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Fire and grazing effects on herbaceous structure, composition and diversity, and plant functional responses to management regimes in Mkomazi, Tanzania

SETTORE SCIENTIFICO DISCIPLINARE DI AFFERENZA: **BIO/03**

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Dedication

To my lovely son Castor Jr. and to the loving memory of my mother & father.

This thesis is organized into five main parts (General introduction, Materials and Methods, Results, Discussions and Conclusions and recommendations).

General introduction: introducing the reader to the background of the study and sets the foundation on which the study is built.

The four other parts have been organized in such a way that each is discussed to reflect the four objectives of the research, which will be referred to in the text by their corresponding roman numerals as sub-headings under each part.

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General introduction

Savanna ecosystems constitute one of the largest biomes of the world covering 20% of the terrestrial land surface (Pratt & Gwynne, 1997; Jeltsch, *et al.,* 2000; Beerling & Osborne, 2006; Buitenwerf *et al.,* 2011), comprising a dynamic mix of trees and grasses that encompasses open woodland and grassland (van Langevelde *et al.*, 2003; Beerling & Osborne, 2006). The balance between herbaceous and woody vegetation is regulated by complex interactions between climate (amount and seasonality of rainfall), soils (soil texture and depth), and disturbance regimes which include fire, grazing, and browsing (Scholes & Archer, 1997; Bond *et a.l*, 2003; Fuhlendorf *et al.,*2008; Sunkaran *et al.,* 2008).

The African savanna ecosystems are among the earth's most productive and valuable ecosystems. The herbaceous component of tropical savanna is dominated by a diverse array of C4 grasses, which contribute significantly to herbaceous productivity and provide forage for both ungulates and domestic stocks (Belsky, 1992; Bond, 2008; Smith *et al*., 2012). They host the world's largest diversity of wild ungulates, and vast areas are managed as protected areas such as national parks and game reserves. The welfare of both human society, wildlife and economic development of many countries in Africa largely depends on their vital functions (Pratt & Gwynne, 1997) and productivity.

In Tanzania, savanna ecosystems support large populations of wildlife which contribute significantly to the country's economic development through a diversity of tourism activities. Tourism is Tanzania's top foreign exchange earner and the second largest contributor to the economy after agriculture, with a contribution of approximately 18 percent to the gross domestic product (GDP) in 2013 (Cunningham *et al*., 2015). About a third of the country's total area is protected to a certain degree as a national park, game reserve, Marine Park, or forest reserve. The

Mkomazi National Park is among the 16 parks in Tanzania. The Park represents the southernmost belt of semi-arid savanna bordering the southern Sahara, and extends as far as in the highlands of Ethiopia (Coe *et al.,* 1999). The park supports a diversity of wildlife populations and tourism activities in the country. Despite of its ecological and economic importance, the effects of management regimes, in particular fire and grazing, on seasonally inundated grasslands of Mkomazi Park are poorly understood.

A substantial body of literature has examined how these disturbance regimes alone each or interactively affect Tropical savanna grasslands (Belsky, 1990; 1992; van Langeverde *et al.,* 2003; Hassan *et al.,* 2007, Furley *et al*., 2008). Fire is a widespread process in the earth system (Bond *et al.,* 2005), an important component in the maintenance of savanna grassland diversity (Freeman, 1998; Uys *et al.,* 2004) and plays a key role in ecosystem composition and distribution (Bond *et al*. 2005). Grazing is another important factor which regulates savanna dynamics. The two disturbances can act independently or additively (Belsky, 1992; Valone, 2003; Savadogo *et al.,* 2008) and the co-occurrence of these disturbances has a synergistic effect on plant communities, both in time and space (Savadogo *et al.,* 2008), which in turn influences the composition and distribution of wildlife populations.

Fire, a management tool and its implications

Both natural and human-induced fires are important ecological factors in many habitats of the world, from forests to dry grasslands (Johnson, 1992; Bradstock, 2010). Many plant communities of the world have evolved to survive fire events and some have even developed specialized relationships with fire or evolved specialized traits or attributes to survive frequent burning. Vegetation communities such as the *chaparral* (Keeley & Keeley, 1988; Beyers & Wakeman, 1997; Keeley, 2005), the tropical savanna of the north and the open forests of the

temperate south in Australia (Bradrock, 2010), the *cerrado* in central Brazil (Gottsberger & Silberauer-Gottsberger, 2006; Loiola *et al.*, 2009), and *miombo* woodlands and savanna grasslands in tropical Africa (Pratt & Gwynne, 1977; Skarpe, 1992; Sheuyange, *et al.,* 2005: Gandiwa, 2011; Smith *et al.,* 2012) offer a good example.

Anthropogenic fire in Africa is an ancient form of environmental disturbance which probably has shaped the savanna vegetation more than any other human disturbance (Sheuyange, *et al.,* 2005: Gandiwa, 2011, Smith *et al.,* 2012). Fire in savanna has long history, dated way back in 2.5 mya when hominids started using it for varying reasons. These include protection against wild animals, hunting, killing vermin and regenerating plant food sources for both humans and livestock among other uses (Pausas & Keeley, 2009). Human activities through the use of fire in savanna habitats have influenced the structure and function of savanna ecosystems (Heady, 1966; Harris, 1980; Trollope, 1982; Pausas & Keeley, 2009). The rise of human has heavily influenced fire regimes often in a way that affects the sustainability of ecosystems (Pausas & Keeley, 2009). For example, fire is known to increase or decrease species richness, affect vegetation cover (Higging *et al.,* 2007) and species abundance (Savadogo *et al.,* 2009), alter population dynamics and vigor of its dominant species (Morgan & Lunt, 1999). Likewise, the ecological effects of fire on soil properties and nutrient composition (DeBano *et al.,* 1977; Viro, 1974; De Ronde, 1990; Shakesby & Doerr, 2006; Mataix-Solera *et al.,* 2011), soil microbiology (Mataix-Solera *et al.,* 2009), the hydrology and geomorphology aspects of soil (Shakesby & Doerr, 2006) are well documented.

The effects of fire on vegetation and soil depend on intensity and frequency, which are in turn influenced by a wide array of biotic and abiotic variables such as the vegetation structure and type of animal utilizing the area, season of burning and weather conditions, topographic and

edaphic features, and fuel (plant biomass) characteristics (Pyne *et al*., 1996; Mataix-Solera *et al.,* 2011). For example, the effect of fire resulting from early burning (i.e. few months after the rains often less than three months) is often less intense than that of late burning (i.e. throughout the dry season) because plants still contain relatively high amount of moisture contents. As a result of low effects on vegetation, early fire is highly utilized as a management tool by wildlife managers in many of protected savanna ecosystems.

Since fire is a natural phenomenon of many savanna ecosystems, it has been used by conservation managers in many different ways and it is often seen as straight-forward habitat management practice in solving ecological problems related to vegetation. In Tanzanian protected areas, fire has been used over decades as a management tool for a variety of purposes such as to reduce the amount of fuel, thereby reducing the effects of unplanned fires/wildfires, to prevent bush encroachment and promote regeneration of young sprouts for grazers. For example, the use of fire in Serengeti National Park is not limited to reduce the population of tsetse flies in tsetse infested areas, but also to increase production of quality forage, control wild fires from outside the protected areas and their spread and to keep animals in tourist areas for visitors' enjoyment (Hassan *et al.,* 2007). Fire exclusion in the Ngorongoro Crater - Tanzania, following the eviction of Maasai pastoralists in 1974, was said to have modify the grassland community to a taller and coarser structure. This in turn is supposed to have favoured Africa buffalo and Burchell's zebra more than wildebeest (Hassan *et al.,* 2007). Although this could have come as a response to multiple of both abiotic and biotic factors, other factors such as the eviction of cattle grazing have been invoked to explain such a change in vegetation structure and composition (Hassan *et al.,* 2007).

These two examples demonstrate that fire is a complex phenomenon and if employed (or excluded) without adequate knowledge, can threaten the biological productivity, biodiversity and sustainability of ecosystems. Indeed, fire is highly variable in space and time and is driven by both, biotic and abiotic factors that dictate it's temporal (seasonality and frequency), spatial (size and patchiness) and magnitude (intensity, severity and type) components (Trollope, 1986; Pyke *et al.,* 2010; Smit *et al.,* 2010; Gandiwa, 2011; Smith *et al.,* 2012).

Nevertheless, fire has long been practiced out of generalization from other areas. This is a dangerous approach to fire (Whalen, 1995), because the beneficial effects of fire in one grassland community do not necessarily mean fire can be used in the same way with the same beneficial effects in other grassland community. Since the responses of community structure and composition and ecosystem processes to fire are generally complex, and vary between biogeographical regions and plant communities, ecological-based studies should provide the management with the guidelines for decision on how best fire regimes be employed or excluded.

Grazing implications

Grazing is second to fire, affecting ecosystem structure and functioning. The two disturbance factors are distributed differently in terms of duration and severity, and are both driven by biotic and abiotic factors that dictate their temporal, spatial and magnitude components. It is well established that grazing by both domestic stocks and wild animals has most notable effects on vegetation structure and composition, and soil nutrient composition (Belsky, 1986; Hiernaux *et al.,* 1999; Yates *et al.,* 2000; Kramer *et al.,* 2006; Keeley *et al.,* 2008; Catorci *et al.,* 2012), mostly in terms of herbage removal, deposition of faeces and urine (dunging), and soil and litter trampling and compaction (Hiernaux *et al.,* 1999).

The impacts of grazing may vary seasonally and as a function of livestock type, stocking density, timing and duration (Keeley *et al.,* 2008). While light grazing is known to allow succession from grassland to woodland (Watkinson & Ormerod, 2001), other forms of grazing, including selective and heavy stocking rate, may alter the floristic composition and in turn, led to a shift from long-lived perennials to herbs (annuals and forbs), accompanied by a decrease in forage production (Fuhlendorf *et al.*, 2001). Similarly, heavy grazing, commonly referred to overgrazing, may lead to the loss of species richness and an increased abundance of unpalatable species (Mwendera *et al.*, 1997), decline in native perennial cover and an increase in exotic annual cover, reduced litter cover as well as the degradation of soil resources (Yates *et al.,* 2000) resulting in an overall rangeland degradation.

Herbage removal (browsing and grazing) is the most notable effect of herbivores affecting vegetation structure and dynamics (Milchunas & Lauenroth, 1993; Díaz, *et al.*, 2001) in terms of area and biomass removal, and is both dependent on, and affects plant morphological and functional traits (Weiher, *et al.,* 1999; Díaz, *et al.,* 2007).

Herbivore dungs are recognized as a potential source of both macronutrients such as N, P, K and several other forms of micronutrients and improves the physical-chemical properties of soils (Harris, 2002; Cumming & Cumming, 2003; Rufino *et al.*, 2006) and may directly or indirectly affects vegetation composition and structure by changing the availability of soil nutrients and their spatial redistribution (Olff & Ritchie*,* 1998; Bardgett & Wardle 2003).

On the other hand, trampling by large herbivores mediated by their hooves can cause soil compaction and reduced aeration. At the same time, trampling impacts vegetation structure by detaching or destroying plant materials (Abdel-Magid *et al.*, 1987; Yates *et al.,* 2000; Hansson, 2004). The type and degree of ecological consequences of grazing on the structure, functioning

and dynamics of savanna ecosystems is dependent upon the type of animal, season and intensity of grazing, soil characteristics and plant communities present. In particular, grazing intensity or seasonality variations are crucial factors in understanding how grazing influences plant community composition (Wartkinson & Ormerd, 2001).

Thus, similarly to those of fire, the effects of herbivores are not necessarily consistent across sites (Augustine & McNaughton, 1998; van Langevelde *et al.,* 2003; Sankaran *et al.,* 2008) due to variability in rainfall patterns and soil nutrient contents across environmental gradients.

Plant functional strategies and the CSR theory

Biodiversity is often measured using simple parameters such as species richness. However, recent research has pointed out that ecosystem level processes are affected by the functional characteristics of organisms involved, rather than by taxonomic identity (Odum, 1969; Hüseyinova *et al.,* 2012). Therefore, functional diversity, rather than the simple number of species, plays a crucial role in regulating ecosystem processes (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; Hooper *et al.,* 2005).

Human activities have changed the ecosystems in unprecedented rates and scale, and predicting responses to global change is a major challenge in ecological science (Díaz *et al.,* 2004; Suding *et al.,* 2008). Present land use change results in profound consequences in disturbance regimes, with pronounced changes in systems where fire and grazing are the major disturbance factors (McIntyre *et al.,* 1999). The recent desire to simultaneously predict vegetation responses to global change factors and changes in terrestrial ecosystems has revived the concept of plant functional classification (McIntyre *et al.,* 1999; Chapin *et al.,* 2000, Garnier

et al., 2007; Garnier & Navas, 2012), in particular the role of plant traits to predict the effects of environmental factors on plant community structure and ecosystem properties and functioning.

A trait-based approach is a conceptual framework to understand and predict the effects of environmental factors on plant community structure and ecosystem properties using plant traits (Chapin *et al.,* 2000; Garnier & Navas, 2012). Although, introduced long ago (Raunkiaer, 1934; Grime, 1977; Noble & Slatyer, 1980; Box, 1981; 1996), the approach is currently gaining a high priority in the research agenda of plant ecology, because it is considered as a primary tool for predicting ecosystem responses to land-use management and climate changes at global scale (Díaz & Cabido, 1997). A long series of both in-depth empirical and theoretical studies in recent years has led to the identification and classification of a set of traits that are often closely correlated to key functional attributes of plants (e.g. leaf net photosynthetic rate, reproductive investment, leaf life-span), facilitating the quantification of these traits in a large number of species (Grime, 1997; Díaz *et al.,* 1997). Being linked to the functional component, plant traits determine species survival and competitive abilities and allow to understand plant species adaptation and distribution to different environments, thereby gaining insight concerning the status of species and role in ecological succession (Yirdirim *et al.,* 2012).

The practical importance of plant traits to ecological studies is demonstrated by a wide range of recent studies. For example, functional traits have been used to provide an insight into how plants have adapted to different environmental pressures (Wright *et al.,* 2005), to clarify the variations in plant life histories (Adler *et al.,* 2014) and to explain the coexistence of species within communities (Pierce *et al.,* 2014) (see also Grime, 1974, 2001; Turkington & Klein, 1993; Cerabolini *et al.,* 2010; Kılınç *et al.,* 2010; Grime & Pierce, 2012; Yirdirim *et al.,* 2012; Negreiros *et al.,* 2014).

The most developed and presently widely applicable system, competitor-C, stress-tolerator-S, ruderal-R (CSR) plant strategy theory (Grime, 1974; 1977; 2001) predicts the occurrence of three suites of plant strategies with regard to species' adaptive responses to tradeoffs in the investment of resources. This includes ability to compete with neighbours (Competitor - C), tolerate stress (Stress tolerator - S) or survive biomass destruction or disturbance (Ruderal plant - R). The practical application of the CSR theory led to the development and advancement of CSR classification methods (Grime, 1988; Hodgson *et al.,* 1999; Pierce *et al.,* 2013).

Based on the theory, plant species can exhibit different proportions of the characteristics related to each of the three primary strategies (C-, S- and R-), including superior stature, an adaptation for a rapid uptake of resources and long-term occupation (C), small stature with longer lifespan, an investment in durable and well-defended structures (S) and variable growth forms, often of short stature, with short lifespans as an adaptation for rapid development and reproduction (R). Reflecting the equilibria that are possible among the primary strategies, four secondary (CR, SR, SC & CSR) and twelve intermediate strategies exist within the CSR system, each exploiting a different intermediate combination of stress and disturbance.

CSR theory has been intensively studied in temperate regions (Caccianiga *et al.,* 2006; Quétier *et al.,* 2007; Cerabolini *et al.,* 2010; Schamp *et al.,* 2011; Frenette-Dussault *et al.,* 2012; Pierce *et al.,* 2013) and elsewhere in the world (Yirdirim *et al.,* 2012; Negreiros *et al.,* 2014). Despite not being universally accepted, it has not been falsified as a theory (Grime & Pierce, 2012), and over time it has continued to be used and is currently seen as a central focus in community ecology. However, it is not certain yet how widely applicable the CSR classification

methodology is across other biogeographical regions and vegetation types (Negreiros *et al.,* 2014). In particular, the theory has never been applied to East African savanna ecosystems.

Objectives

The general objective of the work presented in this thesis was to increase knowledge and understanding of the effects of management regimes on the seasonally inundated herbaceous vegetation community in the semi-arid savanna-woodland in Tanzania. The studies presented in this thesis assess the effects of management regimes (= fire grazing -FG, fire no-grazing - FNG & no-fire no-grazing - NFNG) on species composition and structure, floristic diversity and biomass production, as well as how functional diversity of herbaceous layer in conjunction with management practices governs ecosystem processes. The specific objectives were:

I. Assessing the effects of management regimes (FG, FNG and NFNG) on species composition and vegetation structure (species abundance and dominance, total vegetation cover, percentage of the perennials abundance of seasonally inundated savanna vegetation) as well as on soil properties;

II. Analyzing the effects of management regimes (FG, FNG and NFNG) on species richness, evenness (J'), diversity (H'), and aboveground biomass;

III. Evaluating the relationship between species richness and biomass, i.e. the humpbacked model, the prediction that species richness is highest at an intermediate level of biomass using the combined data from the three types of the management regimes (FG, FNG and NFNG);

IV. Testing the applicability of Grime's Competitors - C, Stress-tolerant - S and Ruderal - R (CSR) strategy scheme and assessing the functional strategies of savanna vegetation in relation to management regimes (FG, FNG and NFNG).

Materials and Methods

Study system

The study was carried out in Mkomazi National Park which lies between (03° 47'S - 37° 45'E) and (04° 33'S - 38^0 45'E), in Same and Lushoto districts in north-eastern Tanzania (Fig. 1). The park is bordered by Tsavo West National Park, in Kenya to the north-east and the Pare mountains to the north-west and covers an estimated area of 3,276 km^2 with an elevation ranging from 230 m to 1,630 m a.s.l (Coe *et al.,* 1999).
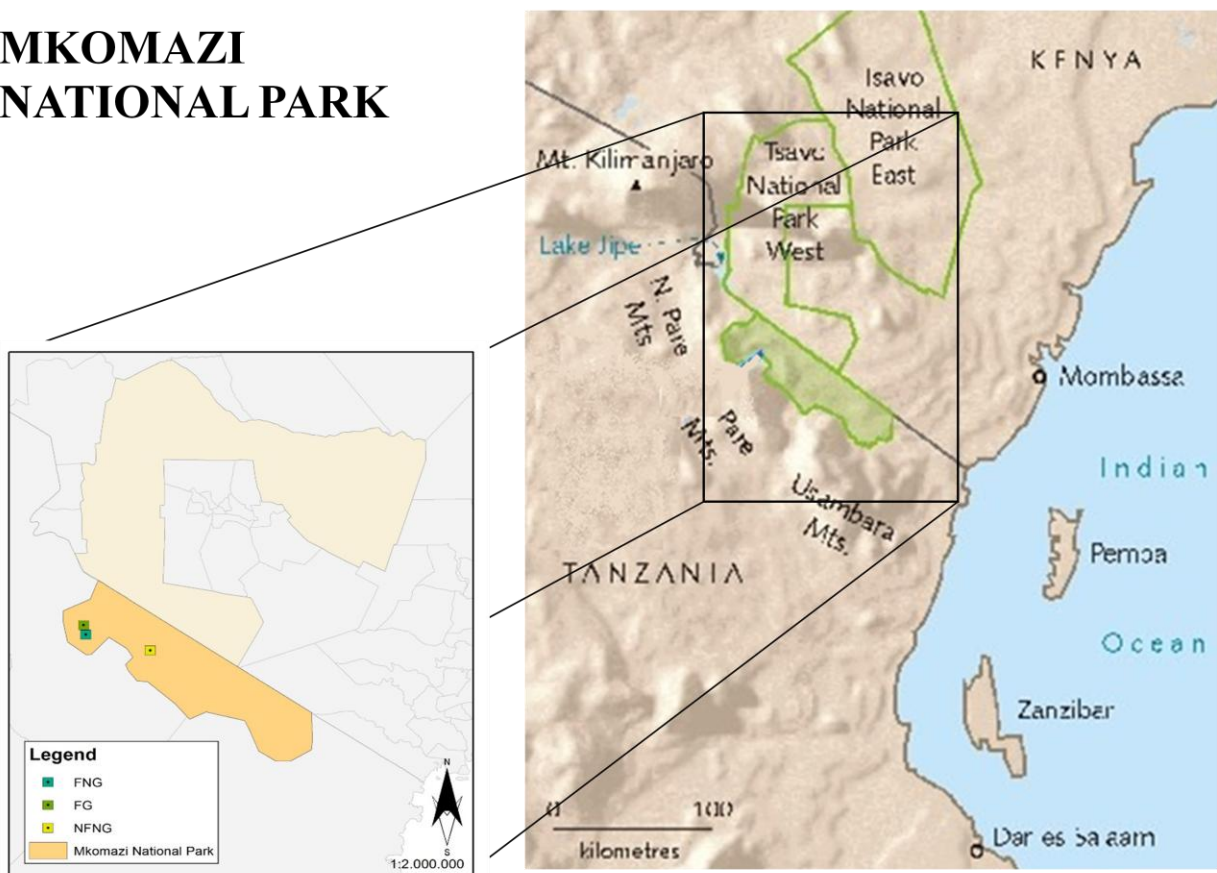

Figure 1 Map of Mkomazi National Park, the park area is indicated by light brown colour. Colored boxes indicate the locations of the study sites where vegetation sampling was done.

The park was a game reserve from 1951 (e.g. allowing for consumptive and non-consumptive uses) and its conservation status was upgraded to a National park in 2005 (e.g. only for non-consumptive uses) as a result of increased degradation of biodiversity.

The climate of the MNP is characterized as semi-arid with evapo-transpiration rates being much higher than rainfall for most of the year (Coe *et al.,* 1999). Annual average rainfall ranges between 570-890 mm (lowlands) and 911-1910 mm (highlands) (Kelvin, 2013). The rainfall is bimodally distributed, with a period of short rains from October to December and the main rain season from March to May (Coe *et al.,* 1999). However, it is ill-distributed and unpredictable and often increase with altitude. This severely impacts the amount of water available to plants and animals within the park. Rainfall is therefore, a primary determinant of the distribution and composition of flora and fauna in the park. The mean annual temperature is 23.1°C with July and August being the coolest and cloudiest months while December-through February are the hottest months. The savanna grassland dries out quickly towards the midst of May to July as the winds increase and the humidity drops. Followed by a period of intense desiccation throughout June to September when the ambient temperature rises, daily sunshine hours are at their longest and the wind velocity increases sometimes to its maximum. However, the degree of desiccation is highly variable amongst areas within the park.

The diversity of wild species is as great as in any other east African protected area with about 26 ungulate species and Buffaloes (*Syncerus caffer*), Elephants (*Loxodonta africana*), Zebras (*Equus burchellii*), Cokes' hartebeests (*Alcelaphus buselaphus cokii*) and Elands (*Taurotragus oryx*) are described as the major grazing species (Coe *et al.,* 1999). Seasonal movements of animals from the Tsavo national park to Mkomazi national park is a common phenomenon during the wet season (Coe *et al.,* 1999).

The vegetation of the park is a characteristic of Somalia-Masai Region and Afromontane Centre of Endemism, and the Zanzibar Inhabane Regional Mosaic dominated by a mosaic of grasses and trees (Coe *et al.,* 1999). Various vegetation types from the highlands to the lowlands predominate the Mkomazi N. Park based on local physiographic features, with *Acacia-Commiphora* woodland/bush lands being very dominant. The seasonally inundate grassland community extends from the central to the west segment of the park. Although the park vegetation has long been studied, inventory to update the vegetation status of the park is inevitable since casual observations suggest a rapid replacement of grassland by bush grassland of some grassland patches.

The soils of the park have been classified based on their colors and location along a catena. They range from red to reddish brown on free drainage hills, ridges and fan slopes to brown and grey brown on slow drainage catena, to black clay on alluvial valley (Anderson, 1967; Harris, 1972).

Research sites and selection criteria

Three sites were discriminated (Fig. 1, Table 1) based on: a) the type of management of the site, namely, fire and grazing, which represent the most widespread management practices in savanna ecosystems; b) site accessibility during the rainy season and c) uniformity in ecological and topographic characteristics and vegetation homogeneity. The sites were selected as follows:

Fire-grazing (FG) site was located in the North West near the former Ibaya camp. The site is burnt every dry season and grazed with an average of 3 to 15 individuals/day (mainly Cokes' hartebeests and Zebras) the year around and occasionally in the wet season, when the site is not inundated, with small herds of Buffaloes, Elephants or Elands of up to 80 individuals (pers. field observations).

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Fire-no grazing (FNG) site was located 20 km south east of the FG site. The site is located between tourists and/or administration roads that connect the park headquarter to the park posts and other areas of tourist attractions. Because of its proximity to the road, animals have learned to avoid this site following past hunting activities in the area. We therefore considered this site to be free from grazing or only rarely grazed. Therefore, no fences to exclude grazers were needed.The site remains flooded for quite some time as compared with the other two sites (FG & NFNG).

No fire-no grazing (NFNG) site was located in the southeastern of FG and FNG sites at a distance of about 70 km away from the two sites, but within the zone of low use and 1 km away from the Rhino sanctuary. Fire is excluded at this site since 2005, when it was gazetted as a national park. Previously, the site was burned every dry season. Based on the experience of park staff, the site was identified as not being used by grazing species with no evidence of grazing throughout the sampling period. The site is located close to the road frequently used by the management, this ascertain the no or little use by herbivores.

Table 1 Characteristics of the three studied sites: FG= Fire grazing, FNG= Fire no grazing, NFNG= no fire no grazing sites.

	FG	FNG	NFNG
Latitude	3° 56' W	$4°$ 0' W	$4°$ 04' W
Longitude	37° 49'N	37° 49' N	$38°$ 05' N
Altitude (min - Max) (m)	841 - 885	829 - 890	715 - 780
Estimated area (Km^2)	409,388	420,197	310,145

The soils of the study sites were atypical of black clay derived from the below and above large rocky inselbergs. The rocks are responsible for the formation of a series of basins into

which eroded minerals and organic matter are washed from the surrounding hills and where physical and chemical changes form extensive grassland patches, referred as *mbuga* and often remain waterlogged throughout the rain season (Coe *et al.,* 1999).

Data collection

Vegetation samples

      Vegetation was sampled in 2014, between April-May when majority of plant species could easily be identified and the vegetation community is at a period of peak standing biomass. In total 80 plots of 2 m x 2 m (4 m^2) were surveyed out in each selected site, according to a stratified random sampling design. For each plot, species composition and abundance were assessed and recorded. Herbaceous plants were identified to species level, their abundances were determined by counting individual shoots. In case of grasses with prostrate stems, tillers were counted to determine species abundance. Names of grasses are those given in Bogdan (1958). Other plant names are those given in Blundell (1987) and those which were matched with specimens in Mweka Herbarium.

      The total vegetation cover per plot was visually estimated by two observers with the aid of a graduated square wooden frame and averaged.

      Biomass harvesting was done once by clipping samples from randomly distributed 0.25 m x 0.25 m quadrats (in total 80 quadrats per site) at ground level with a pair of scissors within each plot after the assessment of floristic composition. Clipped plant material was kept in plastic bags and subsequently weighed while at the camp using a digital scale (Series Cl 201, with maximum 200 g, d = 0.1 g, China) to determine the fresh weight (standing live biomass).

Thereafter plant material was air-dried for 2 weeks in paper bags and later oven-dried at 70°C for 48 hours and weighed.

Soil measurements

Ten samples each measuring 300g were randomly collected to a 20 cm depth from each site using a soil auger. In total 30 samples were collected, appropriately labeled and packed in plastic paper bags. On arrival at the Agricultural Research Institute (ARI) Mlingano Laboratory in Tanga - Tanzania, samples were air-dried, disaggregated and passed through a 2-mm sieve. Soil pH was measured in a soil/water suspension (1:2.5) by electrode and meter (Black, 1965). Part of the air-dried and sieved samples was ground and passed through a 0.25-mm sieve for C and N analysis, respectively. Organic C was determined by the dichromate oxidation procedure of Walkley-Black (Nelson & Sommers, 1982). Total N was measured by the Kjeldahl procedure (UDK140 Automatic Steam Distilling Unit, Automatic Titroline 96, Italy). For elemental (Ca, Mg, K, and Na) analysis, a portion of the < 2mm soil was crushed to a fine powder, following a nitric-perchloric acid digestion (Black, 1965). The soil concentrations of Ca and Mg were determined by Atomic Absorption spectrometry, K and Na by flame emission spectrometry and available P by Bray and Kurts No 1 (1945).

Species trait measurements

Plant trait measurements were performed to determine the three leaf traits necessary for the calculations of the CSR strategies (e.g. Specific Leaf Area -SLA, Leaf Dry Matter Content-LDMC, and Leaf Dry Weight-LDW). Collection of herbaceous (non woody) species was done

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from 25th April 2014 to 20th May 2014, at the peak of the rainy season, the period which is considered most favourable for plant growth in savanna grasslands.

Sampling protocols, and all measurements of traits were done following the standardized methods of Cornelissen *et al.,* (2003). Ten replicates of each of the most abundant species (Table 2) were randomly collected from within the sites, from 8:00 to 10:00 am to avoid the strongest sunlight (Table 2). The whole ramets were collected, preferably with the root portion to avoid desiccation of the leaf material. The shoot portion was collected, in case a species has a woody rootstock (e.g. *Dolichos oliveri*). Sampled individuals were distant at least 10 m from each other, to avoid the risks of taking measurements on the same clonal colony.

Table 2 Number of leaf replicates per site sampled for leaf trait measurements. The species were selected among the most abundant (thus representative) of each site.

Surveyed site	Number of species	10 Individual/ species	4 Leaf replicates/individual
FG	10	100	400
FNG	10	100	400
NFNG	5	50	250
Total	**25**	**210**	**1050**

Although the selection was meant to include the most abundant species, some less abundant species were also sampled to obtain a better representativity of the functional description of the three sites. Most abundant herbaceous species were defined as those species that collectively made up at least 80% of the maximum standing biomass of the community. Such a threshold has been suggested to ensure a satisfactory description of community properties in relation to fluxes of energy and matter through the ecosystem (Pakeman & Quested, 2007; Cerabolini *et al.,* 2010).

Ramets collected were wrapped with soviet paper saturated with water using a spray bottle, packed in plastic bags and sealed. Within 1:30 - 2 hrs, samples were transported to the laboratory and stored in a dark fridge at 4 °C for at least 18 h to retrieve complete turgidity.

Data Analysis

Objective I: the purpose of the study was to assess the effect of management regimes (fire grazing, fire no-grazing & no-fire no-grazing) on plant communities' composition and structure, in particular species abundance and dominance, total vegetation cover, perennials abundance and soil properties.

For each site we calculated a) species abundance; b) total vegetation cover (%) and c) perennials abundance (%), as the average of the plots (n = 80 per site).

To categorize species based on their abundance, we theoretically defined four classes as reported in Table 3.

Table 3 Species abundance classes based on the number of individuals.

SPECIES CATEGORY	N. of individuals per species
Most abundant	> 1000
Abundant	999 - 500
Intermediate abundant	499 - 100
Less abundant	< 100

To detect the most frequent species (i.e. hereafter defined as dominant species) we calculated the percentage of frequency of occurrence of a given species to the total number of plots in each site. The theoretical range for relative dominance is 0 - 100%, so a species was considered as a dominant or a subdominant if its percentage frequency of occurrence is ≥ 70% and ≥ 50% respectively. Only dominant and subdominant species were considered for discussion.

Statistical analyses

We analysed a matrix of 101 species x 240 plots. Floristic gradients were analysed using Detrended Correspondence Analysis (DCA) (McCune & Mefford, 2011). The effects of management regimes on total abundances, percentage vegetation cover (%) and perennials abundances (%) were tested by PERMANOVA, using site as grouping variable (factor with three levels: FG, FNG & NFNG). Also, the differences in the soil parameters among the sites were tested by PERMANOVA. The differences among the sites were separated by the post hoc Tukey HSD test. Statistical analysis was performed using the past software (Hammer *et al.,* 2001). Species dominance was computed using Microsoft® Excel for Window™.

Objective II: the purpose of the study was to test the difference among the management regimes (sites) with respect to i) mean species richness, ii) mean species evenness (J'), iii) mean Shannon index (H'), iv) mean biomass.

Plant species richness (S) i.e. the number of species encountered per plot, was calculated for FG, FNG and NFNG sites (= management regimes).

Plant biomass (gm^{-2}) was calculated for each plot using the below equation:

$$\text{Standing biomass} = \frac{\text{Dry weight (of above ground tissues)}}{\text{Plot area}}$$

Species diversity (H') was calculated for each plot using the equation:

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

where *pi* is the abundance of ith species in a plot (Magurran, 1988).

The evenness or equitability (J') for each plot was calculated as:

$$J' = H'/\ln S$$

where H' is the Shannon index and S is the number of species encountered in each plot, and the lnS is the natural logarithm of species richness encountered in a plot (Magurran, 1988).

Statistical analyses

The effects of treatments (FG, FNG & NFNG) on species richness, evenness and diversity were test by PERMANOVA and the difference among these parameters were separated by Tukey HSD test (PAST software; Hammer *et al.,* 2001).

Objective III: the purpose of this was to evaluate the relationship between species richness and biomass, i.e. the hump-backed model (HBM) (Grime, 1973), the prediction that species richness is highest at an intermediate level of biomass using the combined data from the three types of the management regimes (FG, FNG and NFNG).

Statistical analyses

To analyze the relationship between species richness and biomass (hump-back curve) we used a Generalized Linear Model-univariate (ANOVAs; R software 2.13.1: R, 2011): the number of species in each plot was fitted against biomass as explanatory variable with a Poisson distribution error.

Objective IV: the purpose of the study was to test the applicability of Grime's Competitors - C, Stress-tolerant - S and Ruderal - R (CSR) strategy scheme and to assess the functional strategies of savanna vegetation in relation to management regimes (FG, FNG and NFNG).

To calculate leaf traits, for each ramet, 4 young fully expanded and undamaged herbaceous leaves (including the petiole) (Table 2) were cut and blades were cleaned. Leaf fresh weight (LFW) was measured using a digital analytical scale (KERB/KB/360-03N, Version 07 07/2013 - Germany, with maximum of 360 g and a precision of 0.001 g). Subsequently, the fresh leaves were scanned using a digital scanner (CanoScan LiDE 110, China) and the images were saved as a bitmap file for further analysis. Leaves longer than the surface of the scanner were cut into sizable pieces and leaflets of compound leaves that could not be positioned properly on the scanner surface were detached from their petiole, together they were laid flat in contact with the surface of the scanner. The leaf fresh weight (LFW) was determined with an analytical scale; the

leaf dry weight (LDW) was then determined with the same analytical scale after 24 h of drying in an oven at 105 °C.

Other plant trait data, in particular growth form, life form and clonality, were assessed from field observations supplemented by information reviewed from the literatures.

The Leaf Area (LA) of the replicates was computed using Leaf Area Measurement V-1.3 (A.P. Askew 2003, The University of Sheffield-UK).

The Specific Leaf Area (SLA) values for each leaf replicate were calculated by using the following equation:

$$\text{SLA} = \frac{\text{Mean leaf area (mm}^2)}{\text{Mean leaf dry weight (mg)}}$$

The percentage of the dry matter content of leaf replicates was calculated using the following formula:

$$\text{LDMC (\%)} = \frac{\text{Mean dry weight (mg)}}{\text{Mean fresh weight (mg)}} \times 100$$

All the computations were performed using Microsoft® Excel for Windows™.

The LA, LDMC and SLA values were then used in the classification of the species into categories of CSR strategies (i.e. the 19 possible functional types) using the new classification tool, the CSR triangulator VP provided by Pierce *et al.* (2013), which allows the classification of species within a triangular space corresponding to Grime's theoretical CSR triangle. The CSR classification analyzes the trade-off between the traits LA, LDMC and SLA (high values of this traits are mutually-exclusive and represent extremes of leaf economic and size) to calculate the relative proportion of C-, S- and R-selection exhibited by target species (e.g. C : S : R = 5 : 70 : 25 %).

To examine how plant strategies vary in relation to management practices, we use the CSR values associated with each species to calculate the mean strategy at the community level. In this way, the community-weighted mean (CWM) for each trait t was calculated as the mean of species trait values, t_i of the species, s, in each plot with each species, i, weighted by its relative abundance, p_i (Garnier $et\ al.,$ 2004), according to the following equation:

$$\text{CWM} = \sum_{i=1}^{s} p_i\, t_i$$

We use the CWM values of LA, LDMC and SLA in CSR classification to produce a community-weighted mean CSR strategy for each community with the relative proportion of C-, S- and R-selection expressed as proportions, in the same manner as for individual species.

Statistical analyses

Independent sample T-test was used to test for the difference in leaf traits values for species between two sites.

Results

Objective I: the purpose of the study was to assess the effect of management regimes (fire grazing, fire no-grazing & no-fire no-grazing) on plant communities' composition and structure, in particular species abundance and dominance, total vegetation cover and perennials abundance, as well as on the soil parameters

The three sites were well separated in ordination space (Fig. 2) with FG and FNG sites at the lower extreme of axis 1, resulting more similar to each other compared to NFNG site, which plots concentrated at the higher extreme of axis 1.

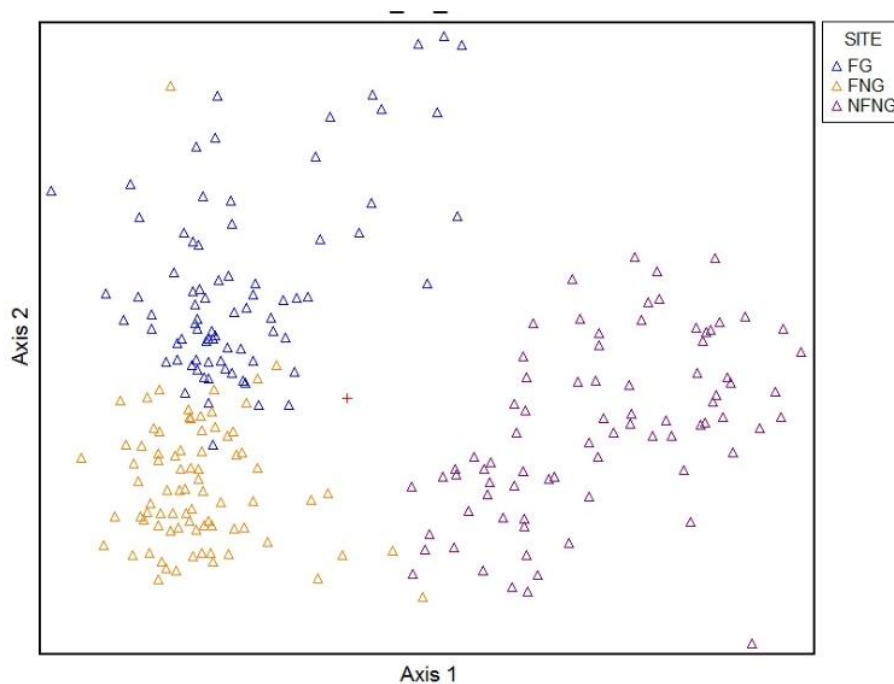**Figure 2** Diagram of DCA ordination of the 240 plots (101 species). Eigenvalues were 0.59 and 0.29 for DCA axis 1 and 2 respectively, and length of gradients were 3.6 and 2.8 SD

NFNG site was characterized by open patches of bare soils, with estimated canopy cover of 60%. The most abundant species (i.e. n. of individuals > 1000) were the grasses *Pennisetum ciliare* and *Echinochloa hapoclada*; four species were abundant (i.e. n. of

individuals between 999 and 500) (*Eustachys paspaloides, Sporobolus* sp., *Bothriochloa insculpta* and *Pennisetum mezianum*). The majority of the species (42 species) had a number of individuals lower than 99 (see Annex 1 – Table 1). Among most abundant and abundant species perennials dominated, while among intermediate and less abundant species, both annuals and perennials were found. However, the community was dominated by perennial species which amounted to 58%. Only three species were present in more than 50% of the plots (*Pennisetum ciliare, Plectoranthus* sp., *Tephrosia volkensii*) (see Annex 1 - Table 2).

FG site was characterized by bare spaces, with a mean plot cover of about 60-70%. Three species were present with more than 1000 individuals (the grasses *Digitaria milanjiana, Themeda triandra* and *Andropogon distachyos*). Abundant species were also perennial grasses as *Ischaemum afrum, Setaria sphacelata* and *Bothriochloa insculpta*. Only an annual species (*Hermannia uhligii*) counted a high number of individuals. Forty-seven species (78%) had a number of individuals lower than 99. Overall, the community was dominated by perennial species which amounted to 56%. Only the grass *Themeda triandra* had a frequency higher than 50% (see Annex 1 - Table 2).

FNG site had a total canopy cover higher than NFNG and FG sites, of 83% on average. Contrary to other sites, the most abundant species was an annual forb (*Commelina petersii*). However, abundant species were again grasses such as *Pennisetum mezianum, Setaria sphacelata, Andropogon distachyos* and *Digitaria milanjiana*. Many species (74%) were among the less abundant. The community resulted dominated by perennial species, although their percentage (54%) slightly diminished compared to the other two sites. Differently from other sites, in FNG site seven species, both grasses and forbs, with a frequency higher than 50% were found.

A total of 21 species were shared among the sites, both perennials (11) and annuals (10) (Annex 1 – Table 1). Shared species were mostly represented by less abundant or

intermediate abundant species. Despite being in common among sites, species were not equally distributed across the sites in terms of abundance, and normally they exhibited a peak of abundance in one site with respect to the others. For example, the grass species *Digitaria milanjiana* was most abundant (e.g. 1841 individuals) in FG site, abundant (e.g. 678 individuals) in FNG site, and an intermediate abundant species (e.g. 194 individuals) in NFNG site (Annex 1 − Table 1). Analogously, the forb *Commelina petersii* was most abundant (e.g. 1838 individuals) in FNG site, intermediate (e.g. 161 individuals) in FG site, and a less abundant species (e.g. 40 individuals) in NFNG site (Annex 1 − Table 1).

The PERMANOVA indicated a significant effect of the site on the analyzed plant community parameters (PERMANOVA test; F= 17.75; p <0.001). The Tukey test (Table 4) evidenced significant differences in all parameters, the only exceptions being the species abundance between NFNG vs. FG and NFNG vs. FNG.

Table 4 Tukey HSD results, comparing the plot means for: species abundance (n), vegetation cover (%), perennial abundance (%) and standing dead biomass (g) of the three sites. NFNG= no fire-no grazing site; FG=fire grazing site; FNG=fire no grazing site.

Species composition parameters (n=240)	FG	FNG	NFNG	FG vs FNG	FG vs NFNG	FNG vs NFNG
Species abundance	121.57±82.48	95.59±51.97	108.06±45.77	*	ns	ns
Vegetation cover	67.25±17.06	83.3±8.93	60.84±15.24	*	*	**
Perennials abundance	76.13±20.50	60.25±26.60	89.09±12.46	*	*	*

*= P<0.05; ** = P<0.01

Soil characteristics

Soil characteristics turned out to be significantly different (PERMANOVA test; F=5.05; p =0.004). However, only NFNG site evidenced significant differences in pairwise comparison (Tukey HSD test) (Annex 1 − Table 3). No significant differences arose between

FG vs. FNG. Overall, NFNG site had a more alkaline pH, and a significantly higher amount of total C% and total N%. NFNG site also evidenced significantly higher Ca and K, while no significant difference arose for Na (Annex 1 – Table 3).

Finally, the mean P differed significantly only between FNG and NFNG sites with FNG site having higher mean value of P.

Objective II: the purpose of the study was to test the difference among the management regimes (sites) with respect to i) mean species richness, ii) mean species evenness (J'), iii) mean Shannon index (H'), iv) standing dead biomass.

A total of 101 plant species (Annex 1 – Table 1) representing 71 genera and 23 families have been recorded. Respectively, 53, 62 and 62 species were identified from no-fire no-grazing (NFNG), fire-grazing (FG) and fire no-grazing (FNG) sites (Annex 1 – Table 1).

The PERMANOVA test (F= 32.6; p = <0.001) evidenced significant differences among the three sites as far as species richness, species evenness, Shannon index and standing biomass are concerned. However, only species richness, species diversity and standing biomass turned out to be significantly different (Tukey HSD test), while evenness remained substantially constant among sites (Table 5). In particular, FNG site evidenced significantly higher species richness, species diversity and standing biomass when compared to both FG and NFNG sites. No significant difference arose when comparing FG vs. NFNG.

Table 5 Plot mean values for species richness, evenness and diversity, and standing dead biomass in the three study sites. NFNG= no fire-no grazing site; FG=fire grazing site; FNG=fire no grazing site. (SE; n = 80, *P < 0·05, **P < 0.01; *** P < 0.001; ns $P > 0·1$)

Community attributes	FG	FNG	NFNG	FG & FNG	FG & NFNG	FNG & NFNG
Richness (n)	8.19±2.56	10.50±2.73	7.43±3.06	*	ns	*
Evenness (E)	0.53±0.14	05.3±0.13	0.53±0.14	ns	ns	ns
Shannon index (H')	1.32±0.41	1.64±0.42	1.28±0.37	*	ns	*
Biomass (gm)	121.46±99.62	231.43±151.76	85.43±62.61	***	ns	***

Objective III: the purpose of the study was to test the relationship between species richness and biomass which predicts that herbaceous species richness is highest at an intermediate level of biomass that corresponds to moderate disturbance (i.e. the humped-back model (HBM).

A significant hump-back pattern was found when the three sites (NFNG, FNG and FG) were analyzed together (Table 6; Fig. 3).

Table 6 Results of Generalized Linear Model (GLZ) for the combined data from all the study sites

	Estimate	Std. Error	z	value	Pr(>|z|)
(Intercept)	144,091	0.21377	6,740	1.58e-11	***
logAllbiomass	0.11922	0.03493	3,413	0.000643	***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
(Dispersion parameter for poisson family taken to be 1)
Null deviance: 267.06 on 239 degrees of freedom
Residual deviance: 255.31 on 238 degrees of freedom
AIC: 1208.2
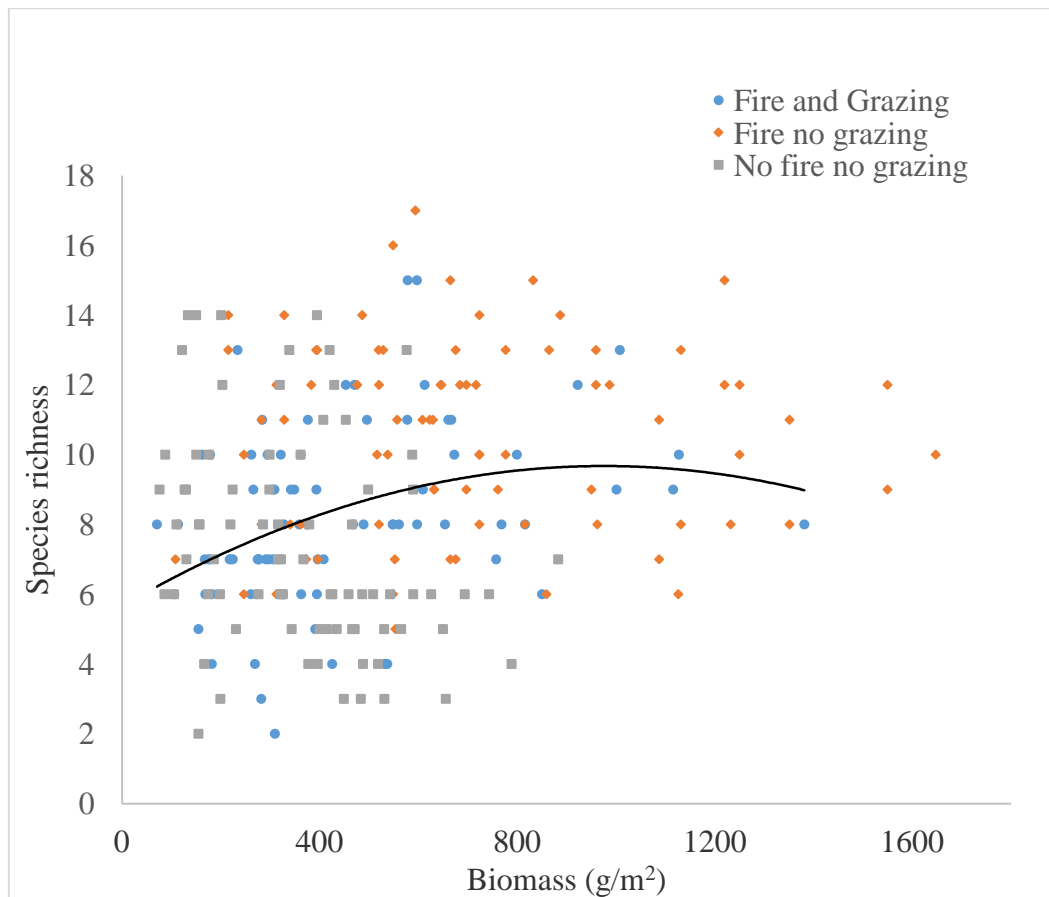
Figure 3 Herbaceous species richness and biomass relationships for the combined data from all the study sites.

When analyzed separately, the three sites demonstrated contrasting trends. NFNG site evidenced a significantly negative relationship ($t_{(1, 79)} = 2.62$, $\beta = 363.43 \pm 24.2$, $p < 0.01$; Fig. 4). Conversely, in FG site the relationship was slightly positive ($t_{(1, 79)} = 3.06$, $\beta = 442.08 \pm 30.6$, $p < 0.002$; Fig 5); while no relationship arose in FNG site ($t_{(1, 79)} = 0.4$, $\beta = 709.09 \pm 50.4$, $p = 0.08$; Fig. 6).

Figure 4 Herbaceous species richness and biomass relationships on the site with no fire and no grazing (NFNG).
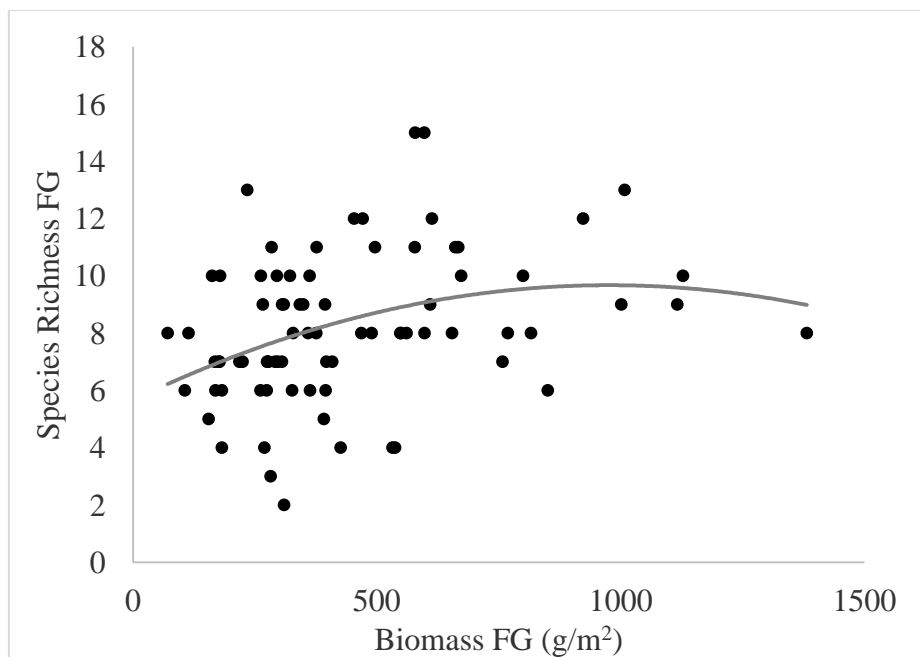
Figure 5 Herbaceous species richness and biomass relationships on the site subjected to annual burning and grazing by herbivores (FG).
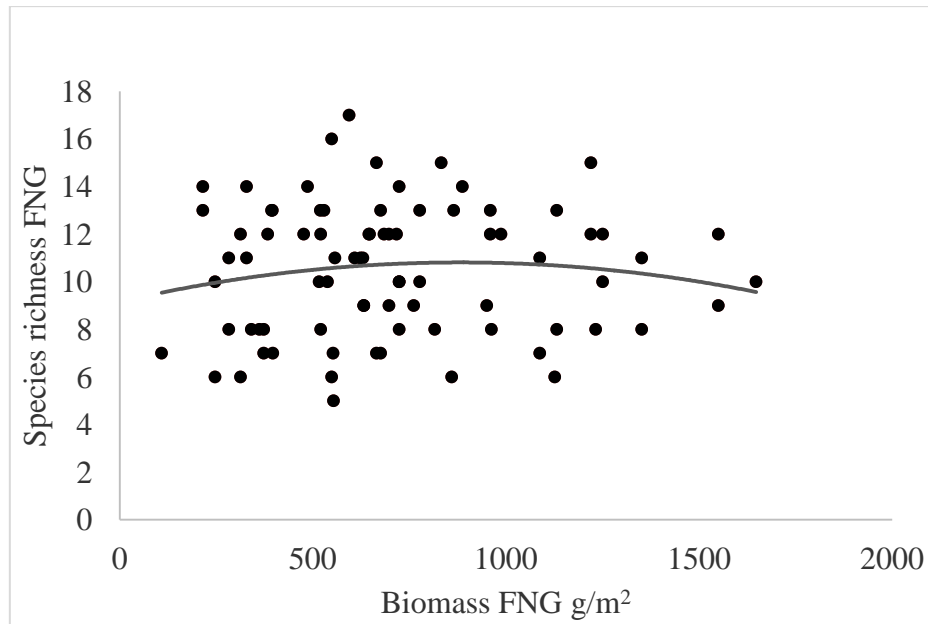
Figure 6 Species richness and biomass relationships on the site subjected to annual burning, but no grazing activities (FNG).

Objective IV: the purpose of the study was to test the applicability of Grime's Competitors - C, Stress-tolerant - S and Rud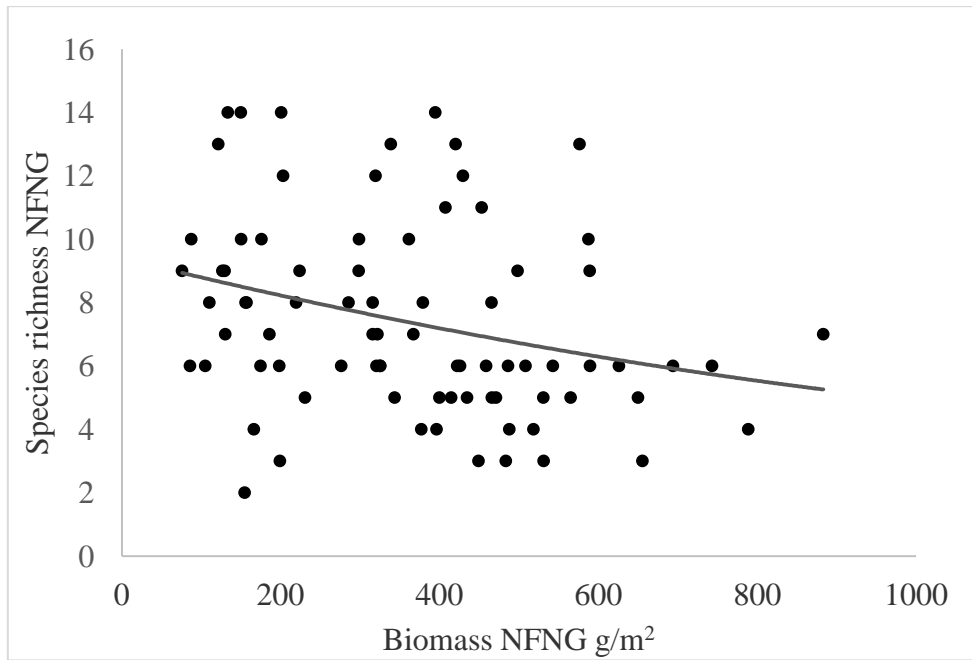eral - R (CSR) strategy scheme and to assess the functional strategies of savanna vegetation in relation to management regimes (FG, FNG and NFNG).

In total 18 species were measured. Species traits means (LA, LDMC & SLA) varied among species within and across sites (Annex 1 – Table 4). Maximum LA was observed in the perennial herb *Dolichos oliveri* in the FNG site, while the lowest LA value was found in the perennial grass *Bothriochloa insculpta* in NFNG site. The maximum LDMC was observed in the perennial grass *Themeda triandra* in the FG site, whereas the minimum was found in the annual forb *Commelina petersii* in FNG site. The highest SLA was observed in the perennial grass *Pennisetum mezianum* in NFNG site, while the lowest SLA value was found in the perennial grass *Ischaemum afrum* in the FG site.

Overall, species of NFNG site showed higher values of SLA compared to species of FG and FNG sites. Conversely, LDMC values of NFNG species were intermediate, with species from FG site having the highest values.

When comparing the species present in two sites, the T-test evidenced some significant differences for the majority of species, being the SLA the most plastic trait. In particular, *Pennisetum mezianum* and *Boithriochloa insculpta* evidenced a higher SLA when growing in NFNG site compared to FNG site. Similarly, *Andropogon distachyos* and *Setaria sphacelata* had significantly higher SLA in FNG site than in FG site. In both cases, also LDMC values varied, although not significantly. The same trend was found in the forb *Commelina petersii* which moving from FNG to FG site showed a significant increase in LDMC and a corresponding decrease in SLA (although not significant).   Only two species, the grass *Digitaria milanjiana* and the herb *Dolichos oliveri*, did not evidenced any significant change in leaf traits across sites.

The 18 plant species were allocated into 13 different strategies as presented in Annex 1 − Table 5. Only *Eustachys paspaloides* and *Pennisetum mezianum* evidenced a primary strategy, Ruderal (R). There was a clear predominance of the stress-tolerant and the ruderal strategy, with only one species, *Dolichos oliveri*, showing a proportion of C above 50 %. Overall, species occurring within a site did not share a common strategy. The species with the greatest abundance in NFNG site, *Pennisetum ciliare*, exhibited a high ratio of stress tolerance (C:S:R = 16:68:15%). Conversely, *Eustachys paspaloides* and *Bothriocloa insculpta*, two abundant species, showed a high ratio of ruderalism (respectively, 12:5:83 and 10:30:60). In FNG site, *Commelina petersii*, the only most abundant species, showed a high ratio of ruderalism (26:0:74). Among the abundant species, only *Pennisetum mezianum* showed a similar ratio of ruderalism (14:22:64), while *Setaria sphacelata* and *Andropogon distachyos* exhibited a high ratio of stress tolerance (respectively 31:40:29 and 24:57:19).

Finally, *Dolichos oliveri* showed a high proportion of competitiveness (65:25:10). Among most abundant species in FG site, only *Andropogon distachyos* and *Themeda triandra* showed a clear polarization towards stress tolerance (respectively, 23:68:9 and 25:63:12), while *Digitaria milanjiana* showed similar ratios of all the components (34:29:37). Abundant species showed a predominance of stress tolerance, either clear (*Ischaemum afrum*, 16:75:9) or in conjunction with ruderalism (*Setaria sphacelata*, 31:49:20; *Bothriochloa insculpta*, 11:46:42).

The species which were shared between two sites evidenced a contrasting pattern, and only 4 species changed the strategy across site. *Pennisetum mezianum* (from R to R/SR) and *Bothriochloa insculpta* (R/CSR to SR/CSR) added a stress component when moving from NFNG to FNG and from NFNG to FG respectively. *Dolichos oliveri* slightly decreased its competitive component in favour of both the ruderal and stress component, when moving from FNG to FG. On the contrary, *Andropogon distachyos* increased its stress component in FNG site compared to FG.

At the community level there was a clear difference of the predominance of stress tolerant and ruderal strategies, with the most abundant species exhibiting proportions of S above 50% and R above 45%, respectively, except for *Digitaria milanjiana* (Fig. 7, Annex 1 – Table 5). Indeed, the CWM strategy of the control site (NFNG) was SR-selected, but tended towards stress-tolerance (10:53:37). Fire on its own, in the FNG site, resulted in a relatively ruderal CWM strategy (R/CSR-selected; 30:24:46), while a combination of fire and grazing selected for a S/CSR mean strategy (26:52:22) (Fig. 7). FNG site had the highest richness in strategies, with CSR and R/CR being the most common, followed by FG site, where the most common strategy was S/CS. Only three different strategies were found in NFNG site.
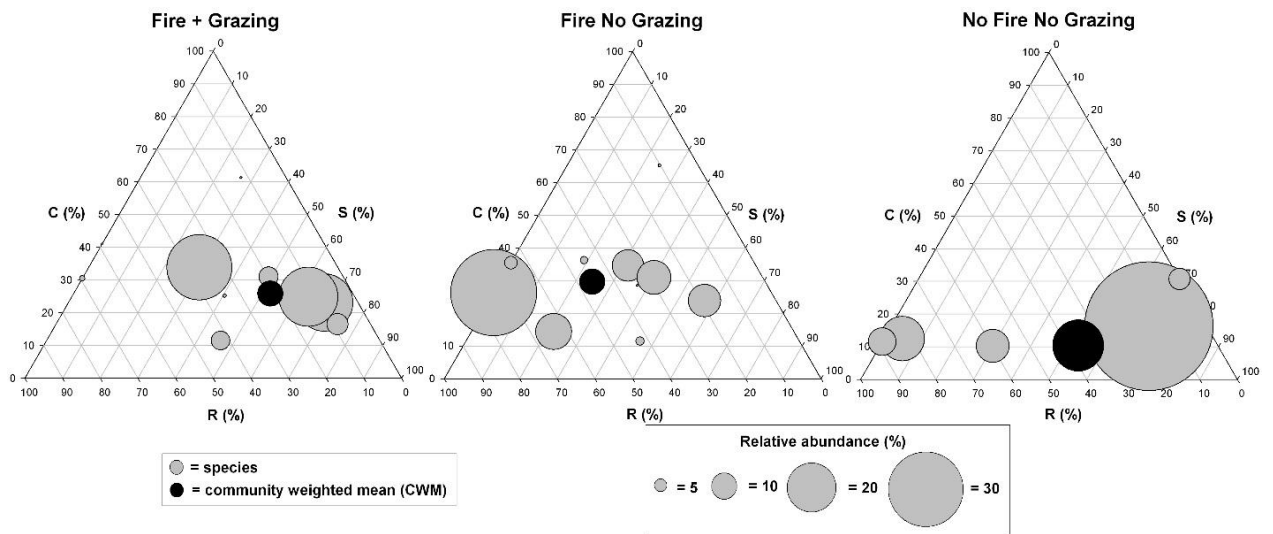
Figure 7 The representativity of the CSR categories in FG: Fire grazing, FNG: Fire no-grazing and

NFNG: No-fire-no-grazing (control) sites, respectively, according the sum of plant, according

to CWM.

Discussion

This study has shown that fire and herbivory have a major impact on savanna ecosystems, with effects on plant community attributes and soil.

Objective I: the purpose of the study was to assess the effect of management regimes (fire grazing, fire no-grazing & no-fire no-grazing) on plant communities' composition and structure, in particular species abundance and dominance, total vegetation cover and perennials abundance.

Overall, the results of this study indicate that management regimes significantly affect species composition and structure (e.g. abundance and dominance, total vegetation cover and perennials abundance). Despite the presence of a group of species in common, the three sites were well characterized in terms of cumulative number of species and species composition, being dominated by different species. Moreover, the species shared across the sites evidenced different abundance values in the three site. The three sites differed also in terms of total vegetation cover and percentage of perennials species which were significantly higher in the control site (i.e. NFNG). Finally, also the fine-scale soil parameters turned out to be significantly different across sites. This suggests that both soil parameters and plant communities composition and structure indeed reflect differences in management regime.

In the present study, NFNG site, strongly dominated by two rhizomatous grass species, *Pennisetum ciliare* and *Echinochloa haploclada*, showed the highest perennials abundance, the lowest cumulative number of species and the lowest mean number of species per plot with respect to both FG and FNG. As already stated (Grime, 1977; Connell, 1978; Valone & Kelt, 1999), the lower level of disturbance in NFNG site could explain the abundance of perennials, since annual ruderal species often dominate when disturbance are

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frequent. Indeed, the two disturbances, fire and grazing, interactively or independently (Belsky, 1992; Valone, 2003; Savadogo *et al.,* 2008) are supposed to strongly influence species presence and abundance by removing the aboveground biomass, increasing light intensity, increasing photosynthesis efficiency, activating dormant meristems thus stimulating growth and reproduction (Noy-Meir, 1993), thus potentially having a positive effect on species richness and diversity. Our results confirmed that fire and grazing have a major interactive effect on floristic composition and structure, and FG site comprised a higher diversity of annual grasses and herbs known to be favoured by disturbance. This study is also consistent with previously reported work that has demonstrated that fire can increase plant species richness (Harrison *et al.*, 2003). Indeed, it has been reported that in different grasslands ecosystems, fire suppression has led to the loss of as many as 50% of the plant species (Leach *et al*., 1996; Uys *et al*., 2004).

However, the way a species is affected by a given type of disturbance strongly depends on its biological and morphological characteristics, which are responsible for the ability of a plant to withstand a cycle of disturbance and recover. In FG site, frequent burning and grazing by resident species (e.g. Zebras, Coke's hartebeest and buffaloes) promote plants with a robust tolerance strategy to stress and disturbance and with the capacity to replace new shoots or regrowth when herbivores are not grazing, as well as plants with clonal growth (e.g. *D. milanjiana, T. triandra, Andropogon distachyos, Ischaemum afrum, Setaria sphacelata,* and *Bothriochloa insculpta*) thus easily recovering from the effects of the two disturbances. This observation is also supported by the greater abundance of *A. distachyos* and *T. triandra* in FG site than their counterparts in FNG site. At the same time, frequent fires promote tall fire-dependent bunchgrass (Archibald *et al.*, 2005). This is evidenced by the predominance of *Themeda triandra* in FG site. The presence or absence of grazing herbivores also affect the mean percentage vegetation cover (%), which was significantly higher in FNG site. In the

absence of herbivores, rhizomatous grass species, stoloniferous forb species and tufted grass seem to be favoured as proved by the abundance of species such as *Pennisetum mezianum*, *Setaria sphacelata*, and, *Commelina petersii* in FG site, or *Pennisetum ciliare* and *Echinochloa hapoclada* in NFNG site. Given their horizontal stem, these species grow aggressively and expansively colonizing open spaces by forming dense matrices of interweave expanded mats with several regenerating tillers and shoots thereby increasing plant cover (Collins, 1987). The present findings are comparable to those of Belsky (1992) in the Serengeti grassland communities, who found that large herbivores prevented several species, included *Pennisetum mezianum* and *Digitaria macroblephara* from growing large enough to outcompete other species in grazed blocks, while, these species grew to their full ungrazed height and overtopped shorter in protected blocks. The abundances of other rhizomatous grass species, such as *B insculpta*, *S. sphacelata* and *P. mezianum* in both FNG and NFNG sites, and the low abundance of bunchgrass (e.g., *T. triandra*) are also likely to be attributed to the absence of herbivores in the two sites.

However, other ecological factors can act promoting the dominance of a species. The high vegetation cover observed in FNG is probably due to the interaction between the type of management and the soil moisture, which varies across the studied sites. Thus the overabundance of *P. ciliare* in NFNG site is mostly likely associated to its high level of tolerate drought and the ability to respond more rapidly to rain than other species (Jackson, 2005). Likewise, the possession of sclerophyllous leaves allow to quickly stop the functioning of the stomata without any damage to tissues in case of water scarcity (Grime, 1977). On the contrary, the abundance of the grass *Eustachys paspaloides* in NFGN site may be attributed to its opportunistic behaviour of growing in depressed locality (restricted geographical locality) which often collects water and deposits of nutrients from adjacent surroundings (Pers. field observation), possibly an opportunistic exploitation of temporarily favorable resources

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(Grime, 1997). Finally, since most of the seedlings of *Hermannia uhligii* were seen emerging from the decomposed animal dung, the high number of individuals probably depends on the contribution of grazers in seed dispersal.

Beside soil moisture, other soil parameters could have governed plant community composition. Fire, in particular, significantly affects soil properties because organic matter is rapidly combusted. The changes in organic matter, in turn, affect several chemical, physical, and microbiological properties of the underlying soil (Neary *et al.*, 2008). Many nutrients essential for plant growth including N, P, S, and some cations are all affected to some extent by fire. When organic matter is combusted, the stored nutrients are either volatilized or are changed into highly available forms that can be taken up readily by microbial organisms and vegetation. However, available nutrients not immobilized are easily lost by leaching or surface runoff and erosion. Nitrogen is the most important nutrient affected by fire. For example, there is a gradual increase in N loss by volatilization as temperature increases (Knight, 1966; White *et al*., 1973) and the amount of total N that is volatilized during combustion is directly proportional to the amount of organic matter destroyed (Raison *et al*., 1985). It has been estimated that almost 99% of the volatilized N is converted to N_2 gas (DeBell & Ralston, 1970), and thus lost into the atmosphere. Phosphorus is the second most limited nutrient found in natural ecosystems. Phosphorus is lost at a higher temperature during soil heating than N, and only about 60 percent of the total P is lost when organic matter is totally combusted (Raison *et al*., 1985). The combustion of organic matter leaves a relatively large amount of highly available P in the surface ash found on the soil surface immediately following fire. Since for most terrestrial plants, the availability of soil resources and light are major environmental constraints (Tilman, 1990), the changes in soil chemical properties could have constrained species survival, growth and reproduction.

Objective II: the purpose of the study was to test the difference among the management regimes (sites) with respect to i) mean species richness, ii) mean species evenness (J'), iii) mean Shannon index (H'), iv) mean biomass and v) mean of soil parameters.

The results of this study indicate that management regimes significantly affect species richness and diversity among the three sites.

Many factors have been hypothesized to influence richness and other measures of species diversity (Palmer, 1994). However, most authors assert that only a small number of factors are responsible for the majority of the variation in richness in nature, and disturbance is widely believed to be one of the main factors influencing variations in species diversity (e.g., Connell, 1978; Huston, 1994; Noss, 1996). Furthermore, species diversity is assumed to be a peaked function of disturbance. The "intermediate-disturbance hypothesis" (IDH; Grime 1973*a,* 1973*b*; Connell, 1978; Huston, 1994) postulates that physical disturbance prevents competitively dominant species from excluding other species from the community, and that there is a trade-off between species' ability to compete and their ability to tolerate disturbance. Therefore, at low levels of disturbance, diversity is low because the best competitors competitively exclude other species. On the contrary, when disturbance is very intense or frequent, few species, the most tolerant, can persist. At an intermediate intensity or frequency of disturbance, conditions allow the coexistence of competitive species and disturbance-tolerant species, thus leading to a peak in species richness. Results emerging from this are in conformity with the intermediate-disturbance hypothesis (IDH; Grime 1973*a,* 1973*b*; Connell, 1978; Huston, 1994).

The results of this study indicate that FG (i.e. high disturbance level) and NFNG (no disturbance) had the lowest richness and diversity when compared with FNG site. These results possibly suggest that fire and grazing interactively, though not necessarily

simultaneously (i.e. not at the same time of the year), impact species richness and diversity by directly consuming or damaging biomass, i.e. kill plants in standing vegetation or destroy seeds in the soils, thereby affecting plant growth and regeneration, and recruitment of young. This process affects both the number of species, selecting those species able to withstand or recover after disturbance, and species abundance, allowing some species to become dominant. At the other extreme, NFNG site evidenced both the lowest cumulative number of species and the lowest number of species per plot. The absence of disturbance led to the predominance of one species, *Pennisetum ciliare*, in turn influencing plant composition and diversity. The effects of this species on the diversity and cover of other species is well documented in different grasslands in many parts of the world (Hussain *et al.,* 1982; Flanks, 1999; Jackson, 2005; Hussain *et al.,* 2010; Marshall & Ostendorf, 2012). On the contrary, at intermediate level of disturbance (i.e. FNG site), fire opens up space for colonization and reduce the competitive superiority of dominant species (Collins, 1987), increase plant vigour and favour the growth of annual herbs, thereby increasing the herb layer diversity and cover. This promoted species richness and diversity in this site.

Our results, however, differ from the previous studies in different grasslands and savanna that have documented significant positive effects of fire and large grazers either collectively or independently on plant species richness and diversity (Heady, 1966; Collins, 1987; Zhang, 1995; Hartnett *et al.,* 1999; Valone & Kelt, 1999). Collins (1987) reported highest species richness on plots that were both burned and grazed at Konza prairie. Meir (1995) found higher species richness and diversity of grazed sites with consistent increase in species richness after a fire on fire-ungrazed sites of the Mediterranean grasslands. However, the analysis of literature arose several inconsistencies, suggesting that the responses of individual plant species or plant communities to fire and grazing vary between geographical regions and plant communities and depend on disturbance intensity and frequency, which are

in turn influenced by a wide range of local variables, both biotic and abiotic (e.g. animal species and density, grazing intensity, climatic condition, vegetation structure or individual species attributes) a few to mention (Pyne, Patricia & Richard, 1996; Mataix-Solera *et al.,* 2011).

Contrary to species richness and diversity, standing biomass was positively influenced by disturbance, being higher in FG and FNG sites. This could be linked to the significant differences in soil variables and nutrient availability, with NFNG soil resulting the poorest. Additionally, the fact that the substrata of FNG site remains moist for a longer period when compared with that of FG and NFNG sites, suggest that the moisture available in the soil probably promoted the growth of short-lived plants, both forbs and grasses thereby regenerating from seed or vegetatively and sprouting throughout the growing season after a fire. These results are supported by past studies documented that limited rainfall affected productivity in semi-arid grassland community (Pratt & Gwynne 1977; Valone and Kelt, 1999).

Thus, in the absence of grazing pressure, perennials together with annuals grow large, thereby accumulating more herbaceous biomass during the growth season in FNG site. Likewise, the available soil moisture at this site probably promoted the growth of ground cover species as compared to FG and NFNG sites which often dries up quickly.

In FG site, both fire and grazing seems to affect biomass and canopy cover at different at times of the year as a result of the observed bare areas. While fire removes both dead and living material in dry season, grazing removes mostly green plants in the wet season, hence when disturbances occur together their effect is augmented. These two disturbances, in different ways and time, reduce the density of viable seeds on the soil surface and of regeneration of buds of perennials thereby reducing the density of seedling and shoots impacting vegetation cover and biomass. These results are in agreement with those of Belsky

(1992) in Serengeti grasslands and Kutt & Wainorski, (2007) in north-eastern Australia, who observed that both grazing and fire reduced ground cover affecting plant biomass.

Objective III: the purpose of the study was to test the relationship between species richness and biomass which predicts that herbaceous species richness is highest at an intermediate level of biomass that corresponds to moderate disturbance (i.e. the humped-back model (HBM).

The relationship between species richness and biomass in the study sites was found to assume a roughly unimodal, or "hump-back" form. Several processes are believed to generate unimodal species richness-curves: some authors suggest that the pattern of productivity-diversity relationship may change with geographical and ecological scales (Waide *et al.,* 1999) or is influenced by other environmental factors (Wright *et al.,* 1993; Waide *et al.,* 1999) including productivity measure, plot size and study system (Mittelbach *et al.,* 2001), abiotic stress (e.g. insufficient water and mineral nutrients) which only few species are able to tolerate (Fraser *et al.,* 2015) and competitive exclusion by a small number of highly competitive species (Grime, 1973; Al-Mufti *et al.,* 1977; Guo & Berry 1998; Fraser *et al.,* 2015). Yet others point out disturbance (Grime, 1973; Connell, 1978), dispersal limitation and evolutionary history (Taylor *et al.,* 1990; Zobel, & Partel, 2008) as the contributing factors.

Our result is in accordance with the intermediate disturbance hypothesis which postulates that the number of species in a community is greatest when levels of disturbance are intermediate. Disturbance reduces the density of competitive species, thereby creating opportunities for less competitive ones. At intermediate level of disturbance, both groups of species can coexist, since dominant species cannot acquire all of the resources leaving pioneering species sites to colonize(Graham & Duda, 2011). However, at local scales, species

richness often increases with increasing productivity (Rosenzweig & Abramsky, 1993). According to this, at the low end, a low level of resources is unable to support many species and species richness is low. As productivity increases, a higher number of species can coexist, up to a point where the number of species begins to decrease because of competition. Hence, at the high end of the gradient, a few highly competitive species monopolize all of the resources and species richness is again low. In our case, this theory fits only to the low end of the gradient, the NFNG site, which soil was the poorest, and both cumulative species number and mean species richness per plot were the lowest. Despite not significant differences in nutrient availability in FG and FNG sites, the two had significantly different mean species richness per plot and standing biomass. The same kind of reasoning could be done for environmental gradients, that when wide enough can generate unimodal relationships (Grime, 1973). Even in this case, soil parameters (e.g., pH, moisture) allow to discriminate only between NFNG site, at the low end, and FG and FNG, at the high end.

When analysing sites separately, only in the FG site the herbaceous species richness increase with increasing biomass. NFNG site evidenced a significant negative relationship while, FNG site showed no significant trend. This pattern indicates that an increase in biomass did not automatically lead to an increase in herbaceous species richness (Zobel & Liira, 1997). Several others have reported similar patterns (Proulx & Mazumber 1998), and several explanations have been suggested for this pattern (Grime 1973; Huston 1994; Oksanen 1996; Guo et al, 2001). In the current study it is probably related mostly to individual identity and dominance by few species which become dominant (Huston, 1979). During sampling period we observed some of the randomly placed quadrats to have fallen on a square meter where a single species dominated with few or no associated species. In all these cases, the competitive superiority of dominant species might have influenced the

number of species per plot and the amount of biomass accumulated within a plot thereby altering the association between species richness and biomass.

The patterns depicted by this study are in conformity with those of Guo and Berry (1998) who found the relationship between species richness and biomass to be positive, negative, or non-existent within microhabitat types, in which the environment was relatively homogeneous. Moreover a study by Oba *et al*. (2001) illustrated a positive relationships between species richness and biomass and a significant hum-back pattern when all plots were analyzed together (exclosure and open plots) in semi-arid Tropical grazing region in northern, Kenya - East Africa. Indeed, in the present study the hump-back pattern was significant only when all plots from the three sites were analyzed together. This supports the idea that the hump-back relationship is most likely to occur when habitats are subjected to different environmental factors and different disturbance regimes as the case of study area.

Objective IV: the purpose of the study was to test the applicability of Grime's Competitors - C, Stress-tolerant - S and Ruderal - R (CSR) strategy scheme and to assess the functional strategies of savanna vegetation in relation to management regimes (FG, FNG and NFNG).

Leaf traits and Grime's Competitors, Stress-tolerant and Ruderal (CSR) strategy scheme proved to be applicable for assessing the functional strategies of savanna vegetation. Our results further demonstrated that CSR classification is a practical method for the categorization of savanna plants, suggesting that Grime's CSR strategy scheme (1974; 1977; 2001) allows the description of a very general ecological phenomenon.

In the present study, mean values of LA, LDMC and SLA varied among species within and across sites. These traits are known to reflect important life history trade-offs between the investment of resources in further resource acquisition versus conservation (Pierce *et al*.,

2014). For example, high values of SLA ensure for high rates of resource acquisition in productive habitats (Grime *et al.,* 1997), while high values of LDMC indicate a conservative leaf economics, implying the acquisition of traits responsible for retention of resource capital in unproductive conditions (Grime *et al.,* 1997). Thus, strategies arise as an adaptive response of plants to site ecological condition (Cerabolini *et al.,* 2010). However, species found in the same site did not share the same adaptive strategy, instead each species have adapted differently to respond to site conditions. Moreover, among the species shared by the three site, some species did not change strategy between sites (e.g. *Commelina petersii* or *Digitaria milanjiana*) while others did (e.g. *Bothriochloa insculpta*, *Pennisetum mezianum*, *Andropogon distachyos*), but even those that did, were very similar, i.e. there was no species that jumped from being R to S, for instance. Mostly, species added up or lost a component of the CSR strategy when moving from one site to another (e.g. *Bothriochloa insculpta* from NFNG to FNG: R/CSR to SR/CSR; *Andropogon distachyos* from FNG to FG: S/CSR to S/CS). This may imply that trait variation may be evident, but changes in the overall strategy within species are either not apparent or are limited. This would suggest that the way in which each species survives does not fundamentally change and that differences between plant communities mainly reflect changes in relative abundance (e.g. *Andropogon distachyos*, from abundant in FNG site to most abundant in FG site) and substitution of species with different life-histories and inherent capacity to survive the stress and disturbance. Thus, both strategy and abundance reflect the adaptive response of plants to site ecological condition, including the kind of treatment. Competitors were not found at any of the sites, for the most competitive species being *Dolichos* (C = 61 to 65 %) but this exhibited an extremely low relative abundance. The difference in soil moisture availability between sites may have acted as the major environmental filter leading to a clear predominance of the stress-tolerant strategy at sites FG and NFNG, whereas fire selected for a greater degree of ruderality at the FNG site.

The substrata of the FNG site stayed moist for quite some time while the substrata of sites FG and NFNG have already started drying up (personal observations of the author). Thus, open spaces once created by fire during the dry period at the FG site become available for colonization by annuals of rapid and high potential growth-rate. It is therefore not surprising to find that *Commelina petersii* (R/CR) rapidly colonizes open spaces, and established very well to become the most abundant species at the FNG site. Indeed, this site was characterised by a significantly low number of perennials, but was species rich especially in terms of annual plants.

Furthermore the functional strategy exhibited by *Dolichos* sheds some light with regard to recent ecological concerns related to this species. This species appears to occur in areas subjected to frequent annual prescribed burning. However, the species had a low abundance in our study sites (i.e. FG & FNG), and it is relatively abundant or rather dominant in other fire prone areas. Its vegetative growth characteristics and dominance in fire-prone areas has been a major concern to Ecologists, as it is usually seen to replace other native species in areas where it occurs. The species had the most features of competitors as described by Grime (1977), which allows its competitive potential to be realized in FG & FNG sites. We recognise competition as 'the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral of nutrient, molecule of water, or volume of space' (Grime, 1977, p. 1170). *Dolichos* is a perennial herb growing from a massive woody rootstock (Blundell, 1987) with extensive underground lateral spread. It has a high, dense canopy of leaves, rapid growth rate often at the onset of rain and a relatively short leaf life-span. It also produces a copious amount of persistent litter. Its characteristic perennial features and persistent rootstock possibly account for the species' ability to compete for space and light, allows for a rapid growth and development of a large standing biomass. Mahmoud & Grime (1974) argue that a rapid accumulation of a large biomass of shoot material, a prerequisite for effective

above-ground competition, is dependent upon high rates of uptake of water and mineral nutrients (Grime, 1977). This suggests that the rootstock structure (i.e. extended surface area) of *Dolichos* in fire prone sites, allows for efficient uptake of mineral nutrients dissolved in soils at the onset of rains and water.

The different abundance evidenced by the species across the sites are in accordance with sites' CWM. This weighting scheme reflects the idea that dominant species should have a greater influence on ecosystem processes (Grime 1998; Díaz *et al.*, 2007; Mokany *et al.*, 2008; Lavorel *et al.*, 2011). Indeed, most common species are supposed to be well adapted to the local conditions and there is strong support for the biomass ratio hypothesis, which states that the extent to which the traits of a species affect ecosystem properties depends on the abundance of the species in the community (Garnier & Navas, 2012). If we accept this scheme, important implications arise. From a practical point of view, in herbaceous vegetation types strongly dominated by one or few species, only these dominant species can be sampled to identify their functional traits, allowing to gather information with relatively little effort (Suding et al. 2008; Frenette-Dussault et al. 2013).

However, recent research has pointed out that not only species diversity, but also functional diversity plays a crucial role in regulating ecosystem processes (Diaz & Cabido 2001; Hooper *et al.* 2005; Lavorel and Garnier 2002), allowing the stability of ecosystems and their adaptability to future changes (Cadotte *et al.* 2009; Hooper *et al.* 2005). Within this framework, our study evidenced that in savanna ecosystem the lack of disturbance (i.e. fire and grazing) leads to a decrease of both species and functional diversity. In NFNG site, environmental conditions prevail (i.e. habitat filtering) leading to convergence of traits within a community due to common adaptation to the physical environment (de Bello *et al.* 2009). Conversely, in FNG site the diversity in terms of strategies when compared with FG and NFNG sites, suggests for a variety of niches the site could offer (Pierce *et al.,* 2012).

On the whole, our study demonstrated the applicability of the CSR strategy scheme in the Savanna ecosystem, outside Europe where the method was originally conceived, practiced and proved, and provides evidence that plant species may co-exist under different environmental conditions but employ distinctive strategies to exploit the available resources differentially.

Conclusions and Recommendations

Our study confirms the hypothesis that the management regimes can have a significant role in influencing seasonally inundated arid vegetation communities. The majority of the variables taken into account evidenced significant differences in the three study sites, particularly striking when comparing the control site (NFNG) with the other two sites (FG and FNG)

Indeed, the control site had the lowest cumulative number of species, the lowest mean species richness per plot and the lowest values of standing biomass. Moreover, also functional diversity (CSR strategies) was at its lowest. This result has important implications in relation to management since the diversity of functional groups in a dynamic ecosystem, the diversity of species, and the diversity of species in functional groups proved to be critical for resilience and the generation of ecosystem services (Chapin *et al*., 1997; Luck *et al*., 2003). Loss of resilience through the combined and often synergistic effects of pressures can make ecosystems more vulnerable to changes that previously could be absorbed. Fire and grazing interactively, though not at the same time of the year, alter species richness and abundances, and herbaceous layer, promoting the growth of plants with a robust tolerance strategy to stress and disturbances and clonal organs with reserved energy to recover easily from stress and disturbance. The ecological effects of fire alone on grass composition, biomass and productivity turned out to be positive, assuring the highest richness, both in terms of species and strategies, and the highest productivity. Fire increases plant vigor, allows perennials and annuals to grow large and significantly increases the percentage of annual herbs, and consequently, increases herb layer diversity and cover, and in turn, increases biomass production. However, our study also evidenced how the output of a given management regime is influenced by the physical environment. The highlighted cover differentiation is a

combined result of management regimes (presence or absence of grazers) and the difference in soil moisture among the studied sites.

Our study clearly illustrates how management regime shifts in savanna ecosystems may alter community abundance, structure, and composition implying functional changes that may lead to alterations in ecosystem functions. Since fire and grazing act in combination with biotic and other abiotic factors interacting and/or competing in altering savannas ecosystem, management plans in MNP should be based on the actual knowledge of their effects on the biotic (flora and fauna) and abiotic components of the ecosystems and should adopt an adaptive approach.

Since the area is characterised by erratic rainfall and the seasonally inundated grassland dries out quickly due to high rate of evapo-transpiration, we recommend for long-term studies to be able to account for other physical parameters, including but not limited to fire and moisture intensity, duration of inundation, rainfall variation if any across the sites. Vegetational changes in response to fire and grazing and variations in climate and other environmental parameters need long-term period of study to come up with sound conclusion for the recommendations.

The responses of the herbaceous flora to stress and disturbances, particularly fire and grazing, were site-specific, suggesting the importance of landscape-scale approaches to understand the impact of stress and disturbances on the composition, structure and diversity, soil parameters and biomass production of seasonally inundated arid savanna grassland communities.

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ANNEX 1

Table 1: List of species sampled in the three study sites. Numbers indicate the cumulative number of individuals of each species in each site. Most abundant species are in bold. For each species the presence of clonal organs, the growth form and the life history are also reported. Symbols are as follows: NFNG= no fire-no grazing site; FG=fire grazing site; FNG=fire no grazing site. For Growth Form: F= F; G= Grass; H= Herb; DS= Dwarf shrub; S= Shrub. For Life history: A=Annual; P=Perennial. n.a.=not available.

	Clonal organ	Growth form	Life history	NFNG	FG	FNG
Cumulative number of species				53	62	62
% perennials				58.49	56.45	54.84
% cover				60.84±15.24	67.25±17.06	83.30±8.93
average n. of species/plot (± SD)				7.43±3.06	8.19±2.56	10.50±2.73
Pennisetum ciliare (L.) Link	Rhizomatous	G	P	**2485**	4	.
Echinochloa haploclada L.	Rhizomatous	G	P	**1178**	.	114
Eustachys paspaloides (Vahl.)	Rhizomatous.	G	P	862	.	.
Sporobolus sp.	BunchG	G	P	767	.	.
Bothriochloa insculpta (Hochst. Ex A. Rich.)	Rhizomatous	G	P	644	533	188
Pennisetum mezianum Leeke.	Rhizomatous	G	P	542	68	769
Plectoranthus sp.	None clonal	DS	P	417	.	.
Chloris myriostachysHochst.	BunchG	G	P	206	.	.
Digitaria milanjiana (Rendle.) Stapf.	Rhizomatous	G	P	194	**1841**	678
Tephrosia volkensii L.	Non clonal	H	A	144	9	28
Panicum sp.	BunchG	G	P	113	.	.
Hermannia uhligii Engl.	None clonal	F	A	83	560	236
*Justicia flava (*Vahl) Vahl.	None clonal	H	A	81	.	3
Commelina benghalensis L.	Stoloniferous	F	A	78	62	.
Abutilon hirtum (Lam.) Sweet.	Non clonal	H	A	78	.	.
Shrub sp.2	n.a.	S	P	61	.	.
Hypoestes sp.	None clonal	H	A	60	49	38
Cassia sp.	None clonal	H	A	47	120	144
Vernonia sp.	None clonal	H	P	45	18	.
Justicia ornatopila Ensermu.	None clonal	H	A	41	184	15
Commelina petersii Hassk.	Stoloniferous	F	A	40	161	**1838**
Sida sp.	None clonal	H	P	40	.	.
Cynodon dactylon L.	Stoloniferous	G	P	37	111	11
Eragrostis sp.	None clonal	G	A	36	1	.
Vernonia galamensis L.	None clonal	H	A	33	.	276
Rhynchosia elegans A. Rich.	Clonal	H	P	30	23	163
Cyperus sp.	Clonal	G	A	27	16	25
Commelina sp.	Stoloniferous	F	A	25	11	.
Herb sp.2	n.a.	n.a.	P	25	.	2
Thunbergia alata Sims.	Clonal	H	A	23	69	18

Aristida adscensionis L.	None clonal	G	A	19	186	.
Orthosiphon parvifolius Vatke.	None clonal	H	P	19	72	9
Asparagus aspergillus Jessop.	None clonal	S	A	19	.	.
Tetrapogon tenellus (Roxb.)	None clonal	G	P	19	.	.
Sida ovata Forssk.	None clonal	H	P	17	25	6
Leucas glabrata (Vahl) R. Br.	None clonal	H	A	16	13	30
Aeschynomene indica L.	None clonal	H	A	12	162	18
Crotalaria sp.	None clonal	H	A	12	13	.
Blepharis sp.	None clonal.	H	P	12	3	1
Dactyloctenium aegyptium L.	None clonal.	G	P	10	.	.
Solanum incanum L.	None clonal.	H	P	8	1	.
Shrub sp.1	n.a.	n.a.	P	8	.	22
Euphorbia sp.	n.a.	n.a.	A	6	14	.
Schoenefeldia transiens (Pilger.)	None clonal	G	P	6	.	42
Anthericum sp.	Tuberous	F	P	3	5	23
Hibiscus cannabinus L.	None clonal	H	A	3	.	29
Acacia mellifera (Vahl.)	n.a.	S	P	3	.	.
Brachiaria sp.	n.a.	n.a.	A	3	.	.
Tragia impedita (Prain.)	Clonal	H	P	2	106	186
Acacia drepanolobium Sojostedt	None clonal	S	P	2	2	4
Grewia bicolor Juss.	None clonal	S	P	2	.	3
Commiphora sp.	None clonal	S	P	1	.	.
Themeda triandra Forssk.	BunchG	G	P	.	**1668**	54
Andropogon distachyos L.	Rhizomatous	G	P	.	**1617**	696
Ischaemum afrum (J.F. Gmel.)	Rhizomatous	G	P	.	607	.
Setaria sphacelata (Schumach.)	Rhizomatous	G	P	.	548	727
Heteropogon contortus L.	n.a.	G	P	.	326	.
Eragrostis macilenta (A. Rich.)	None clonal.	G	A	.	78	.
Cassia mimosoides L.	None clonal.	H	A	.	76	24
Dolichos oliveri Schweinf.	Tuberous rootstock	H	P	.	69	71
Pennisetum polystachyon L.	n.a.	G	P	.	44	.
Panicum maximum Jacq.	BunchG	G	P	.	36	14
Aspilia mossambicensis (oliv.)	Clonal	H	P	.	32	60
Sarga purpureo-sericea A**. & S.**	None clonal.	G	A	.	30	96
Indigofera arrecta A. Rich	H	H	P	.	21	50
Tragus berteronianus Schult.	None clonal.	G	P	.	20	39
Tephrosia purpurea L.	Clonal	H	P	.	16	83
Rottboellia exaltata L.f.	None clonal.	G	P	.	15	142
Eragrostis superba Peyr.	None clonal.	G	P	.	15	.
Herb sp.1	n.a.	n.a.	P	.	11	.
Thunbergia gregorii S.Moore.	n.a.	H	A	.	9	.
Abutilon sp.	Non clonal	H	A	.	8	123
Indigofera schimperi Jaub.	None clonal	H	P	.	5	54
Pavonia sp.	None clonal	H	A	.	5	4
Digitaria sp.	n.a.	G	A	.	5	.
Eragrostis chalcantha Trin.	Non clonal	G	A	.	4	.

Striga laterices Vatke.	n.a.	H	A	.	4	.
Anthericum cameronii (Bak.)	Tuberous	F	P	.	3	18
Anthericum cooperi Baker	Tuberous	F	P	.	3	.
Sesbania subalata Gillett.	None clonal.	H	A	.	2	56
Hibiscus sp.	None clonal.	H	A	.	2	.
Solanum sp.	None clonal.	H	P	.	2	.
Sporoborus pyramidalis P. Beauv.	None clonal	G	P	.	2	.
Scilla sp.	n.a.	H.	P	.	1	.
Agrostis sp.	None clonal	G	A	.	.	194
Digitaria gayana (Kunth) Stapf ex A. Chev	None clonal	G	A	.	.	112
Anthericopsis sepalosa (C. B. Clarke.) Engl.	Tuberous	F	P	.	.	27
Lintonia nutans Stapf.	Stoloniferous	G	P	.	.	25
Indigofera volkensii Taub.	None clonal.	H	A	.	.	18
Digitaria velutina (Forsk.)	Stoloniferous	G	A	.	.	13
Dichrostachys cinerea L.	None clonal.	S	P	.	.	5
Kalanchoe sp.	n.a.	n.a.	A	.	.	5
Cyperus esculentus L.	Tuberous	G	A	.	.	4
Chlorophytum macrophyllum (A. Rich.)	Rhizomatous	F	P	.	.	3
Maerua sp.	None clonal.	S	P	.	.	3
Stapelia semota N.E.Br.	n.a.	F	A	.	.	3
Brachiaria eruciformis (Sw.)	Rhizomatous	G	A	.	.	2
Ocimum americanum L.	None clonal.	H	A	.	.	1
Setaria phragmitoides Stapf.	Rhizomatous	G	P	.	.	1
Tephrosia villosa L.	None clonal.	H	A	.	.	1
Cordia ovalis R.Br. ex A.DC.	None clonal.	DS	P	1	.	
Total no. of individuals				8736	9726	7647

Table 2: Dominant (frequency > 70%) and subdominant (frequency > 50%) species in the three study sites. NFNG= no fire-no grazing site; FG=fire grazing site; FNG=fire no grazing site.FG.

Species name	NFNG freq.	FG freq.	FNG freq.
Themeda triandra Forssk.		75	
Pennisetum mezianum Leeke.			76
Setaria sphacelata (Schumach.)			73
Commelina petersii L.			71
Cassia sp.			63
Hermannia uhligii Engl.			58
*Vernonia galamensis*L.			53
Pennisetum ciliare (L.) Link	88		
Plectoranthus sp.	69		
Tephrosia volkensii L.	54		

Table 3 Tukey HSD results comparing the plot means for soil parameters (SE; n = 10) in the three study sites. NFNG= no fire-no grazing site; FG=fire grazing site; FNG=fire no grazing site.FG.

Soil characteristics	FG	FNG	NFNG	Tukey HSD test		
				FG vs FNG	FG vs NFNG	FNG vs NFNG
pH (H_2O)	7.06±0.11	7.17±0.13	8.02±0.21	ns	*	*
Total C%	1.48±0.20	1.41±0.17	2.61±0.75	ns	*	*
Total N	0.09±0.02	0.10±0.14	0.18±0.49	ns	*	*
P (mg/kg)	5.91±1.70	4.93±1.97	3.27±0.25	ns	*	ns
Ca (Cmol/kg)	20.98±7.00	15.64±6.61	32.38±14.44	ns	*	*
K (Cmol/kg)	0.36±0.11	0.55±0.17	1.97±0.56	ns	*	*
Na (Cmol/kg)	0.72±0.14	0.76±0.36	0.45±0.34	ns	ns	ns

*Values are means ±standard deviations; *P < 0·05, ns P > 0·1*

Table 4 The leaf area (LA, mm^2), leaf dry matter content (LDMC, %) and specific leaf area (SLA, mm^2 mg^{-2}) for the most abundant species in the three sites (i.e. Fire grazing-FG, Fire non-grazing- FNG & No fire no grazing-NFNG), each with 4 leaf replicates (total n =1000); significant results from T-tests are in bold.

Species name	NFNG			FNG			FG		
	LA	LDMC	SLA	LA	LDMC	SLA	LA	LDMC	SLA
Eustachys paspaloides	281.0±30.12	17.4±3.34	58.7±16.58	.	.	.	.	.	.
Pennisetum ciliare	413.2±43.47	33.2±1.46	13.5±0.57	.	.	.	.	.	.
Plectoranthus sp.	659.0±45.82	27.4±0.96	9.0±0.50	.	.	.	.	.	.
Pennisetum mezianum	257.1±25.63	16.0±3.17	**68.8±19.52**	285.4±27.62	20.1±1.90	**32.4±41.26**	.	.	.
Boithriochloa insculpta	226.8±15.77	22.8±3.93	**37.3±8.65**	.	.	.	384.76±49.29	31.3±2.28	**33.4±5.80**
Andropogon distachyos	.	.	.	1102.4±95.09	34.3±0.98	**16.2±0.82**	959.2±151.59	37.6±0.72	**12.2±0.39**
Commelina petersii	.	.	.	572.1±76.28	**14.5±3.07***	32.7±4.36	693.9±61.15	**15.8±0.89**	30.2±5.77
Digitaria milanjiana	.	.	.	1359.4±116.57	22.7±0.60	19.8±0.43	1352.7±402.38	22.3±1.82	21.3±1.20
Dolichos oliveri	.	.	.	19774.0±3189.70	28.7±3.80	15.7±1.67	14431.9±3494.92	28.5±3.99	16.2±2.74
Setaria sphacelata	.	.	.	1419.6±76.2	26.2±0.87	**19.4±0.70**	1662.9±146.98	30.5±1.08	**16.3±0.57**
Indigofera arrecta	.	.	.	1395.5±78.28	26.1±0.77	23.7±1.26	.	.	.
Rhynchosia elegans	.	.	.	2368.4±7239.80	21.2±0.69	33.4±1.77	.	.	.
Vernonia galamensis		.	.	1106.3±77.44	13.8±0.52	38.4±1.31	.	.	.
Sarga purpureosericea	.	.	.	1453.3±486.67	0.3±0.04	25.9±2.87	.	.	.
Ischaemum afrum	.	.	.	.	.	.	441.2±74.20	36.1±0.91	11.8±0.33
Commelina benghalensis	.	.	.	.	.	.	816.0±62.65	15.6±0.03	21.0±2.45
Themeda triandra	.	.	.	.	.	.	1374.4±134.50	39.4±0.91	13.9±0.41
Tragia impedita	.	.	.	.	.	.	862.1±60.29	25.3±0.47	20.7±1.20

Table 5 Results of the CSR strategies analysis of the 18 most abundant plant species computed using the CSR classification tool of Pierce *et al.* (2013), which analyzes the trade-off between the traits LA, LDMC and SLA to calculate the relative proportions (%) of C-, S- and R-selection exhibited by individual species in fire grazing (FG), fire non-grazing (FNG) and no fire no grazing (NFNG) sites.

| | The C-S-R proportions (%) | | | | | | | | | Species strategy | | |
| | NFNG | | | FNG | | | FG | | | | | |
Species name	C	S	R	C	S	R	C	S	R	NFNG	FNG	FG
Andropogon distachyos	.	.	.	24	57	19	23	68	9	.	S/CSR	S/CS
Bothriochloa insculpta	10	30	60	.	.	.	11	46	42	R/CSR	.	SR/CSR
Commelina benghalensis	.	.	.	.	.	.	41	0	59	.	.	CR
Commelina petersii	.	.	.	26	0	74	30	0	70	.	R/CR	R/CR
Digitaria milanjiana	.	.	.	35	31	34	34	29	37	.	CSR	CSR
Dolichos oliveri	.	.	.	65	25	10	61	27	12	.	C/CS	C/CSR
Eustachys paspaloides	12	5	83	.	.	.	.	.	.	R	.	.
Indigofera arrecta	.	.	.	28	37	34			.	.	CSR	.
Ischaemum afrum	.	.	.	.	.	.	16	75	9	.	.	S/CS
Pennisetum ciliare	16	68	15	.	.	.	.	.	.	S/CS	.	.
Pennisetum mezianum	12	0	88	14	22	64	.	.	.	R	R/SR	.
Plectoranthus sp.	31	69	0	.	.	.	.	.	.	S/CS	.	.
Rhynchosia elegans	.	.	.	36	19	45	.	.	.	.	CR/CSR	.
Setaria sphacelata	.	.	.	31	40	29	31	49	20	.	S/CS	S/CS
Sarga purpureosericea	.	.	.	32	43	25	.	.	.	.	SC/CSR	.
Themeda triandra	.	.	.	.	.	.	25	63	12	.	.	S/CS
Tragia impedita	.	.	.	.	.	.	25	40	34	.	.	CSR
Vernonia galamensis	.	.	.	35	0	65	.	.	.	.	R/CR	.

Table 6 Relative abundance of the most abundant species used in the determination of the Community Weighted Mean (CMW) for computation of community CSR strategies.

Species names/Site	Total abundance (n)	Relative abundance (%)	Strategy
Fire grazing site			
Andropogon distachyos	1617	22.4	S/CS
Bothriochloa insculpta	533	7.4	SR/CSR
Commelina benghalensis	62	0.9	.
Commelina petersii	161	2.2	.
Digitaria milanjiana	1841	25.5	.
Dolichos oliveri	69	1.0	.
Ischaemum afrum	607	8.4	.
Setaria sphacelata	548	7.6	.
Themeda triandra	1668	23.1	.
Tragia impedita	106	1.5	.
Sum	**7212**	**100**	
Fire no grazing site			
Commelina petersii	1838	33.7	.
Pennisetum mezianum	769	14.1	.
Setaria sphacelata	727	13.3	.
Andropogon distachyos	696	12.8	S/CSR
Digitaria milanjiana	678	12.4	.
Vernonia galamensis	276	5.1	.
Sarga purpureosericea	188	3.4	.
Rhynchosia elegans	163	3.0	.
Indigofera arrecta	50	0.9	.
Dolichos oliveri	71	1.3	.
Sum	**5456**	**100**	
No fire no grazing			
Pennisetum ciliare	2485	50.2	.
Eustachys paspaloides	862	17.4	.
Bothriochloa insculpta	644	13.0	R/CSR
Pennisetum mezianum	542	10.9	.
Plectoranthus sp.	417	8.4	.
Sum	**4950**	**100**	

Estratto per riassunto della tesi di dottorato

Studente: Oliver Castor Nyakunga matricola: 956032

Dottorato: Scienze ambientali

Ciclo: 28°

Titolo della tesi[1] : Fire and grazing effects on herbaceous structure, composition and diversity, and plant functional responses to management regimes in Mkomazi, Tanzania

Abstract: Fire and grazing are the major ecological disturbances shaping species composition and diversity, abiotic factors and productivity in seasonally inundated savanna ecosystems. The study examines the effects of management regimes on plant communities' composition and structure, species richness and functional diversity in Mkomazi National Park (Tanzania). The study confirms the hypothesis that the management regimes have a significant role in influencing seasonally inundated arid vegetation communities and that management regime shifts may alter community abundance, structure, and composition implying functional changes that may lead to alterations in ecosystem functions. Fire and grazing act in combination with biotic and abiotic factors interacting and/or competing in altering savannas. Our results suggest that management plans should be based on an actual knowledge of their effects on the biotic and abiotic components of the ecosystems, and should adopt an adaptive approach.

Abstract: Il fuoco e il pascolo sono tra i maggiori fattori ecologici di disturbo capaci di determinare composizione in specie, diversità, parametri abiotici e produttività degli ecosistemi di savana. Il presente studio è volto ad esaminare gli effetti di diverse pratiche di gestione su composizione, struttura, ricchezza specifica e diversità funzionale delle comunità vegetali di savana del Parco Nazionale di Mkomazi (Tanzania). I risultati ottenuti hanno confermato l'ipotesi secondo cui la gestione ricopre un ruolo significativo nell'influenzare le comunità vegetali, e che differenze nella tipologia di gestione possono portare ad alterazioni diverse nelle comunità e nella funzionalità dell'ecosistema. Il fuoco e il pascolo agiscono in combinazione a fattori biotici ed abiotici nell'alterare le comunità vegetali di savana. I nostri risultati suggeriscono come futuri piani di gestione debbano prendere le mosse da una conoscenza accurata dei loro effetti, adottando un approccio di tipo adattativo.

Firma dello studente

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[1] Il titolo deve essere quello definitivo, uguale a quello che risulta stampato sulla copertina dell'elaborato consegnato.