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Fire and grazers in the West African savanna

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Chapter 1

Introduction

1.1 INTRODUCTION

Recent forest fires in Greece burned around 3000 km² or over 2% of the country (Boschetti *et al.* 2008), killing 84 people and causing immediate damage of over two billion euros. In October 2007, wildfires in California burned around 2000 km², killing nine and leading to the evacuation of half a million people. Notwithstanding the impact of these two events, the area that was burned amounted to not even 0.15% of the global area that is burned every year. Recent studies based on satellite data estimated the global extent of vegetation fires at around 300 to 350 million hectares, with the most extensive burned area located in sub-Saharan Africa (Van der Werf *et al.* 2003, Tansey *et al.* 2004, Giglio *et al.* 2006a, b, FAO 2007) (Fig. 1).

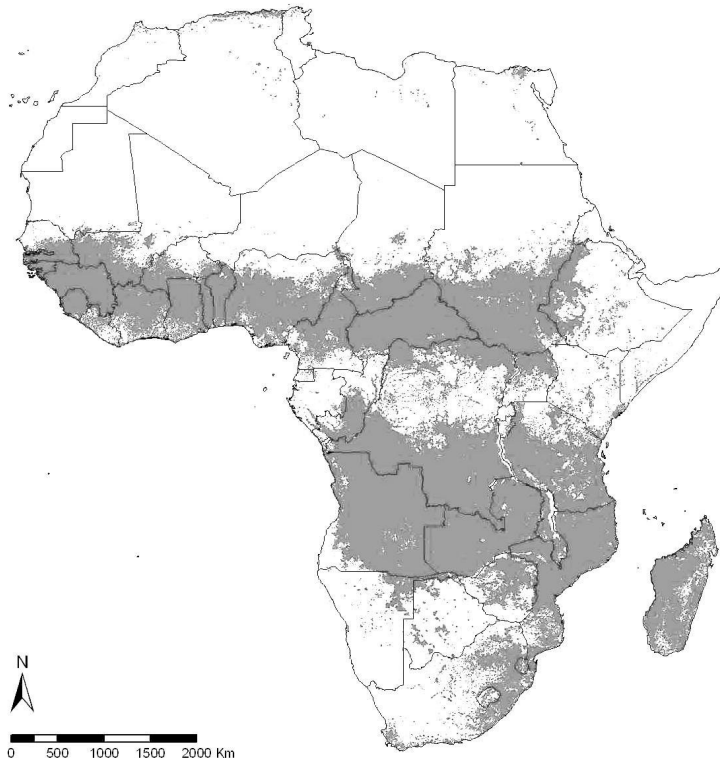


Fig. 1. Fires recorded in Africa in 2007 based on Modis satellite observations (Justice *et al.* 2002).

As can be seen in Fig. 1, the distribution of fire in Africa roughly follows the extent of the savanna biome. Savannas are characterised by the coexistence of trees and grasses, the balance of which is governed by fire, herbivory, moisture and nutrients (Scholes & Archer 1997). The herbaceous layer in tropical savannas is dominated by grasses of the C₄ photosynthetic pathway, which is more efficient than C₃ photosynthesis at low levels of CO₂ and high temperatures (Ehleringer *et al.* 1997, Sage & Kubien 2007). The CO₂ efficiency of C₄ photosynthesis led to the hypothesis that the origin and rapid expansion of the savanna biome in the late Miocene, around six to eight million years ago (Ma), was triggered by low atmospheric CO₂ levels (Cerling *et al.* 1997, Ward 2004, Beerling & Osborne 2006, Osborne 2008). However, recent evidence of CO₂ levels during the Oligocene and Miocene does not support this hypothesis (Pagani *et al.* 1999, 2005) and Keeley & Rundel (2005) argued that the Miocene expansion of C₄ grasslands was driven by an increase in fire activity. Increased seasonality during the Miocene, characterized by high biomass production in the wet season followed by a pronounced dry season, created a highly favourable fire climate, which facilitated the conversion of woodlands into grasslands (Keeley & Rundel 2005). Ecological differences between C₃ and C₄ grasses in relation to fire are also highly relevant for the structure and functioning of contemporary savanna ecosystems. Compared to C₃ grasses, tropical C₄ grasses are characterized by low protein levels and high fibre contents (Caswell *et al.* 1973, Barbehenn *et al.* 2004). Accordingly, decomposition rates are slow and productive C₄ grasslands promote fire by rapidly building up substantial fuel loads (Bond *et al.* 2003a). Indeed, hundreds of millions of hectares of savanna areas are burned annually (Hao *et al.* 1990), making tropical C₄ grasslands the most frequently and extensively burned biome in the world (Hao & Liu 1994, Barbosa *et al.* 1999, Bond *et al.* 2005).

Since fire requires oxygen and fuel, the history of vegetation fires starts in the late Silurian period (around 420 Ma) after the earliest vascular land plants had originated and O₂ levels were sufficiently high (Glasspool *et al.* 2004, Scott & Glasspool 2006). Vegetation biomass increased and became less moisture-dependent in the Devonian, leading to the first widespread forest fires in the early Carboniferous (Mississippian) around 360 Ma when woody vegetation had spread over the land and O₂ levels had risen sharply (Scott & Glasspool 2006). Throughout the geologic time scale, fire activity varied with fluctuating O₂ levels in the atmosphere (Scott 2000). Fire ignition was mainly by lightning strikes (Scott 2000) until the domestication of fire by man in the Pleistocene. The first use of fire by hominids is subject to debate, however (James 1989). Conservative estimates point at the late Middle Pleistocene, about 0.3–0.5 Ma (James

1989), although indirect evidence from South Africa (Brain & Sillen 1988) and China (Weiner *et al.* 1998; but see Wu 1999, Lopez-Gonzalez *et al.* 2006) suggests that the use of fire goes back over 1 million years. Fire activity increased considerably in the middle and late Holocene, mainly as a result of slash-and-burn agriculture and charcoal production (Carcaillet *et al.* 2002).

At present, vegetation fires are common in many temperate, tropical and boreal ecosystems (Bond & Keeley 2005). In Africa alone, an estimated 2.3 million km² or 7.7% of the land area was burned in the year 2000, equalling 64% of the global burned area (FAO 2007). Most vegetation fires occur in savannas and grasslands, Mediterranean shrublands (e.g., fynbos) and boreal forests (Bond *et al.* 2005). The far majority of present-day wildfires are of anthropogenic origin, with lightning contributing no more than 10% of global biomass burning (Crutzen & Andreae 1990). Areas are burned for numerous reasons. Throughout the tropics, fire is widely used as a land management tool and reasons for burning include the preparation of agricultural fields, stimulating off-season regrowth for cattle or wild herbivores and providing firebreaks around houses or villages (Laris 2002). Lewis (2002) argued that these reasons represent the vestiges of a European pastoralists' burning regime, and that traditional burning practice can be based on very different reasons such as hunting, ceremonial purposes or to drive away dangerous supernatural beings. Regardless of the background, widespread vegetation fires have shaped the distribution of the biomes of the world (Bond & Keeley 2005). The existence of mesic savannas (>650 mm rainfall) critically depends on fire and herbivory (Bond *et al.* 2003a, Sankaran *et al.* 2008) and it has been estimated that without fire the global extent of closed forests would double in area (Bond *et al.* 2005).

1.2 EFFECTS OF FIRES ON THE ENVIRONMENT

Vegetation fires can have significant ecological and environmental impacts (Gonzalez-Perez *et al.* 2004), including changes in soil characteristics (e.g., organic matter content, soil microbial populations, susceptibility to erosion), vegetation quality and structure (e.g., leaf tissue nutrient levels, sward structure, tree–grass balance) and atmospheric impact due to burning emissions.

Soil nutrient levels and organic matter content can be substantially altered by wildfires. Shortly after a fire, the availability of soil nutrients can be increased because of ash deposition, leading to an increase in soil pH and a corresponding increase in cation

exchange capacity (González-Pérez *et al.* 2004). For example, in acid soils phosphorus availability is enhanced by an increase in soil pH due to ashes (Certini 2005). However, increased nutrient availability is often temporary and the long-term effects of fire on savanna nutrient budgets are more complicated. Fire-induced changes in soil organic matter content are highly variable and depend on the fire regime, soil type and moisture content, and the vegetation that is burned (González-Pérez *et al.* 2004). Various studies have shown that grassland fires can lead to decreased nitrogen availability and mineralization rates (e.g., Ojima *et al.* 1994, Blair 1997, Turner *et al.* 1997, Fynn *et al.* 2003; but see Coetsee *et al.* 2008) and substantial decreases in the soil carbon pool (Bird *et al.* 2000, Mills & Fey 2004), leading to the widespread concern that repeated burning results in a net loss of nitrogen and carbon from the system. Reductions in the soil carbon pool seem to be less affected by the frequency of burning than whether or not an area is burned at all, probably because of the feedback between fire frequency and fuel load (Bird *et al.* 2000). Reported decreases of nitrogen are usually greater than the loss of carbon, resulting in widened C:N ratios and a vegetation that is tolerant of low nitrogen levels (Tilman & Wedin 1991, Ojima *et al.* 1994, Fynn *et al.* 2003). In contrast to abovementioned studies, fires have also been reported to increase soil organic matter content in forest and savannas (Johnson & Curtis 2001, Brye 2006) as a result of the accumulation of charcoal, the deposition of charred plant material and the encroachment of nitrogen-fixing vegetation (Johnson & Curtis 2001, Johnson *et al.* 2004, González-Pérez *et al.* 2004). In addition, heavy grazing by herbivores can reduce nitrogen losses by fire due to decreased fuel loads or even shift the balance towards a net nitrogen gain (Hobbs *et al.* 1991).

In addition to any fire-induced changes to the abiotic environment, fires can also result in reduced soil microbial biomass because of heating of the topsoil (Andersson *et al.* 2004, Certini 2005). However, these effects depend strongly on soil moisture content (Certini 2005) and the impact of fire on soil microbial biomass is generally small compared to the substantial seasonal variation (Andersson *et al.* 2004).

Burning of savanna grasslands has important consequences for the quality and structure of the grass sward. Concentrations of some macronutrients such as nitrogen, phosphorus and potassium in post-fire regrowth are generally higher than in unburned vegetation (Christensen 1977, Boerner 1982, Singh 1993, Van de Vijver *et al.* 1999, Laclau *et al.* 2002), although in East Africa nutrient levels have been shown to decline within three months to the levels of unburned vegetation (Van de Vijver *et al.* 1999). In addition,

fires increase digestibility and alter the structure of the grass sward by increasing leaf:stem ratios and live:dead proportions (Van de Vijver *et al.* 1999). Raised nutrient levels in post-fire regrowth have been attributed to a variety of causes, such as the effect of nutrient supply through ash deposition, relocation of nutrients from roots to shoots and the distribution of nutrients over less biomass (see Van de Vijver *et al.* 1999 and references therein). Van de Vijver *et al.* (1999) concluded that in a nutrient-rich savanna in East Africa increased nutrient levels were the effect of increased leaf:stem ratios and rejuvenatory processes. The exact effects of fire on the grass sward, however, may depend on a variety of factors including fire intensity, local soil conditions, and precipitation patterns.

Fire is among the principal factors governing the tree–grass balance in savannas, together with moisture, nutrients and herbivory (Scholes & Archer 1997). In arid and semi-arid savannas (200–700 mm rainfall), maximum woody cover increases linearly with rainfall and is relatively independent of fire (Sankaran *et al.* 2005, 2008). In contrast, in mesic savannas (>650 mm) moisture availability is sufficient to support a closed woody canopy and the coexistence of trees and grass depends principally on fire and herbivory (Bond *et al.* 2003a, Sankaran *et al.* 2005, 2008). Surface fires in savannas usually do not kill adult trees but constrain the establishment of saplings (Higgins *et al.* 2000, Bond *et al.* 2003b). However, woody saplings can escape the ‘fire trap’ when fire frequencies are low, and woody cover becomes independent of burning at fire return intervals greater than 12–15 years (Sankaran *et al.* 2008). The tree–grass balance is also directly affected by the interactive effects between fire and herbivory, as for example grazing decreases fuel loads and therefore promotes tree establishment (Van Langevelde *et al.* 2003).

Global climate change has led to an increased interest in the atmospheric impact of biomass burning. Savanna fires are the largest source of biomass burning emissions worldwide (Hobbs *et al.* 2003), and the African savannas contribute a major part of the global amount of carbon emission from burning (Van der Werf *et al.* 2003). However, the net emission of carbon dioxide (CO₂) from savanna fires is nil since the emission from burning is balanced by the CO₂ uptake by grass regrowth during the wet season. Savanna fires are a net source of several trace gases and particles that are not reassimilated during regrowth (Bird *et al.* 2000, Scholes 1995). Although emission estimates in the literature vary widely (Van der Werf *et al.* 2003), the most important emissions by savanna fires apart from CO₂ are carbon monoxide (CO), methane (CH₄),

non-methane hydrocarbons, ozone (O₃), nitrogen oxides (NO_x), carbonaceous aerosols and particles (Bird *et al.* 2000, Sinha *et al.* 2003, Korontzi *et al.* 2004). Dry savanna fires are typically efficient fires that have high emission proportions of fully oxidized products such as CO₂ and NO_x (Korontzi *et al.* 2004). However, the combustion completeness depends on the moisture content of the grass sward and therefore varies with season and fire intensity (Korontzi *et al.* 2003). Moist swards early in the dry season can result in low intensity fires which are likely to produce high proportions of products of incomplete combustion such as CO and CH₄ (Hoffa *et al.* 1999). Some trace gases such as CO₂, CH₄ and N₂O are important greenhouse gases, and organic compounds and CO from African savanna fires have been shown to lead to widespread increases in the concentration of ozone (O₃) over the South Atlantic region (Sinha *et al.* 2003).

1.3 FIRE AND HERBIVORY

African savannas are well-known for their high species richness of ungulates. Nearly a hundred species of ungulates occur in Africa (Kingdon 1997), and in some areas such as the Serengeti–Mara ecosystem more than 30 of these species coexist (Sinclair & Arcese 1995, Sinclair & Norton-Griffiths 1979). Regular burning is likely to have significant ecological effects on the herbivores living in savanna ecosystems. As described above, fires affect the nutritional quality and structure of the grass sward and the structure of the habitat, both of which can affect resource selection patterns, the partitioning of resources among potential competitors, and species diversity patterns or assemblage structure of savanna ungulates. In addition, by changing the vegetation structure fires can lead to changes in the availability of shelter or predation risk.

Probably the most important effect of fire to herbivores is a change in food availability. Wet season rainfall leads to a high biomass grass sward of inferior nutritional quality because of high fibre contents and low digestibility (Bremner & De Wit 1983). During the growing season grazing herbivores therefore prefer foraging on grazing lawns, since heavily grazed grass swards of low height and biomass have been shown to be nutritionally superior to ungrazed swards (Verweij *et al.* 2006). In the dry season, fires can replace the entire moribund grass sward by nutritious regrowth that contains higher nutrient levels, higher leaf:stem ratios and higher digestibility than unburned vegetation (Van de Vijver *et al.* 1999). Because of the improved structure and quality of burned grass swards, grazing herbivores are able to reach higher forage intake rates on post-fire regrowth compared to unburned areas due to increased foraging efficiency (Hobbs *et al.*

1991, Moe & Wegge 1997). As a result, grazers tend to feed on grass regrowth following savanna fires rather than on unburned grass swards (e.g., Moe *et al.* 1990, Wilsey 1996, Moe & Wegge 1997, Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002, Archibald & Bond 2004). Although the preference of grazing herbivores for post-fire regrowth is widely acknowledged, resource selection patterns by herbivores on burned areas may not be uniformly distributed over time and space. Levels of nitrogen and other macronutrients in post-fire regrowth have been shown to decline rapidly and can reach sub-maintenance levels of ruminants in weeks or months after burning (Van de Vijver *et al.* 1999). In addition, variation in the terrain or the temperature and humidity during burning can lead to variation in fire intensity, thereby affecting regrowth structure such as the amount of dead stems in the sward that reduce the foraging efficiency of grazing herbivores.

Besides characteristics of the grass sward itself, utilization of post-fire regrowth may also be affected by species-specific parameters such as water dependency or body mass. Body mass is considered to be a main determinant of resource partitioning among ungulates (Jarman 1974, Prins & Olf 1998), since large species are able to digest lower quality food than small species because of longer gut retention times and lower metabolic rate per unit body mass (Van Soest 1982, Demment & Van Soest 1985; but see Pérez-Barberia *et al.* 2004, Clauss *et al.* 2007). Based on this, Wilsey (1996) suggested that the selection of post-fire regrowth by herbivores is governed by body weight whereby preference for burned grassland decreases with increasing size. However, Tomor & Owen-Smith (2002) did not support this conclusion and emphasized instead the importance of biotic interactions and resource partitioning in the differential use of post-fire regrowth.

Since fires affect tree:grass ratios in moist savanna ecosystems, long-term burning is likely to affect the balance of grazers and browsers (De Bie 1991). In the absence of fires, mesic savannas would transform into dense woodland or forest thickets (Swaine *et al.* 1992, Bond & Keeley 2005), which are habitats favoured mostly by browsers. In contrast, burning can favour grazers by keeping the savanna open. Because of the feedback between fuel load and fire intensity, interactive effects between herbivory and fire can affect habitat suitability for both grazers and browsers (Van Langevelde *et al.* 2003). Patches of heavy grazing such as on grazing lawns usually have very low grass biomass which reduces fire intensity or even prevents the spread of fire (Hobbs *et al.* 1991). Consequently, grazing can favour bush encroachment to the

advantage of browsers (D'Odorico *et al.* 2006, Kraaij & Ward 2006). Similarly, browsers can reduce woody biomass and accordingly promote grass growth, leading to increased fire intensities to the advantage of grazers (Van Langevelde *et al.* 2003).

1.4 RESEARCH GOALS

As described in the previous sections, savanna fires can have substantial effects on both the abiotic and biotic components of the environment. The interactions between fire and herbivory play a paramount role in savanna dynamics (Frost & Roberston 1987) as is shown by e.g., the interactive effects of fire and grazing on the tree–grass balance. However, many aspects of the effects of fire on herbivores in the African savannas are unclear. Although it is well-known that grazing herbivores prefer post-fire regrowth compared to unburned vegetation, there is little information on many effects of fire on African herbivores such as fire-induced changes in forage quality, resource selection and partitioning, assemblage structure and broad-scale diversity patterns. In addition, it is unclear how species-specific ecological parameters such as herbivore body mass or feeding guild affect these relationships. The goal of this thesis is therefore to describe and quantify the effects of savanna fires on various aspects of the ecology of West African savanna herbivores, thereby explicitly taking into account the effects of body mass and guild membership. Based on this research goal, this thesis attempts to answer the following research questions:

1. What are the effects of fire seasonality on the quality and structure of post-fire regrowth, and how do these effects relate to the food requirements of grazing herbivores?
2. Which factors govern resource selection patterns by ungulates on post-fire regrowth, and what is the influence of body mass on these selection patterns?
3. What is the importance of herbivore body mass, diet composition and diet quality on resource partitioning between savanna herbivores?
4. Do savanna fires govern the structure of ungulate assemblages at the local scale, such as co-occurrence patterns and guild dominance?
5. To what extent are broad-scale patterns in species richness and assemblage composition of ungulates related to patterns in fire occurrence, climate, and soil fertility?

1.5 THESIS OUTLINE

As described in the previous sections, this thesis attempts to describe and quantify the effects of savanna fires on the ecology of West African herbivores. The outline of this thesis is given in Fig. 2. Starting with examining the effects of fire on the grass sward, this thesis then moves on to assess patterns of herbivore foraging such as the selection and partitioning of resources on burned grass swards. It is then investigated whether and how savanna fires govern local community structure, for example by affecting competitive interactions. Finally, the importance of fire on regional diversity patterns of herbivores is described. Note that Fig. 2 is simplified in the sense that feedback mechanisms such as the effects of grazing on the grass sward and hence, fuel loads and fire activity, are not shown.

This thesis starts with this Introduction, after which in Chapter 2 the study area is

described. In Chapter 3 the effects of the fire regime on the quality of post-fire regrowth as a food source for grazing herbivores are assessed. This is done by means of a burning experiment where the experimental plots are burned either early, middle or late in the dry season, with the control plots left unburned. The quality of the post-fire regrowth is measured by concentrations of macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium), digestibility, and parameters of sward structure such as green leaf biomass. The quality and sward structure of the experimental grass swards are then compared to the nutrient requirements of herbivores.

Chapter 4 attempts to disentangle the effects of different habitat and grass sward characteristics on the utilization of post-fire regrowth, using resource selection functions based on logistic regression. This is done for nine species of ungulates

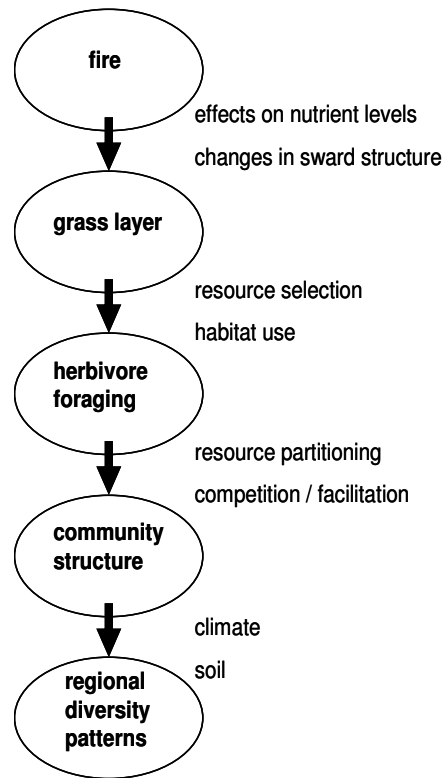


Fig. 2. Conceptual outline of this thesis.

throughout the dry season. Besides taking into account several habitat characteristics such as vegetation cover and distance to the river, and grass sward parameters such as regrowth age and the amount of dead stem material, the importance of herbivore body mass on resource selection patterns is explicitly assessed.

In Chapter 5 the importance of diet composition, diet quality and herbivore body mass on the partitioning of resources by eight species of savanna herbivores is investigated. Resource overlap among herbivore species is quantified by means of the composition (i.e., the range of food plants consumed) and quality of the diet (expressed as fibre contents and the concentrations of nitrogen and phosphorus). Both the composition and the quality of the diet are based on faecal samples. The relationship between body mass and diet composition and quality is assessed to test the hypothesis that smaller herbivores select on higher quality forage compared to larger herbivores.

In Chapter 6 the effects of savanna fires on the structure of local ungulate assemblages are investigated by testing the hypothesis that species are randomly distributed over burned and unburned areas. Using data on the distribution of 11 herbivore species over burned and unburned sites, fire-induced changes in body mass distribution, co-occurrence patterns, species richness, species density and guild dominance of herbivore assemblages are examined. Patterns of community structure are also related to biotic interactions such competition and facilitation.

Chapter 7 attempts to relate broad-scale diversity patterns of ungulates to fire occurrence, moisture availability and soil fertility. Based on satellite images and digital maps of several environmental variables, patterns in species richness (alpha diversity) and differences in species composition between ungulate assemblages (beta diversity) are related to gradients in fire occurrence, actual evapotranspiration and soil fertility throughout western Africa. This is done for both the entire species set of West African ungulates as well as the two main guilds, i.e., grazers versus browsers/frugivores.

Chapter 8 provides a broad discussion of the results of this research. Here, the results are integrated and placed in a broader context. In addition, any implications of this research for the management of fire and wildlife are discussed. This thesis concludes with English and Dutch summaries of this research.

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