management tool to minimize the risk of severe late fire (occurring from February to May), to improve pasture production for wildlife and to maintain species composition and richness (Bellefontaine *et al.* 2000; Sawadogo *et al.* 2005; Laris and Wardell 2006). It is generally believed that fires burning early in the dry season tend to be of lower intensity as the predominantly herbaceous fuel still holds high moisture than later during dry season (Liedloff *et al.* 2001).

Fire behavior is defined as what the fire achieves the dynamics of the fire event, the manner in which it occurs and the factors that influence the release of heat energy (Trollope 1983). It is often characterized by fire intensity, rate of spread, flame height and fuel consumption (Trollope 1984). Fire intensity is the most important parameter since it determines the amount of heat released per time unit during conflagration and is thus a useful indicator of its impact on plants (Trollope 1984; Gambiza *et al.* 2005). It is influenced by a wide range of variables such as topography, fuel characteristics, vegetation structure, the season of burning, and weather conditions (Pyne *et al.* 1996). The species composition and spatial distribution of available fuel loading affect the ease of ignition as well as fire size and intensity while fuel moisture content increases the amount of heat necessary to reach the point of ignition (Cochrane 2003). In tropical savanna ecosystems, the fuel load is mainly composed of herbaceous vegetation that makes up 75-90% of total annual biomass (Frost and Robertson 1987) with high amounts of standing dead fuel, resulting in high combustibility and fire risk (Hennenberg *et al.* 2006). In terms of species composition, the herbaceous fuel is composed of both annuals and perennials with varying proportions, which in turn influence fire behavior. The annual grasses dry earlier at the end of the rainy season and burn easily, while the perennial grasses hold relatively high moisture content and burn more slowly. Weather conditions including ambient air temperature, relative humidity, and wind direction and velocity affect fire behavior (Trollope 1984; Trollope *et al.* 2002). Wind conditions have a dominant influence on fire behavior, particularly wind speed affects the rate of fire spread and flame height (Bilgili and Saglam 2003). Relative air humidity and air temperature affect fire behavior indirectly through their effect on the moisture content of vegetation and litter (Bond and van Wilgen 1996).

Herbivores generally reduce fuel load by herbage removal and trampling and therefore lower intensity and frequency of fires. For example, moderate levels of grazing and prescribed burning early in the dry season are used for limiting the extent and severity of late fire in southern Africa (Frost *et al.* 1986; Shea *et al.* 1996). Since fire and grazing regimes can be manipulated directly, they are potentially important ecosystem management tools (Frost *et al.* 1986; Liedloff *et al.* 2001). In West Africa, the management of savanna-woodland ecosystem entails application of prescribed early fire while precluding grazing by livestock (Bellefontaine *et al.* 2000). Recent studies, however, have shown that moderate level of grazing has no detrimental effect on seedling and saplings recruitment of woody species (Zida *et al.* 2007), on coppice growth (Sawadogo *et al.* 2002) as well as on herbaceous plant cover and phytomass (Sawadogo *et al.* 2007). An understanding of the relationship between grazing and fire behavior is essential to

critically examine the current management prescription. Thus, this study was performed to address the following questions: (1) Do fuel characteristics vary between grazed and non-grazed plots, as well as between plots dominated by annual or perennial grasses? (2) Do grazing treatment, dominant grass type and wind direction influence fire behavior, maximum fire temperature and residence time of lethal temperatures? (3) Do fuel characteristics and weather data satisfactorily predict fire behavior?

2. Materials and methods

2.1 Description of study site

The study was conducted in Tiogo State forest (12°13' N, 2°42' W) located at an altitude of 300 m above sea level in Burkina Faso, West Africa. The Tiogo State forest (forêt classée) was delimited by the colonial French administration in 1940 and covers 30,000 ha. It is situated along the only permanent river in the country (Mouhoun formerly known as Black Volta). Phyto-geographically, it is situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (White 1983). The unimodal rainy season lasts about 6 months, from May to October. The mean annual rainfall for the years 1992-2005 was 851 ± 49 mm (mean \pm SE) with inter-annual variability. The number of rainy days per annum during this period was 67 ± 3 (mean \pm SE). Mean daily minimum and maximum temperatures were 16°C and 32°C in December/January (the coldest months) and 26°C and 40°C in April (the hottest month). Most frequently encountered are Lixisols according to the FAO soil classification system (Driessen *et al.* 2001). The soils are mainly deep (>75 cm) silt-clay and are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo 1998).

The vegetation is a tree and bush 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. and *Diheteropogon amplexans* W. D. Clayton (Sawadogo *et al.* 2005). In the study area, these perennial grasses are the most important species owing to their fodder value and their use in local construction (roof-thatching and fences) and handicraft. The main forb species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC.) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Linn. The woody vegetation component is dominated by species in the families Mimosaceae and Combretaceae. The most common woody species are *Acacia macrostachya* Reichenb. ex Benth., *Combretum nigricans* Lepr. ex Guill. & Perr. and *Combretum glutinosum* Perr. ex DC. The Tiogo State forest is subjected to annual early fire and grazing. The livestock carrying capacity at Tiogo State forest was estimated at 1.4 Tropical Livestock Unit ha⁻¹ (T.L.U. ha⁻¹) (Sawadogo 1996) and the grazing pressure at the experimental site was about half of this capacity. The mean herbaceous biomass production during the period 1993-2003 was 3.47 ± 1.37 t DM ha⁻¹ (mean \pm SE) from (Savadogo *et al.* 2007).

2.2 Experimental set-up and burnings

The present study is part of a larger factorial experiment with four replicates of 4.5 ha each established for studying the long-term ecological effects of grazing, prescribed fire and selective tree cutting on savanna-woodland ecosystems (Sawadogo *et al.* 2005). In this study, we examined the effects of grazing (with or without), vegetation types (annual versus perennial grass), wind direction (backfire versus head fire) on fire behavior parameters. The experimental site was first divided into two main plots: grazed plot (open for livestock grazing) and non-grazed plot (fenced at the start of the experiment in 1992 to exclude livestock). The grazing intensity in the grazed main plot was moderate; i.e., half the carrying capacity. A total of 32 plots (20 × 20 m) were used in the present study ensuring homogeneous vegetation type, of which 16 plots were from each grazed or non-grazed area. The 16 plots were further grouped into 8 plots based on the dominant vegetation type (annual versus perennial grasses). Four of the 8 plots were subjected to backfire while the other four were subjected to head fire. The experimental lay-out is shown in Fig. 1. All plots were located on flat ground to eliminate the influence of slope on fire behavior; the density of trees (from an inventory done in 2002) on these plots subjected to annual burning was 572 ± 39 individuals per ha. Fire was ignited with a drip torch along one side of each plot a time to rapidly establish a fire line and to ensure linear ignition. To examine the influence of wind direction on fire behavior, fire was ignited in east to west direction (head fire) in half of the plots or in opposite direction, west to east, in the other half (back fire). Each plot was surrounded by fire breaks and five to eight people were standing-by to extinguish the fire once it reached the plot edge. All burnings (32 fires) were conducted early in the morning (5.00 to 7.00 a.m.) or late in the afternoon (5.00 to 7.00 p.m.) for five consecutive days from November 30 to December 4 in 2005. Such a schedule enabled us to reduce the variation in fuel moisture that could be caused by extended period of burning.

2.3 Assessment of fuel characteristics

Fuel characteristics were described by the following variables: fuel load (kg m^{-2}) and composition, moisture content of the fuel (%), and vegetation cover (%) and height (cm). Fuel characteristics were assessed at two occasions, pre and post burning in order to compute fuel consumption later on. To assess fuel loads, six quadrats of 1 × 1 m in each plot were established, which were further divided into four equal parts. Fuels were collected in two diagonal parts of each quadrat shortly before burning to determine the pre-burn fuel load while fuels in the other two diagonal parts were collected after the fire was extinguished to determine the post-burn fuel load. Both the pre and post burning fuels 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. For moisture content determination, 32 samples of litter, dead and live fuels were bagged separately, sealed and then oven-dried at 80°C until constant dry weight was reached. Moisture content was then calculated on a dry weight basis. The height and cover of the vegetation were determined as the vertical

distance (to the nearest 5 cm) from the ground to the tip of the shoot and using the point intercept sampling procedure (Levy and Madden 1933), respectively.

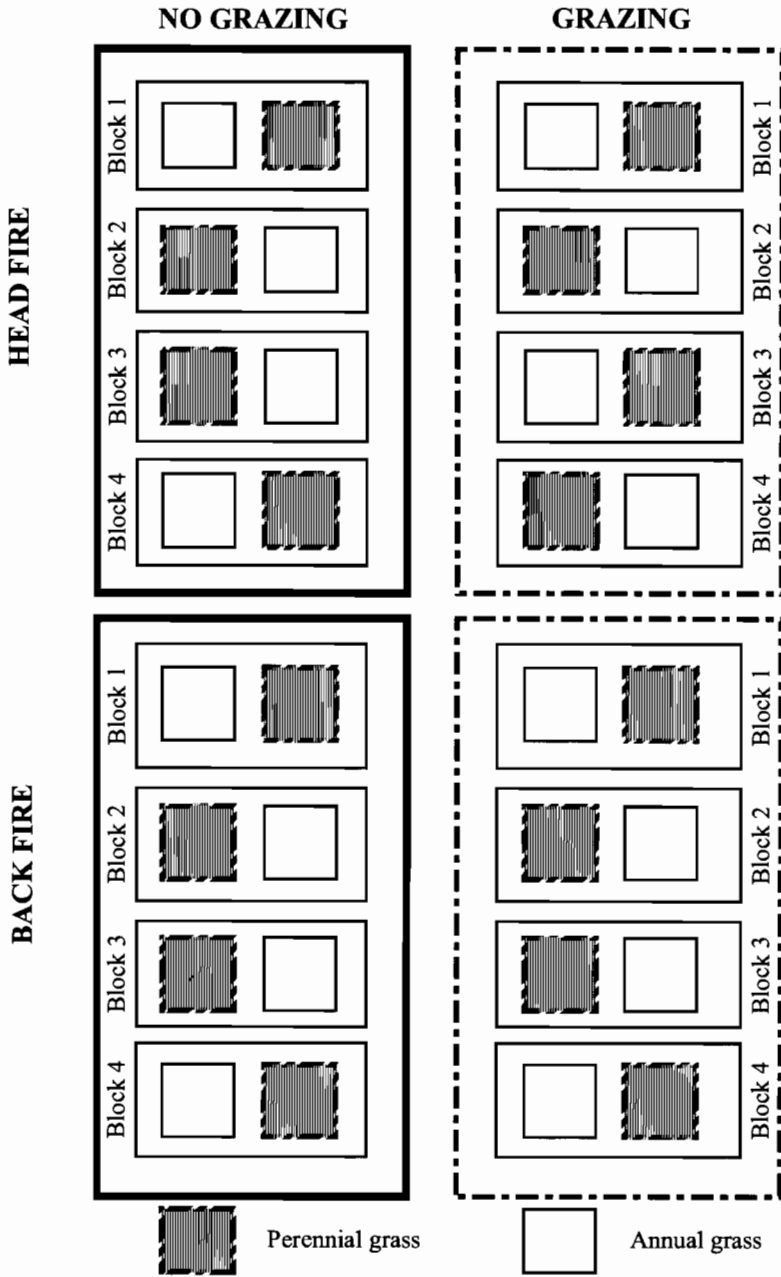


Fig. 1. Experimental set up.

2.4 Weather data

During the experimental fires, open wind speed, air temperature and relative humidity were recorded every minute on each plot using in situ automatic weather station placed at 1.8 m. The wind speed and air temperature were recorded using a hand-held anemometer with integrated temperature reader (Model Silva ADC Summit, Switzerland) while the relative humidity was recorded using a digital thermo-hygrometer (Model S-631 07 Termometerfabriken, Sweden). The recorded values were averaged over the period of fire propagation for each plot.

2.5 Fire behavior parameters

The fire behavior was characterized by the following parameters: fuel consumption, rate of spread, fire intensity, and flame height. The fuel consumption was computed 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 arrive at the pre-placed, 5 m apart poles on either side of the burning plot. A reading on the progression of the fire was recorded for every 5 m distance to estimate the mean rate of spread during head fire and back fire. Fire intensity was estimated using Byram's (1959) equation:

$$I = H \times w \times r$$

I = fire intensity ($\text{kJ s}^{-1} \text{m}^{-1}$), H = heat yield of the fuel (kJ kg^{-1}), w = weight of fuel consumed per unit area (kg m^{-2}), r = rate of spread (m s^{-1}). The heat value (H) developed for grass fuel of head ($16\,890 \text{ kJ kg}^{-1}$) and back fires ($17\,781 \text{ kJ kg}^{-1}$) (Trollope 1983) were adopted to calculate the fire intensities. Flame height of the moving fires was measured vertically from the ground. The pre-placed poles along the sides of the plots at an interval of 5 m were used to measure the mean flame height. The occasional higher flashes when the foliage of a tree or shrub burst into flames were not considered. Each fire was photographed with the painted poles in sight. These photographs were used to verify the height of the flames later on.

2.6 Fire temperature and residence time

To examine whether maximum temperature and residence time show spatial variation (vertical position) with elevation below or above the surface of the plot, we registered fire temperatures at 10, 5, 2 cm below ground, at the surface (0 cm) and at 20, 50, 150, 300, 500 cm above the surface of each plot using MiniCube data loggers with 10 thermo elements type-K (Model VC, Environmental Measuring Systems, BRNO, Czech Republic). Each probe was made of 30 m length of double stranded wire (High temperature thermocouple cable type HH-KI-24-SIE) by removing 1 cm of insulation and twisting the bare ends together. The probes were connected to the loggers programmed to record data every 5 seconds and to store the average of two measurements every 10 seconds. For each burnt plot, the maximum temperature at each probe position from 10 cm below ground to 500 cm above ground was considered during data analysis. The series of temperature measurements at each probe position were used to calculate residence time above 60°C , defined as the time taken by maximum fire temperature to stay

above 60°C as temperature above 60°C is considered lethal for plant tissues (Daniell *et al.* 1969).

2.7 Statistical analyses

The effects of grazing treatments (G_i), vegetation type (V_j), wind direction (W_k), probe location (P_l) and their interactions, with m replicates (varying from 1 to 4), on pre-burn fuel characteristics (model 1), fire behavior parameters (model 2) and maximum fire temperature and the residence time above 60°C (model 3) were subjected to analysis of variance using the following general linear models:

$$Y_{ijm} = \mu + G_i + V_j + G_iV_j + e_{ijm} \quad (1)$$

$$Y_{ijkm} = \mu + G_i + V_j + W_k + G_iV_j + G_iW_k + V_jW_k + G_iV_jW_k + e_{ijkm} \quad (2)$$

$$Y_{ijklm} = \mu + G_i + V_j + W_k + P_l + G_iV_j + G_iW_k + G_iP_l + V_jW_k + V_jP_l + W_kP_l + G_iV_jW_k + G_iV_jP_l + G_iW_kP_l + V_jW_kP_l + G_iV_jW_kP_l + e_{ijklm} \quad (3)$$

Data were checked for normality and homoscedasticity before running ANOVA, and no assumptions were violated. Multiple comparisons were made with Tukey's test to detect differences between probe locations at 5% level of significance. Correlation analyses were also performed to examine the relationship between fire behavior parameters and fuel characteristics and weather data. Fire behavior prediction models were derived by stepwise multiple regressions (backward elimination with 5% significance level) using both fuel characteristics and weather data as predictors. The magnitude of grazing effect was determined by a statistic called partial eta squared (η_p^2), and the effect was considered as small, moderate or large if the value of this statistic was 0.01, 0.06 or 0.14, respectively (Cohen, 1988).

3. Results

3.1 Fuel characteristics

Pre-burn fuel characteristics were differentially affected by the grazing treatment, the vegetation type and their interaction. Vegetation height ($F_{1, 28} = 11.70$, $p = 0.002$), total fuel load ($F_{1, 28} = 25.04$, $p < 0.0001$), dead fuel load ($F_{1, 28} = 13.38$, $p = 0.001$) and live fuel load ($F_{1, 28} = 13.59$, $p = 0.001$) were significantly reduced on grazed plots compared to non-grazed plots (Table 1). The magnitude of grazing effect was large for these fuel characteristics ($\eta_p^2 = 0.472$, 0.327, 0.323 and 0.295 for total fuel consumption, live fuel load, dead fuel load and plant height, respectively). At all levels of grazing treatments, plots dominated by perennial grasses had significantly higher values for vegetation height ($F_{1, 28} = 79.42$, $p < 0.0001$), total fuel load ($F_{1, 28} = 16.76$, $p < 0.0001$), live fuel load ($F_{1, 28} = 54.54$, $p < 0.0001$) than plots dominated by annual grasses. The interaction effect of grazing treatment and vegetation type was significant for the quantity of litter fuel ($F_{1, 28} = 12.35$, $p = 0.002$) and live fuel fractions ($F_{1, 28} = 13.19$, $p = 0.001$). The amount of litter fuel fraction was higher on non-grazed than on grazed plots that

were dominated by annual grasses while it was nearly the same in both grazed and non-grazed plots that were dominated by perennial grasses (Fig. 2). The amount of live fuel fraction was lower on grazed than on non-grazed plots where perennial grasses dominated, whereas it was at a similar (and much lower) level when annual grasses dominated (Fig. 2). Among the different fuel characteristics, vegetation cover, and moisture content of litter and dead fuel fractions were insensitive to grazing treatment, vegetation type or both (Table 1).

Table 1. Main effects of grazing and vegetation type on pre-burn fuel characteristics (mean \pm standard error)

Characteristics	Grazing treatment		Vegetation type	
	Grazing	No Grazing	Annual	Perennial
VH (cm)	122.71 \pm 16.25*	170.21 \pm 21.21	84.58 \pm 4.28*	208.33 \pm 16.14
VC (%)	92.06 \pm 5.86	82.31 \pm 5.16	82.13 \pm 7.17	92.25 \pm 3.05
Litter FL (kg m ⁻²)	0.20 \pm 0.01	0.24 \pm 0.025	0.24 \pm 0.02	0.20 \pm 0.01
Dead FL (kg m ⁻²)	0.14 \pm 0.02*	0.24 \pm 0.02	0.21 \pm 0.02	0.17 \pm 0.03
Live FL (kg m ⁻²)	0.09 \pm 0.028*	0.25 \pm 0.08	0.00 \pm 0.00*	0.34 \pm 0.06
Total FL (kg m ⁻²)	0.42 \pm 0.034*	0.73 \pm 0.07	0.45 \pm 0.04*	0.70 \pm 0.07
Litter MC (%)	4.69 \pm 2.27	3.99 \pm 2.46	4.24 \pm 2.17	4.44 \pm 2.55
Dead fuel MC (%)	6.95 \pm 2.93	3.68 \pm 1.76	2.60 \pm 1.00	8.02 \pm 3.17
Live fuel MC (%)	19.95 \pm 6.14	27.48 \pm 6.64	0.00 \pm 0.00*	43.26 \pm 3.94

VH: vegetation height; VC: vegetation cover; FL: fuel load; MC: moisture content;
 * Significant, $p < 0.05$.

3.2 Weather and fire behavior parameters

During the 32 experimental fires over five days, the average air temperature, relative air humidity and wind speed were $34.43 \pm 1.22^\circ\text{C}$, $54.56 \pm 0.72\%$ and 0.53 ± 0.10 m/s (mean \pm SE), respectively. Generally, fires were burnt under a relatively narrow range of weather conditions. The vegetation type had no effect ($p > 0.05$) on any of the fire behavior parameters, but the effects of grazing treatment and wind direction were significant for some fire behavior parameters. The amount of fuel consumed during burning was significantly lower on grazed than non-grazed plots ($F_{1, 24} = 6.11$, $p = 0.021$), and the magnitude of grazing effect was large ($\eta_p^2 = 0.203$). The rate of spread ($F_{1, 24} = 7.43$, $p = 0.012$) and flame height ($F_{1, 24} = 4.52$, $p = 0.044$) were significantly shorter for back fire than head fire, but fire intensity remained similar in both grazed and non-grazed plots, in plots dominated by annual and perennial grasses or in plots subjected to head fire or back fire (Fig. 3). Fuel consumption during head fire showed significant correlations with vegetation height, dead fuel load, live fuel load and total fuel load, while the rate of spread and fire intensity showed negative correlation with relative air humidity but positive correlation with wind speed (Table 2A). During back fire, fuel consumption was significantly correlated with total fuel load and the different fuel load fractions; flame height correlated significantly with litter fuel load; fire intensity was negatively correlated with vegetation height while the rate of spread showed significant negative correlations with vegetation height, live fuel load and total fuel load (Table 2B).

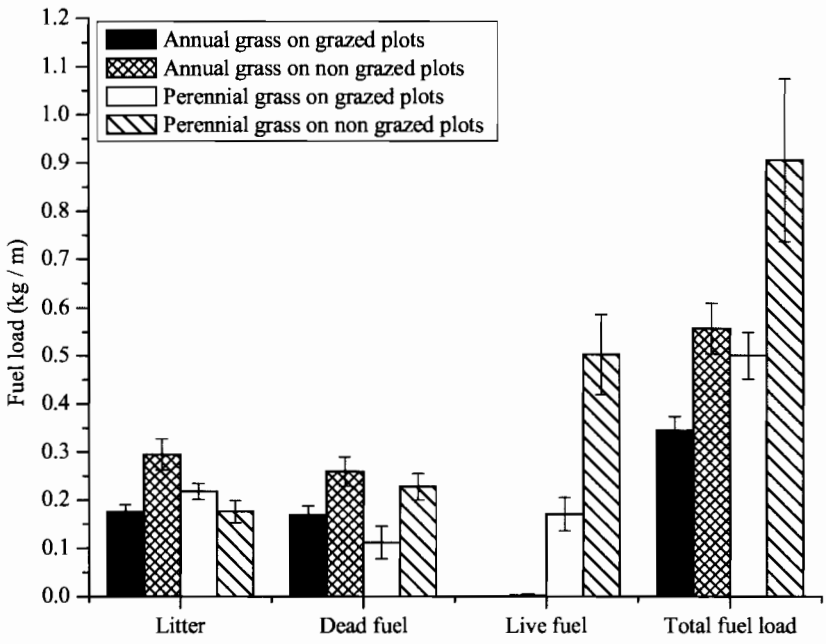


Fig. 2. Above ground fuel load (mean \pm standard error) before burning.

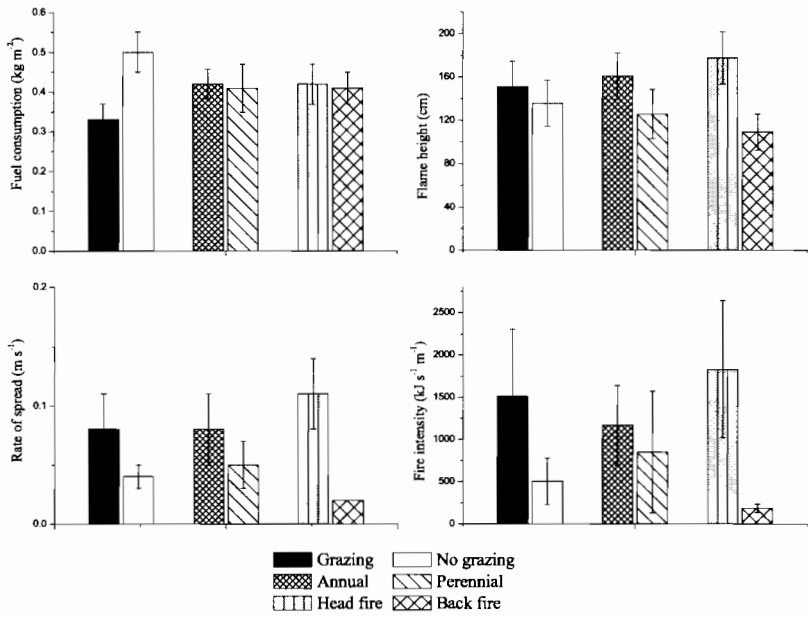


Fig. 3. Main effects of grazing, vegetation type and wind direction on fire behavior parameters (mean \pm standard error).

Table 2. Correlations between fire behavior parameters and fuel characteristics and weather variables

A. Head fire

	Ht	VC	FL _l	FL _d	FL _f	TFL	MC _l	MC _d	MC _f	T	RH	W
w	0.48*	-0.14	0.32	0.90*	0.56*	0.93*	-0.27	-0.08	-0.19	0.16	0.08	-0.01
FH	-0.19	0.37	0.20	-0.15	-0.37	0.27	0.21	0.06	0.15	0.21	-0.23	0.08
r	-0.29	-0.43	0.02	-0.22	-0.32	-0.33	0.12	0.03	0.08	0.45	-0.62*	0.71*
I	-0.31	-0.38	0.19	-0.08	-0.35	-0.22	0.12	0.04	0.09	0.43	-0.63*	0.82*

B. Back fire

	Ht	VC	FL _l	FL _d	FL _f	TFL	MC _l	MC _d	MC _f	T	RH	W
w	0.29	-0.14	0.64*	0.49*	0.27	-0.84*	0.17	0.10	0.12	-0.03	0.11	-0.42
FH	-0.20	0.16	0.60*	-0.37	-0.41	0.16	0.23	0.13	0.16	-0.33	0.00	0.03
r	-0.70*	-0.19	0.14	-0.17	-0.73*	-0.48*	0.25	0.14	0.18	-0.35	-0.41	0.30
I	-0.49*	-0.15	0.40	-0.26	-0.49*	-0.08	0.23	0.13	0.16	0.23	-0.42	0.19

Ht, mean vegetation height (cm); VC, vegetation cover (%); FL_l, litter fuel load (kg m⁻²); FL_d, Dead fuel load (kg m⁻²); FL_f, Live fuel load (kg m⁻²); TFL, total fuel load (kg m⁻²); MC_l, moisture content of litter (%); MC_d, moisture content of dead fuel (%); MC_f, moisture content of live fuel (%); w, fuel consumption (kg m⁻²); r, temperature (°C); RH, relative air humidity (%); W, wind speed (m s⁻¹); FH, Flame height (cm); T, rate of fire spread (m s⁻¹); I, fire intensity (kJ s⁻¹ m⁻¹). * Significant correlation, p < 0.05.

The most pertinent fire behavior prediction models are presented in Table 3. Wind speed and total fuel load explained 56% and 73% of the variations in rate of spread and fire intensity during head fire, respectively. 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 explained 81% and 63% of the variations in fire intensity and rate of spread, respectively. The total fuel load described 71% of the variation in fuel consumption during back fire.

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

3.3 Fire temperature and residence time

The average maximum fire temperature varied significantly between grazing treatment ($F_{1, 216} = 33.01$, $p < 0.0001$), vegetation type ($F_{1, 216} = 10.77$, $p = 0.001$), wind direction ($F_{1, 216} = 6.37$, $p = 0.012$) and probe position ($F_{8, 216} = 34.67$, $p < 0.0001$). It was higher on non-grazed than grazed plots, on plots dominated by annual than perennial grasses, and on plots subjected to head fire than back fire (Table 4). The magnitude of grazing effect on maximum temperature was nearly moderate ($\eta_p^2 = 0.133$). It was also significantly higher at the soil surface (0 cm) than either at 20, 50, 150, 300 and 500 cm above the soil surface or at 2, 5, 10 cm below the soil surface (Fig. 4). Generally fire temperature in the sub-surface (ranging from $34.61 \pm 1.28^\circ\text{C}$ to $88.91 \pm 16.34^\circ\text{C}$) tended to be lower than that above the soil surface (ranging from $108.99 \pm 16.41^\circ\text{C}$ to $289.21 \pm 36.59^\circ\text{C}$).

There were also significant interaction effects of vegetation type \times probe position ($F_{8, 216} = 5.97$, $p < 0.0001$), wind direction \times probe position ($F_{8, 216} = 2.37$, $p = 0.018$) and vegetation type \times grazing treatment \times wind direction ($F_{1, 216} = 4.55$, $p = 0.034$) on maximum fire temperature. The average maximum temperatures at 0 and 20 cm probe positions were $511.39 \pm 41.29^\circ\text{C}$ and $401.16 \pm 50.02^\circ\text{C}$, respectively on plots dominated by annual grasses, which were nearly twice the

maximum temperature recorded on plots dominated by perennial grasses ($298.00 \pm 51.97^\circ\text{C}$ at 0 cm and $177.26 \pm 36.89^\circ\text{C}$ at 20 cm probe position). The average maximum temperatures during head fire was substantially higher at 50 cm ($269.36 \pm 41.10^\circ\text{C}$), 150 cm ($180.65 \pm 31.23^\circ\text{C}$) and 500 cm ($164.41 \pm 47.91^\circ\text{C}$) probe positions than during back fire ($166.92 \pm 23.23^\circ\text{C}$, $114.49 \pm 18.71^\circ\text{C}$ and $100.12 \pm 19.55^\circ\text{C}$ at 50, 150 and 500 cm). During head fire, the average maximum temperature was higher on plots dominated by annual grasses ($172.55 \pm 27.76^\circ\text{C}$) than by perennial grasses ($91.57 \pm 17.82^\circ\text{C}$), both subjected to grazing while the variation was insignificant for non-grazed plots. During back fire, the maximum fire temperature was still higher on plots dominated by annual ($211.41 \pm 36.80^\circ\text{C}$) than by perennial grasses ($142.12 \pm 18.78^\circ\text{C}$) that were not subjected to grazing treatment.

The residence time above 60°C also varied significantly with respect to grazing treatment ($F_{1,216} = 4.89$, $p = 0.028$) and probe position ($F_{8,216} = 20.90$, $p < 0.0001$). The residence time was shorter on grazed than non-grazed plots at all levels of probe position (Table 4) although the magnitude of grazing effect was nearly small ($\eta_p^2 = 0.022$). The residence time was longer at the soil surface (0 cm) than either above or below the surface at all levels of grazing treatment, vegetation type and wind direction (Fig. 4). The residence time was also longer at the first two probe positions above the soil surface than those below the surface. Further below the surface (-10 cm), the residence time was nil as the temperature did not reach 60°C at this position (Fig. 4). The residence time was insensitive to vegetation type and wind direction.

Table 4. Main effects of grazing, vegetation type and wind direction on maximum fire temperature and residence time above 60°C (mean \pm standard error)

Main factors	Max. Temperature ($^\circ\text{C}$)	Residence time (minutes)
Grazing	126.57 ± 12.74	0.72 ± 0.11
No grazing	200.16 ± 15.54	1.02 ± 0.10
p-value	< 0.0001	0.028
Annual grass-dominated	189.53 ± 16.38	0.88 ± 0.09
Perennial grass-dominated	137.21 ± 12.03	0.86 ± 0.12
p-value	0.001	0.843
Head fire	174.65 ± 14.74	0.77 ± 0.10
Back fire	152.08 ± 14.26	0.97 ± 0.11
p-value	0.012	0.147

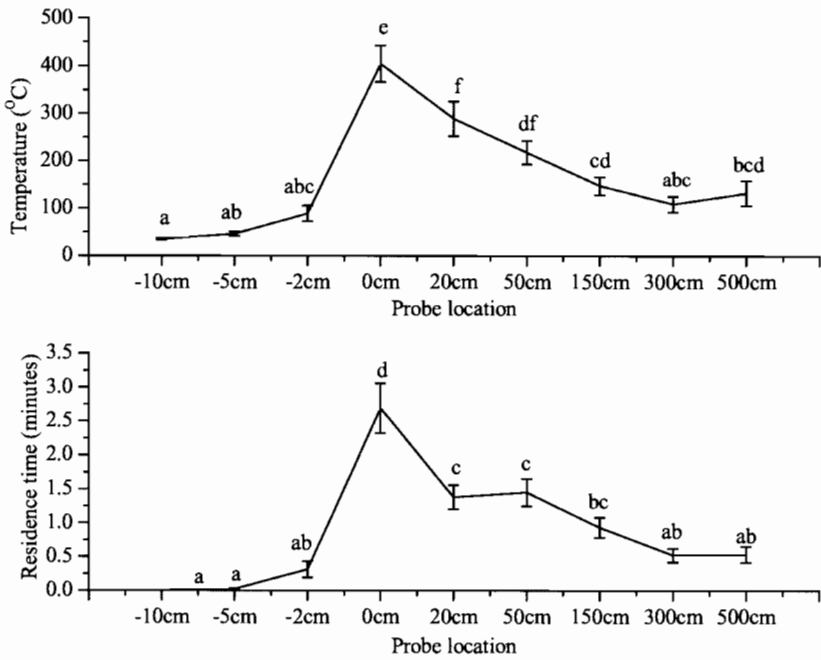


Fig. 4. Main effects of probe location on maximum fire temperature and residence time above 60°C (mean \pm standard error). Means with different letters are significantly different based on Tukey's HSD test.

4. Discussion

The quantity of pre-burn fuel load and vegetation height was significantly lower on grazed than non-grazed plots. This effect is related to herbage removal and trampling pressure (static load) exerted by the animals, which are the most known grazing disturbance factors affecting vegetation structure and dynamics in savannas (Frost *et al.* 1986; Rietkerk *et al.* 2000). The effect of grazing on fuel load also interacts with vegetation type. On plots dominated by annual grasses (*Loudetia togoensis* and *Andropogon pseudapricus*), the quantity of litter fuel was higher on non-grazed than grazed plots while the effect of grazing was insignificant on plots dominated by perennial grasses (*Andropogon gayanus* and *Diheteropogon amplexans*). By preferentially grazing on high-quality plant species, such as annual grasses and forbs, livestock enhances the dominance of perennial grass that can tolerate grazing pressure. 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 from significantly lower fuel consumption by fire on grazed than non-grazed plots. Further more, the incomplete consumption of fuel is beneficial for livestock that can graze on

remaining grass during the dry season. Despite significant effects on total fuel load, both grazing treatment and vegetation type did not affect the rate of spread and fire intensity. Most savanna-woodlands have mosaic architecture with bush clumps and open areas (Menaut *et al.* 1995), which creates spatial heterogeneity in fuel load that has potential to influence fire behavior (Whelan 1995). In addition, 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 behavior that in turn might not sufficiently decrease the horizontal and vertical fuel continuity on the plots. The rate of spread was faster during head than back fire. Fire intensity and rate of spread were also closely related to wind speed in head fire. Apparently both wind direction and speed have a strong effect on fire behavior in the Sudanian savanna-woodland, as documented previously in other vegetation communities (Cheney *et al.* 1993; Trollope *et al.* 2002; Bilgili and Saglam 2003). The positive effect of wind speed is attributed to enhanced supply of oxygen to the fire (Trollope *et al.* 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 due to tilting the flames towards the fuel ahead of the fire. Generally increased wind speed results in exponential increase in rate of spread during head fire than during back fire (e.g. Govender *et al.* 2006). The rate of spread and fire intensity were negatively correlated with relative air humidity. 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 behavior parameters during head and back fire were not significantly correlated with ambient air temperature, most likely due to narrow range of air temperature during fire. The ranges of fire behavior variables found in the present study were comparable with those reported from the savanna-woodland ecosystems of southern Africa (Shea *et al.* 1996; Gambiza *et al.* 2005).

Our fire behavior prediction models show that rate of spread and fire intensity during head fire can be predicted with reasonable precision based on wind speed and total fuel load while fuel consumption can be predicted from total fuel load. During back fire, rate of spread and fire intensity can be predicted from wind speed, vegetation cover and height data while fuel consumption could be predicted from total fuel load. Since the models are statistically significant and conceptually meaningful and logical, they can serve as a guide for predicting fire behavior 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 *et al.* 1998). This is further supported by the large quantity of live perennial fuel load with high moisture content observed during prescribed early fire during our study (Table 1). 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 behavior in West African savanna ecosystem, our result is comparable to studies made in other savanna or grass land ecosystems (e.g. Trollope *et al.* 2002).

The present study indicated that livestock grazing significantly reduced fire temperature and residence time of temperature above 60°C since it removes the biomass and creates patchiness in the fuel bed. Also plots dominated by annual grasses were hotter than that dominated by perennial grasses, which can be explained by the level of desiccation during prescribed early burning. The moisture content of live fuel in perennial grass dominated plots was substantially higher than those in annual grass dominated plots. The overall temperature was higher in head fire than in back fire, however the majority of back fires were hotter than the head fires at the surface (0 cm), which is consistent with findings by Trollope *et al.* (2002). Fire temperature and residence time also varied significantly with respect to probe location. The highest values were recorded at the soil surface (0 cm). Generally fire temperatures and residence times above the soil surface were higher than below the soil surface with increasing soil depth. Our result is in agreement with previous reports from comparable ecosystem types (Bradstock and Auld 1995; Miranda 1993; Auld and O'Connell 1991; Silva *et al.* 1990). It is generally believed that fire temperature decreases with increasing soil depth in a negatively exponential manner (De Luis *et al.* 2004), which is related to the thermal conductivity across the soil profile (Valette *et al.* 1994).

Conclusions

Grazing by livestock reduced herbaceous fuel load thus decreased fire severity by lowering fire temperature and lethal temperature residence time. Thus, moderate levels of grazing can be used as a potential tool to modify fire behavior in the savanna-woodlands. Recent studies on our experimental sites have also shown that the effect of moderate grazing on species richness, abundance and recruitment of both herbaceous and woody species is marginal or insignificant. Therefore, the current management practice that prohibits grazing in savanna-woodland reserves may need revision so that the management of savanna-woodlands for wood production could be integrated with livestock husbandry as the latter is one of the main sources of income for local people. The dominant grass type influenced the moisture content of the fuel, which in turn reduced fire temperature. Wind direction affected fire temperature, the residence time, flame height and rate of spread implying that managers should consider back fire under moderate weather conditions to control fire propagation and intensity. Our empirical fire behavior model is reasonably good, thus could serve as a tool to guide prescribed burning in the study area. However, larger experiments with broader weather and fuel conditions as well as greater geographical spread are required to further improve the model and to make it “global” for the region.

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Herbaceous species responses to long-term effects of prescribed fire, grazing and selective tree cutting in the savanna-woodlands of West Africa

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Abstract

Grazing, fire and selective tree cutting are major disturbances that shape species diversity in savanna ecosystems, yet their effects are highly variable. We carried out a factorial experiment with two levels to examine the effects of grazing, fire and selective tree cutting on herbaceous species richness, abundance and diversity on two sites in the Sudanian savanna-woodlands of Burkina Faso and assessed it for 10 years (1994 – 2003). The results show significant inter-annual variation in species richness, abundance and diversity at both sites ($p < 0.001$), while main or interactive effects of fire, grazing and selective cutting were limited and varied between life forms and sites. Grazing favoured the diversity of perennial grasses, fire favoured the richness of annual and perennial grasses while 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. In many cases, the responses of herbaceous species to treatments were clearer on the site with deep soils than the one on shallow soils. The vegetation dynamics cannot be attributed solely 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. Rainfall accounted for 62% and 54% of the inter-annual variations of richness and diversity of forbs species on deep soils while the relationship was less than 24% on shallow soil. The fact that the response varied between sites accentuates the importance of landscape-scale approaches to understand the impacts of disturbances on composition, structure and diversity of savanna ecosystems.

Keywords: Burkina Faso; Disturbance; Diversity; Herbivory; Savanna ecosystems; Species richness

1. Introduction

Savanna ecosystems are often subjected to multiple disturbances, such as grazing, fire and selective tree cutting (Breman and Kessler, 1995), which are major factors that shape species diversity (McNaughton, 1983; van Langevelde et al., 2003). Generally, local species richness and diversity of savanna ecosystems are maintained by a dynamic interaction between local colonization processes from species pools at larger spatial scales and local extinction due to competitive exclusion processes, which in turn are influenced by disturbances (Gibson and Brown, 1991).

Herbivores affect plant diversity through either or both of these processes (Olf and Ritchie, 1998). For example, herbivores enhance local colonization processes through enhanced propagule dispersal and increasing availability of light and improving soil conditions while reducing local extinction rates by preferentially consuming competitively dominant plants; they are allowing more functionally different plant species to coexist. Conversely, herbivores reduce the colonization process through consumption of seeds and reproductive structures, and counterbalancing the positive effect of increased water and nutrient availability in gaps by unfavourable thermal conditions that increase soil evaporation and plant evapotranspiration while enhancing the extinction processes by preferentially grazing on rare, high-quality plant species, such as forbs, and enhancing the dominance of few species that can tolerate high grazing pressure.

Fire is a prominent feature of most tropical savanna ecosystems, and between 25 and 50% of the Sudanian zone burns annually primarily due to anthropogenic causes (Menaut et al., 1991). Its effect on herbaceous vegetation could be positive or negative depending on the intensity and severity of burning (Garnier and Dajoz, 2001; Hoffmann, 1999). Fire burning early in the dry season tends to be of low intensity as the predominantly herbaceous fuel still holds moisture from the wet season (Liedloff et al., 2001). It, thus, enhances the colonization processes by inducing a flush of germination and flowering, a transient increase in overall productivity due to removal of litter that enhances the availability of nutrients, space and light, as well as maintaining tussocks and increasing their cover by favouring tillering (Garnier and Dajoz, 2001; Whelan, 1995; Williams et al., 1999). High-intensity fires may create pH and osmotic conditions unfavourable for germination of some species. Post-fire gaps may be drought-prone, as the increased exposure may lead to elevated evaporation and thus reduced moisture availability at shallow depths where germination occurs; and hence contributes to enhance extinction processes (Elberse and Breman, 1990).

Canopy gaps created by tree removal is expected to result in increased diversity and abundance due to reduced competition for water and nutrients as well as increased availability of light (Casado et al., 2004; Frost et al., 1986), thus contributing to enhanced local colonization processes, although the opposite has sometimes been found (Akpo et al., 1999) especially for isolated trees (Belsky, 1992). In arid and semi-arid areas, the canopy gaps created by selective removal of

trees may create 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 (Ky-Dembele *et al.*, 2007; Sawadogo *et al.*, 2002), the compensatory response of trees may lead to increased competition for water and nutrients to the detriment of the herbaceous vegetation.

These disturbances can act independently or additively (Belsky, 1992; Drewa and Havstad, 2001; Valone, 2003; Valone *et al.*, 2002). Generally, the co-occurrence of fire and grazing has a synergistic effect on plant communities both in time and space. Many grazers are attracted to recently burnt ground to feed on the 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 provides more space and resources for the growth of herbaceous species temporarily, which in turn attracts more grazers and the relatively high grazing intensity reduces fire-severity by reducing the fuel load. Selective cutting may favour the dominance of drought-tolerant species (e.g. perennial grasses) while grazing and fire reduce their abundance and the combined effect of these three factors eventually reduces the overall diversity of herbaceous flora. Nonetheless, it is still difficult to make generalizations as effects of these disturbances are still highly variable depending on the types of plant community and their interaction with site specific ecological factors, such as soil and precipitation (e.g. Belsky, 1992; Harrison *et al.*, 2003).

Fire, livestock grazing, the overlying tree canopy in savannas, and soil heterogeneity are sources of spatial patterning, diversity and community organisation in grasslands and woodlands. They are not independent, but rather interact in complex ways that remain far from fully understood (McNaughton, 1983). The focus of models and experimental studies investigating the roles of biotic and abiotic factors such as fire and grazing influencing the coexistence of the ligneous and herbaceous vegetation has mainly been on tree population dynamics (Gignoux *et al.*, 1997; Sawadogo *et al.*, 2002). Most scholars have focused on plant community responses to single treatments of either grazing (Hiernaux, 1998) or burning (Garnier and Dajoz, 2001); few studies have examined how these disturbances interact (Belsky, 1992; Collins, 1987; Drewa and Havstad, 2001; Valone, 2003; Valone and Kelt, 1999). Additionally, most studies have been of relatively short duration rather than as time series investigations, and therefore unable to evaluate long-term responses. Long-term multi-factor studies are essential to get a complete picture of the responses of herbaceous vegetation to several disturbance regimes and their interaction with other ecological factors such as rainfall, which is a key growth limiting factor in dry savanna ecosystems. The interaction of these disturbances with climate unveils vegetation responses that would not have shown if fire, grazing, or woody presence had been studied individually.

In this paper, we presented 10 years data (1994-2003) on the effects of repeated burning, grazing and selective tree cutting done once at the beginning of the experiment, on species richness, abundance and diversity of herbaceous vegetation

at two sites in the Sudanian savanna-woodlands of Burkina Faso: Laba (shallow sandy soil) and Tiogo (deep clay soil). Current policies for management of State forests in Burkina Faso entail prohibition of grazing, application of annual early fire and selective tree cutting of 50% of the merchantable standing volume on a 20-year rotation period (Bellefontaine et al., 2000), all of which are not based on scientific evidence. The results from the present study will therefore provide scientific evidence for an informed discussion on the effects of these management regimes on the herbaceous vegetation. The specific questions were: (1) how does herbaceous vegetation respond to fire, grazing and selective tree cutting as well as treatment combinations thereof? (2) Is there inter-annual variation in the response of herbaceous vegetation and if so how does this variation interact with disturbance regimes? (3) Could the inter-annual variation be explained by ecological factors; mainly amount and distribution of rainfall?

2. Materials and Methods

2.1 Site description

The experimental sites are located on flat areas in Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) State forests (forêts classées), both at an altitude of 300 m a.s.l 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 (Mouhoun, formerly known as Black Volta) in the country. The unimodal rainy season lasts for about six months, from May to October. The mean annual rainfall during the study period (1994-2003) was 883 ± 147 mm for Laba and 856 ± 209 mm for Tiogo, and the number of rainy days per annum was 75 ± 16 and 70 ± 9 for Laba and Tiogo, respectively (Fig. 1). Mean daily minimum and maximum temperatures ranged from 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 and Lugo, 1982) of 3.5 and 3.7 for Laba and Tiogo, respectively. Most frequently encountered soils are Lixisols (Driessen et al., 2001), and the soil at Laba is shallow (< 45 cm depth) silty-sand while it is mainly deep (>75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998).

Phyto-geographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (Fontes and Guinko, 1995). The vegetation type at both sites is a tree/bush 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 asciodis* 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 handicraft. 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 families Mimosaceae and Combretaceae 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.

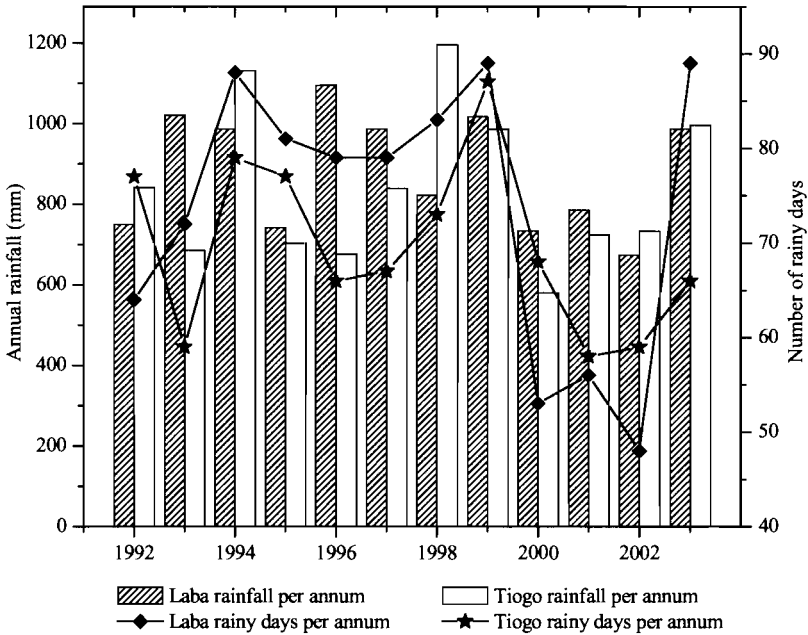


Fig. 1. Total annual rainfall (mm) and number of rainy days during the study period at Laba and Tiogo.

Before 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). Livestock is dominated by cattle although sheep and goats also graze on these sites. The sites are also, occasionally, visited by elephants. The presence of livestock in the two State forests varies spatially and temporally, 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.. They then graze on straws in the bush clumps that have escaped the fire as well as

the young shoots of perennial grass species and young woody foliage induced by the fire. The livestock carrying capacity at Laba State forest was estimated at 1.0 Tropical Livestock Unit per ha (T.L.U. ha⁻¹) and that of Tiogo at 1.4 T.L.U. ha⁻¹ (Sawadogo, 1996). The grazing pressure at both experimental sites was about half of this capacity. The mean herbaceous biomass production for the study period was 3.47 ± 1.37 t DMha⁻¹ at Laba site and 4.01 ± 1.51 t DM ha⁻¹ for Tiogo (Sawadogo et al., 2005).

2.2 Experimental design

A factorial experiment was established in each of the two State forests to examine the effects of grazing, early fire, selective cutting and their interaction on composition, abundance and diversity of herbaceous vegetation. Each experimental site (18 ha) was divided into eight blocks (2.25 ha); four of which were fenced to exclude livestock (hereafter referred to as non-grazed plots) and the other four were open for grazing (hereafter referred to as grazed plots). Each block was further divided into four plots of 0.25 ha (50 x 50 m), separated from each other by 20 – 30 m fire-breaks. To the four plots within each block, the following treatments were randomly assigned: No cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire. The selective cutting was done in December 1993 at Tiogo and a month later in January 1994 at Laba by removing 50% of the merchantable standing volume. Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and fuelwood, and fuelwood and others (Hagberg et al., 1996; Sawadogo, 1996). Except protected species, individuals of other categories 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 (Sawadogo et al., 2002). The prescribed early fire was applied at the end of the rainy season (October – November) each year beginning 1993 when the grass layer humidity was approximately 40%. The grazing main plots at both study sites were open for grazing by livestock (a mixed herd of cattle, sheep and goats) mainly but also wild animals. The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit ha⁻¹ (T.L.U. ha⁻¹) and that of Tiogo was 1.4 T.L.U. ha⁻¹ (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo et al., 2005). The presence of the livestock in the two forests varied spatially and temporally; grazing mainly occurs during the rainy season when grasses were green and surrounding area cultivated.

2.3 Data collection and analyses

The assessment was carried out every year from 1994 to 2003 at the end of the rainy season (September to October) when most of the species are flowering and fruiting, which allows for easy species identification. The point-intercept sampling procedure (Levy and Madden, 1933) was used to gather species-cover data. The presence of species was recorded along a 20 m permanent line laid in each plot at an interval of 0.20 m. 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 follows Hutchinson et al. (1954).

Abundance, richness and diversity of herbaceous species were computed for each replicate in each treatment. 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). Abundance, species richness and diversity were also computed by life form; i.e., annual grasses, perennial grasses and forbs, as well as for some selected species that were encountered in all treatment plots. Prior to statistical analyses, abundance and species richness data were checked for normality. We used repeated-measures analysis of variance (Davis, 2002) to determine whether abundance, species richness and diversity were affected by year, grazing, fire, selective cutting and their interactions. The analysis of variance was performed for each experimental site separately following the general linear model (GLM) repeated measures:

$$Y_{ijk} = \mu + \beta_i + \lambda_j + (\beta\lambda)_{ij} + \epsilon_{j(i)} + \epsilon_{j(k)}$$

where Y_{ijk} was the response variable for the herbaceous vegetation, μ was the overall mean, β_i was the effect of the between-subject factors, i (fire, grazing, selective cutting treatments and their combinations), λ_j was the effect of the within-subject factor, j , year, $(\beta\lambda)_{ij}$ was the interaction of the between- and within-subject factors. The parameters $\epsilon_{j(i)}$ and $\epsilon_{j(k)}$ are random error of the between-subject and the within-subject factor, respectively with k number of replicates. When the homogeneity of variance assumption was violated, according to Mauchly's test of Sphericity, the degrees of freedom for testing the significance of the within-subject factors were adjusted using Huynh-Feldt correction factor, which is less biased than other correction factors (Davis, 2002). All statistical analyses were done with SPSS 14 software package (Copyright SPSS for Windows, Release 2005 Chicago: SPSS Inc.). In addition, the relationship between vegetation parameters (i.e. species richness, diversity and abundance) and rainfall data were explored by means of multiple linear regressions combining the amount of rainfall and precipitation pattern expressed in number of rainy days. The amount of rainfall and number of rainy days were standardized to zero mean and unit variance. Differences were judged to be significant when the probability of a greater F value was less than 0.05.

3. Results

3.1. Main effects of treatments

The main effects of grazing on total species richness, abundance and diversity of herbaceous flora were not significant at either experimental site, except total abundance which was significant at Tiogo (Table 1, between-subject factors). Among life forms, grazing had a marginally significant effect on abundance of perennial grasses at Laba ($F_{1,24} = 4.206$, $p = 0.051$) and a significant effect on their diversity at Tiogo ($F_{1,24} = 4.909$, $p = 0.036$). The total abundance of herbaceous flora was higher on ungrazed than grazed plots at Tiogo, and perennial grasses were more abundant on ungrazed than grazed plots at Laba while they were more diverse on grazed than ungrazed plots at Tiogo (Table 2). The main effects of fire on total species richness, abundance and diversity of herbaceous vegetation were not significant at either Laba or Tiogo (Table 1); however fire had significant effects on richness of annual grasses at Tiogo ($F_{1,24} = 4.336$, $p = 0.048$) and abundance ($F_{1,24} = 4.787$, $p = 0.039$) and marginally on diversity ($F_{1,24} = 4.218$, $p = 0.051$) of perennial grasses at Laba. The number of annual grasses was higher on burnt than unburnt plots at Tiogo while abundance and diversity of perennial grasses were higher on unburnt than burnt plots at Laba (Table 3). Selective tree cutting affected neither the total species richness nor abundance and diversity of herbaceous flora at either experimental site (Table 1). Selective cutting did not have effect either on species richness, abundance and diversity of different life forms (Table 4).

3.2. Interaction effects of treatments

None of the treatment interactions were significant at both experimental sites, except fire \times cutting treatment that had a significant effect on total species richness and abundance of herbaceous flora at Laba (Table 1). At all levels of grazing at Laba, the richness of herbaceous flora was slightly lower on plots subjected to fire \times cutting treatment than plots subjected to either fire or cutting treatments while the reverse held true for total abundance (Table 5). At life form level, fire \times grazing treatment significantly reduced the species richness of forbs at Tiogo ($F_{1,24} = 5.427$, $p = 0.029$) compared to grazing treatment alone while fire \times grazing treatment resulted in significantly higher forbs diversity ($F_{1,24} = 5.363$, $p = 0.029$) than either grazing or fire (Table 5). The diversity of forbs was also significantly influenced by the interaction of the three factors at Tiogo ($F_{1,24} = 4.941$, $p = 0.036$). Forb diversity was higher on plots subjected to fire \times grazing \times cutting than on plots subjected to neither of these treatments (Table 5).

Table 1: Summary of repeated measures ANOVA for testing the significance of the between- and within-subject effects on total species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna woodlands at Laba and Tiogo

A) Laba

Source	Richness			Abundance			Diversity		
	df	F	p	df	F	p	df	F	p
Between subject factors									
Fire	1	0.726	0.403	1	0.617	0.440	1	0.412	0.527
Grazing	1	2.750	0.110	1	3.590	0.070	1	2.097	0.097
Cutting	1	0.213	0.648	1	0.016	0.899	1	0.122	0.729
Fire × Grazing	1	1.447	0.241	1	0.580	0.454	1	0.112	0.740
Fire × Cutting	1	4.357	0.048	1	5.238	0.031	1	1.973	0.173
Grazing × Cutting	1	0.251	0.621	1	0.017	0.896	1	0.024	0.879
Fire × Grazing × Cutting	1	0.147	0.705	1	1.707	0.204	1	0.259	0.615
Error	24			24			24		
Within subject factors									
Year	9	6.227	0.000	7	5.375	0.000	9	5.963	0.000
Year × Fire	9	0.631	0.770	7	0.457	0.853	9	1.079	0.379
Year × Grazing	9	0.595	0.800	7	0.704	0.659	9	0.529	0.852
Year × Cutting	9	0.587	0.807	7	0.601	0.743	9	1.729	0.084
Year × Fire × Grazing	9	1.062	0.392	7	2.155	0.045	9	0.965	0.470
Year × Fire × Cutting	9	1.887	0.055	7	1.985	0.065	9	2.971	0.002
Year × Cutting × Grazing	9	0.974	0.463	7	1.154	0.333	9	0.751	0.662
Year × Fire × Cutting × Grazing	9	0.692	0.716	7	0.855	0.537	9	0.671	0.735
Error	216			157			216		

Note that the degrees of freedom for the within-subject factor for testing abundance were Huynh-Feldt adjusted. Significant ($p < 0.05$) difference in bold italic.

Table 1 (continued)

B. Tiogo

Source	Richness			Abundance			Diversity		
	df	F	p	df	F	p	df	F	p
Between subject factors									
Fire	1	0.937	0.343	1	2.093	0.161	1	2.275	0.144
Grazing	1	0.916	0.348	1	4.474	0.045	1	0.731	0.401
Cutting	1	0.281	0.601	1	0.814	0.376	1	0.008	0.927
Fire × Grazing	1	2.261	0.146	1	3.180	0.087	1	2.227	0.149
Fire × Cutting	1	2.294	0.143	1	2.892	0.102	1	1.291	0.267
Grazing × Cutting	1	0.611	0.442	1	0.508	0.483	1	0.787	0.384
Fire × Grazing × Cutting	1	3.854	0.061	1	3.766	0.064	1	1.636	0.213
Error	24			24			24		
Within subject factors									
Year	9	16.473	0.000	5	9.323	0.000	7	13.135	0.000
Year × Fire	9	1.407	0.186	5	1.472	0.199	7	1.656	0.118
Year × Grazing	9	3.585	0.000	5	2.694	0.021	7	1.782	0.089
Year × Cutting	9	0.897	0.529	5	0.744	0.603	7	1.091	0.371
Year × Fire × Grazing	9	0.962	0.473	5	0.671	0.658	7	0.717	0.665
Year × Fire × Cutting	9	0.918	0.510	5	0.797	0.563	7	0.487	0.852
Year × Cutting × Grazing	9	0.639	0.763	5	0.909	0.483	7	0.683	0.694
Year × Fire × Cutting × Grazing	9	1.141	0.335	5	1.483	0.195	7	0.699	0.681
Error	216			130			178		

Significant ($p < 0.05$) difference in bold italic.

Table 2. The main effects of grazing on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna woodlands at Laba and Tiogo (Values are mean \pm SE)

		Laba			Tiogo		
		grazed	ungrazed	p-value	grazed	ungrazed	p-value
Richness	An	8 \pm 1	7 \pm 1	0.118	7 \pm 1	6 \pm 1	0.565
	Pr	2 \pm 0	2 \pm 0	0.279	3 \pm 1	2 \pm 1	0.174
	Fb	7 \pm 1	6 \pm 1	0.081	5 \pm 1	5 \pm 2	0.618
	Total	16 \pm 1	15 \pm 2		4 \pm 1	13 \pm 3	
Abundance	An	7.9 \pm 1.0	7.4 \pm 1.1	0.706	6.5 \pm 1.2	9.3 \pm 0.9	0.087
	Pr	12.0 \pm 5.5	16.7 \pm 3.5	0.051	18.0 \pm 1.8	16.4 \pm 6.5	0.485
	Fb	2.7 \pm 0.5	2.8 \pm 0.5	0.455	3.0 \pm 0.3	3.1 \pm 0.5	0.635
	Total	22.5 \pm 4.4	26.8 \pm 4.1		27.4 \pm 2.4	28.7 \pm 6.5	
Diversity	An	1.63 \pm 0.15	1.38 \pm 0.25	0.111	1.28 \pm 0.13	1.35 \pm 0.37	0.458
	Pr	0.50 \pm 0.14	0.68 \pm 0.17	0.195	0.83 \pm 0.15	0.60 \pm 0.16	0.036
	Fb	0.85 \pm 0.10	0.73 \pm 0.10	0.218	0.60 \pm 0.22	0.55 \pm 0.19	0.597
	Total	3.00 \pm 0.08	2.78 \pm 0.15		2.68 \pm 0.10	2.53 \pm 0.43	

An: Annuals; Pr: Perennials; Fb: forbs; Significant ($p < 0.05$) difference in bold italic.

Table 3. The main effects of fire on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna woodlands at Laba and Tiogo (Values are mean \pm SE)

		Laba			Tiogo		
		burnt	unburnt	p-value	burnt	unburnt	p-value
Richness	An	8 \pm 1	7 \pm 1	0.079	7 \pm 0	6 \pm 1	0.048
	Pr	2 \pm 0	2 \pm 0	0.531	3 \pm 0	2 \pm 0	0.091
	Fb	7 \pm 1	7 \pm 1	0.908	5 \pm 1	5 \pm 2	0.233
	Total	16 \pm 1	16 \pm 3		14 \pm 1	13 \pm 3	
Abundance	An	7.8 \pm 0.9	7.6 \pm 1.2	0.436	7.7 \pm 1.9	8.0 \pm 1.9	0.554
	Pr	11.5 \pm 3.1	17.1 \pm 5.2	0.039	14.1 \pm 3.3	20.3 \pm 3.4	0.072
	Fb	3.0 \pm 0.4	2.4 \pm 0.2	0.096	3.2 \pm 0.4	2.8 \pm 0.2	0.319
	Total	22.3 \pm 2.7	27.1 \pm 5.1		24.9 \pm 1.2	31.2 \pm 4.5	
Diversity	An	1.63 \pm 0.15	1.38 \pm 0.25	0.119	1.45 \pm 0.13	1.18 \pm 0.30	0.126
	Pr	0.48 \pm 0.10	0.70 \pm 0.16	0.051	0.75 \pm 0.17	0.68 \pm 0.22	0.300
	Fb	0.83 \pm 0.10	0.75 \pm 0.13	0.435	0.53 \pm 0.13	0.63 \pm 0.25	0.355
	Total	2.93 \pm 0.17	2.85 \pm 0.17		2.73 \pm 0.13	2.48 \pm 0.39	

An: Annuals; Pr: Perennials; Fb: forbs; Significant ($p < 0.05$) difference in bold italic.

Table 4. The main effects of selective cutting on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna-woodlands at Laba and Tiogo

		Laba			Tiogo		
		cut	uncut	p-value	cut	uncut	p-value
Richness	An	7 ± 1	7 ± 1	0.984	7 ± 1	6 ± 1	0.408
	Pr	2 ± 0	2 ± 0	0.680	3 ± 1	2 ± 1	0.676
	Fb	7 ± 1	6 ± 1	0.326	5 ± 1	5 ± 2	0.923
	Total	16 ± 1	16 ± 2		14 ± 1	13 ± 3	
Abundance	An	7.8 ± 1.2	7.5 ± 1.0	0.635	7.7 ± 2.5	8.0 ± 1.1	0.516
	Pr	13.0 ± 4.5	15.7 ± 5.7	0.447	16.0 ± 4.0	18.5 ± 5.2	0.505
	Fb	2.9 ± 0.4	2.6 ± 0.4	0.183	3.0 ± 0.5	3.1 ± 0.2	0.729
	Total	23.6 ± 3.6	25.8 ± 5.7		26.5 ± 2.3	29.6 ± 6.2	
Diversity	An	1.53 ± 0.21	1.48 ± 0.29	0.734	1.35 ± 0.19	1.28 ± 0.34	0.670
	Pr	0.53 ± 0.13	0.65 ± 0.21	0.329	0.70 ± 0.24	0.73 ± 0.15	0.768
	Fb	0.85 ± 0.06	0.73 ± 0.13	0.268	0.58 ± 0.10	0.58 ± 0.28	0.817
	Total	2.90 ± 0.14	2.88 ± 0.21		2.63 ± 0.05	2.56 ± 0.46	

Table 5. The interaction effects of grazing (G), fire (F) and selective cutting (C) on species richness, abundance and diversity of herbaceous vegetation in the Sudanian savanna-woodlands

		Control	GF	GC	CF	GCF
A) Laba						
Richness	An	5 ± 2	8 ± 2	8 ± 1	7 ± 1	7 ± 1
	Pr	2 ± 0	2 ± 0	2 ± 0	2 ± 0	2 ± 0
	Fb	5 ± 1	7 ± 2	8 ± 2	6 ± 1	7 ± 1
	Total	12 ± 3	16 ± 2	18 ± 3	15 ± 3*	16 ± 2
Abundance	An	8.9 ± 3.0	7.4 ± 1.5	8.2 ± 1.3	7.4 ± 1.8	9.0 ± 1.7
	Pr	20.7 ± 3.6	9.3 ± 3.7	9.5 ± 3.3	15.4 ± 5.8	8.8 ± 1.9
	Fb	2.5 ± 0.8	3.2 ± 0.9	2.4 ± 0.8	3.4 ± 0.6	3.1 ± 0.6
	Total	32.0 ± 5.9	20.0 ± 4.5	20.1 ± 3.4	26.1 ± 6.5*	20.9 ± 2.7
Diversity	An	1.10 ± 0.17	1.73 ± 0.28	1.68 ± 0.18	1.42 ± 0.23	1.72 ± 0.17
	Pr	0.87 ± 0.11	0.39 ± 0.10	0.48 ± 0.11	0.48 ± 0.13	0.39 ± 0.10
	Fb	0.57 ± 0.15	0.93 ± 0.31	0.87 ± 0.30	0.83 ± 0.23	0.85 ± 0.21
	Total	2.55 ± 0.32	3.05 ± 0.35	3.03 ± 0.27	2.74 ± 0.34	2.96 ± 0.23
B) Tiogo						
Richness	An	4 ± 2	7 ± 3	6 ± 2	6 ± 2	7 ± 2
	Pr	2 ± 1	3 ± 0	3 ± 1	3 ± 1	3 ± 0
	Fb	3 ± 1	4 ± 2*	5 ± 1	4 ± 2	4 ± 2*
	Total	9 ± 3	13 ± 4	14 ± 2	13 ± 4	14 ± 3
Abundance	An	9.4 ± 4.0	6.7 ± 1.3	5.3 ± 1.3	10.3 ± 3.1	9.0 ± 1.7
	Pr	25.1 ± 6.9	15.6 ± 5.2	18.8 ± 4.4	10.0 ± 4.3	8.8 ± 1.9
	Fb	3.1 ± 0.8	3.3 ± 1.1	2.7 ± 0.8	3.7 ± 1.1	3.1 ± 0.6
	Total	37.7 ± 8.6	25.6 ± 6.8	26.8 ± 3.6	23.6 ± 7.1	26.2 ± 6.4
Diversity	An	0.84 ± 0.46	1.35 ± 0.51	1.08 ± 0.43	1.49 ± 0.30	1.28 ± 0.43
	Pr	0.75 ± 0.21	0.39 ± 0.10	0.48 ± 0.11	0.63 ± 0.22	0.86 ± 0.23
	Fb	0.32 ± 0.16	0.93 ± 0.31	0.87 ± 0.30	0.54 ± 0.17	0.48 ± 0.17
	Total	1.91 ± 0.44	3.05 ± 0.35	3.03 ± 0.27	2.66 ± 0.27	2.62 ± 0.36

An: Annuals; Pr: Perennials; Fb: forbs; * Significant ($p < 0.05$) (values are mean ± SE)

3.3 Inter-annual variations

Total species richness, abundance and diversity of herbaceous flora exhibited a highly significant inter-annual variation at both experimental sites (Table 1, within-subject factor). Some of the treatments interacted significantly with the within-subject factor, year. At Laba, the annual variation in total abundance of the herbaceous flora was significantly high on fire \times grazing plots while at Tiogo the annual variations in total species richness and abundance were significant on grazed plots (Table 1). The richness, abundance and diversity of different life forms also showed significant inter-annual variations, except richness of perennial grasses at Laba and abundance of forbs at both Laba and Tiogo, as well as affected by interaction effects of year and treatments. Generally, the change in species richness (Fig. 2), abundance (Fig. 3) and diversity (Fig. 4) of herbaceous flora across the study years was somehow quadratic.

At Laba, the interaction effect of year \times fire \times selective cutting was significant for richness of annual grasses ($F_{9,216} = 1.99$, $p = 0.041$) and marginally significant for total species richness ($p = 0.055$). Total species richness was considerably higher on plots subjected to fire \times selective tree cutting treatment than the control plots, particularly in 1994 (17 *vis-à-vis* 14 species), 1995 (19 *vis-à-vis* 14 species) and 1996 (20 *vis-à-vis* 16 species) while the richness of annual grasses was twice higher on fire \times selective cutting plots (7 species) than the control plots (3 species) in 2000 (Fig. 2A).

At Tiogo, the effect of year \times grazing interaction was significant for total species richness ($p < 0.001$), and richness of annual grasses ($F_{9,162} = 2.93$, $p = 0.003$) and forbs ($F_{9,216} = 2.36$, $p = 0.014$). In addition, the interaction effect of year \times fire on richness of annual grasses ($F_{9,216} = 2.61$, $p = 0.007$), and effects of year \times grazing \times selective cutting ($F_{8,193} = 2.31$, $p = 0.022$) and year \times grazing \times selective cutting \times fire ($F_{8,193} = 2.20$, $p = 0.029$) on richness of perennial grasses were significant. Total species richness, and richness of annual grasses and forbs were substantially higher on grazed than control plots through out the study period, especially remarkable during 1997-2001 (Fig. 2B). The effect of fire on richness of annual grasses was more pronounced after three (1996) and nine (2002) years when species richness was doubled on burnt plots (10 species) than unburnt plots (5 species). Richness of perennial grasses was higher on grazing \times selective cutting plots in 1999 and 2003, and on grazing \times selective cutting \times fire plots in 2003 than the control plots (Fig. 2B).

The interaction effects of year and treatments on abundance differed between experimental sites. At Laba, the abundance of annual grasses were significantly affected by year \times selective tree cutting \times fire ($F_{7,166} = 2.29$, $p = 0.030$) and year \times grazing \times fire ($F_{7,166} = 2.50$, $p = 0.019$) so also the total abundance of herbaceous flora ($F_{7,157} = 2.15$, $p = 0.045$). Over the study period, the total abundance of herbaceous flora was higher on control plots than plots subjected to selective cutting \times fire and grazing \times fire treatments; especially the variation was marked in 2000 (c.f. 43.1% and 27.0% for untreated and treated plots, respectively) in the former and in 2000 (43.1% *vis-à-vis* 26.0%) and in 2002 (35.9% *vis-à-vis* 13.2%)

in the latter (Fig. 3A). In 1998, annual grasses were less abundant on selective cutting × fire plots (8.4%) than control plots (12.9%), so also in 2000 (c.f. 7.7% and 12.1% for treated and untreated plots, respectively); grazing × fire treatment also reduced the abundance of annual grasses by half (6.6%) compared to the control (13.3%) in 1999 (Fig. 3A).

At Tiogo, the interaction effect of year × grazing was significant for total abundance ($F_{5,130} = 2.69$, $p = 0.021$) and abundance of annual ($F_{6,143} = 2.49$, $p = 0.026$) and perennial grasses ($F_{5,121} = 2.37$, $p = 0.043$). Grazing had a decreasing effect on total abundance in 1994 (24.3% and 13.8% for the ungrazed and grazed plots, respectively), 1998 (49.1% and 26.9% for the ungrazed and grazed plots, respectively) and 2003 (49.1% and 25.1% for the ungrazed and grazed plots, respectively). During the first four years (1994-1997), annual grasses were more abundant on grazed than ungrazed plots, but thereafter the relationship reversed (Fig. 3B). The abundance of perennial grasses tended to be lower on grazed than ungrazed plots during the study period, particularly reduced by three-fold in 1994 and nearly by half in 1998 compared with the control (Fig. 3B).

The interaction effects of year and treatments on diversity of herbaceous flora differed between life forms and experimental sites. At Laba, total diversity was significantly affected by year × selective cutting × fire ($F_{9,216} = 2.97$, $p = 0.002$) while diversity of perennial grasses was affected by year × grazing ($F_{9,216} = 1.93$, $p = 0.049$) and year × grazing × selective cutting × fire ($F_{9,216} = 2.50$, $p = 0.010$). Generally, total diversity of herbaceous flora and diversity of perennial grasses tended to be higher on the plots subjected to cutting × fire treatment than the control (Fig. 4A), but the variation was considerably high in 2000 when total diversity was 2.55 and 1.87 and diversity of perennial grasses was 1.73 and 0.73 for treated and control plots, respectively. The diversity of perennial grasses tended to be higher on ungrazed than grazed plots during the first five years (1994-1998) and particularly in 1996 it was considerably higher on ungrazed ($H' = 1.06$) than grazed ($H' = 0.61$) plots (Fig. 4A).

At Tiogo, the interaction effect of year × grazing was significant for diversity of annual grasses ($F_{6,150} = 2.65$, $p = 0.016$) and forbs ($F_{9,216} = 2.34$, $p = 0.016$), so also the effect of year × fire on diversity of annual grasses ($F_{6,150} = 3.09$, $p = 0.006$). Over the study period, the diversity of annual grasses was generally higher on either burnt or grazed plots than the control plots; particularly it was nearly tripled in 1995, 1997 and 1998 on burnt or grazed plots compared to the control plots (Fig. 4B). The diversity of forbs was generally high on grazed than ungrazed plots across the study period (Fig. 4B), but it was substantially high in 1999 ($H' = 0.88$ *vis-à-vis* 0.12), in 2000 ($H' = 0.81$ *vis-à-vis* 0.17) and in 2003 ($H' = 1.35$ *vis-à-vis* 0.34).

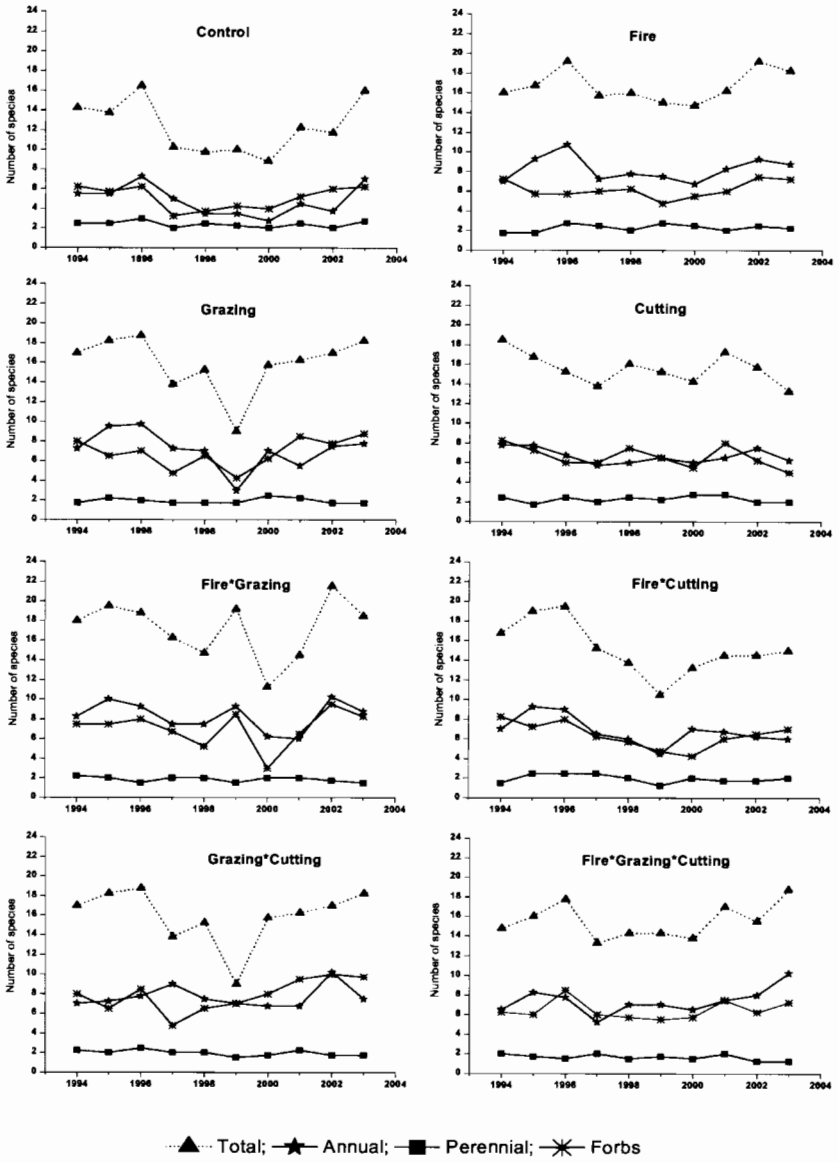


Fig. 2 A. Inter-annual variations in species richness of herbaceous flora (number of species/plot) at Laba

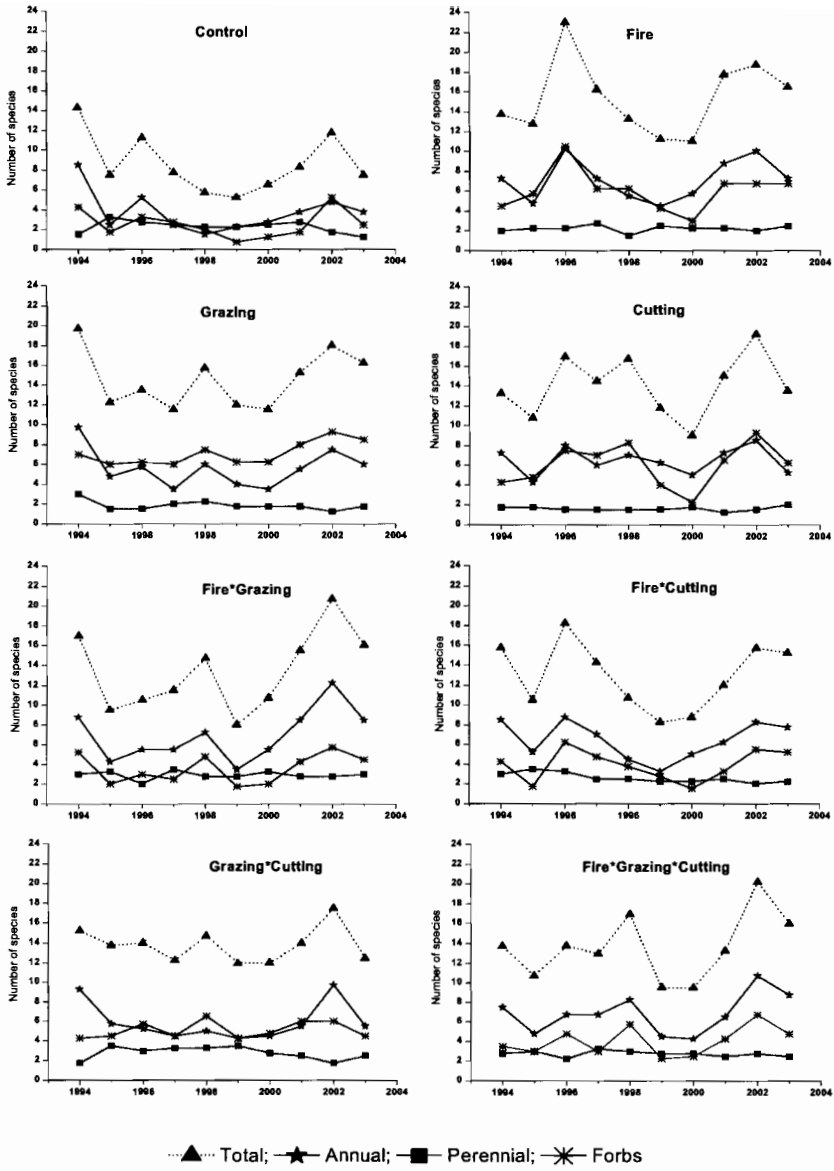


Fig. 2 B. Inter-annual variations in species richness of herbaceous flora (number of species/plot) at Tiogo.

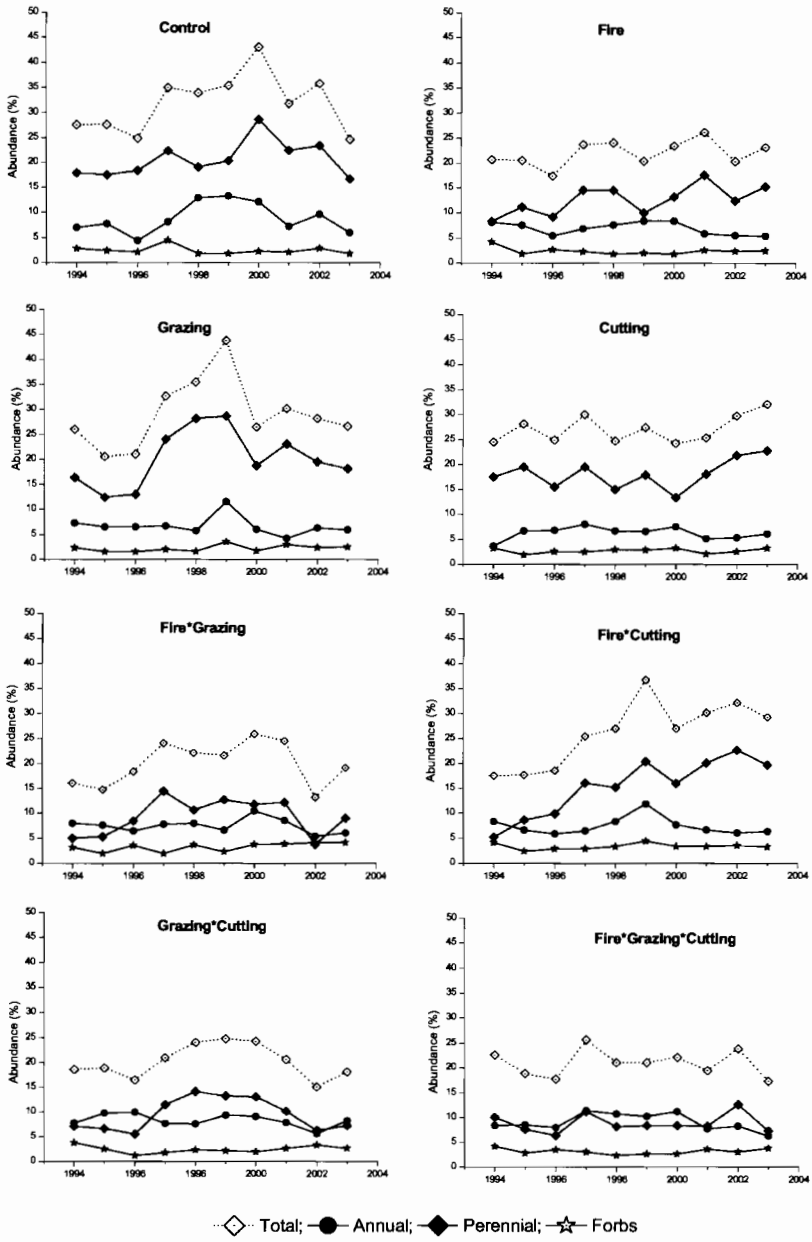


Fig. 3 A. Inter-annual variations in abundance of herbaceous flora (% cover) at Laba.

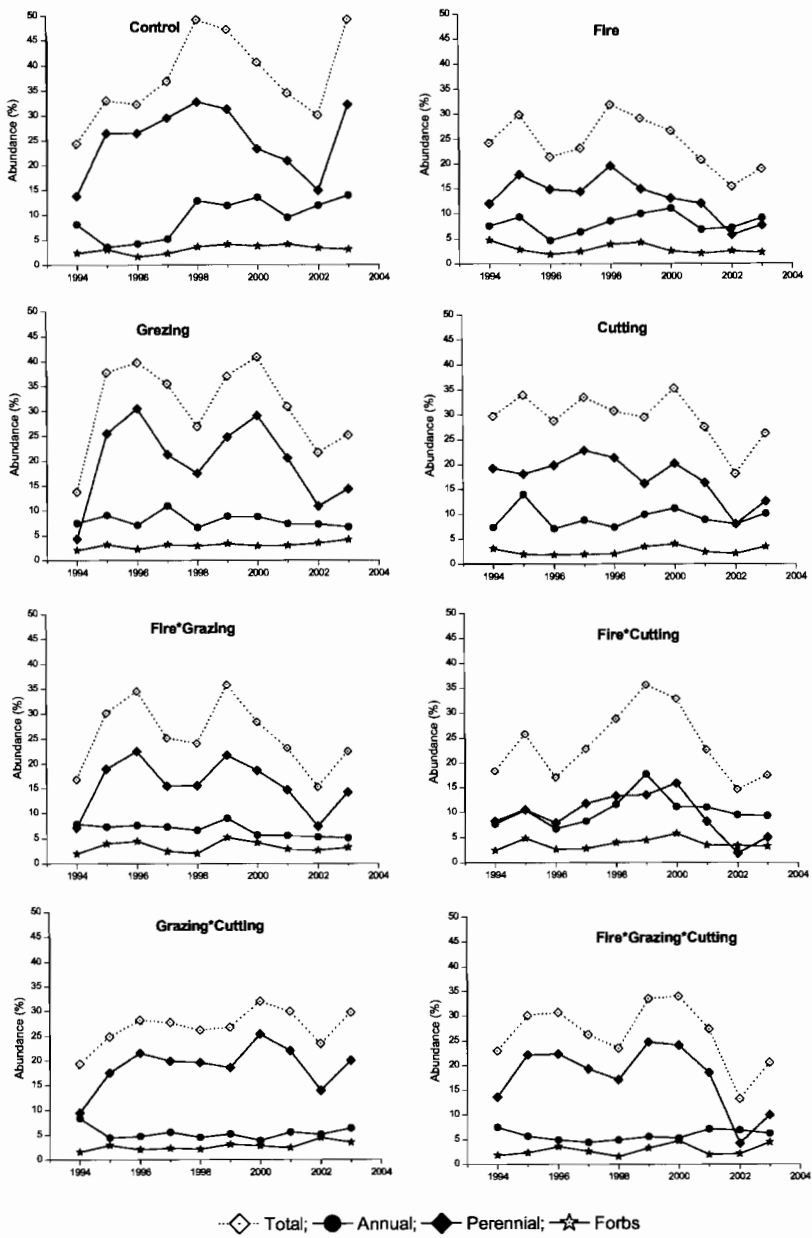


Fig. 3 B. Inter-annual variations in abundance of herbaceous flora (% cover) at Tiogo.

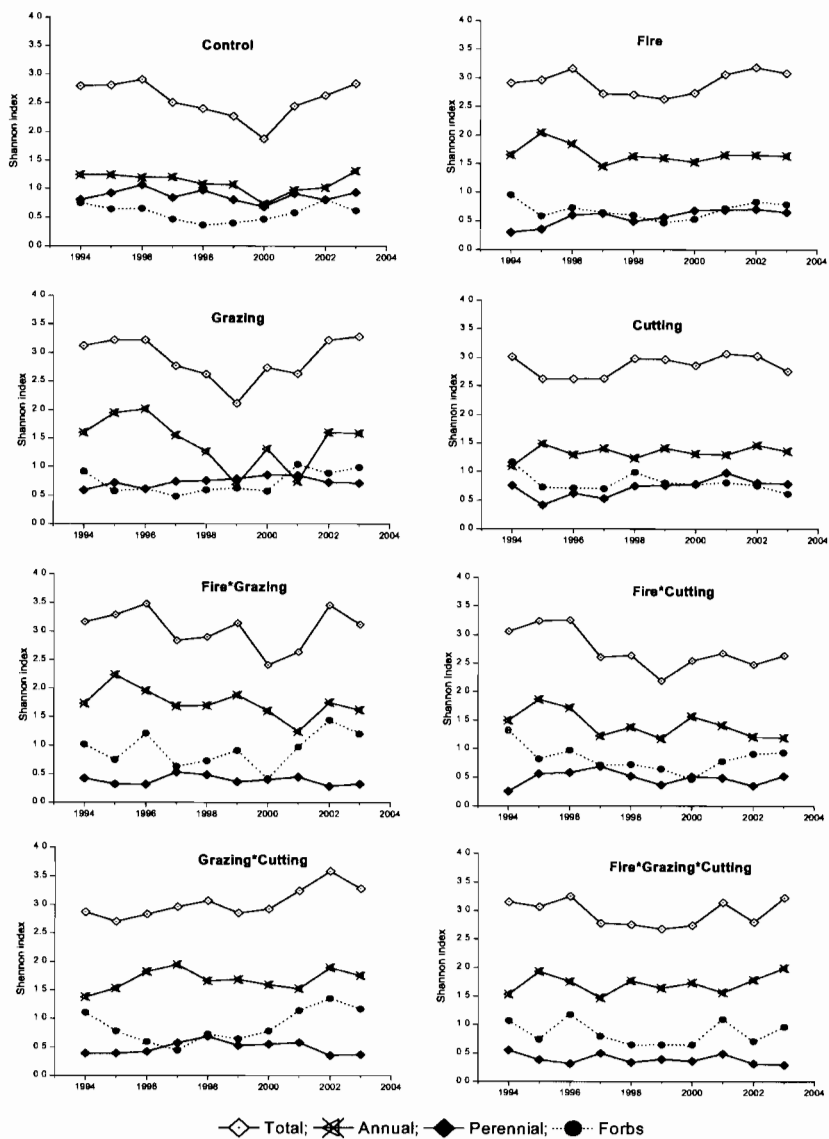


Fig. 4 A. Inter-annual variations in diversity of herbaceous flora (Shannon-Wiener's index) at Laba.

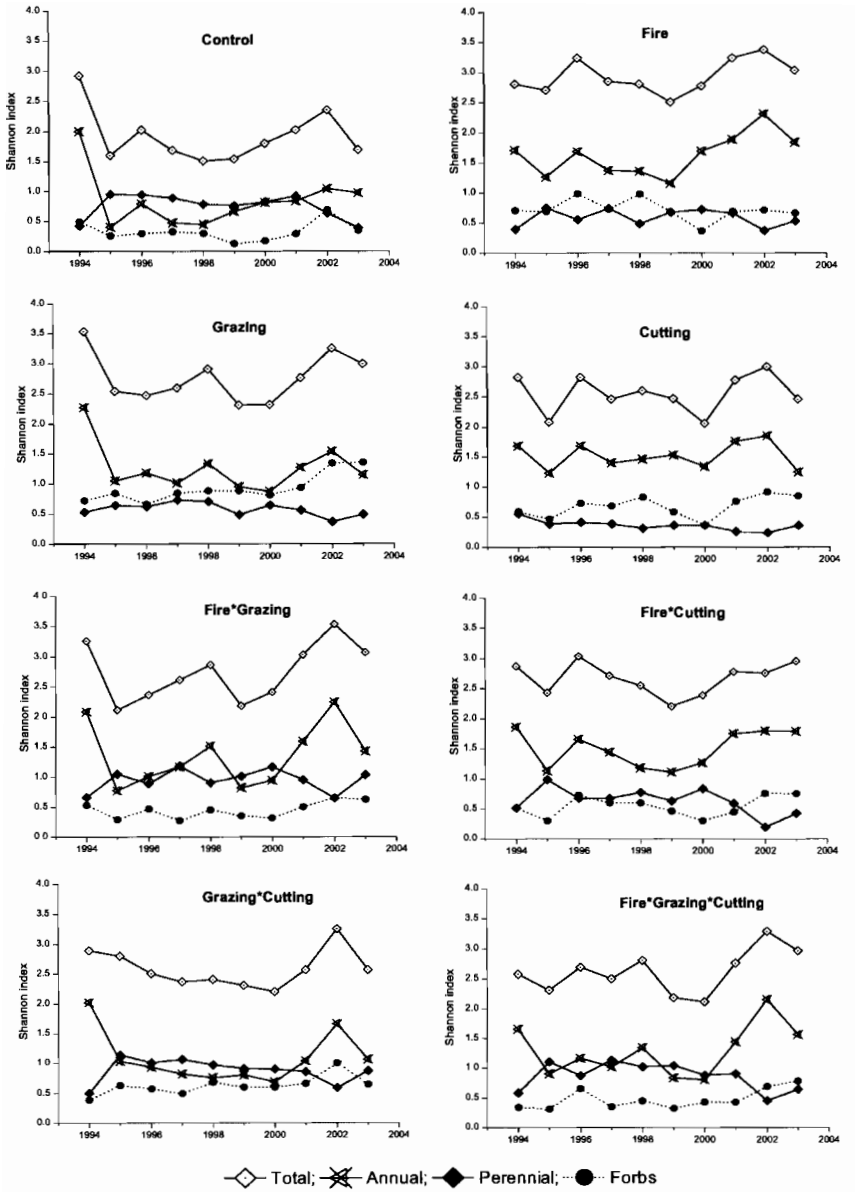


Fig. 4 B. Inter-annual variations in diversity of herbaceous flora (Shannon-Wiener's index) at Tiogo.

3.4. Dominant species

Four species, *Andropogon ascinodis* and *Diheteropogon hagerupii* at Laba and *Andropogon gayanus* and *Loudetia togoensis* at Tiogo were the most common species on nearly all experimental plots for analysis on species level. Among these species, the abundance of *L. togoensis* was significantly ($F_{1,24} = 4.746$, $p = 0.039$) increased by fire ($12.50 \pm 3.08\%$ on burnt versus $5.85 \pm 2.05\%$ on unburnt plots) and reduced ($F_{1,24} = 4.565$, $p = 0.043$) by grazing ($5.21 \pm 3.08\%$ on grazed versus $13.15 \pm 3.21\%$ on non grazed) and grazing \times cutting ($F_{1,24} = 4.643$, $p = 0.041$) treatments. For all species except *A. ascinodis*, the annual variation in abundance was significant ($p < 0.01$ in all cases). For *L. togoensis*, the annual variation in abundance was more pronounced on grazing ($p = 0.006$) and grazing \times cutting ($p = 0.006$) plots.

3.5. Vegetation response to rainfall

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. For annual and perennial grasses, the relationship between vegetation attributes and rainfall parameters was very weak, especially at Laba. For instance on the annually burnt plots mean perennial grass richness and diversity significantly increased with importance of precipitation amount and precipitation pattern ($r^2 = 0.56$, $F_{2,8} = 5.13$, $p = 0.037$ and $r^2 = 0.56$, $F_{2,8} = 5.03$, $p = 0.038$ for richness and diversity, respectively). At Tiogo, annual species diversity was also positively related to rainfall parameters on annually burnt ($r^2 = 0.61$, $F_{2,8} = 6.29$, $p = 0.023$), burnt and grazed plots ($r^2 = 0.58$, $F_{2,8} = 5.55$, $p = 0.031$) and simultaneously burnt grazed and cut plots ($r^2 = 0.58$, $F_{2,8} = 5.59$, $p = 0.030$). At the same site growing season precipitation amount and pattern best expressed the variation of forbs diversity on cut ($r^2 = 0.71$, $F_{2,8} = 9.62$, $p = 0.007$) and cut and burnt plots ($r^2 = 0.54$, $F_{2,8} = 4.64$, $p = 0.046$). The abundance of forbs species increased significantly with rainfall data on burnt plots ($r^2 = 0.57$, $F_{2,8} = 5.23$, $p = 0.035$) and burnt and grazed plots ($r^2 = 0.60$, $F_{2,8} = 6.11$, $p = 0.024$) while for annual grass the same effect was observed on grazed plots ($r^2 = 0.61$, $F_{2,8} = 6.36$, $p = 0.022$).

4. Discussion

4.1 Temporal variation

The total number of herbaceous species identified during the 10 years at both sites was 176 and 152 at Laba and Tiogo, respectively. These taxa were made up of 43 families and 112 genera at Laba and 47 families and 117 genera at Tiogo site.

Prior to applying the treatments in 1993, the pool of herbaceous species at Laba was 8, 22, 38 perennial grasses, annual grasses and forbs, respectively and the corresponding values at Tiogo were 5, 23 and 43 perennial grasses, annual grasses and forbs, respectively. The results showed a conspicuous inter-annual variation in herbaceous species richness, abundance and diversity. These could be partly explained by the difference in precipitation patterns between and within years. The composition of the herbaceous layer in dry savannas appears to be affected primarily by year to year and longer-term variation in rainfall. The change in diversity and herbaceous cover are in many places found to be related to weather conditions and in particular spatial and temporal distribution of rainfall (Frost et al., 1986; Seghieri et al., 1994) and water catchments among the plots. In the present study, a fairly good relationship was found between rainfall parameters and abundance and diversity at one of the study sites (Tiogo). The specific nature of this relationship could very well depend on the soil characteristics and nutrient status, moisture availability and disturbance regime. 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 et al., 2005). These two species also accounted substantially for the high abundance found at this site. The general relationship between herbaceous species richness and the site location was similar to that described by Fontes and Guinko (1995).

The variation between years of total species richness and diversity may be related to different precipitation patterns between and within years which was suggested by Frost et al. (1986); an effect also found at both study sites for some specific growth forms and disturbance regimes. In the present study the correlation coefficient was improved when considering annual precipitation amount and number of rainy days. This observation was consistent with Nippert et al. (2006) who reported that variability in rainfall patterns, independent of seasonal amount increase soil moisture variability and reduced soil water content, which lead to increased plant water stress and decreased productivity. The correlation increased slightly when considering annual grasses and forbs. This could be explained by the fact that perennial grasses may be more drought resistant. At the same site the correlation between herbaceous biomass and rainfall was 38% (Sawadogo et al., 2005).

Early heavy rains stimulated seed germination within three days (personal observation) but gaps in rainfall distribution caused wilting of emerging seedlings; also in the field, 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 and Breman, 1990); dry spells following the first rains favour slow germinating species. Thus timing of rains, speed of germination and drought tolerance of seedlings are important in determining what species establish at a given site each year, while the

production of seeds for the seed bank is decisive for the species composition in the following year. The discrepancy between years may be explained by the loss of seeds due to herbivores (insects and rodents) or due to failed germination because of insufficient soil moisture. Herbaceous vegetation may also be influenced by inter site differences in soil texture and fertility as well as the patchiness of the soil at micro-site level, the discontinuous tree vegetation (out in the open and under trees in bush clumps) changing the micro-environment. Apart from climatic and other abiotic variables, the herbaceous spatial distribution was also influenced by anthropogenic disturbances such as burning frequency, livestock grazing, and tree removal.

4.2 Effects of grazing

Results from the present study show that grazing had no effect on total species richness and diversity of herbaceous vegetation at either experimental site (Table 1). There are three possible reasons why grazing had no negative impact on total species richness and diversity of herbaceous species. 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 and Ritchie, 1998). This is further proven by the dominance of *Andropogon gayanus* (47.1% cover) on ungrazed plots and from the significantly lower abundance of herbaceous species on grazed than ungrazed plots, particularly at Tiogo (Table 2). 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 grazing on total species richness interacted significantly with year, especially at Tiogo (Fig. 2B), suggesting spatial and temporal variations in terms of grazing intensity, stocking rate and feeding behaviour, which could average out the overall effect of grazing. Temporal variation in grazing intensity, stocking rate and feeding behaviour is common in the Sahel (Hiernaux, 1998) where free grazing by mixed herds – cattle, sheep and goats, is practiced (which is also the case on our sites). Grazing, however, reduced the abundance of herbaceous flora, particularly perennial grasses 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 cessation of trampling (Cole, 1995).

The effects of grazing were more pronounced when it interacted with the factor year, particularly at Tiogo. Total species richness, richness of annual grasses and forbs tended to be higher on grazed than ungrazed plots over the study period (Fig. 2B), but substantially higher in 1998 when the mean annual rainfall was the highest during the study period (1195 mm; Fig. 1). Although soil fertility is generally low at both experimental sites, the soils at Tiogo are mainly deep (> 75 cm) silty-clay while they are shallow (< 45 cm) silty-sand at Laba. Clay soils are more productive than sandy soils during years of above average rainfall (e.g. 1998, Fig. 1) and maintain greater quantities of available soil water over a longer period (Seghieri et al., 1994), thereby contributing to enhanced local colonization

rates. Evidence shows that the effects of herbivores is somewhat predictable and varies across environmental gradients; notably soil fertility and precipitation gradients (Belsky, 1992; Fuhlendorf et al., 2001; Harrison et al., 2003), and grazing is expected to have a strong positive effect on diversity in systems with higher productivity (Bakker et al., 2006; Milchunas and Lauenroth, 1993; Osem et al., 2002; Proulx and Mazumder, 1998).

We also found some species, namely *Borreria stachydea*, *Zornia glochidiata* and *Pandiaka heudelotii*, on 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 improving soil conditions by enhancing water infiltration and localized fertilization effects of dung and urine (Hansson, 2004; Herault and Hiernaux, 2004; Kohler, 2004; Oconnor and Pickett, 1992), thereby enabling species to colonize grazed sites. The new species that appeared on grazed plots in our study sites are previously described as indicators of grazing disturbance in the Sudanian savanna (Cesar, 1992).

4.3 Effects of prescribed fire

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 on species richness of annual and perennial grasses at Tiogo (Table 3), 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 et al., 2001) that results in increased seed mortality, and an inverse relationship has been observed between fire severity and species richness (Jensen and Friis, 2001). However, early fire is often of low intensity and severity due to high moisture in the fuels and thus has a minor impact on seed viability while creating conditions favourable for germination and favouring tillering by removal of litter cover (Garnier and Dajoz, 2001; Whelan, 1995). Germination of several herbaceous species is also stimulated by smoke released during burning (Adkins and Peters, 2001).

The effect of fire on species richness and diversity of annual grasses interacted significantly with the factor year, especially at Tiogo. For example the richness of annual grasses was two times higher on burnt than unburnt plots after three (1996) and nine (2002) years (Fig. 2B) while diversity of annual grasses was nearly tripled after two (1995), four (1997) and five (1998) years (Fig. 4B) 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 (Cheney et al., 1993; Coughenour, 1991), and the ability of some grasses to fully recover after fire, which may require 2 to 4 years or more (Bock and 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, 2003; Valone and Kelt, 1999). At Laba, fire significantly reduced the abundance of perennial grasses (Table 3). 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. Also, germination of some species is inhibited by unfavourable pH and osmotic conditions on post fire seedbeds and due to reduced moisture availability on drought-prone postfire gaps (Elberse and Breman, 1990).

4.4 Effects of selective tree cutting

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). For example, higher densities of summer annuals have been found away from the cover of competitively superior shrubs than under them (Guo, 1998). 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. 2-4), but the overall main effect of selective cutting of trees was not significant (Table 4). 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 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 (Nygård et al., 2004; Sawadogo et al., 2002) that shows vigorous resprouting and suckering ability of most savanna-woodland 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.

4.5 Interaction effects

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; even the limited interactions were life form and site specific. Furthermore, similar interaction effects involving grazing, fire and selective cutting were not detected for species individually regardless of the site. Species such as *A. gayanus* or *A. pseudapricus* responded differently to similar manipulation at different sites. These results conform with Belsky (1992) namely that grassland species cannot be divided into functional groups in which all species respond in a similar manner to all major environmental variables. As a whole, the combined effects of fire, selective cutting and grazing were significant for diversity of forbs at Tiogo while grazing \times fire treatment enhanced the richness and diversity of forbs at Tiogo, and cutting \times fire reduced the total species richness and abundance at Laba. 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, 1987; Collins and Barber, 1985). In mesic grasslands, burning opens space for colonists and grazing limits the ability of competitively dominant C₄ grass species to outcompete other plants, resulting in opportunities for colonization by C₃ grasses and forbs (Collins, 1987; Collins et al., 1998). In arid savannas, plant communities tend to have less ground cover and presumably less competition for space (Valone and Kelt, 1999). It is therefore the resource availability that limits local diversity (Collins et al., 1998). Such limited interaction effects of grazing and fire have been observed in other arid plant communities (Belsky, 1992; Drewa and Havstad, 2001; Valone, 2003; Valone and Kelt, 1999). 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 removal of trees creates evaporative stress and limits the growth of annual grasses, as can be seen from the relatively lower abundance values during the first three years of post-treatment (Fig. 3A); and abundance further decreased due to intensive grazing compared to untreated plots. Selective cutting possibly favoured the dominance of drought-tolerant perennial grasses, which in turn serve as good fuel and result in high-intensity fire that eventually reduced the overall abundance of herbaceous species. It should be noted that the treatment combination also showed significant interactions with year, suggesting temporal variability in grazing and fire intensities, as well as competition with profoundly regenerating individuals following cutting disturbance, which could average out the overall interaction effects.

Conclusions

The study provides evidence that the species composition, diversity and abundance in the Sudanian savanna-woodlands exhibit significant inter-annual variability that balances the main or interactive effects of grazing, fire and selective tree cutting. The responses of herbaceous flora to treatments particularly fire and grazing, was site-specific, suggesting the importance of landscape-scale approaches to understand the impact of disturbances on composition, structure and diversity of savanna-woodland ecosystems. Provided that grazing is kept at low intensities, the management of savanna-woodlands could be integrated with livestock husbandry, as it is the main sources of livelihood and source of revenue for the local people in Burkina Faso. The application of early fire could continue to be used as a management tool with due caution to the timing of burning, weather conditions and other possible factors that increase fire intensity. The current level of selective cutting (50% of the basal area of all trees) seems to have less beneficial effect on herbaceous vegetation, further research is, therefore, required to determine the appropriate cutting intensity that balances the composition and diversity of the herbaceous and woody components.

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Multivariate analysis of dynamic responses of herbaceous vegetation communities to disturbances in the Sudanian savanna-woodland using Principal Response Curves

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Abstract

Savanna-woodlands in West Africa are subjected to major disturbances that shape the landscape both spatially and temporally, yet the ecological effects are not fully understood. We carried out a long-term factorial experiment, from 1994–2006, to examine the effects of grazing, fire and selective tree cutting on herbaceous species abundance both at the community and individual species levels. Community abundance data recorded from line intercept sampling at two sites, mainly differing in their soil attributes, were analyzed using a multivariate ordination technique known as Principal Response Curves (PRC). The results indicate that disturbance regimes, independently or interactively, influenced species abundance over time with inter-site specificity. The PRC ordination accounted for 38% and 34% of the variation within the data set for sites with deep and shallow soils, respectively. At the site with deep soils, more than one PRC axis was needed to summarize the community response sufficiently, suggesting that the species reacted in different ways to disturbances. The PRC method allowed us to distil the complexity of the community responses to those of individual species and to identify species that can serve as indicators of certain disturbance regimes.

Keywords: multivariate ordination techniques; disturbance regimes; savanna ecosystem.

1. Introduction

Savannas are often subjected to multiple anthropogenic disturbances, including grazing, browsing, fire and selective tree cutting (Breman & Kessler, 1995). These disturbance regimes are often regarded as sources of spatial patterning, diversity and community organisation in grasslands and woodlands (McNaughton, 1983; van Langevelde *et al.*, 2003). Generally, the local species richness and the diversity of savanna ecosystems are maintained by dynamic interactions between local colonization from species pools at larger spatial scales and local extinction due to competitive exclusion. These are, in turn, influenced by disturbance (Gibson & Brown, 1991; Olff & Ritchie, 1998). In savanna woodlands,

characterized by mixtures of woody and herbaceous life forms, understanding the effect of various types of disturbance on the herbaceous community is essential for designing multiple use management plans. This is because the herbs account for 75-90% (Frost & Robertson, 1987) of the total annual biomass in tropical savanna ecosystems and play a major ecological as well as socio-economic role (Le Mire Pecheux, 1995).

Current policies for sustainable management of savanna-woodlands in Burkina Faso focus on woody vegetation and entail prohibition of grazing, setting annual early fires and selective tree cutting of 50% of the basal area over a 20-year rotation (Bellefontaine, Gaston & Petrucci, 2000). This approach is not based on scientific evidence. To generate scientific information to use in developing appropriate management strategies, long-term experimental plots were established in 1992 to examine the ecological effect of repeated burning, grazing and selective tree cutting on both the woody and herbaceous components of the Sudanian savanna woodland (Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004; Sawadogo, Tiveau & Nygård, 2005; Savadogo, Sawadogo & Tiveau, 2007; Zida *et al.*, 2007). This ongoing experiment is generating large data sets, comprising information on temporal changes in the abundance of herbaceous vegetation in the control and treatment plots. From these large datasets, however, only information about a limited number of taxa (usually the most abundant ones) or overall means have, so far, been properly analyzed with standard univariate statistical methods (Sawadogo, Tiveau & Nygård, 2005; Savadogo, Sawadogo & Tiveau, 2007). Although such techniques are well documented and robust, in general, vegetation studies that include multivariate analysis tend to explain much more of the total variation especially for species density (Grace, 1999). Previously, we applied repeated measures analysis to large part of the data set reported in this paper, but it was not possible to discern treatment effects at the level of individual species (P. Savadogo *et al.* Unpublished data 2007). In order to obtain a complete picture of disturbance dynamics and their effect on the vegetation community, an appropriate multivariate analysis technique that combines the interaction between treatment and time effects, both at community and individual species levels is needed.

In this study, the main research question was: how do the effects of disturbance regimes on herbaceous vegetation abundance change over time? The research question could also be phrased: what is the response, over time, of the herbaceous vegetation community to fire, grazing and selective cutting disturbances? To answer these questions, the abundance of herbaceous vegetation recorded over 13 years (1994-2006) was analyzed using a multivariate ordination technique called Principal Response Curves (PRC). PRC analysis is an ordination method based on partial redundancy analysis and developed specifically for analysis of community response data from designed experiments sampled repeatedly over time (van den Brink & ter Braak, 1998; Van den Brink & Ter Braak, 1999). Associated with each PRC is a set of species weights, which reflect the influence of each species on the overall community response described by the PRC scores over time.

2. Materials and Methods

2.1 Site description

The experimental sites are located on flat areas in Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) State forests (forêts classées), both at an altitude of 300 m a.s.l 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 (Mouhoun, formerly known as Black Volta) in the country. Phyto-geographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (Fontes & Guinko, 1995). The vegetation type at both sites is a tree/bush 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, local construction (roof-thatching and fences) and handicraft. The main forb species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC.) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Linn. Species in the families Mimosaceae and Combretaceae 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 was 10.7 m² ha⁻¹ at stump level (20 cm) and 6.3 m² ha⁻¹ at breast height (130 cm) with a stand density of 582 individuals ha⁻¹ for stems ≥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.

The unimodal rainy season lasts for about six months, from May to October. The mean (± SE) annual rainfall (Fig. 1) during the period (1994-2006) was 869 ± 39 mm for Laba and 848 ± 49 mm for Tiogo, and the number of rainy days per annum was 69 ± 5 and 66 ± 3 for Laba and Tiogo, respectively. 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. Most frequently encountered soils are Lixisols (Driessen, Deckers & Spaargaren, 2001), and the soil at Laba is shallow (< 45 cm depth) silty-sand while it is mainly deep (>75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998).

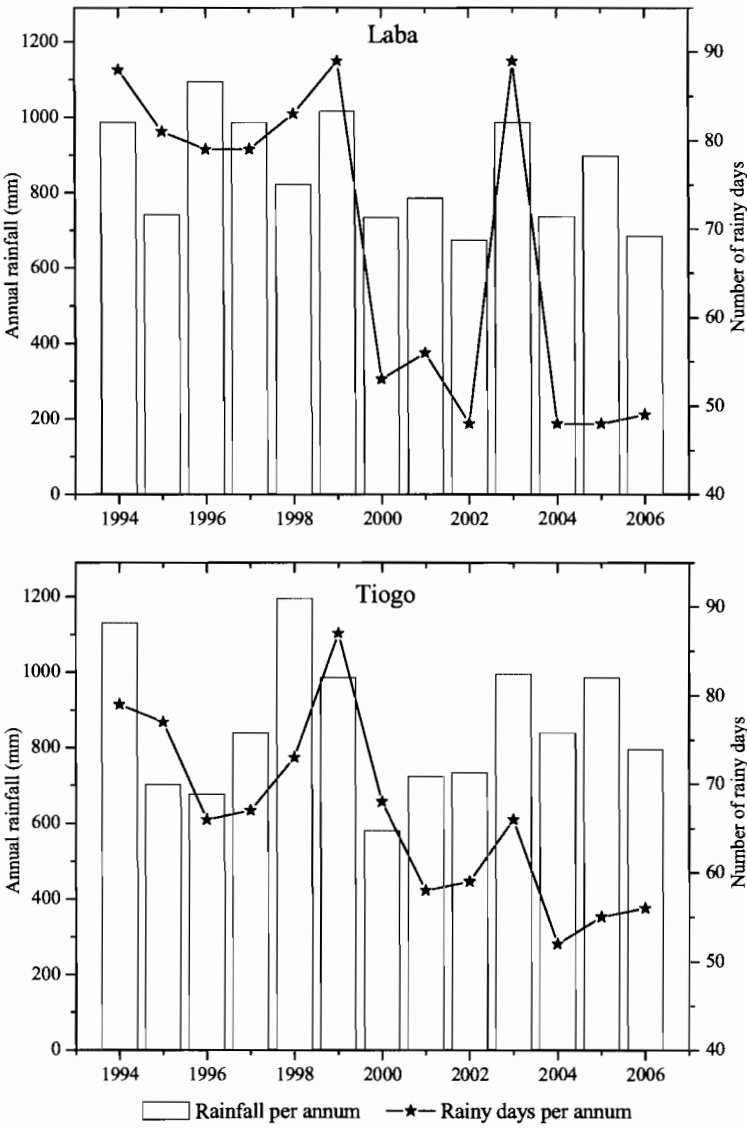


Fig. 1. Annual rainfall and number of rainy days for Tiogo and Laba across the study period.

2.2 Experimental design

A factorial experiment was established in each of the two State forests to examine the effects of grazing, early fire, selective cutting and their interaction on abundance of herbaceous vegetation (Fig. 2). Each experimental site (18 ha) was divided into eight blocks (2.25 ha); four of which were fenced to exclude livestock

(hereafter referred to as non-grazed plots) and the other four were open for grazing (hereafter referred to as grazed plots). Each block was further divided into four plots of 0.25 ha (50 x 50 m), separated from each other by 20 – 30 m fire-breaks. To the four plots within each block, the following factorial treatments were randomly assigned: No cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire. The selective cutting was done in December 1993 at Tiogo and a month later in January 1994 at Laba by removing 50% of the merchantable standing volume.

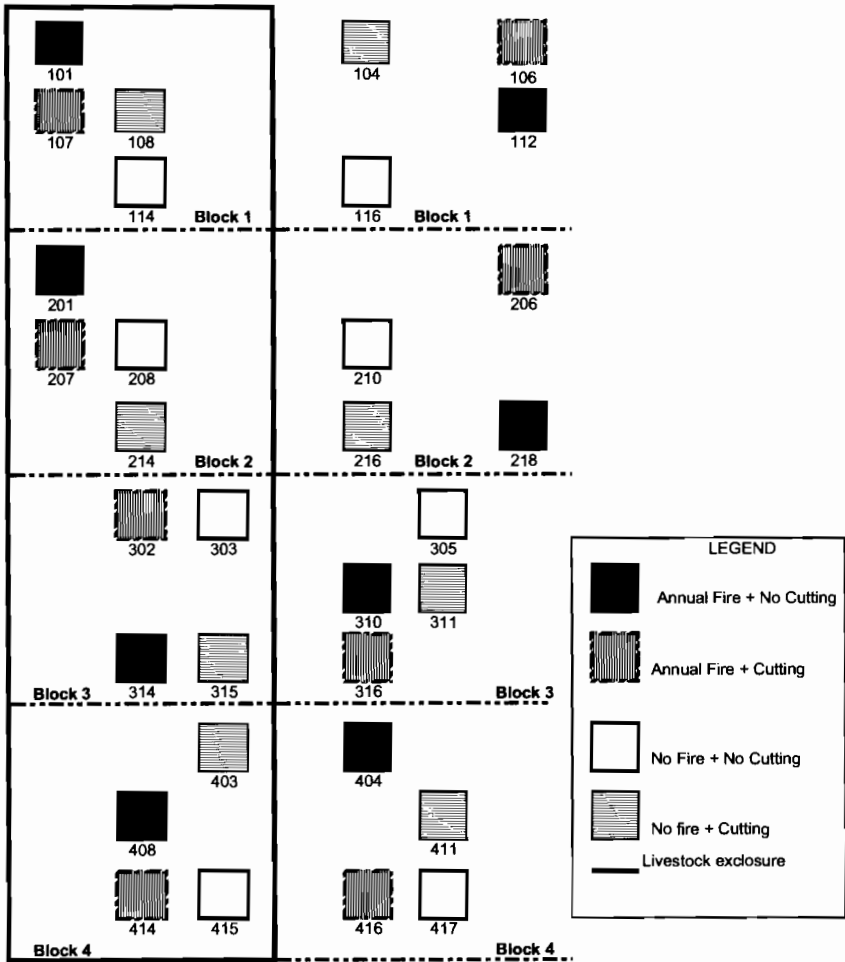


Fig. 2. Lay-out of the factorial experimental design.

Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and fuelwood, and fuelwood and others (Hagberg, Gomgnimbou & Somé, 1996; Sawadogo, 1996). Except protected species, individuals of other categories 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 (Sawadogo, Nygård & Pallo, 2002). The prescribed early fire was applied at the end of the rainy season (October – November) each year beginning 1993 when the grass layer humidity was approximately 40%. The grazing main plots at both study sites were open for grazing by livestock (a mixed herd of cattle, sheep and goats) mainly but also wild animals. The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit ha⁻¹ (T.L.U. ha⁻¹) and that of Tiogo was 1.4 T.L.U. ha⁻¹ (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo, Tiveau & Nygård, 2005). The presence of the livestock in the two forests varied spatially and temporally; grazing mainly occurs during the rainy season when grasses were green and surrounding area cultivated.

2.3 Data collection and analysis

The abundance of herbaceous vegetation was assessed every year from 1994 to 2006 at the end of the rainy season (September to October) when most of the species are flowering and fruiting, which allows for easy species identification. The point-intercept sampling procedure (Levy & Madden, 1933) was used to gather species-cover data. The presence of species was recorded along a 20 m permanent line laid in each subplot at an interval of 20 cm, giving a total of 100 sampling points. At each point record, a pin of 6 mm diameter taller than the maximum height of the vegetation was projected from above, and all contacts were recorded if the pin hit any of the live parts of a grass species. The positions of the transect lines were permanently marked to ensure accurate relocation each year. Identification of species and families of plants follows Hutchinson *et al.* (1954).

Initial data exploration to investigate the range of variation in the data set was carried out using detrended correspondence analysis (DCA), a method of indirect gradient analysis (ter Braak & Smilauer, 2002). However, the gradient length for the first axis was 1.05 and 1.33 for Tiogo and Laba, respectively, which are less than the recommended values, 3.0; thus species data set was ordinated with Principal Component Analysis (PCA). The abundance data for all herbaceous species (152 and 176 at Tiogo and Laba respectively) in response to fire, grazing, selective cutting and their interactions over the study period were then analyzed using Principal Response Curves (PRC) analysis. This technique is based on the ordination technique called partial redundancy analysis and developed specifically for analysis of community response data from designed experiments sampled repeatedly through time (van den Brink & ter Braak, 1998; Van den Brink & Ter Braak, 1999). Time coded as dummy variable was considered as covariable and only time by treatment interaction (also coded as dummy variable) were considered as explanatory variables. PRC plots the first principal component of the

treatment effects against time, expressed as deviations from the control/reference treatment (van den Brink & ter Braak, 1998). The general model for the first principal component can be expressed as:

$$Y_{d(j)tk} = \check{y}_{otk} + b_k c_{dt} + \varepsilon_{d(j)tk}$$

where $Y_{d(j)tk}$ is the abundance of species k in replicate j of treatment d at year t , \check{y}_{otk} is the mean log-abundance of species k in year t in the control ($d = 0$), c_{dt} is the score of the d^{th} treatment at year t , b_k is the weight of the k^{th} species and $\varepsilon_{d(j)tk}$ is an error term with mean zero and variance σ_k^2 . The coding used in the PRC standardized the control to be zero-valued $c_{dt} = 0$ for all times i.e. horizontal line in the PRC diagram. Species abundance was $\ln(x+1)$ -transformed to approximate the normal distribution while accounting for large number of zeros in the initial species data matrices, for which $\ln 0$ is undefined. In this case the reference (the control) was taken as the no fire + no cutting + no grazing plots. The underlying assumption for choosing this treatment as reference was that a system in undisturbed state is fairly stable and the effect of any disturbance can be gauged against this stable state. 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. Species with high positive scores are positively correlated, species with negative scores respond oppositely, and species with near-zero scores are indifferent to the trend recognized by the PRC axes (ter Braak & Smilauer, 2002). The statistical significance of the resulting PRC axes was evaluated using Monte Carlo permutation tests ($p < 0.05$ after 499 permutations under split-plot constraints) by permuting freely data from the whole treatments within each year. Changes in treatment effects through time were evaluated in sequential tests for each sampling year by permuting the census data. Monte Carlo permutation test was also performed to determine the effects of each treatment separately in time, plus their interactions with other treatments. The statistical analyses were performed using the software package CANOCO 4.5 and the ordination diagrams drawn in CANODRAW (ter Braak & Smilauer, 2002).

3. Results

The initial ordination of the herbaceous vegetation using PCA showed a low degree of variation in the abundance of species between treatments averaged over the study period, as evidenced from the low eigenvalue for the first axis, which was 0.34 for Tiogo and 0.41 for Laba. The PCA score/loading biplot further showed a low affinity of species to particular treatment at both Tiogo (Fig. 3A) and Laba (Fig. 3B). Although species affinity to treatments appeared low, it was still difficult to visualize, quantify and test for treatment by year interactions within the classic ordination framework provided by PCA. It should be noted that we averaged the abundance across the study years in order to clearly see how the responses of individual species spread over the different treatments.

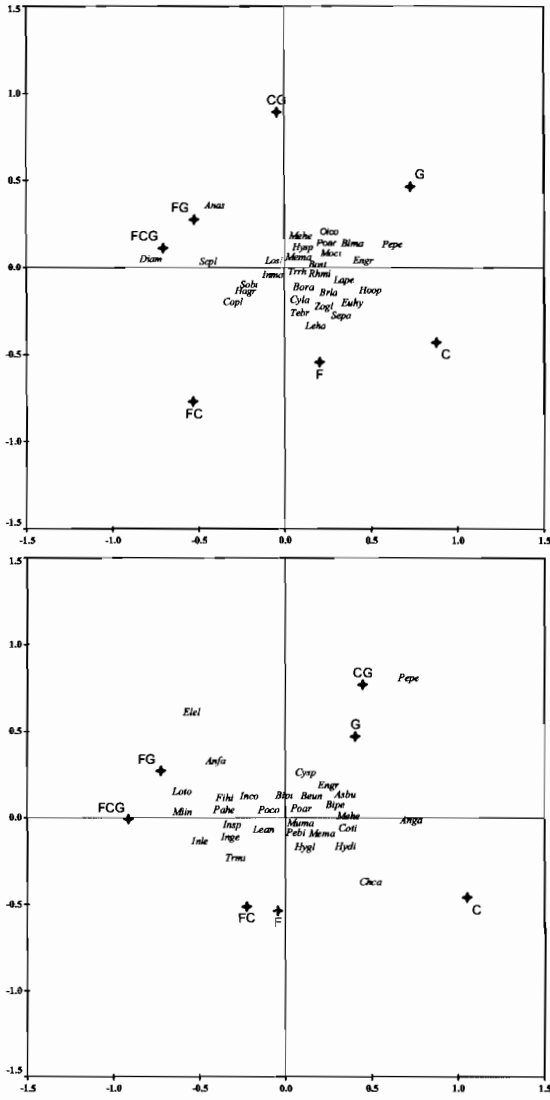


Fig. 3. Principal Component Analysis (PCA) biplots of an ordination of species by treatment regimes for the two study sites (upper panel for Tiogo and lower panel for Laba). A complete list of species is given in the appendix and the treatment regimes abbreviated as follows: F = fire, G = grazing, C = selective cutting, FG = fire x grazing, CG = cutting x grazing, FC = fire x cutting, FGC = fire x grazing x cutting.

The PRC ordination accounted for 38% and 34% of the variation within the data set for Tiogo and Laba, respectively (Table 1). The PRC models for the first axis in the full data showed that 13% and 8% of the total variation were attributed to

sampling years at Tiogo and Laba, respectively while treatment regime accounted for 25% and 26% of the total variation at Tiogo and Laba, respectively (Table 1).

Table 1. Percentage (%) of the total variance (Var.) that can be attributed to time and treatment regime within the data sets collected at Tiogo and Laba experimental sites. The treatment regime includes the interaction between treatments and time. The remaining fraction of variance is residual variance. The fractions of variance explained by the treatment regime that are captured by the first and second Principal Response Curves are also presented

	Full Data set	Data subsets						
		F	G	C	FG	FC	CG	FCG
A. Tiogo								
Var. accounted for by								
Time	13	19	23	19	25	20	25	23
Treatment regime	25	18	15	19	17	25	12	15
Explained Var. captured by								
First PRC	25*	58*	61	65*	58*	72	55*	63*
Second PRC	21*	26	27	29	33	31	25	23
B. Laba								
Var. accounted for by								
Time	8	8	13	16	10	10	12	11
Treatment regime	26	20	17	11	25	16	18	30
Explained Var. captured by								
First PRC	35*	23*	65	54*	75*	68	69*	79*
Second PRC	20	1	27	16	25	25	25	1

* Significant axes ($p < 0.05$); F: Fire; G: Grazing; C: Cutting

At both study sites, the first axis captured 25% to 35% of the total variation and was significant (Table 1). The second axis was also significant for Tiogo but not for Laba. The effects of each treatment separately in time, plus their interactions with other treatment indicated that the variation accounted for by the first axis ranged from 55% to 72% at Tiogo and 23% to 79% at Laba. At Tiogo, the first PRC axis was significant for all treatments and their interactions except grazing and fire \times cutting treatment, while at Laba it was significant for cutting, fire \times grazing and fire \times cutting \times grazing treatments. The PRC diagram for the first axis showed that there were two directions of departure from the control plots at Tiogo where fire, grazing and selective cutting were not applied (Fig. 4A). The main effects of fire, selective cutting and grazing on abundance were generally positive for the herbaceous vegetation community through out the study period; particularly these treatments favoured species, such as *Loudetia togoensis*, *Andropogon fastigiatus*, and *Andropogon pseudapricus*. The interaction effects were generally negative at community level compared to the control across the study period while having pronounced positive effects on species such as *Andropogon gayanus*, *Chasmopodium caudatum* and *Andropogon ascinodis*. Several species had their weight close to zero, indicating that they seemed insensitive to the treatments over time.

The Monte Carlo tests per sampling year revealed that the treatment regimes had significant effects on herbaceous species abundance after 4 (1998), and 6-10 (2000-2004) years at Tiogo (Table 2). Particularly, abundance declined in almost all plots in 2003. The PRC diagram also showed that the extent of the fire, selective cutting, and fire \times cutting \times grazing interaction effects was larger than the effects of grazing and other interactions as evidence from the large deviation of these lines from the control (Fig. 4A).

Table 2. Summary of the Monte Carlo permutation tests (number of permutation 499) of PRC axes 1 and 2, and sequential tests on data subsets for each treatment separately in time

	Full data set	Data subsets						
		F	G	C	FG	FC	CG	FCG
A. Tiogo								
All axes	0.247*	0.182*	0.150	0.194*	0.170*	0.246	0.115	0.153*
PRC axis 1	0.062*	0.106*	0.091	0.127*	0.098*	0.178	0.063*	0.097*
PRC axis 2	0.039*	0.020	0.016	0.019	0.024	0.021	0.013	0.013
1994	0.060	0.117	0.115	0.081	0.146	0.074	0.068	0.113
1995	0.092	0.251	0.185	0.325	0.127	0.336*	0.159	0.129
1996	0.104	0.269	0.150	0.277	0.183	0.324*	0.129	0.125
1997	0.109	0.198	0.131	0.281*	0.155	0.314*	0.116	0.134
1998	0.133*	0.232	0.134	0.280*	0.208	0.278*	0.136	0.154
1999	0.105	0.207	0.184	0.214	0.142	0.270*	0.172	0.174
2000	0.155*	0.303	0.145	0.288	0.204	0.308*	0.162	0.176
2001	0.153*	0.289	0.186	0.289	0.317*	0.462*	0.116	0.190
2002	0.118*	0.281*	0.246*	0.248	0.252	0.395*	0.168	0.368*
2003	0.131*	0.185	0.269*	0.156	0.322*	0.237	0.259*	0.239*
2004	0.102*	0.252	0.231*	0.243*	0.292*	0.360*	0.175	0.238
2005	0.099	0.216	0.282*	0.239	0.332*	0.356*	0.143	0.282
2006	0.091	0.159	0.239*	0.212	0.236	0.300*	0.154	0.188
B. Laba								
All axes	0.257*	0.179	0.168	0.106	0.253	0.164	0.180	0.295
PRC axis 1	0.089*	0.123	0.110	0.057*	0.189*	0.112	0.125	0.232*
PRC axis 2	0.033	0.013	0.016	0.008	0.016	0.013	0.014	0.019
1994	0.054	0.129	0.156	0.103	0.156	0.116	0.148	0.099
1995	0.093	0.199	0.147	0.129	0.249*	0.125	0.175	0.241
1996	0.095	0.154	0.202	0.093	0.220	0.136	0.195	0.268
1997	0.079	0.139	0.120	0.123	0.209	0.118	0.150	0.210
1998	0.116	0.200	0.175	0.150	0.271*	0.156	0.151	0.325*
1999	0.120*	0.276	0.184	0.210	0.346*	0.259	0.214	0.311
2000	0.133	0.203	0.191	0.125	0.272	0.221	0.231	0.413*
2001	0.138*	0.240*	0.166	0.135	0.264*	0.240	0.205	0.405*
2002	0.119	0.231	0.205	0.127	0.304*	0.171	0.255*	0.344*
2003	0.139*	0.199	0.197	0.084	0.296*	0.164	0.208*	0.392*
2004	0.165*	0.238	0.264*	0.117	0.400*	0.260*	0.234	0.426*
2005	0.145*	0.187	0.262*	0.116	0.342*	0.202	0.245*	0.393*
2006	0.166*	0.266	0.242*	0.136	0.327*	0.234	0.244	0.488*

* Significant eigenvalue ($p < 0.05$); F: Fire; G: Grazing; C: Cutting

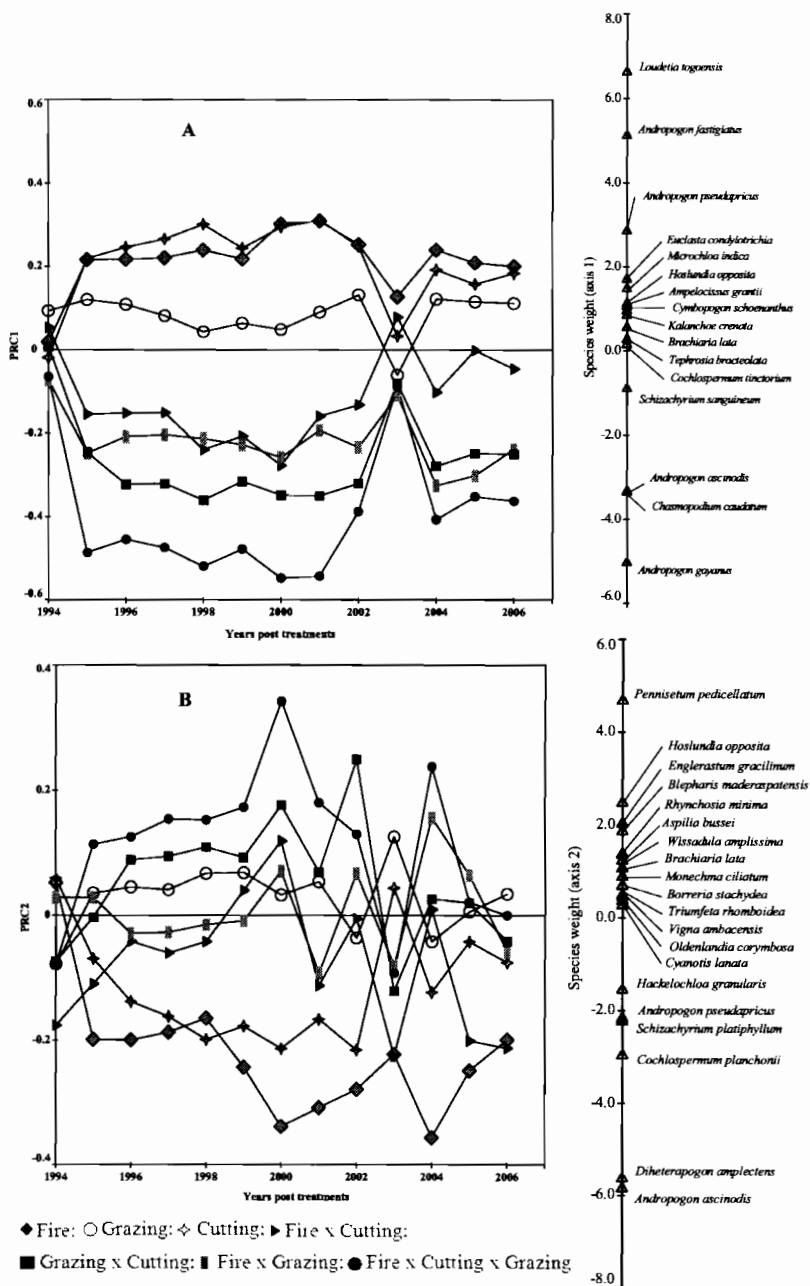


Fig 4. Principal response curves (PRC) together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and their interactions over 13 years at Tiogo site: A) for PRC axis 1 and B) for PRC axis 2. Only species with relatively strong responses are shown for the sake of clarity.

For the second axis, the PRC diagram revealed additional treatment effects as evidenced from a new set of species (Fig. 4B). The extent of fire and selective cutting main effects was larger than the oppositely oriented main effect of grazing, shown by the lines directed to the negative side of the vertical axis. Apparently, fire enhanced the abundance of *Andropogon ascinodis* and *Diheteropogon amplexans* throughout the study period, so also selective cutting during most of the study period. Among treatment interactions, cutting × grazing and fire × cutting × grazing had a larger positive influence on the abundance of species such as *Pennisetum pedicellatum* during most of the study period. Several other species also responded differentially to treatments during the study period as shown by their weights.

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 where the main effects of fire, grazing and selective cutting are oriented in the negative side of the vertical axis while the interaction effects are oppositely oriented except grazing × cutting (Fig. 5). Fire strongly influenced the abundance of herbaceous species during the study period by favoring species such as *Elionurus elegans*, *Andropogon fastigiatus*, *Diheteropogon hagerupii* and *Loudetia togoensis* while disfavoring *Andropogon gayanus*, *Schizachyrium sanguineum*, *Andropogon ascinodis* and *Monocymbium ceresiiforme*. 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 main effects of fire and grazing. On the basis of Monte Carlo tests per sampling year, the treatment regimes had significant effects on herbaceous species abundance after 8-12 years (2002-2006) while marginally significant after 5 (1999) and 7 (2001) years (Table 2).

Summary of the test for each treatment effect over time for Tiogo is presented in Table 2A, and the pattern is graphically depicted in Fig. 4A. The main effect of fire was significant in 2002 where abundance of herbaceous vegetation was relatively low compared with the previous sampling years. The effect of grazing was significant during the last five years of sampling (2002-2006) where abundance was higher in these sampling years except 2003 when grazing resulted in reduced abundance compared to the other sampling years. Selective cutting had more positive effect on the abundance of herbaceous vegetation community in 1997, 1998 and 2004 than the rest of the sampling years. The interaction effect of fire × cutting was positive in 1994 and 2003 than the other sampling years when abundance was relatively lower than the control. The fire × grazing treatment had a decreasing effect on abundance for the sampling years 2001, 2003 and 2005 and an increasing effect in 2004. The abundance of the herbaceous vegetation generally decreased in cutting × grazing and fire × grazing × cutting plots throughout the sampling years except 2003 in the former and in 2002 and 2003 in the latter when abundance was closer to the control.

Similar Monte Carlo tests results for the second case study site, Laba, is given in Table 2B, and the pattern of this inter-annual variation depicted in Fig. 5. The fire

treatment resulted in significantly lower abundance in 2001 than in some of the sampling years (e.g. 1994, 1997, 2005), while grazing reduced the abundance of herbaceous vegetation during the last three years (2004-2006) compared with the previous years. The effects of selective cutting did not vary across sampling years. In fire \times grazing treatment, the response of herbaceous vegetation was positive in 1995, 1998 and 2001-2006 while negative in 1994 and 1999. Abundance was lower in 2004 for fire \times cutting treatment, in 2002-2006 for cutting \times grazing and in all sampling years except 1995-1997 for fire \times grazing \times cutting treatment than the other sampling years.

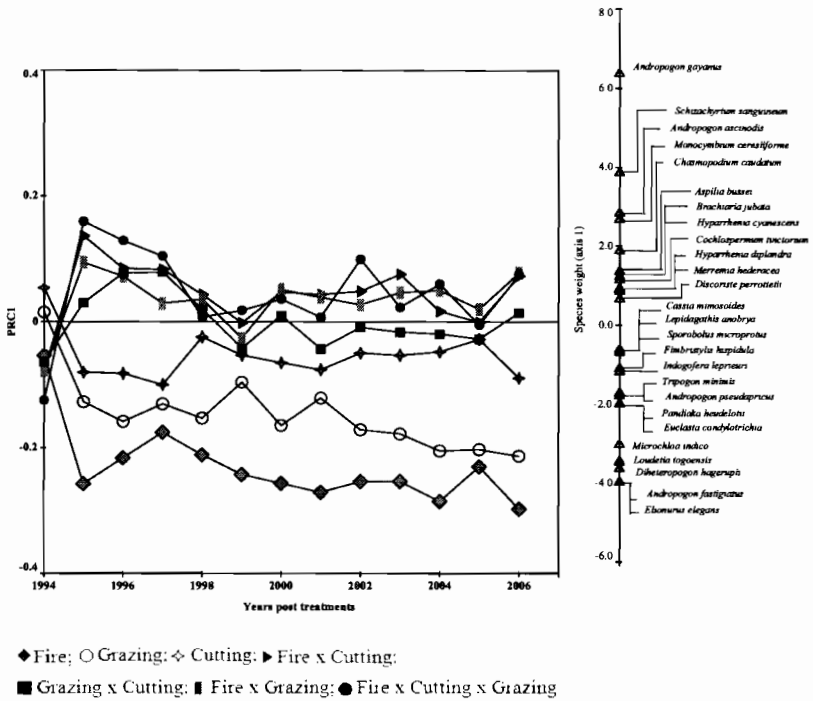


Fig. 5. Principal response curves (PRC) together with species weight diagrams representing the changes in herbaceous community response to fire, grazing, selective cutting and their interactions over 13 years at Laba site. Only species with relatively strong responses are shown for clarity.

4. Discussion

4.1 PRC model overview

The PRC model summarized the extensive species by sample data with one or two significant axes, depending on the case study site. Dimensional complexity is an important factor in the interpretation of multivariate analysis and models with few dimensions (axes) are often highly preferred. The proportion of variation accounted in the PRC ordination was higher for the treatment regime (involving time by treatment interaction) than for time for both study sites. This suggests that the treatment effects on species abundance were more important than the time per se. The fact that more than one PRC axis was needed to summarize the large data set from Tiogo suggests that the species reacted in quantitatively different ways to the treatments, as can be deduced from their weights.

4.2 Responses to individual treatments

The species composition of savanna ecosystems is maintained by a dynamic interaction between local colonization and local extinction due to competitive exclusion. In turn, these are influenced by disturbances, such as fire, herbivory and selective cutting (McNaughton, 1983; Gibson & Brown, 1991; Breman & Kessler, 1995). At the Tiogo study site, the effect of fire, selective cutting or grazing on the perennial grasses *Andropogon gayanus*, *Andropogon ascinodis* and *Schizachyrium sanguineum* in the herbaceous vegetation community was negative compared to the control, but not for the annual grass *Chasmopodium caudatum*. On the deep soils of Tiogo, these treatments tended to favour annual grass species and adversely affect perennial ones. Low intensity fire (such as early fire) enhances the colonization processes by inducing a flush of germination and flowering, a transient increase in overall productivity due to removal of litter that increases the availability of nutrients, space and light, as well as maintaining tussocks and increasing their cover by favouring the tillering of perennial grass (Whelan, 1995; Garnier & Dajoz, 2001). In contrast, recurrent fires may create unfavourable conditions for the germination of some species and can exhaust the below-ground reserves of perennials leading to their disappearance and replacement with more competitive annuals. In addition, post fire gaps may be drought-prone as a result of elevated evaporation that reduces moisture availability at the shallow depths where germination occurs, thus contributing to extinction processes (Elberse & Breman, 1990). The opposite effect was noted at the Laba study site: in the shallow soils at this site the perennial grass species *Andropogon gayanus*, *Schizachyrium sanguineum*, *Andropogon ascinodis*, *Monocymbium cerasiiforme* were favoured by the treatments while the annual grass species were adversely affected. The inter-site variability in the fire effect could be due to the occurrence of only short-lived fires at Laba because of the dominance of annual grass species with lower biomass compared to Tiogo where perennials dominate. The inter-site variability in fire effect could be due to relatively high fire intensity at Laba, which, in turn, is related to the increased availability of fuel in the form of biomass from annual grasses.

During the first half of the study period (1994-1999), the abundance of herbaceous vegetation increased somehow steadily in response to fire treatment, particularly at Tiogo. This initial increase may be related to increased availability of nitrogen and other nutrients essential for plant growth through deposition of ash (Jensen, Michelsen & Gashaw, 2001; Wan, Hui & Luo, 2001). The treatment effect was statistically significant (Monte Carlo tests) for 2001 at Laba and 2002 at Tiogo, which could be explained by interaction of fire with other environmental factors, such as rainfall. The mean annual rainfall was low for three consecutive years (2000-2002) at both study sites compared to the immediate sampling years before and after these years. Fire treatment might exacerbate drought in the post burn environment and result in reduced abundance of herbaceous vegetation. As a whole, the effect of fire on herbaceous vegetation community depends on growth form, fire frequency and intensity (Bennett, Judd & Adams, 2003; Sawadogo, Tiveau & Nygård, 2005), and the latter in turn depends on fuel load, moisture content of the fuel and weather conditions (Goldammer, 1990; Scholes & Walker, 1993).

The species composition and abundance of the understory increases following the formation of canopy gaps created by tree removal; this is due to reduced competition for water and nutrients as well as increased availability of light and growing space (Frost *et al.*, 1986; Akpo, Bada & Grouzis, 2003). There is evidence of this in the first PRC diagram for the Tiogo study site, where abundance increased steadily during the first five years of the study period. In contrast, at Laba the effect of selective cutting on the abundance of herbaceous vegetation over time was slightly negative. This could be related to drought effects, exacerbated by the selective removal of trees at Laba where the soil is mainly shallow, silty-sand with a low water holding capacity. It is indeed expected that the canopy gaps created by selective removal of trees may create unfavourable thermal conditions in arid and semi-arid areas and favour the growth of drought-tolerant species only, thereby contributing to competitive exclusion process.

Although grazing had a positive effect on the herbaceous vegetation community during the study period, the extent of its effect was lower than that of fire or selective cutting at Tiogo. The grazing intensity in our subplots, particularly at Tiogo, was half the carrying capacity (Sawadogo, 1996), thus many species could survive intermediate levels of grazing that allows succession to proceed but limits the ability of a few highly competitive species to dominate the community. Generally, moderate grazing enhances plant diversity through enhanced propagule dispersal, increased availability of light, and improving soil conditions while reducing local extinction rates by preferentially consuming competitive, dominant plants (Olf & Ritchie, 1998). The dynamics of grazing effects during the course of the study period are, in fact, related to the spatio-temporal variation in stocking rate and grazing intensity, which are common in the Sahel region (Hiernaux, 1998). At Laba, grazing had a greater negative impact at community level during the study period. This negative effect could be a consequence of the low biomass production at this site (Sawadogo, Tiveau & Nygård, 2005) coupled with heavier grazing pressure (Sawadogo, 1996) than at Tiogo.

4.3 Responses to treatment interactions

Generally all treatment interactions had a negative effect on the herbaceous vegetation community at Tiogo site during most of the study period. Their effects, however, were positive (increasing abundance) for perennial grasses *Andropogon gayanus*, *Andropogon ascinodis* and *Schizachyrium sanguineum*. The fire × cutting × grazing treatment effect was more pronounced than the other interaction effects. The removal of trees in 1994 created more growing space and probably enhanced the abundance of herbaceous vegetation. The increased availability of forage, in turn, might attract more herbivores and/or resulted in intense fire that eventually decreased the abundance of herbaceous species. The negative effect of this treatment interaction slightly fluctuated across the sampling years until 2002 and 2003 when abundance increased significantly closer to the control. This dynamics can be explained by the gradual decrease in the positive effect of selective cutting (increased growing space and reduction of competition) due to rapid colonization during the first few years (as can be seen from steady-state increase in selectively cut plots), which in turn reduced the availability of fuels and fire intensity. From the PRC diagram (Fig. 4A) it appears that the extent of selective cutting × grazing effect was more pronounced than the effect of fire × cutting or fire × grazing. This indicates high grazing pressure and stocking rate in response to abundance of forage following selective removal of trees, which might be the reason for limited effect of this treatment over the study period. Contrary to Tiogo, treatment interactions resulted in higher abundance of herbaceous vegetation community relative to the control during most of the study years, except cutting × grazing treatment. This site-specificity could be partly explained by the spatial distribution of herbaceous species at each case study site. At Laba, 12 dominant species responded positively for treatment combinations than 4 dominant species at Tiogo (c.f. Fig. 4A and 5).

4.4 Methodological importance

Analysis of large scale studies on disturbance dynamics is often centred around the use of conventional statistical methods, such as analysis of variance (Sawadogo, Tiveau & Nygård, 2005) or repeated measures analysis (P. Savadogo et al. Unpublished data 2007) based on data pooled over time or data from just a few individual species. Such analyses fail to reflect how the effects of disturbance vary over time or they do not allow the interpretation of results simultaneously at both community and individual species levels. PRC is a novel method for the visualization of results of repeated measurements analysis, focusing on time-dependent treatment effects (van den Brink & ter Braak, 1998; Van den Brink & Ter Braak, 1999). It has the capacity to reveal trends at a major community level within a large data matrix, combined with an increased ecological relevance to studies at lower levels of biological organization (Kedwards, Maund & Chapman, 1999). 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), vegetation and disturbance dynamics (Pakeman *et al.*, 2003; Pakeman, 2004; Vandvik *et al.*, 2005; Kohler *et al.*, 2006; Britton & Fisher, 2007) to the 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 more powerful tool for analyzing community responses to different perturbations over time than the conventional univariate methods and multivariate ordination techniques (e.g. DCA). Compared to our previous results based on repeated measures analysis of variance (P. Savadogo *et al.* Unpublished data 2007), PRC enabled us to interpret treatment effects not only at the community level but also at the individual species level. Such information is indispensable for identifying species that can serve as indicators of particular disturbance regimes. 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 to identify potential indicator species. In our study, *Loudetia togoensis*, *Andropogon gayanus*, *Andropogon fastigiatus*, *Andropogon ascinodis*, *Chasmopodium caudatum* and *Pennisetum pedicellatum* have the highest weights at Tiogo, while *Andropogon gayanus*, *Andropogon fastigiatus*, *Elionurus elegans* and *Schizachyrium sanguineum* have the highest weights at Laba. Therefore, these species could potentially serve as indicators of fire, grazing and selective cutting disturbances in the Sudanian savanna woodland.

Conclusions

This study illustrates that the herbaceous vegetation component of savanna-woodland responds differently along a time gradient to single or combined disturbances of fire, grazing and tree removal. Furthermore these effects are site-specific, suggesting that their effects interact with other environmental factors such as soil characteristics. The dynamics of these disturbance regimes also interact, to some extent, with rainfall. The PRC approach to the analysis of disturbance dynamics in this study appears to be indispensable, in that it allows identification of potential indicator taxa that could be used for monitoring the effects of disturbance regimes on the herbaceous community in savanna-woodlands.

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Appendix

A complete list of species together with their growth form (GF = growth form, Pe = perennial grass, An = annual grass, Fb = forbs) displayed in Principal Component Analysis biplots for both Tiogo and Laba

Species	Code	GF	Family
<i>Andropogon ascinodis</i> C. B. Cl.	Anas	Pe	Poaceae
<i>Andropogon fastigiatus</i> Sw.	Anfa	An	Poaceae
<i>Andropogon gayanus</i> Kunth	Anga	Pe	Poaceae
<i>Andropogon pseudapricus</i> Stapf	Anps	An	Poaceae
<i>Aspilia bussei</i> O. Hoffm. Et Muschl.	Asbu	Fb	Asteraceae
<i>Blepharis maderaspatensis</i> (L.) Heyne ex Roth	Blma	Fb	Acanthaceae
<i>Borreria radiata</i> DC.	Bora	Fb	Rubiaceae
<i>Borreria scabra</i> DC.	Bosc	Fb	Rubiaceae
<i>Borreria stachydea</i> DC.	Bost	Fb	Rubiaceae
<i>Brachiaria distichophylla</i> (Tri) Stapf	Brdi	An	Poaceae
<i>Chasmodium caudatum</i> (Hack.) Stapf	Chca	An	Poaceae
<i>Chlorophytum senegalense</i> (Bak.) Hepper	Chse	Fb	Liliaceae
<i>Cochlospermum planchonii</i> Hook. F.	Copl	Fb	Coclospermaceae
<i>Cymbopogon schoenanthus</i> Mair & Weiller	Cysc	Pe	Poaceae
<i>Digitaria horizontalis</i> Wild.	Diho	An	Poaceae
<i>Diheteropogon amplexens</i> (Nees) W.D. Clayton	Diam	Pe	Poaceae
<i>Diheteropogon hagerupii</i> Hitchc.	Diha	An	Poaceae
<i>Elionurus elegans</i> Kunth	Elel	An	Poaceae
<i>Euclasta condylotricha</i> (Hochst ex Steud.) Stapf	Euco	An	Poaceae
<i>Hackelochloa granularis</i> (L.) O. Ktze.	Hagr	An	Poaceae
<i>Hoslundia opposita</i> Vahl	Hoop	Fb	Lamiaceae
<i>Kaempferia aethiopica</i> (Schweinf.) Solm-Laub.	Kaae	Fb	Zingiberaceae
<i>Loudetia togoensis</i> (Pilg.) Hubb.	Loto	An	Poaceae
<i>Microchloa indica</i> Beauv.	Miin	An	Poaceae
<i>Pandiaka heudelotii</i> (Moq.) Hook.	Pahe	Fb	Amaranthaceae
<i>Pennisetum pedicellatum</i> Trin	Pepe	An	Poaceae
<i>Pennisetum polystachion</i> (Linn.) Schult.	Pepo	An	Poaceae
<i>Rhytachne triaristata</i> (Steud.) Stapf	Rhtr	An	Poaceae
<i>Rottboellia exaltata</i> Linn. .	Roex	An	Poaceae
<i>Schizachyrium exile</i> (Hochst.) Pilger	Scex	An	Poaceae
<i>Schizachyrium sanguineum</i> (Retz.) Alston	Scsa	Pe	Poaceae
<i>Sorghastrum bipennatum</i> (Hack.) Pilger	Sobi	An	Poaceae
<i>Tephrosia pedicellata</i> Bak.	Tepe	Fb	Fabaceae
<i>Tripogon minimis</i> Hochst. ex Steud.	Wiam	Pe	Poaceae

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Effects of grazing intensity and prescribed fire on soil physical and hydrological properties and pasture yield in the savanna woodlands of Burkina Faso

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Abstract

In West Africa policies for prescribed early fire and livestock grazing in the savanna woodlands are rarely based on long-term experimental studies. The inherently different management characteristics and their effects on the vegetation dynamics make landscape degradation a contentious issue. The effects of grazing intensity were investigated by a comparison of non-grazed areas, lightly grazed areas, moderately grazed areas, heavily grazed areas and very heavily grazed areas that received one of two fire treatments: early burning and fire protection in a long-term 12-year study. The parameters assessed reflected changes in herbaceous plant cover, biomass as well as soil physical and hydrological properties. The main findings were by and large specific for the grazing level. This supports the argument for devolution of management responsibility to the local level where there is indigenous site-specific knowledge but at the same time insufficient management capacity.

A comparison of composite soil samples taken at a depth of 0–10 cm did not differentiate significantly between treatments. This is probably because the composite soil sampling procedure hid the properties of the top first few centimeters. Grazing pressure had a tendency to reduce total above ground biomass ($p = 0.081$). This was related to increased biomass removal and the trampling pressure (static load) exerted by the animals. The infiltration measurements indicated that the deleterious impact of cattle trampling increased as stocking rate increased. Livestock grazing significantly ($p = 0.038$) lowered the infiltrability. Prescribed early fire had a tendency ($p = 0.073$) to reduce the soil water infiltration rate. The subplots subjected to prescribed burning had a lower steady state infiltration rate compared to unburnt areas (means of $49.2 \pm 27.5 \text{ mm h}^{-1}$ versus $78 \pm 70.5 \text{ mm h}^{-1}$ for burnt and unburnt subplots, respectively). A partial least squares projection to latent structures showed that 34% of the steady state infiltrability was explained by the stocking rate and soil organic matter. Also all soil characteristics were significantly connected to steady state infiltrability suggesting that they are related to the soil hydrological response to trampling.

From a management perspective, adoption of a short duration grazing system should avoid high stocking rates because they may adversely affect soil infiltrability, increase susceptibility to erosion in the savannas and decrease biomass productivity.

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Keywords: Trampling; Soil compaction; Vegetation cover; Net primary production; Infiltration

1. Introduction

Rapid deforestation due to shifting cultivation, over-grazing, fire and woodcutting is a serious problem in Burkina Faso as in most countries in the Sudano-sahelian

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region (Fries and Heermans, 1992). Livestock grazing is one of the main causes of soil and vegetation degradation (Warren et al., 2001). Livestock grazing may affect the properties of pastureland by altering plant cover by the mechanical effects of the hooves (Mwendera and Saleem, 1997a) and deposition of feces and urine. The impact of animal trampling depends on soil texture, phenological status of herbaceous vegetation, soil moisture and stocking rate at the time of grazing (Hiernaux et al., 1999). The stocking rate may alter the floristic composition of rangeland vegetation and may result in a shift from long-lived perennials to annuals and forbs with a concomitant decrease in production (Fuhlendorf et al., 2001). Severe grazing can lead to land degradation or desertification (Keya, 1998). Indeed, studies report an increase of soil bulk density, a decrease of water infiltration rate and an increase of surface runoff (Mwendera and Saleem, 1997b). Light grazing promotes succession from grassland to woodland (Watkinson and Ormerod, 2001). Livestock reduces grass biomass and often creates patchy vegetation alternated by bare soil. It has been found that vegetated patches positively affected soil moisture through less runoff and higher infiltration of rainwater compared to patches of bare soil (Rietkerk et al., 2000).

Fire is a prominent feature of most tropical savannas. Between 25% and 50% of the Sudanian zone burns annually (Delmas et al., 1991), primarily due to anthropogenic causes (Menaut et al., 1991). It favours the release of nutrients at the soil surface (Snyman, 2003) but also leads to losses due to leaching. Fire decreases the vegetation cover leading to increased ground temperature as well as disturbance of hydrological cycle and soil compaction. Fires burning early in the dry season tend to be of low intensity as the predominantly herbaceous fuel still holds moisture from the wet season (Liedloff et al., 2001). These fires often burn in a patchy manner and while removing litter and much of the grass layer, they have little effect on the vegetation the following year (Williams et al., 1999).

Fire and grazing are interrelated and their co-occurrence has a synergistic effect on plant communities. The effects depend on the type of vegetation and the phenological state of the plants, season, frequency and intensity of burning, grazing pressure, physical structure of the landscape and climatic conditions (Frost et al., 1986; Coughenour, 1991). Herbivory interacts with fire both in time and space. Many grazers are attracted to recently burnt ground to feed on the post fire regrowth of grasses. Grazers in turn reduce the fuel load by consumption and trampling (Mwendera et al., 1997) and therefore lower the intensity and frequency of accidental fire. Patchy grazing consequently causes patchy fire and vice versa (Frost et al., 1986). Since fire and grazing regimes can be manipulated directly, they are potentially important management tools to maintain quality pasture (Frost et al., 1986; Liedloff et al., 2001). The objectives and consequences of such regimes should be evaluated before incorporating them into any management system.

The sustainability of cattle grazing systems in dry savannas depends on assessment and maintenance of pasture productivity. Few guidelines for development and management of sustainable pastoral systems have been successfully developed so far. The impact of livestock grazing is poorly documented because of the scarcity of data obtained under controlled stocking rates and types of herd management (Hiernaux et al., 1999). In Burkina Faso, livestock presence in state forests is illegal (M.E.E., 1997) although in reality, these forests are the only rangelands available especially during the rainy season when the surrounding areas are occupied by crop cultivation. Therefore, the clandestine presence of livestock in the forest is harmful due to practices such as overgrazing and repeated pollarding of forage trees. To avoid these negative effects, it is important for forest management strategies to take the presence of livestock into account. It is therefore crucial to understand plant–animal interactions in order to ensure sustainable use of these grazing systems. Previous studies in the same forest found positive effects of livestock on stump survival and coppice growth after selective tree cutting (Savadogo et al., 2002) but the shortcoming of these studies was the unknown grazing intensity. Therefore, the key question is “how much livestock could graze in a forest without jeopardizing the sustainability of different forest products?”

The objectives of this study were to quantitatively describe the influence of prescribed fire, selected grazing intensities including grazing exclusion on soil characteristics, infiltration rate, forage production and vegetation cover after a short duration grazing experiment.

It was hypothesized that (1) herbaceous cover, species composition and biomass would be greater on the ungrazed and unburnt treatments compared to grazed and burnt ones and (2) annually prescribed early fire and increased grazing intensity will affect soil physical features while lowering nutrient contents and resulting in poor aggregate structure and infiltration rate. These properties are important for soil fertility and land management in the savanna woodlands.

2. Materials and methods

2.1. Site description

The study was conducted in Tiogo State Forest (12°13'N, 2°42'W) at an altitude of 300 m above sea level in Burkina Faso, West Africa. The Tiogo State Forest (forêt classée) was delimited by the colonial French administration in 1940 and covers 30,000 ha. It is located along the only permanent river (Mouhoun formerly known as Black Volta) in the country. Phyto-geographically it is situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (White, 1983). The unimodal rainy season lasts about 6 months, from May to October. The mean annual rainfall for the years 1992–2003 was 841 ± 187 mm with large inter-annual variability. The number of rainy days

per annum during this period was 69 ± 8 (Table 1). Mean daily minimum and maximum temperatures were 16 and 32 °C in January (the coldest month) and 26 and 40 °C in April (the hottest month), yielding an aridity index (Brown and Lugo, 1982) of 3.6.

Most frequently encountered are Lixisols (LX) according to the FAO soil classification system (Driessen et al., 2001). The soils are mainly deep (>75 cm) silty-clay and are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998). The vegetation is a tree and bush 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. and *Andropogon asciodis* C.B. Cl. (Savadogo et al., 2005). In the study area, these two perennial grasses are the most important species because of their fodder value and also because they are used for construction purposes (roof-thatching and fences) and handicraft. The main forb species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC) Hutch. and Dalz., *Borreria radiata* DC and *Wissadula amplissima* Linn. Mimosaceae and Combretaceae dominate the woody vegetation component. The most common woody species are *Acacia macrostachya* Reichenb. ex Benth., *Combretum nigricans* Lepr. ex Guill. and Perr. and *Combretum glutinosum* Perr. ex DC.

Bush fires occur almost every year, often late in the dry season (November–May). Nevertheless, most forest management plans include early burning (October–November). Livestock is dominated by cattle, sheep and goats as well as wild animals. The presence of livestock in Tiogo State Forest varies spatially and temporally, mainly occurring during the rainy season (June–October) when the grass is green and the surrounding areas are cultivated. During the dry season, when the crops have been 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 as well as the young shoots of perennial

grass species and young woody foliage induced by the fire. The livestock carrying capacity in Tiogo State Forest was estimated at 1.4 tropical livestock unit ha⁻¹ (TLU ha⁻¹) (Savadogo, 1996) and the grazing pressure at the experimental site was about half of this capacity.

2.2. Experimental design and grazing regimes

This study is part of a larger split-plot experiment with four replicates of 4.5 ha established for long-term studies of the ecological effects of grazing, prescribed fire and selective tree cutting (Fig. 1). The experimental site (18 ha) was split into two contiguous main plots of which one was fenced off at the beginning of the dry season in December 1992 to exclude livestock. Each main plot was further divided into 4 blocks of 2.25 ha, each containing 9 subplots of 0.25 ha (50 m × 50 m). The subplots were separated from each other by 20–30 m firebreaks. To the nine subplots within each block, three treatments were randomly assigned as no cutting, selective cutting of 50% of the basal area at stump level and selective cutting of 50% of the basal area followed by direct seeding of tree species. Three fire treatments were also applied: “fire protection”, “2-year fire protection followed by early annual fire” and “early annual fire since the establishment of the trials”. The prescribed early fire was applied at the end of the rainy season (October–November) each year beginning 1992, when the grass layer humidity was approximately 40%. In June 2003 a short duration grazing experiment was added to the half of the experiment that is open to livestock grazing. In this study, the treatment 2-year fire protection followed by early fire was not considered. Indeed, the subplots with this treatment were protected from 1992 to 1994 and since then they have received annual early burning treatment. All the subplots open to livestock grazing had a similar history of moderate, discontinuous use throughout the year and were in good condition in terms of carrying capacity when the controlled grazing experiment was implemented. The area was divided into four blocks separated by a barbed wire fence to regulate the number of cattle in each block. Due to the animals’ preference for the firebreaks where grass is greener compared to unburnt subplots where litter from previous year hinders grazing, the subplots were further enclosed by a second barbed wire fence for strict control. The intensity of grazing was defined according to the number of livestock per grazing area unit and frequency of grazing activities. To simulate the grazing pressure, 20, 40, 60 and 80 cattle were allowed to graze/trample each subplot for 4 h during 10 consecutive days per month from June to September (rainy season). The confinement of the livestock during these short periods while the soil was moist created a herd effect and the cumulative trampling pressure of the soil surface by the static load exerted by the animal was therefore overestimated. The animals were local zebu cows with an average live weight of 280 kg and they received a salt/mineral supplement. The grazing frequencies were applied

Table 1
Annual rainfall for 1992–2003 at Tiogo state forest in the Sudanian zone of Burkina Faso

Year	Rainfall (mm)	Number of rainy days
1992	841	77
1993	686	59
1994	1131	79
1995	703	77
1996	676	66
1997	839	67
1998	1195	73
1999	986	87
2000	581	68
2001	723	58
2002	733	59
2003	996	66
Mean ± S.D.	841 ± 195	70 ± 9

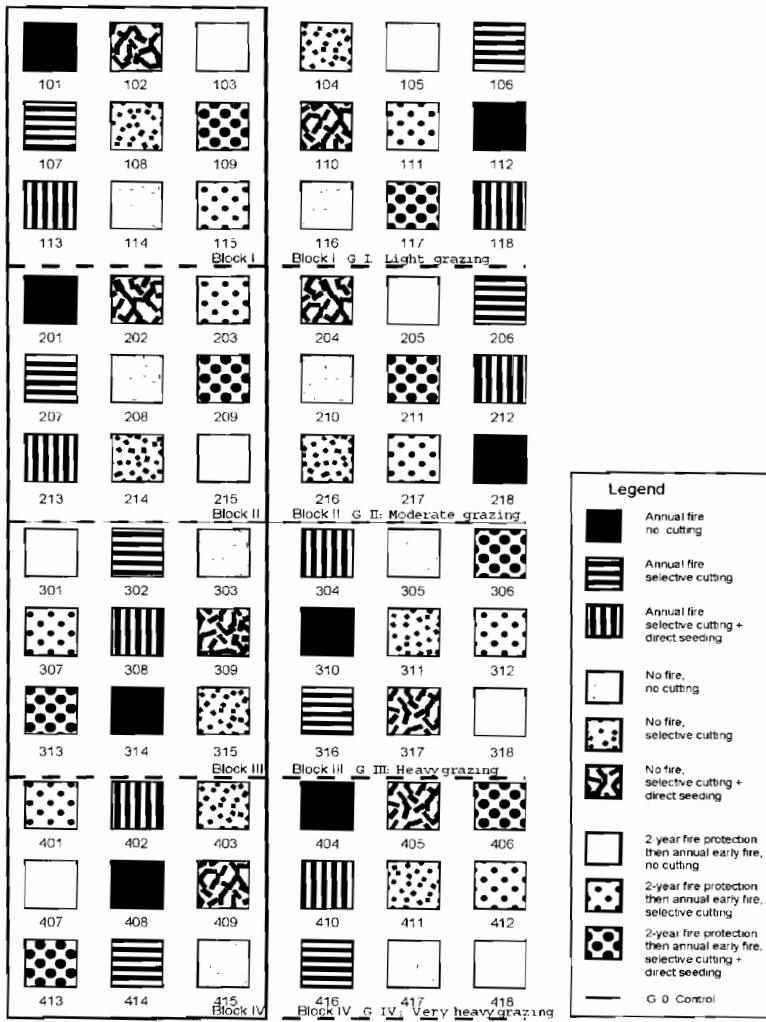


Fig. 1. Experimental set-up in Tiogo state forest, Burkina Faso.

to allow regrowth of vegetation by letting the area rest and were converted to stocking density and stocking rate using the formula proposed by Scarnecchia (1985). Stocking density was calculated as: $SD = AU/A$ where SD is the stocking density in animal-unit per hectare ($AU\ ha^{-1}$); AU is animal-unit and A is area in ha. The daily stocking rate was calculated by the equation $SR = SDt$ where SR is the stocking rate in animal unit per day and per hectare ($AUD^{-1}\ ha^{-1}$) and t is duration of grazing in days. The experiment therefore had the following grazing levels:

- G0: control with zero grazing, these plots have been protected for 11 years;

- GI: light grazing stocked at $2\ AUD^{-1}\ ha^{-1}$;
- GII: moderate grazing stocked at $4\ AUD^{-1}\ ha^{-1}$;
- GIII: heavy grazing stocked at $6\ AUD^{-1}\ ha^{-1}$;
- GIV: very heavy grazing stocked at $8\ AUD^{-1}\ ha^{-1}$.

2.3. Vegetation assessment

Biomass yield and vegetation percentage cover were determined in each subplot shortly before infiltration measurements were done in November 2003. The herbaceous vegetation biomass and cover were assessed each year beginning 1992. The herbaceous biomass assessment was done by hand clipping at peak biomass (mid October) of six $1\ m^2$

quadrats in each 50 m × 50 m subplot. The location of these quadrats was chosen at random. The samples were sorted according to species, bagged, dried and weighed. In this study, for each treatment, the mean herbaceous standing phytomass was analysed by considering the total herbaceous biomass and litter. The phytomass yield from the ungrazed subplots was compared to that from the grazed subplots to determine changes in aboveground biomass due to increased grazing pressure. The assessment of the herbaceous understorey percentage cover was carried out using the point intercept sampling procedure (Levy and Madden, 1933). The presence of species was recorded at 0.20 m intervals along one 20 m permanent line located in each subplot. At each point record, a pin taller than the vegetation maximum height was projected from above; a species was present if the pin hit any of its live parts. Identification of species and families of plants were made according to Hutchinson et al. (1954). The species were grouped per growth form (annual and perennial grasses and forbs) and analysed.

2.4. Infiltration measurement

Water infiltration rate was measured with two double ring infiltrometers (Bouwer, 1986). The internal diameters of the inner and outer rings were 30 and 55 cm for the first infiltrometer and 28 and 53 cm for the second. The height of each ring was 25 cm. The infiltrometers were placed on four randomly selected points in each subplot. The water level in the outer ring was kept constant and the reading of the water level in the inner continued until a steady state was reached.

The data in this study were collected after several years of moderate discontinuous grazing, with no information on the progress of infiltration rates over time. Water infiltration data were therefore used to assess the relative effects of levels of animal compaction on the soil, and not the effect of grazing system on the total hydrology of the savanna (Gifford and Hawkins, 1978).

2.5. Soil sampling and analysis

Soil sampling was done after measuring the infiltration in the same subplots. Topsoil samples at 0–10 cm were taken at 4 random selected points in each subplot using a cubic soil auger with 10 cm sides. The soil samples from each location were bulked, thoroughly mixed and air-dried. A composite sample was taken, bagged, labeled and analysed. The following list of physical and chemical parameters was determined according to standard procedures for soil analysis:

- soil particle size distribution according to the procedure described by Day (1965);
- soil bulk density using the methods described by Blake (1965);
- soil pH-value: in distilled water;

- the total N (N_{tot}) using Kjeldahl procedure;
- organic matter was determined according to Walkley and Black (1934);
- available K, Ca and Mg were extracted using atomic absorption spectrometry;
- available P using a Bray-1 extract as described by Olsen and Dean (1965).

2.6. Statistical analyses

Data were statistically analysed using the following general linear model (GLM):

$$Y_{ij} = \mu + G_i + F_j + GF_{ij} + e_{ij}$$

where Y_{ij} is the response variable for the herbaceous phytomass, or cover, or the steady infiltrability respectively, μ was the overall mean, G_i was the effect of livestock grazing and F_j was the effect of fire. Significant differences at $p < 0.05$ were further tested using Tukey's HSD multiple comparisons' test. A partial least squares projection to latent structures analysis was run in SIMCA software using the results from the laboratory together with the treatments to detect to what extent the infiltrability can be explained by the different main components. The measured infiltration rates were fitted to the model developed by Philip (1957):

$$I(t) = st^{1/2} + At \text{ derived as } i(t) = \frac{1}{2}st^{-1/2} + A$$

where I represents the cumulative volume of water infiltrated at time t per unit area of soil surface, i is the infiltrability as the volume of water entering a unit soil surface area per unit time and s is the so-called the sorptivity. When t approaches infinity, the infiltration rate decreases to its final asymptotic value $i(\infty) \approx A$. A is the steady state infiltration rate which in turn corresponds to the hydraulic conductivity of the soil's upper layer and was analysed using an ANOVA.

3. Results

3.1. Vegetation richness and cover

During the 12-year period there was no clear successional trend of the species richness and there was large variability among years (Fig. 2). The overall mean species richness per year ranged from 49 to 81 species at the experimental site. For the last year when the short duration grazing experiment was carried out, the herbaceous vegetation was rich with 49 species identified at both burnt and unburnt subplots. Although there was no clear trend in species richness with increased grazing intensity, there was nevertheless a net decrease of species between non-grazed and very heavily grazed subplots with fire protection. The total number of taxa included 23 families and 38 genera. The most frequently encountered families were Poaceae, Leguminosae and Rubiaceae. The number of taxa per growth form

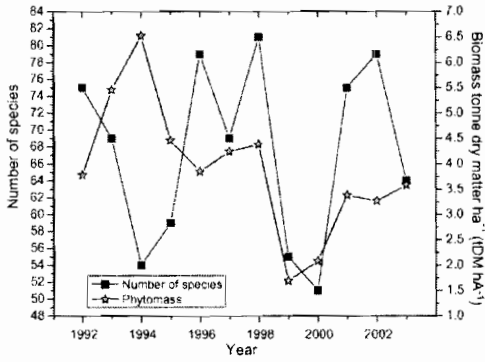


Fig. 2. Trend in annual herbaceous total biomass and species richness for 1992–2003 at Tiogo site, Burkina Faso.

were 18 annual, 5 perennial grasses and 26 forbs (Table 2). Total dominant plant species cover was highest for annual grasses, followed by perennials, whereas the forb cover was the lowest among the three growth forms (Table 3). On burnt subplots, the vegetation cover of forb species was highest following moderate grazing (15%) and very heavy grazing (8.2%) whereas on unburnt subplots the cover of forbs was highest at heavy (10.8%) and light (5.8%) grazing levels. Without fire, perennial grass cover was highest with moderate grazing whereas with early fire the highest cover was found for the livestock enclosure treatment. The vegetation cover was not proportional to the increase in the intensity of grazing for any of the growth forms.

3.2. Phytomass yield

In general, the mean above ground biomass of herbaceous species at the study site from 1992 to 2003 was 3.9 (± 1.31) Tonnes DM ha⁻¹. There was a large interannual variation of above ground biomass during the study period. For example, herbaceous biomass varied from 6.5 Tonnes DM ha⁻¹ in 1993 to 1.7 Tonnes DM ha⁻¹ in 1999 and increased the following years (Fig. 2). Also an inverse relation was seen between species richness and above ground phytomass; highest pasture yield was measured during a season with average rainfall. The results for

Table 2
Mean grass species richness for five grazing levels with two fire treatments at Tiogo site in 2003, Burkina Faso

	Fire					No Fire				
	G0	G1	GII	GIII	GIV	G0	G1	GII	GIII	GIV
Perennial	4	2	3	2	1	3	1	3	2	3
Annual	8	11	7	10	10	4	7	4	5	4
Forbs	7	5	6	4	6	9	2	9	4	2
Total	19	18	16	16	17	16	10	16	11	9

G0: control with zero grazing; G1: light grazing; GII: moderate grazing; GIII: heavy grazing; GIV: very heavy grazing.

Table 3
Percentage ground cover for dominant herbaceous species per growth form for different treatment combinations at Tiogo site in 2003, Burkina Faso

Fire			
G0			
<i>Andropogon gayanus</i> Kunth.	gv		34.10
<i>Andropogon fastigiatus</i> Sw. Prod	ga		26.05
<i>Euclasta condylotricha</i> (Hochst ex Steud) Stapf.	ga		25.71
Others			0.14
Bare ground			14
G1			
<i>Euclasta condylotricha</i> (Hochst ex Steud) Stapf.	ga		17.03
<i>Schizachyrium platyphyllum</i> (Franch) Stapf.	ga		11.85
<i>Andropogon gayanus</i> Kunth.	gv		11.85
Others			48.27
Bare ground			11
GII			
<i>Andropogon gayanus</i> Kunth.	gv		28.75
<i>Crinum ornatum</i> (L.f. ex Ait.) Bury	fb		15.00
<i>Schizachyrium platyphyllum</i> (Franch) Stapf.	ga		12.5
Others			3.75
Bare ground			40
GIII			
<i>Andropogon pseudapricus</i> Stapf.	ga		29.92
<i>Euclasta condylotricha</i> (Hochst ex Steud) Stapf.	ga		29.13
<i>Loudetia togoensis</i> (Pilger) C.E. Hubbard	ga		11.02
Others			17.93
Bare ground			12
GIV			
<i>Andropogon pseudapricus</i> Stapf.	ga		35.61
<i>Andropogon gayanus</i> Kunth.	gv		15.06
<i>Borreria stachydea</i> (DC) Hutch. and Dalz.	fb		8.21
Others			14.12
Bare ground			27
No Fire			
G0			
<i>Andropogon gayanus</i> Kunth.	gv		43.30
<i>Rottboellia exaltata</i> Linn.	ga		40.65
<i>Chasmopodium caudatum</i> Stapf.	ga		10.44
Bare ground			0.61
			5
G1			
<i>Pennisetum pedicellatum</i> Trin.	ga		75.00
<i>Borreria stachydea</i> (DC) Hutch. and Dalz.	fb		5.77
<i>Andropogon gayanus</i> Kunth.	gv		4.80
Bare ground			0.43
			14
GII			
<i>Andropogon gayanus</i> Kunth.	gv		54.81
<i>Andropogon ascinosidis</i> C.B. Cl.	gv		14.81
<i>Chasmopodium caudatum</i> Stapf.	ga		5.92
Others			17.46
Bare ground			7

Table 3 (Continued)

GIII		
<i>Pennisetum pedicellatum</i> Trin.	ga	40.54
<i>Schizachyrium exile</i> (Hochst.) Pilger.	ga	13.51
<i>Aspilia bussei</i> O. Hoffm. and Muschl.	fb	10.81
Others		19.14
Bare ground		16
GIV		
<i>Andropogon gayanus</i> Kunth.	gv	48.72
<i>Andropogon pseudapricus</i> Stapf.	ga	17.95
<i>Andropogon ascinosus</i> C.B. Cl.	gv	15.38
Others		5.95
Bare ground		12

The growth forms are indicated by: ga (annual grass), gv (perennial grass) and fb (forbs). G0: control with zero grazing; GI: light grazing; GII: moderate grazing; GIII: heavy grazing; GIV: very heavy grazing.

the year 2003, when the short duration grazing experiment was established on burnt and unburnt subplots, showed that protection from grazing resulted in higher biomass production compared to grazed subplots (Fig. 3). *Andropogon gayanus* Kunth., *A. ascinosus* C.B. Cl., *A. pseudapricus* Stapf. and *Pennisetum pedicellatum* Trin. were the main grass species and they made up 48% and 65% of the total biomass on burnt and unburnt subplots, respectively. The quantity of plant litter on the ground, in other words the old plant litter from previous years as well as fresh plant litter from the year under investigation, varied depending on the intensity of grazing and fire treatment. The burnt subplots showed the existence of litter on the ground in zero and light grazing (8 and 17 g/m², respectively) while subplots subject to livestock enclosure and fire protection held the highest amount of litter (42 g/m²). At the highest grazing pressure no plant litter was found. At burnt subplots, the total aboveground phytomass declined as the intensity of grazing increased but for unburnt subplots it was slightly lower for heavily grazed subplots compared to very heavy grazing.

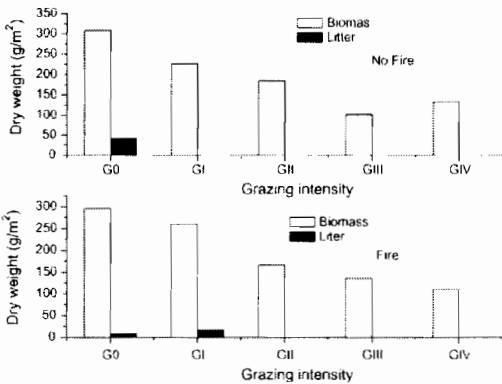


Fig. 3. Mean herbaceous biomass and litter in 2003 for the different treatment combinations at Tiogo site, Burkina Faso.

Table 4

Two way-ANOVA for herbaceous biomass, plant litter and steady state infiltrability at Tiogo site, Burkina Faso

Parameters	Fire		Grazing		Fire × Grazing	
	F	P	F	P	F	P
Aboveground biomass	0.21	0.65	2.16	0.08	0.81	0.52
Litter	0.67	0.42	5.67	0.00	4.01	0.00
Steady state infiltrability	3.46	0.07	3.18	0.03	0.64	0.08

Increased grazing pressure from moderate to very heavy grazing did not have a significant effect ($p = 0.081$) on grass biomass. The effects of prescribed early fire as well as the interaction between grazing and fire were not significant ($p = 0.646$ and 0.521 , respectively) for the total biomass (Table 4).

3.3. General soil characteristics

Soil chemical characteristics (Table 5) were not affected in composite soil samples taken down to a depth of 10 cm from burnt and unburnt subplots having received the five levels of grazing. For the grazing level G0 repeated prescribed burning during 12 years lowered accumulatively the soil organic matter content by 0.1%. There was a decrease in the amount of soil organic matter in both unburnt and burnt subplots from the control G0 to GIV (loss was estimated at 0.6% and 0.2%, respectively for unburnt and burnt subplots). The reduction in total C and N content had a proportional relation to the increment in the intensity of grazing from G0 to GIV, particularly in unburnt subplots (0.3% and 0.02 mg kg⁻¹, respectively). All subplots from all treatments had a very low N concentration ranging from 0.05 to 0.07 mg kg⁻¹. Total N and Ca also have their lowest values in very heavily grazed and unburnt subplots with concentrations of 0.05 and 395.9 mg kg⁻¹, respectively. Mg concentration was highest (235.7 mg kg⁻¹) at light grazing and fire protected subplots while its lowest concentration (80.4 mg kg⁻¹) was at very heavily grazed subplots with the same fire treatment. A similar pattern was found for soil bulk density with an average of 1.4 g cm⁻³ for all subplots; the highest bulk density (1.5 g cm⁻³) was found in unburnt subplots with high grazing pressure. Clay content was higher for G0 (31.3%) compared to GIV (11%) for exclusion of prescribed early fire. On burnt subplots it was the opposite. In this study soil pH was slightly acidic and did not show significant differences when comparing burnt and unburnt subplots. Soil pH ranged between 6.3 and 6.9; all pH values are quite high but below the limit for alkaline soils. The sum of exchangeable bases (SEBs) did not vary among the fire treatments.

3.4. Infiltration rate

The mean values of the steady state infiltrability showed that increased grazing pressure reduced infiltration rate on

Table 5
Soil characteristics from samples taken in 2003 to a depth of 10 cm for the different treatment combinations at Tiogo site, Burkina Faso

	No fire					Fire				
	G0 ^a	G1 ^a	GII ^a	GIII ^a	GIV ^a	G0 ^a	G1 ^a	GII ^a	GIII ^a	GIV ^a
OC (%)	1.8	1.7	1.6	1.6	1.2	1.7	1.7	1.9	1.7	1.5
Clay (%)	31.3	36.0	32.3	29.3	11.0	26.3	35.3	38.5	38.5	35.8
Fine silt (%)	15.2	16.3	15.3	16.5	8.5	15.5	16.0	16.8	16.0	16.5
Silt (%)	33.7	30.0	35.1	35.2	33.9	35.8	30.0	29.7	31.7	32.6
Fine sand (%)	6.5	5.7	2.8	6.5	15.8	8.2	6.1	5.1	4.8	5.2
Sand (%)	13.4	12.1	14.5	12.5	30.9	14.4	12.7	10.0	9.0	10.0
C tot. (%)	1.0	1.0	1.0	0.9	0.7	1.0	1.0	1.1	1.0	0.9
N (mg kg ⁻¹)	0.07	0.06	0.06	0.06	0.05	0.06	0.07	0.06	0.06	0.06
K (mg kg ⁻¹)	66.0	84.6	52.8	72.7	34.8	73.9	76.7	87.6	75.7	80.6
P ass. (mg kg ⁻¹)	1.1	0.8	1.0	1.5	1.6	3.0	1.0	1.4	1.9	1.8
Ca (mg kg ⁻¹)	881.9	1019.4	908.4	737.4	395.9	901.4	887.2	964.7	891.8	816.7
Mg (mg kg ⁻¹)	179.2	235.7	212.6	192.5	80.4	184.8	235.5	230.8	210.7	205.1
pH	6.6	6.7	6.7	6.5	6.7	6.8	6.8	6.6	6.5	6.3
Density (g cm ⁻³)	1.4	1.4	1.4	1.4	1.5	1.4	1.4	1.4	1.4	1.4

G0: control with zero grazing; G1: light grazing; GII: moderate grazing; GIII: heavy grazing; GIV: very heavy grazing; C tot. (%): total carbon (%); OC (%): organic matter (%); P ass. (mg kg⁻¹): assimilated phosphorus (mg kg⁻¹).

^a Grazing treatment.

both burnt and unburnt subplots (Table 6). The mean steady state infiltration rate was 78.0 (± 70.5) and 49.2 (± 27.5) mm h⁻¹ (respectively in unburnt and burnt subplots) at the study site. Subplots treated with early fire had a steady state infiltrability ranging from 21.3 to 82.6 mm h⁻¹ while infiltrability ranged from 16.4 to 109.7 mm h⁻¹ for subplots protected from fire. Fire only had a tendency ($p = 0.073$) to affect steady state infiltration. However, there was a statistically significant ($p = 0.028$) main effect of livestock trampling (Table 4) with a size effect (eta squared = 0.297) indicating that the actual difference in the mean value is relatively high. Post hoc comparison using Tukey's test indicated that there was a significant impact ($p = 0.004$) of heavy grazing compared to the zero grazing. Very heavy grazing and light grazing showed significantly different values for the infiltrability ($p = 0.009$). The pair wise comparison did not show any significant differences for any of the other grazing levels. The main effect of fire as well as the interaction between fire and grazing was not statistically significant (Table 4). The infiltration rates were lower on very heavily grazed subplots than on heavily,

moderately, lightly and non-grazed subplots (Fig. 4). However, the infiltration rate for light grazing on unburnt subplots was slightly higher compared to exclusion from grazing. The initial water infiltration was higher in non-grazed and unburnt subplots. In general the infiltration rate was higher in non-burnt subplots than in the burnt one. The infiltration rate was faster at first but slower as the soil reached saturation.

The results from the PLS modeling (Fig. 5) in the present study indicated that the steady state infiltrability was mostly dependent on grazing intensity. The values of the R^2Y (cum) and Q^2Y (cum) were 0.416 and 0.340, respectively indicating that 34% of the infiltration was explained by the two first components. Grazing intensity had the largest influence (this variable importance value in projection VIP was 1.46) followed by soil organic matter and soil C; these last two elements had similar levels of influence (VIP was 1.31 in both cases). Prescribed fire, Ca (mg kg⁻¹) and pH were (in

Table 6
Mean values of steady state infiltration (mm h⁻¹) for the different treatment combinations at Tiogo site, Burkina Faso

Grazing treatment	Fire		No fire	
	Mean	S.D.	Mean	S.D.
G0, zero grazing	82.6 a	54.2	109.7 a	29.9
G1, light grazing	51.8 a	23.5	123.6 a	123.8
GII, moderate grazing	49.3 ab	13.9	79.5 ab	67.2
GIII, heavy grazing	40.8 ab	25.4	60.6 ab	31.9
GIV, very heavy grazing	21.3 b	14.9	16.4 b	10.4
Mean total steady state infiltration	49.2	27.5	78.0	70.5

Mean with the same letter in column are not different ($p < 0.05$) following Tukey's HSD multiple comparisons test.

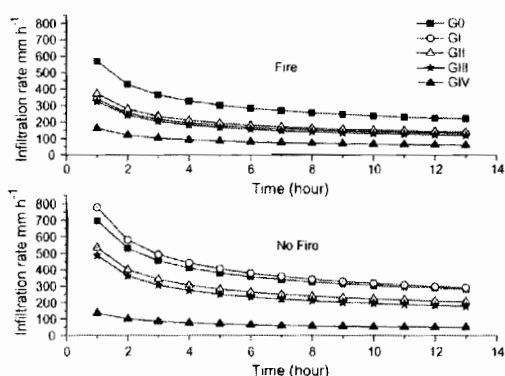


Fig. 4. Infiltration rate as a function of time for the different treatment combinations at Tiogo site in 2003.

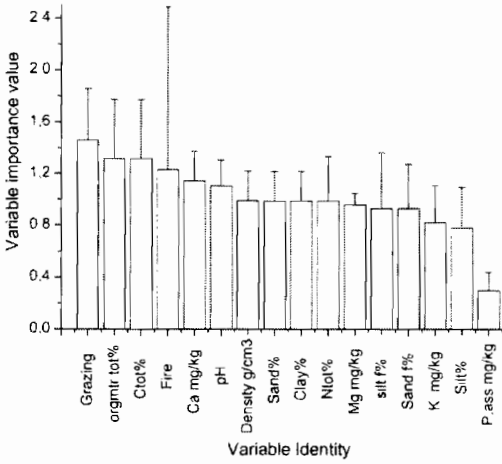


Fig. 5. Contribution of components affecting infiltration at Tiogo site according to partial least squares projection to latent structures test.

decreasing order), also relevant in explaining infiltration with a VIP > 1. All other variables included in the PLS-test were significantly connected to the steady state infiltration but had a VIP < 1.

4. Discussion

4.1. Vegetation characteristics

The variation between years for total species richness found at the experimental site may be related to climatic conditions and in particular spatial and temporal distribution of rainfall. This is supported by the hypotheses proposed by Frost et al. (1986) that the composition of the herbaceous layer in dry savannas appears to be affected primarily by year-to-year and longer-term variation in rainfall. Early heavy rains stimulated seed germination within three days but frequently gaps in the rainfall distribution caused wilting of emerging seedling (personal field observation). Thus timing of rains, speed of germination and drought tolerance of seedlings were important in determining which species establish each year, while the production of seeds for the seed bank appeared decisive for the species composition in the following year.

In this study, effects of prescribed early fire did not have significant influence on total species richness, diversity and cover compared to no fire. Species showed different degrees of sensitivity to fire; some were stimulated by the fire and some reacted negatively. Fires burning early in the dry season tend to be of low intensity as the fuel dominated by the herbaceous layer still holds moisture from the wet season (Liedloff et al., 2001). The seed loss was likely minor; moreover favourable germination conditions may have been

created. Inhibition of herb regeneration in savannas is related to high fire temperatures (Jensen and Friis, 2001) because of increased seed mortality. Increasing fire severity is negatively correlated with species richness (Jensen and Friis, 2001). Early fire creates favourable conditions for germination (Lacey et al., 1982) by removing litter or breaking seed dormancy and consequently maintains herbaceous diversity in savannas. Grazing intensity did not have a significant effect on species richness and vegetation cover; however patchy bare soil was locally observable as grazing intensity increased (personal field observation). The reason why the results were not significant could be the short duration of the grazing and compensatory regrowth as a response to it (McNaughton, 1983). The interaction between fire and grazing was not significant. This result coincides with findings by Archibald et al. (2005) who recognize that fire and grazing are important modifiers in savannas but their interaction on grass communities is difficult to identify. Other important factors like soil characteristics, species palatability and endozoochorous or hydrochorous seed dispersal surely had influence on the species richness and cover. This work shows that, by influencing where, when, and for how long animals graze an area, fire can influence the competitive balance between grazing-tolerant and grazing-intolerant grass species and affect their distributions in the landscape.

4.2. Above ground phytomass

The observation of large inter-annual variability of the biomass was most likely related to the rainfall patterns. A correlation coefficient of 38% was found between herbaceous biomass and annual rainfall at the same experimental site (Savadogo et al., 2005). This coefficient increased slightly when taking the number of rainy days per year into account. Rainfall had the most marked effect on variability of herbaceous production (Fynn and O'Connor, 2000) through its temporal distribution. Inter-annual variation of fire intensity and grazing pressure are other factors that influence the annual herbaceous biomass.

This study showed that increased grazing intensity had a tendency to reduce the measured above ground phytomass because of grazing 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, Savadogo et al. (2005) found that the lack of overall effect of prescribed fire was because annual grasses increased and perennial grasses decreased. The total biomass decreased with increasing grazing intensity, which is likely due to increased biomass removal and the trampling pressure (static load) exerted by the animals. Cattle 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 the seasonal production. The loss of vegetation and litter cover allows direct impact of raindrops on the soil (Russell et al., 2001) and may also produce hydrophobic substances that can reduce infiltration (Emmerich and Cox, 1992). Soil temperature tends to increase after burning and litter removal because of greater exposure to sunlight and this increases the drying and crusting processes.

4.3. Soil characteristics

Soil physical and chemical properties of the 10 cm surface layer sampled from burnt and unburnt plots were not statistically significant between treatments. This result is in accordance with previous work (Raison, 1979; Menaut et al., 1992; Dembele et al., 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 carbon change (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 first 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 the composite soil sampling procedure down to a depth of 10 cm that hides the properties of the top first few centimeters. 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 of 0–10 cm. This shows the importance of the first centimeters of the soil regarding nutrient dynamics in rangelands (Snyman, 2005). Furthermore, the fact that fire did not affect soil properties was most likely due to a low rise in soil temperature at a depth of 10 cm in the burnt subplots. Herbaceous biomass reduction by grazing and trampling led to reduced fire intensity. This observation was consistent with Gonzalez-Perez et al. (2004) who reported the effect of fire on soil to be dependent on the intensity of fire, soil moisture as well as type and nature of the combustibles. The amount of change in soil physical and chemical properties in this experiment could have also been dependent on a low amount of energy radiated by the prescribed early burning onto the soil surface and transferred downward into the underlying duff and mineral soil. DeBano et al. (1998) attributed the changes in organic matter and other soil properties as a consequence of the increased temperature induced by the radiated heat. The soil surface in some burnt subplots showed patchy crust formation (personal field observation). Similar results were reported for fire prone savannas in South Africa where frequent burning increases the tendency of a soil to crust, enhances runoff, decreases soil organic matter and stability of the aggregates, reduces soil porosity, and water infiltration rate (Mills and Fey, 2004).

Moreover, fire and grazing are recognized as having an important ecological role in the development and maintenance of savanna ecosystems. This in combination with the short time frame of this experiment could explain why the expected results on soil surface characteristics were not found.

4.4. Infiltration

This study indicated that prescribed early fire only had a tendency to decrease steady state infiltrability. Although burning was repeated 11 consecutive years, only slight differences were observed. Some studies however (Snyman, 2003), find infiltrability changes after one single accidental late fire. In our experiment, fire intensities were difficult to control due to fuel load heterogeneity (savanna mosaic). The varying intensities gave different effects on soil properties, which are not well detected by composite sampling, especially regarding steady state infiltrability. In this experiment, 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 due to the fire removing above ground biomass and leaf litter; fire is known to increase the exposure of the soil surface to the impact of raindrops (Moyo et al., 1998) which in turn often leads to crusting (Mills and Fey, 2004). The mechanical energy input from raindrops increases the dispersion of clay and results in the blockage of surface pores and reduced infiltration in most soil types even for soils with low clay content (Hillel, 2004). At the experimental site crusting could be attributed mostly to low content of organic matter, which probably reduced aggregate stability.

Another factor affecting infiltration rate is the increased soil temperature while the vegetation burns; combustion of grass in savannas can generate temperatures of 700 °C (Van de Vijver, 1999). The removal of vegetation tends to increase exposure to sunlight and the drying processes of the soil.

The steady state infiltrability with grazing was significantly lower than without livestock presence; the subplots with low grazing had a large infiltration rate, which indicates the importance of livestock management on soil hydrology. Several studies report similar results (Mwendera and Saleem, 1997b; Rietkerk et al., 2000). Grazing pressure was moderate at 0.7 TLU ha⁻¹ for 10 years before this short duration grazing experiment was implemented during the rainy season. Cattle grazing results in mechanical pressure on the ground as animal trampling contributes to altered soil structure like soil compaction and reduction of soil porosity. The effects of soil compaction are greater when the soil is wet (Warren et al., 1986), which was the case during this experiment. The increased stocking rate in the short duration grazing experiment compared to the earlier grazing level of 0.7 TLU ha⁻¹ contributed to the compaction. Grazing also decreases the infiltration rate by reducing vegetation cover and amount of organic matter in the

topsoil, especially at high stocking rates (Mwendera et al., 1997). A decrease of organic matter content in the soil will lower macro-porosity, which reduces infiltrability (Stroosnijder, 1996). The steady state infiltrability decreased with increased grazing pressure due to compaction by trampling. This decrease could also be explained by reduced soil macrofauna (mostly termites and ants) activity. Faunal activity has been found to be an important agent for control of soil crusting. It improves the physical properties of the soil and contributes considerably to increased infiltration in seasonally dry ecosystems (Mando et al., 1996; de Rouw and Rajot, 2004). The high infiltrability observed with light grazing (GI) in unburnt subplots 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 and remoulding resulting from animal trampling. The lower infiltration rate may be attributed to the development of soil crust under no grazing, which hindered infiltration. Grazing exclusion management system in semi-arid savanna ecosystem decreases the plant cover and biomass and increases runoff overtime due to crust colonization (Casenave and Valentin, 1992). These results support earlier work suggesting that trampling and compaction are important reducers of soil hydrology only under high stocking rates while light to moderate grazing improve infiltration by reduction of surface crusts (Hiernaux et al., 1999). Higher steady state infiltrability at control subplots (ungrazed and unburnt) could be due to the development and maintenance of porosity, particularly macropores (network of galleries built by termites), which constitute the main pathways for water infiltration. For the subplots that received the low grazing treatment as well as the ones that didn't receive any grazing, macroporosity could have influenced the steady state infiltrability. Macropores were found in different locations, beneath trees, on shrub-covered surfaces, as well as at sites with a dominance of herbaceous cover.

The partial least squared projection to latent structures test indicated that prescribed fire was the fourth variable affecting infiltrability while livestock grazing was the most important one. All other characteristics included in the PLS-test were significantly connected to steady state infiltrability. This could be explained by the particular role of each component for maintaining characteristics of soil structure (Hillel, 2004).

The variation in contents of organic matter among all subplots was small (1–2%), despite different treatment histories. A larger variation of organic matter is likely to give larger effect on changes in steady state infiltrability as indicated by the PLS modeling, according to which organic matter is the second most important variable affecting infiltrability. The highest steady state infiltrability and the highest content of organic matter were found in G0 for prescribed fire and this corresponds well with the expected results. For the burning treatment, the low infiltration rate corresponds well with the high content of clay, but, as

indicated in PLS test, the high grazing pressure affected the infiltration rate even more. The high infiltrability most likely depends on the protection from grazing and fire since 1992, as these subplots had the highest steady state infiltrability in this study. Total N and Ca also have their lowest values in very heavily grazed and unburnt subplots with concentrations of 0.05 and 395.9 mg kg⁻¹, respectively. Ca contributes to good aggregate structure (Hillel, 2004), due to its divalent ion, and low content of Ca is therefore expected to lead to low infiltrability. Total N (%) gives a rather large contribution to infiltrability according to PLS test but as most N is bound in organic matter it can also be the organic matter contributing to good soil structure, not the N itself. The highest bulk density (1.5 g cm⁻³) was found in unburnt and very heavily grazed subplots where compaction and low content of organic matter lead to low infiltrability. At the same location the lowest concentration of Mg was found. It is a variable that according to the PLS-test has a relatively large impact on infiltrability, which is due to its divalent ion improving aggregate structure in the soil (Hillel, 2004).

5. Conclusions

Grazing and fire are known to reduce infiltration and cause runoff and erosion in arid environments. In this study fire did not significantly affect steady state infiltrability. This could be explained by the fact that the fire was applied early in the dry season when the vegetation was still moist and less organic matter was destroyed. Therefore, prescribed early fire seems like a good compromise between protection from fire and late burning as it did not negatively influence soil infiltrability.

Grazing had significant impact on steady state infiltrability in these Lixisols. Results obtained in this experiment indicated that adoption of a high stocking rate in savanna grazing systems may adversely affect soil infiltrability and above ground phytomass production. To avoid long-term damage on the environment, livestock grazing should ideally not exceed the moderate level.

More research is needed to assess the cumulative long-term effects of grazing and trampling on vegetation, soil, and hydrology of savanna woodlands. Such knowledge is needed for a sustainable multipurpose use of the savanna woodlands.

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Dry matter production and nutrient content of four grass species in a Sudanian savanna-woodland subjected to repeated early fire

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Abstract

Fire is known to be an integral ecological factor in African savanna ecosystems, but the effects of frequent fire on savanna productivity are highly variable and less understood. We conducted a field experiment to quantify and compare changes in dry matter production and nutrient composition in a Sudanian savanna-woodland subjected to annual early fire from 1993 to 2004. The effects of the fires were then assessed on two perennial and two annual grass species that have high forage values in West African livestock production. Fire at the end of the previous growing season significantly reduced above-ground dry matter ($p = 0.03$), crude protein ($p = 0.022$), neutral detergent insoluble crude protein ($p = 0.016$) and concentrations of Ca, Fe, and Mn ($p < 0.05$). The perennial grasses tended to have higher dry mass but lower total crude protein and fat than annual grasses, with marked variation within growth forms. Non-structural carbohydrates tended to be higher for annuals and fibre and lignin contents higher for perennials. Except Na and Fe, the concentration of mineral elements varied between species. Fire did not affect measures of digestibility and metabolizable energy, but they differed among species. In conclusion, the results illustrate that long-term frequent fire will counterbalance the short term increases in soil fertility and plant nutrient concentrations claimed to be accrued from single or less frequent fire.

Keywords: Early burning; Pastures quality; Tropical grass; Semi-arid; Burkina Faso

1. Introduction

Fire has been an important ecological component of African savanna ecosystems for millennia acting not only as a destructive force but also as a selective and regulatory agent (Goldammer, 1990; Scholes and Walker, 1993; van Langevelde *et al.*, 2003). In the Sudanian savanna-woodland alone, an area stretching from Senegal in the west to the Ethiopian highlands in the east at 6°-13° N (Menaut *et al.*, 1995), between 25 and 50% of the savanna-woodland burns annually (Delmas *et al.*, 1991), while the entire area burns every second or third year, primarily due

to human activities (Menaut *et al.*, 1991). In addition, prescribed burning has been adopted as an ecosystem management tool in most protected savanna-woodlands to minimize the risk of severe late fire, to improve pasture production for wildlife and to maintain species composition and richness (Richards *et al.*, 1999; Bellefontaine *et al.*, 2000; Sawadogo *et al.*, 2005). An understanding of the effects of recurrent fire on growth and nutrient composition of the herbaceous vegetation is essential to attenuate the need for multiple use management of the savanna-woodlands. In most parts of Africa, the herbaceous vegetation of savanna-woodlands provides both essential forage for domestic and wild animals (Ouedraogo-Kone *et al.*, 2006; Sanon *et al.*, 2007) and raw materials for local construction, handicrafts and traditional medicine (Le Mire Pecheux, 1995).

The first and most obvious effects of fire on the ecosystem are the removal of old, dead vegetation and the following flush of young regrowth. Burning also results in a short-term increase in available nitrogen and other mineral nutrients in the soil immediately after burning (Jensen *et al.*, 2001; Wan *et al.*, 2001), which in turn stimulates growth of perennial grasses. The increases in productivity and nutrient concentrations in above-ground post-fire regrowth, particularly in mesic environments, are attributed to a combination of factors including improvements in the microclimate due to the removal of accumulated litter (Dhillon and Anderson, 1994; Briggs and Knapp, 1995), enhanced nutrient availability due to nutrient release and increased microbial activity (Wan *et al.*, 2001). They are also related to changes in plant nutrient use efficiency and carbon allocation (Bowen and Pate, 1993; Ojima *et al.*, 1994), rejuvenation and associated changes in plant tissue composition (Kauffman *et al.*, 1994; Van de Vijver *et al.*, 1999). Overall, burning of mesic grasslands increases productivity due to increase in resources such as light, temperature and nutrients.

In contrast, burning of savannas in semi-arid zones often reduces growth and biomass for one or more growing seasons, depending on growth form, fire frequency and intensity (Bennett *et al.*, 2003; Sawadogo *et al.*, 2005). The decrease in grass production following burning is partly attributed to water stress in the post-burn environment (Meurer, 1994). In a recent study made in the Sudanian savanna, Savadogo *et al.* (2007) found a decreasing tendency in steady state infiltration rate on burnt sites, implying reduced soil water availability. Thus, fire may reduce productivity of semi-arid savannas if it reduces a primary growth limiting factor such as water availability. In addition, burning could exacerbate mineral nutrient limitations in semi-arid savannas owing to increase nutrient losses during burning from the already nutrient-limited environment.

The effects of fire, positive or negative, on the productivity of savannas strongly depend on the fire frequency and intervals (Jensen and Friis, 2001; Bennett *et al.*, 2003; Andersson *et al.*, 2004). Generally, frequent burning may disrupt the "savanna equilibrium" and may have long-term consequences on soils through accumulative nutrient losses that, in turn, influence vegetation and animal life. Most previous studies have focused on short-term effects of fire frequency on soil fertility and nutrient cycling (Jensen *et al.*, 2001; Wan *et al.*, 2001; Andersson *et al.*, 2004; Ferran *et al.*, 2005), plant composition and productivity in shrublands

and prairies (Shay *et al.*, 2001; Delitti *et al.*, 2005), and nutrient contents and demography of selected grass species (Van de Vijver *et al.*, 1999; Garnier and Dajoz, 2001; Bennett *et al.*, 2003). However, the effects of recurrent fire on the productivity of herbaceous vegetation of semi-arid savannas have been less thoroughly researched than its effects on mesic grasslands. We therefore need more data before we can draw general conclusions regarding the effects of fire in these ecosystems. In this paper, we present 12-year data (1993-2004) on the effects of annual early fire on dry matter production and the cumulative fire effects 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.) all of which are commonly used to feed livestock in West Africa. The main objectives of the study were to increase our understanding of fire effects in the Sudanian savanna-woodland and to evaluate the merit of prescribed fire as an ecosystem management tool thereby ensuring multiple use woodland management.

2. Materials and methods

2.1 Site description

The study was conducted in Tiogo State forest (12°13' N, 2°42' W) located 300 m above sea level in Burkina Faso, West Africa. The Tiogo State forest (forêt classée) was delimited by the colonial French administration in 1940 and covers 30,000 ha. It is situated along the only permanent river (Mouhoun, formerly known as Black Volta) in the country. Phyto-geographically, it is situated in the Sudanian regional centre of endemism in the transition from the north to the south Sudanian Zone (White, 1983). The vegetation is characterized as a tree and bush savanna with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard, and the perennial grasses *Andropogon gayanus* Kunth. and *Diheteropogon amplexans* W. D. Clayton (Sawadogo *et al.*, 2005). *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC.) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Linn are the main forbs species, and *Acacia macrostachya* Reichenb. ex Benth., *Combretum nigricans* Lepr. ex Guill. & Perr. and *Combretum glutinosum* Perr. ex DC are the most common woody species. The unimodal rainy season lasts for about six months from May to October. The mean annual rainfall for the years 1993-2004 was 841 ± 195 mm, and the number of rainy days per annum was 68 ± 10 (Figure 1). Mean daily minimum and maximum temperatures ranged from 16°C and 32°C in January (the coldest month) to 26°C and 40°C in April (the hottest month), yielding an aridity index (Brown and Lugo, 1982) of 3.6. The most frequently encountered soils type are Lixisols (Driessen *et al.*, 2001), which mainly consist of deep silt-clay (>75 cm), and are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998). Some of the physical and chemical properties of composite samples of the soil taken at a depth of 10 cm from burnt and unburnt plots are presented in Table 1.

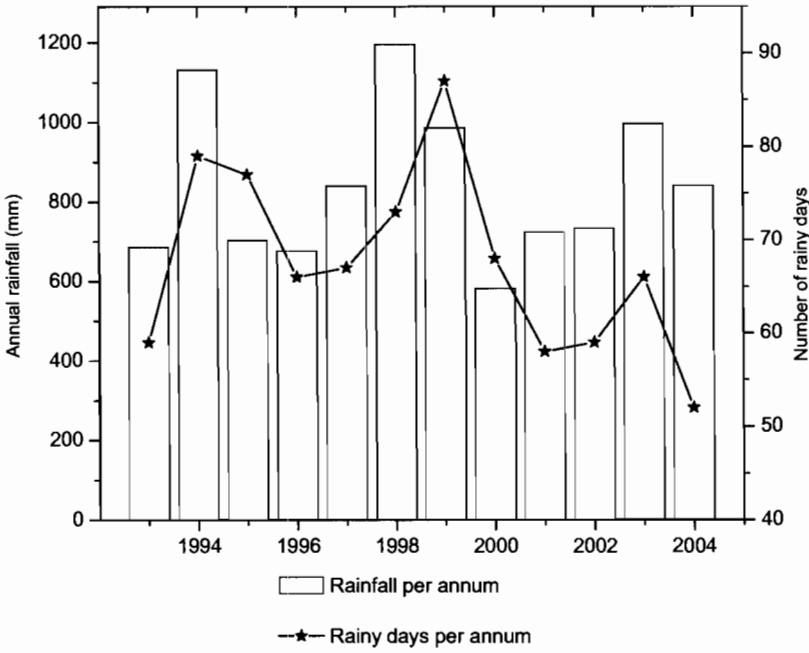


Figure 1. Total annual rainfall (mm) and number of rainy days during the study period at Tiogo.

Table 1. 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 (%)	35.77 ± 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

2.2 Grass species

Two annual (*Chasmopodium caudatum* Stapf. and *Rottboellia exaltata* Linn) and two tufted perennial grasses (*Andropogon gayanus* Kunth. and *Diheteropogon amplexans* W. D. Clayton), all of which provide socio-economically important forage and conserved fodder for livestock, were selected as study species. All studied species have C-4 photosynthetic pathway as most sahelian grasses (Breman, 1991). The annuals grasses are shade-loving compared to the perennial grasses.

2.3 Experimental set up and sampling

The present study is part of a large factorial experiment with four replicates of 4.5 ha established to study the long-term effects of grazing, prescribed fire and selective tree cutting on the ecology and productivity of the Sudanian savanna-woodland (Sawadogo *et al.*, 2005). The experimental site was first split into two areas; grazed (open for livestock grazing) and non-grazed (fenced at the start of the experiment in 1992 to exclude livestock). Within each grazed or ungrazed area, there were 36 subplots. 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%. In each burnt or unburnt subplot, six 1 × 1 m quadrats were marked for sampling 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 bagged, air-dried until constant mass and weighed to determine dry matter content.

2.4 Chemical analysis

For each species, two composite samples were taken on the ungrazed area from burnt and unburnt plots separately in 2004. The whole plant cut at the base including green stems, leaves, flowers and capsules were collected in 2004 when at the beginning of the flowering stage of the grasses. Samples were dried in a forced draught oven at 60 °C and were ground to pass through 1.0 mm sieve using a Christy & Norris Laboratory Mill before being analyzed according to the Cornell net carbohydrate and protein (CNCPS) system (Sniffen *et al.*, 1992). All CNCPS-analysis were performed in a commercial laboratory in the USA that specializes in CNCPS-analysis (Dairy One, Ithaca, NY, USA). Neutral detergent fiber (NDF) and acid detergent fiber (ADF) were analyzed by the ANKOM A200 Filter Bag Technique (Komarek, 1994). The solutions used for the NDF-analysis were the same as in AOAC Method 973.18 (AOAC, 1990). Alpha amylase and sodium sulfite were added at the start of the NDF digestion. The solutions for the ADF analysis were the same as in Van Soest *et al.* (1991). Lignin was analyzed sequentially after ADF according to AOAC Method 973.18 and crude fiber (CF) according to AOAC Method 962.09 (AOAC, 1990). The samples were analyzed for crude protein (CP), neutral detergent insoluble crude protein (NDICP) using

6.25 times the Kjeldahl-N concentration (Block Digestion and Tecator Kjelttec Auto 1030 Analyser – a modified Kjeldahl procedure with automatic distillation and titration). Crude fat was determined using ether extraction according to AOAC Method 2003.05 (AOAC, 1990). *In vitro* true digestibility (IVTD) was determined and expressed as a percentage of dry matter (DM) and neutral detergent fiber digestibility (NDFD) as a percentage of NDF. Non structural carbohydrates (starch + sugars) were determined using an YSI 2700 SELECT Biochemistry Analyzer (YSI Inc.) for starch and the water soluble sugar method published by Hall *et al.* (1999) for sugar.

The total mineral content (ash) was measured according to AOAC Method 942.05. The macro-minerals (Ca, P, Mg, K, Na) and the trace elements (Fe, Zn, Cu, Mn, Mo) were analyzed using a Thermo Jarrell Ash IRIS Advantage Inductively Coupled Plasma (ICP) Radial Spectrometer (Sirois *et al.*, 1994). To characterize digestibility and metabolizable energy of the samples, we estimated total digestible nutrients (TDN), net energy for maintenance (NEM), net energy for lactation (NEL), relative feed value (RFV), and relative forage quality (RFQ).

2.5. Statistical analysis

Data on dry matter production and chemical composition were subjected to Two-Way ANOVA to examine the effects of fire and species based on the following linear model:

$$Y_{ij} = \mu + F_i + S_j + FS_{ij} + e_{ij}$$

where Y_{ij} is the response variable, μ is the overall mean, F_i is the effect of fire, S_j is the effect of species, FS_{ij} is the fire by species interaction, and e_{ij} is the error term with k replicates. The parameters F_i , S_j , and FS_{ij} were regarded as fixed effects. All statistical analyses were done using the SPSS 15 software package (SPSS 15 for Windows, Release 2006 Chicago: SPSS Inc.).

3. Results

3.1. Dry matter production

Dry matter production varied significantly between burnt and unburnt plots ($F_{[1, 24]} = 10.97$; $p = 0.03$), as well as between grass species ($F_{[3, 24]} = 11.83$; $p < 0.0001$). For all grass species, above-ground biomass was higher on unburnt than burnt plots (Table 2). At both levels of fire treatment, the mean above-ground biomass was higher for *A. gayanus* than *D. amplexans*, *C. caudatum* and *R. exaltata*. There was no significant fire \times grass species interaction effect ($F_{[3, 24]} = 1.08$; $p = 0.376$). Inter-annual variations in above-ground biomass during the study period on both burnt and unburnt plots are shown in Figure 2. For *A. gayanus*, above-ground dry matter production was three-fold higher in 1997/98 than in the preceding years on unburnt plots, while the variation was small on burnt plots. For *D. amplexans*, dry matter production was considerably higher on burnt plots after one year, but

continually decreased thereafter until the end of the study period, whereas dry matter production on unburnt plots increased in the second year and the following two years, then started to decline again. For the two annual grass species, *C. caudatum* and *R. exaltata*, dry matter production was relatively higher at the beginning and at the end of the study period on both burnt and unburnt plots.

Table 2. Main effects of fire and species differences on above ground biomass ($t DMha^{-1}$) of native grass in semi-arid savanna of Burkina Faso (values are mean \pm SE)

	<i>A. gayanus</i>	<i>D. amplexens</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)
Fire	1.34 \pm 0.46	0.15 \pm 0.10	0.11 \pm 0.08	0.39 \pm 0.09	0.50 \pm 0.17*
No Fire	2.37 \pm 0.38	1.20 \pm 0.39	0.30 \pm 0.15	0.84 \pm 0.34	1.18 \pm 0.25
Main effect (species)	1.85 \pm 0.34a	0.68 \pm 0.27b	0.21 \pm 0.09b	0.62 \pm 0.19b	

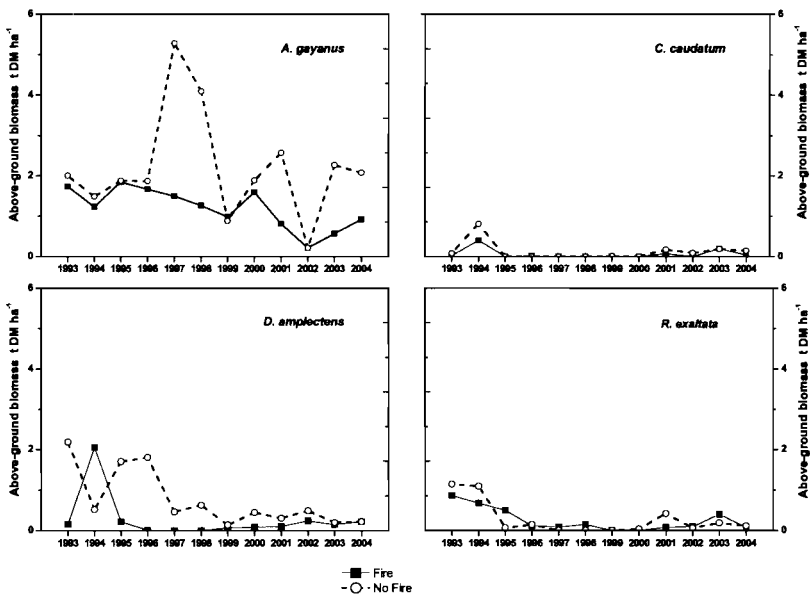


Figure 2. Trend in annual above-ground biomass ($t DM ha^{-1}$) of *A. gayanus*, *D. amplexens*, *C. caudatum*, *R. exaltata* during 1993-2004 at Tiogo.

3.2 Composition of organic compounds

The main effect of fire was significant for crude protein ($F_{[1, 8]} = 8.04$; $p = 0.022$) and neutral detergent insoluble crude protein ($F_{[1, 8]} = 9.33$; $p = 0.016$) while crude protein ($F_{[3, 8]} = 43.08$; $p < 0.0001$), soluble protein ($F_{[3, 8]} = 12.50$; $p = 0.002$), and crude fat ($F_{[3, 8]} = 22.64$; $p < 0.0001$) varied significantly among grass species.

Neither fire nor grass species had a significant effect on degradable protein concentration. The total crude protein and fat concentrations were generally lower for perennial grasses than annual grasses (Table 3), but marked variations within grass species were also observed. The annual grass, *R. exaltata*, had the highest crude protein and neutral detergent insoluble crude protein concentrations, while the perennial grass *D. amplexans* had the lowest soluble protein concentrations. Crude fat concentrations were lowest in the perennial grass *A. gayanus* and highest in the annual grass *R. exaltata*. There were no fire \times grass species interaction effects ($p > 0.05$) on crude protein, protein fractions or crude fat.

The fire treatment had no significant effect on any of the carbohydrate moieties in the forages, while sugar ($F_{[3, 8]} = 16.83$; $p = 0.001$), starch ($F_{[3, 8]} = 5.69$; $p = 0.022$), lignin ($F_{[3, 8]} = 7.68$; $p = 0.010$), crude fiber ($F_{[3, 8]} = 4.23$; $p = 0.046$), acid detergent fiber ($F_{[3, 8]} = 8.62$; $p = 0.007$) and neutral detergent fiber ($F_{[3, 8]} = 19.28$; $p = 0.001$) varied significantly among grass species. The perennial grass *A. gayanus* had the highest concentration of fibers (ADF, NDF and CF) than the annual grass *R. exaltata* while non-structural carbohydrates (starch and sugar) were higher in the latter than the former species (Table 4). The lignin concentration was lower in the annual grass *C. caudatum* than in the perennial grasses. No significant interaction effect of fire and grass species on any of the carbohydrate moieties was found.

3.3. Composition of mineral elements

The ash concentration of forages, a measure of their total mineral concentrations, was not affected by fire treatment ($F_{[1, 8]} = 4.76$; $p = 0.061$), but it varied significantly among grass species ($F_{[3, 8]} = 73.73$; $p < 0.0001$). Generally the ash concentration of annual grasses was higher than that of perennial grasses, with notable variations within growth forms (Table 5). The ash concentration was highest for the annual grass, *R. exaltata*, and lowest for the perennial grass, *A. gayanus*. There was also a significant interaction effect of fire and grass species on ash concentration ($F_{[3, 8]} = 6.04$; $p = 0.019$). The ash concentrations of *A. gayanus*, *D. amplexans*, and *R. exaltata* were higher on unburnt than on burnt plots while the reverse was true for *C. caudatum* (Table 5).

Among the various mineral elements analyzed in the forages, the concentrations of calcium ($F_{[3, 8]} = 21.19$; $p = 0.002$), iron ($F_{[3, 8]} = 5.68$; $p = 0.044$), and manganese ($F_{[3, 8]} = 25.31$; $p = 0.001$) were significantly affected by fire. Samples of forage collected from burnt plots had lower concentrations of Ca, Fe, and Mn than those collected from unburnt plots (Table 5). The concentrations of calcium ($F_{[3, 8]} = 84.08$; $p < 0.0001$), phosphorus ($F_{[3, 8]} = 21.38$; $p < 0.0001$), magnesium ($F_{[3, 8]} = 108.85$; $p < 0.0001$), potassium ($F_{[3, 8]} = 20.85$; $p < 0.0001$), zinc ($F_{[3, 8]} = 108.71$; $p < 0.0001$), copper ($F_{[3, 8]} = 9.06$; $p = 0.006$), manganese ($F_{[3, 8]} = 282.77$; $p < 0.0001$), and molybdenum ($F_{[3, 8]} = 6.22$; $p = 0.017$) varied significantly among grass species. The concentrations of P, K, and Zn in annual grasses were higher than those in perennial grasses, while the concentrations of Cu and Mb tended to be higher in annual grasses than perennials. There were marked variations within

grass species for some of the mineral elements analyzed. The concentrations of Ca, Mg, and Mn were higher for the perennial grass, *D. amplexans*, compared to the other perennial grass species and the two annual grass species. Significant fire \times grass species interaction effects were found for concentration of P ($F_{[3, 8]} = 4.91$; $p = 0.032$), Zn ($F_{[3, 8]} = 5.18$; $p = 0.028$), and Mn ($F_{[3, 8]} = 6.09$; $p = 0.018$). Among all grass species, the concentration of P in *C. caudatum* was higher for forage samples collected from unburnt than burnt plots while the concentration of Mn in both perennial grass species was higher in unburnt than burnt plots (Table 5). With regard to concentration of Zn, the grass species exhibited variations between burnt and unburnt plots. *A. gayanus* forage samples collected from burnt and unburnt plots had the same concentration of Zn, while it was considerably higher on unburnt than burnt plots for *D. amplexans* and *R. exaltata*. For *C. caudatum*, the concentration of Zn was higher on burnt than unburnt plots.

3.4. Digestibility and metabolizable energy

Prescribed early fire did not significantly affect any of the measures of digestibility or metabolizable energy of forages. However significant differences among grass species were found for net energy for lactation ($F_{[3, 8]} = 7.78$; $p = 0.009$), net energy for maintenance ($F_{[3, 8]} = 6.87$; $p = 0.010$), relative feed value ($F_{[3, 8]} = 15.55$; $p = 0.001$) and relative forage quality ($F_{[3, 8]} = 5.85$; $p = 0.012$). The net energy for lactation, an estimate of the energy value of a feed used for maintenance plus milk production during lactation and for maintenance plus the last two months of gestation for dry pregnant cows, was the highest in the annual grass, *R. exaltata* while it was the lowest for the two perennial grasses (Table 6). The relative feed value, an index for ranking forage based on digestibility and intake potential calculated from ADF and NDF, was also higher in annual than perennial grasses; the highest being in the annual grass, *R. exaltata* and the lowest in the perennial grass, *A. gayanus*.

Table 3. Main effects of fire and species differences on crude protein, protein fractions and crude fat (% DM) in native grass of semi-arid savanna of Burkina Faso (values are mean \pm SE)

	<i>A. gayanus</i>	<i>D. amplexiens</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)
CP%	Fire	3.35 \pm 0.35	3.35 \pm 0.25	4.45 \pm 0.05	5.30 \pm 0.40
	No Fire	3.30 \pm 0.00	3.55 \pm 0.15	5.40 \pm 0.30	6.25 \pm 0.25
	Main effect (species)	3.33 \pm 0.14a	3.45 \pm 0.13a	4.93 \pm 0.30b	5.78 \pm 0.34c
NDICP%	Fire	1.55 \pm 0.25	1.80 \pm 0.30	1.65 \pm 0.05	1.95 \pm 0.05
	No Fire	1.55 \pm 0.05	1.95 \pm 0.05	1.95 \pm 0.05	2.75 \pm 0.05
	Main effect (species)	1.55 \pm 0.10a	1.88 \pm 0.13a	1.80 \pm 0.09a	2.35 \pm 0.23b
DP% CP	Fire	54.00 \pm 1.00	53.50 \pm 3.50	61.50 \pm 0.50	60.00 \pm 1.00
	No Fire	54.50 \pm 1.50	59.00 \pm 9.00	60.00 \pm 3.00	57.50 \pm 0.50
	Main effect (species)	54.25 \pm 0.75a	56.25 \pm 4.25a	60.75 \pm 1.32a	58.75 \pm 0.85a
SP % CP	Fire	18.50 \pm 3.50	10.00 \pm 1.00	21.00 \pm 3.00	20.50 \pm 0.50
	No Fire	21.00 \pm 1.00	11.00 \pm 1.00	21.00 \pm 2.00	16.00 \pm 0.00
	Main effect (species)	19.75 \pm 1.65b	10.50 \pm 0.65a	21.00 \pm 1.47b	18.25 \pm 1.31b
Crude fat%	Fire	0.90 \pm 0.10	1.30 \pm 0.10	1.50 \pm 0.00	1.90 \pm 0.00
	No Fire	0.85 \pm 0.05	1.60 \pm 0.00	1.60 \pm 0.00	2.05 \pm 0.35
	Main effect (species)	0.88 \pm 0.05a	1.45 \pm 0.10b	1.55 \pm 0.03bc	1.98 \pm 0.15c

CP: Crude Protein; SP: Soluble Protein (% CP); DP: Degradable Protein (% CP); 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.

Table 4. Main effects of fire and species differences on carbohydrates (% DM) in native grass of semi-arid savanna of Burkina Faso (values are mean \pm SE)

	<i>A. gayanus</i>	<i>D. amplexiens</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)	
ADF%	Fire	52.90 \pm 3.40	51.15 \pm 1.55	47.55 \pm 0.05	44.65 \pm 1.35	49.06 \pm 1.42
	No Fire	51.55 \pm 0.85	50.25 \pm 0.95	44.60 \pm 1.70	45.60 \pm 1.40	48.00 \pm 1.22
	Main effect (species)	52.23 \pm 1.48a	50.70 \pm 0.79ab	46.08 \pm 1.10bc	45.13 \pm 0.84c	
NDF%	Fire	77.70 \pm 0.50	74.30 \pm 2.50	70.90 \pm 1.40	67.80 \pm 1.60	72.68 \pm 1.53
	No Fire	79.30 \pm 0.10	72.95 \pm 0.95	70.75 \pm 0.45	67.60 \pm 2.30	72.65 \pm 1.69
	Main effect (species)	78.50 \pm 0.51a	73.63 \pm 1.16b	70.83 \pm 0.60bc	67.70 \pm 1.15c	
Lignin%	Fire	7.50 \pm 1.10	8.45 \pm 0.45	5.50 \pm 0.60	6.45 \pm 0.55	6.98 \pm 0.50
	No Fire	8.10 \pm 0.40	7.45 \pm 0.85	5.40 \pm 0.50	5.60 \pm 0.30	6.64 \pm 0.49
	Main effect (species)	7.80 \pm 0.51a	7.95 \pm 0.49a	5.45 \pm 0.32b	6.03 \pm 0.35ab	
CF%	Fire	43.60 \pm 2.80	39.05 \pm 1.65	35.75 \pm 0.55	33.20 \pm 0.70	37.90 \pm 1.60
	No Fire	40.10 \pm 0.60	37.20 \pm 1.90	35.45 \pm 1.45	36.00 \pm 4.70	37.19 \pm 1.21
	Main effect (species)	41.85 \pm 1.54a	38.13 \pm 1.16ab	35.60 \pm 0.64ab	34.60 \pm 2.10b	
NFC%	Fire	14.80 \pm 0.40	16.00 \pm 1.70	15.55 \pm 1.05	17.75 \pm 1.55	16.03 \pm 0.63
	No Fire	13.00 \pm 0.30	16.10 \pm 0.50	15.95 \pm 0.25	15.65 \pm 1.95	15.18 \pm 0.62
	Main effect (species)	13.90 \pm 0.56a	16.05 \pm 0.72a	15.75 \pm 0.46a	16.70 \pm 1.18a	
Starch%	Fire	1.50 \pm 0.40	1.15 \pm 0.05	1.75 \pm 0.25	2.15 \pm 0.05	1.64 \pm 0.16
	No Fire	1.05 \pm 0.05	1.30 \pm 0.10	2.00 \pm 0.30	2.25 \pm 0.55	1.65 \pm 0.22
	Main effect (species)	1.28 \pm 0.21a	1.23 \pm 0.06ab	1.88 \pm 0.18ab	2.20 \pm 0.23b	
Sugar%	Fire	6.20 \pm 0.30	8.10 \pm 0.80	8.30 \pm 0.30	11.00 \pm 0.40	8.40 \pm 0.67
	No Fire	5.85 \pm 0.35	8.25 \pm 0.05	9.25 \pm 0.75	8.55 \pm 0.85	7.98 \pm 0.53
	Main effect (species)	6.03 \pm 0.21a	8.18 \pm 0.33b	8.78 \pm 0.43b	9.78 \pm 0.80b	

For species, means with different letters are significantly different based on Tukey's HSD test.

ADF: Acid Detergent Fiber; NDF: Neutral Detergent Fiber; CF: Crude Fiber; NFC: Non Fiber Carbohydrates

Table 5. Main effects of fire and species differences on minerals in native grass of semi-arid savanna of Burkina Faso (values are mean \pm SE)

		<i>A. gayanus</i>	<i>D. amplexans</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)
Ash%	Fire	4.85 \pm 0.04	6.82 \pm 0.70	9.29 \pm 0.38	9.19 \pm 0.30	7.54 \pm 0.71
	No Fire	5.10 \pm 0.16	7.81 \pm 0.21	8.29 \pm 0.52	11.22 \pm 0.18	8.10 \pm 0.83
	Main effect (species)	4.98 \pm 0.10a	7.31 \pm 0.41b	8.79 \pm 0.39c	10.20 \pm 0.60d	
Ca%	Fire	0.19 \pm 0.01	0.41 \pm 0.04	0.18 \pm 0.01	0.24 \pm 0.02	0.25 \pm 0.04 *
	No Fire	0.20 \pm 0.01	0.52 \pm 0.02	0.23 \pm 0.02	0.31 \pm 0.03	0.31 \pm 0.05
	Main effect (species)	0.19 \pm 0.01a	0.46 \pm 0.03c	0.20 \pm 0.02a	0.27 \pm 0.03b	
P%	Fire	0.08 \pm 0.01	0.07 \pm 0.01	0.08 \pm 0.00	0.12 \pm 0.02	0.09 \pm 0.01
	No Fire	0.06 \pm 0.00	0.06 \pm 0.00	0.13 \pm 0.01	0.12 \pm 0.01	0.09 \pm 0.01
	Main effect (species)	0.07 \pm 0.00a	0.06 \pm 0.00a	0.10 \pm 0.01b	0.12 \pm 0.01b	
Mg%	Fire	0.12 \pm 0.02	0.24 \pm 0.00	0.18 \pm 0.01	0.14 \pm 0.01	0.17 \pm 0.50
	No Fire	0.13 \pm 0.01	0.25 \pm 0.01	0.17 \pm 0.00	0.16 \pm 0.00	0.18 \pm 0.02
	Main effect (species)	0.12 \pm 0.01a	0.24 \pm 0.00c	0.17 \pm 0.00b	0.15 \pm 0.01b	
K%	Fire	1.23 \pm 0.05	1.12 \pm 0.18	1.62 \pm 0.02	1.57 \pm 0.08	1.38 \pm 0.09
	No Fire	1.18 \pm 0.01	1.06 \pm 0.08	1.62 \pm 0.08	1.80 \pm 0.12	1.41 \pm 0.12
	Main effect (species)	1.20 \pm 0.02a	1.09 \pm 0.08a	1.62 \pm 0.03b	1.68 \pm 0.10b	
Na%	Fire	0.011 \pm 0.001	0.001 \pm 0.000	0.002 \pm 0.000	0.002 \pm 0.000	0.004 \pm 0.002
	No Fire	0.002 \pm 0.000	0.001 \pm 0.000	0.002 \pm 0.000	0.002 \pm 0.000	0.002 \pm 0.000
	Main effect (species)	0.006 \pm 0.004a	0.001 \pm 0.000a	0.002 \pm 0.000a	0.002 \pm 0.000a	

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

Table 5 (continued)

		<i>A. gayanus</i>	<i>D. amplexens</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)
Fe ppm	Fire	137.00 ± 4.00	177.00 ± 22.00	325.00 ± 68.00	185.00 ± 4.00	206.00 ± 30.09*
	No Fire	203.00 ± 47.00	250.00 ± 48.00	257.00 ± 47.00	389.00 ± 38.00	274.75 ± 31.22
	Main effect (species)	170.00 ± 27.10a	213.50 ± 30.14a	291.00 ± 39.04a	287.00 ± 60.92a	
Zn ppm	Fire	18.00 ± 2.00	19.00 ± 1.00	41.00 ± 0.00	34.00 ± 1.00	28.00 ± 3.74
	No Fire	18.00 ± 0.00	22.00 ± 1.00	36.00 ± 3.00	40.00 ± 1.00	29.00 ± 3.54
	Main effect (species)	18.00 ± 0.82a	20.50 ± 1.04a	38.50 ± 1.89b	37.00 ± 1.83b	
Cu ppm	Fire	3.00 ± 0.00	3.00 ± 0.00	5.00 ± 1.00	5.50 ± 0.50	4.13 ± 0.48
	No Fire	3.50 ± 0.50	4.00 ± 1.00	5.50 ± 0.50	6.00 ± 0.00	4.75 ± 0.45
	Main effect (species)	3.25 ± 0.25a	3.50 ± 0.50ab	5.25 ± 0.48bc	5.75 ± 0.25c	
Mn ppm	Fire	82.50 ± 1.50	124.50 ± 6.50	61.00 ± 5.00	33.00 ± 2.00	75.25 ± 12.73 *
	No Fire	91.50 ± 2.50	157.00 ± 4.00	65.00 ± 3.00	40.50 ± 2.50	88.50 ± 16.47
	Main effect (species)	87.00 ± 2.86a	140.75 ± 9.89b	63.00 ± 2.65c	36.75 ± 2.53d	
Mb ppm	Fire	0.20 ± 0.00	0.10 ± 0.00	0.15 ± 0.05	0.25 ± 0.05	0.18 ± 0.03
	No Fire	0.10 ± 0.00	0.10 ± 0.00	0.25 ± 0.05	0.45 ± 0.15	0.23 ± 0.06
	Main effect (species)	0.15 ± 0.93a	0.10 ± 0.00a	0.20 ± 0.04ab	0.35 ± 0.10b	

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

Table 6. Main effects of fire and species differences on digestibility and metabolizable energy (mean \pm SE) in native grass of semi-arid savanna of Burkina Faso

	<i>A. gayanus</i>	<i>D. amplexens</i>	<i>C. caudatum</i>	<i>R. exaltata</i>	Main effect (fire)	
TDN%	Fire	42.00 \pm 1.00	40.00 \pm 1.00	44.00 \pm 5.00	49.00 \pm 1.00	43.75 \pm 1.61
	No Fire	47.50 \pm 10.50	43.00 \pm 2.00	48.00 \pm 2.00	47.50 \pm 0.50	46.50 \pm 2.20
	Main effect (species)	44.75 \pm 4.59a	41.50 \pm 1.26a	46.00 \pm 2.48a	48.25 \pm 0.63a	
NEI (Mcal/kg)	Fire	0.53 \pm 0.02	0.59 \pm 0.07	0.73 \pm 0.11	0.88 \pm 0.07	0.68 \pm 0.07 *
	No Fire	0.55 \pm 0.13	0.66 \pm 0.04	0.79 \pm 0.02	0.86 \pm 0.04	0.70 \pm 0.04
	Main effect (species)	0.55 \pm 0.07a	0.64 \pm 0.04a	0.77 \pm 0.04ab	0.86 \pm 0.02b	
NEm (Mcal/kg)	Fire	0.55 \pm 0.04	0.48 \pm 0.04	0.64 \pm 0.18	0.81 \pm 0.04	0.62 \pm 0.07
	No Fire	0.73 \pm 0.37	0.59 \pm 0.06	0.77 \pm 0.06	0.79 \pm 0.02	0.73 \pm 0.07
	Main effect (species)	0.64 \pm 0.15a	0.55 \pm 0.04b	0.70 \pm 0.09a	0.79 \pm 0.02c	
RFV	Fire	57.50 \pm 3.50	61.50 \pm 3.50	68.00 \pm 1.00	74.50 \pm 3.50	65.38 \pm 2.70
	No Fire	57.00 \pm 1.00	63.50 \pm 1.50	71.00 \pm 1.00	74.00 \pm 4.00	66.38 \pm 2.65
	Main effect (species)	57.25 \pm 1.49a	62.50 \pm 1.66ab	69.50 \pm 1.04bc	74.25 \pm 2.18c	
IVTD%	Fire	58.50 \pm 0.50	57.00 \pm 1.00	64.00 \pm 6.00	66.00 \pm 1.00	61.38 \pm 1.83
	No Fire	65.00 \pm 12.00	61.00 \pm 2.00	67.00 \pm 2.00	68.00 \pm 2.00	65.25 \pm 2.57
	Main effect (species)	61.75 \pm 5.25a	59.00 \pm 1.47a	65.50 \pm 2.72a	67.00 \pm 1.08a	
RFQ	Fire	46.50 \pm 8.50	46.50 \pm 4.50	61.50 \pm 8.50	72.50 \pm 1.50	47.13 \pm 1.90
	No Fire	62.50 \pm 21.50	52.50 \pm 4.50	75.50 \pm 7.50	74.00 \pm 2.00	52.00 \pm 3.33
	Main effect (species)	54.50 \pm 6.71a	49.50 \pm 1.31a	68.50 \pm 3.43b	73.25 \pm 1.11b	
NDFD%	Fire	46.50 \pm 0.50	42.50 \pm 0.50	49.50 \pm 7.50	50.00 \pm 3.00	56.75 \pm 4.81
	No Fire	56.00 \pm 15.00	46.00 \pm 2.00	53.50 \pm 2.50	52.50 \pm 4.50	66.13 \pm 5.64
	Main effect (species)	51.25 \pm 10.51a	44.25 \pm 3.12a	51.50 \pm 6.14a	51.25 \pm 2.32a	

TDN: Total Digestible Nutrients; NEm: Net Energy for Maintenance; NEI: Net Energy for Lactation; RFV: Relative Feed Value, RFQ: Relative Forage Quality. For species, means with different letters are significantly different based on Tukey's HSD test. *In vitro* true digestibility (IVTD); neutral detergent fiber digestibility (NDFD) a

4. Discussion

The results of this study demonstrate that post-fire regrowth had lower above-ground dry matter than unburned vegetation. There are three possible explanations for this. First, fire may have exacerbated water stress in this semi-arid savanna-woodland by removing standing dead/live vegetation, thereby increasing mortality in burnt plots. In a previous study conducted on the same experimental plots, Savadogo *et al.* (2007) found that recurrent early fire tended to decrease steady state infiltration rate, which in turn is believed to enhance water stress on post-burn plots. Second, the recurrent fires may have exacerbated mineral nutrient limitation in the already nutrient-poor semi-arid environment through increased nutrient losses during burning, thereby reducing plant growth. This is further evidenced from the relatively lower concentrations of organic carbon, total carbon and nitrogen on burnt than unburnt plots (Table 1). Furthermore, losses of mineral nutrients, especially nitrogen, following frequent burning have been previously documented (Wan *et al.*, 2001; Laclau *et al.*, 2002), and such losses are also reflected in the nutrient composition of above-ground biomass, notably the reduced total protein concentration in post-burn regrowth in our study. Third, the old-growth in the unburnt plots may play an important role in sustaining growth in this semi-arid environment by ameliorating the micro-climate and maintaining reserves of plant and soil water. It is believed that the 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 *et al.*, 2003). Overall, a combination of these factors would result in significant variations in above-ground dry matter production between burnt and unburnt plots.

Marked inter-species variations in above-ground dry matter production were observed on both burnt and unburnt plots; notably in both cases the productivity of the perennial grass, *A. gayanus*, was higher than that of the three other species. Given the high water stress and nutrient-limitation in this semi-arid environment and that fire exacerbates these growth limiting factors, perennial grass species have better chances of thriving in such environments than annual grass species that are shade-lovers due to their greater photosynthetic efficiency and other anatomical and biochemical features that enable them to cope more effectively with high temperature and high light intensity. Fire is known to reduce the tree cover (Scholes and Walker, 1993). 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 (Savadogo *et al.*, 2005). It could then out-compete some species like *R. exaltata* and *C. caudatum* in burnt areas. The seeds of these two species have not adaptation for burial after the last rains like those of *L. togoensis*. They are then exposed at ground level to the high temperature during burning that could kill them. Indeed, inhibition of herb regeneration was related to high fire temperature (Jensen and Friis, 2001) because of increased seed mortality. The significant variation in above-ground dry matter production between perennial grass species (*A. gayanus* versus *D. amplexens*)

makes generalization at growth form level difficult and suggests that growth performance in resource-limited environments is instead species specific.

The inter-annual variability observed in above-ground dry matter production during the study period could be partly explained by the annual rainfall pattern. A correlation of 38% has been found between total herbaceous biomass and annual rainfall at the same experimental site (Sawadogo *et al.*, 2005). However, it should be noted that not only the amount of rainfall but also its frequency influences plant growth. Our result is consistent with the study conducted in tussock grassland of semi-arid Australia, where above-ground biomass remained smaller on burnt plots for the entire study period (Bennett *et al.*, 2003). Thus, rainfall not only in the first season but also during subsequent growing seasons seems to influence the post-burn productivity of herbaceous vegetation in semi-arid environments. The fluctuation between years could also be related to the heterogeneous distribution of the studied species on the plots.

Burning significantly reduced the crude protein and neutral detergent insoluble crude protein concentrations in post-fire regrowth. This reflects the limiting soil N conditions under which the grass species grew. Indeed, in burnt plots soil N concentration was slightly lower than in unburnt plots (Table 1), and numerous studies have recorded losses of soil N due to volatilization during frequent burning (Laclau *et al.*, 2002). Fire did not, however, affect the amounts of crude fat, or cell wall and non-structural carbohydrates, in post-burn regrowth, most likely due to translocation of stored reserves between below- and above-ground biomass of the herbaceous vegetation. Most living herbaceous biomass in savannas is generally found below-ground (Laclau *et al.*, 2002), and therefore acts as a strong carbon sink. The stored carbon is then translocated during the early stages of regrowth following fire and may add-up to the photosynthetic production to such an amount equivalent to the unburnt vegetation. This phenomenon of inter-organ translocation has been observed for a number of mineral nutrients in post-burn regrowth (Villegant *et al.*, 1979; Menaut, 1983; Laclau *et al.*, 2002). All organic compounds analyzed, however, varied significantly among grass species. The perennial grasses tended to have lower concentrations of crude protein and fat while annual grasses tended to have higher concentration of non-structural carbohydrates. Despite this general pattern, a substantial variation in organic compounds was observed between grasses within each growth, which is consistent with the findings by Scheirs *et al.* (2001).

The low quantity of total crude protein and fat in perennial grasses could also be the result of increased allocation of proteins and fats to the below- than above-ground organs for perennials as an adaptation strategy to drought and other non-drought stressors in the semi-arid environment as hypothesized by several researchers (Villegant *et al.*, 1979; Menaut, 1983; Laclau *et al.*, 2002). These results are consistent with an earlier study in the Sudanian Zone where crude protein and fat concentrations of perennial grasses were found to be significantly lower than in annual grasses (Kabore-Zougrana, 1995). Owing to their growth habit, it is also apparent that the perennial grasses utilize most assimilates for structural maintenance while the annual grasses utilize the same for rapid growth

and reproduction as evidenced from the substantially higher lignin and fibre concentrations in perennial grasses than annual grasses in our study.

Fire did not affect the concentration of mineral elements analyzed in the present study except that of Ca, Mn and Fe, which were significantly lower in post-fire regrowth than the unburned vegetation. Generally, burning oxidizes organically bound elements in the vegetation and litter, and these nutrient elements are either released in forms available to plants through ash deposition or are lost through volatilization and ash convection (Frost and Robertson, 1987). As evidenced from soil sample analyses, fire enhances the concentrations of K, P, Ca and Mg in the soil but that was not followed by concomitant increases in post-fire regrowth. The extent to which 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, which is consistent with result reported by Van de Vijver *et al.* (1999) in 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 foliar leaching.

The concentrations of mineral elements also varied significantly between grass species; notably that of P, Mg, K, Ca, Zn, Cu, Mn and Mb. This could be related to nutritional requirements and uptake efficiency of each individual species as also documented in an earlier study (Kabore-Zoungana, 1995). Interestingly, all studied grass species irrespective of the fire treatment have higher concentrations of most mineral elements than the relative requirements for livestock production in tropical grassland ecosystems (Payne and Wilson, 1999), and therefore appear to be suitable for animal production systems although deficient in Ca, P, Na and Mb. This finding is consistent with other studies from tropical grasslands (Jumba *et al.*, 1995; Kabore-Zoungana, 1995). Knowledge of the energy concentration of a particular feed is helpful in feeding animals according to their nutrient requirement 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 affect significantly 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 concentration of proteins, fats, starch and sugar than the perennial grasses.

Conclusions

Annual fire reduces the above-ground biomass of post-fire regrowth of the studied species. However, its effects on the nutrient composition, digestibility and net energy concentration of post-fire regrowth, compared to unburnt vegetation, are

not substantial. The results confirm that in the long term the adverse effects of frequent fires will counterbalance the short term benefits (increases in soil fertility and plant nutrient concentrations) claimed to accrue from single or less frequent fires. In this semi-arid savanna-woodland, factors such as available soil water and nutrients play important roles, as well as fire, in regulating vegetation growth, as evidenced by the marked inter-annual variations observed in above-ground dry matter in the control plots and an overall paucity of soil nutrients. Although annual early fires resulted in lower above-ground dry mass in the present study, their effects are still weaker than those often observed of severe late fires. It should be noted that very intense late fire is inevitable in the study area if early fire is not applied. Thus, the application of annual early fire as a tool for multiple uses management of savanna-woodland should continue, but with due caution regarding the timing of burning, weather conditions and other factors that may increase fire intensity.

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Structural and functional responses of herbaceous vegetation in the Sudanian savanna-woodland ecosystem to effects of herbivory, fire and selective tree cutting were investigated. Moderate grazing intensity reduces fuel consumption during fire, thus decreasing temperature and lethal temperature residence time. Structural responses exhibited significant temporal variation, while main or interactive effects of disturbances were limited, and varied between life forms, species and sites. High grazing intensity reduced soil water infiltration and aboveground biomass. Fire reduced above-ground phytomass and grass nutrients concentration.

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