Fire, Plant-derived Smoke and Grazing Effects on Regeneration, Productivity and Diversity of the Sudanian Savanna-woodland Ecosystem

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Cover: Mid-season fire (top left), smoke produced during early burning (top right), grazing (bottom left), seeds of *Borreria radiata* DC. (bottom right)
(Photo: S. D. Dayamba)

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Abstract

The establishment and subsequent dynamics and productivity of many plants is affected by diverse environmental factors, some of the most important in savanna ecosystems being herbivory, fire and its related cues. This thesis assessed the effects of these factors on the woody and herbaceous regeneration, productivity and diversity of Sudanian savanna-woodlands.

The time (season) of fires and soil depth were found to affect both fire temperature and temperature residence time, which in turn affected the germination of seeds buried in the soil. Fairly good germination of unburied or superficially buried seeds could be obtained after early burning which is not the case of mid-season and late-season fires. Analysis of seeds' germination responses to smoke generated by burning revealed that smoke responsiveness is a species-specific attribute that transcends plant species' ecological characteristics, notably their fire response categories. In addition, the type and dose of smoke strongly affect germination parameters of responsive species, and for some species an appropriate combination of smoke and heat is required for maximal germination responses. Further, certain levels of heat induce temporary physiological dormancy in some species, which, in field conditions, might be beneficial in synchronizing the start of germination with the onset of rainy season. The effects of grazing and fire on the biomass dynamics of resprouts from cut stumps of selected tree species were also examined. The responses to the treatments were found to be species-specific, fire being deleterious in some cases and grazing generally having no significant effect. Finally, the time (season) of fires was found to have no significant effects on the richness, diversity, biomass or abundance of the herbaceous layer.

In conclusion, grazing could be integrated in management prescriptions to promote multi-purpose uses of the forests. In addition, more attention should be paid to burning conditions to reduce fire severity as complete fire exclusion is utopian in this savanna ecosystem. Further, assuming optimal dosage levels are identified, fire-related cues (smoke and heat) could have potential uses in reforestation with native species.

Keywords: Fire, smoke, heat, herbivory, germination, resprouts, biomass, diversity, Burkina Faso, West Africa.

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Contents

List of Publications

This thesis is based on the work described in the following papers, which are referred to by the corresponding Roman numerals in the text:

I. Sidzabda Djibril Dayamba, Patrice Savadogo, Didier Zida, Louis Sawadogo, Daniel Tiveau, Per Christer Oden (2010). Fire temperature and residence time during dry season burning in a Sudanian savanna-woodland of West Africa with implication for seed germination. *Journal of Forestry Research (in Press).*

II. Sidzabda Djibril Dayamba, Mulualem Tigabu, Louis Sawadogo, Per Christer Oden (2008). Seed germination of herbaceous and woody species of the Sudanian savanna-woodland in response to heat shock and smoke. *Forest Ecology and Management* 256, 462–470

III. Sidzabda Djibril Dayamba, Louis Sawadogo, Mulualem Tigabu, Patrice Savadogo, Didier Zida, Daniel Tiveau, Per Christer Oden (2010). Effects of aqueous smoke solutions and heat on seed germination of herbaceous species of the Sudanian savanna-woodland in Burkina Faso. *Flora* 205, 319‐ 325.

IV. Sidzabda Djibril Dayamba, Patrice Savadogo, Louis Sawadogo, Didier Zida, Daniel Tiveau, Per Christer Oden (2010). Dominant species' resprout biomass dynamics after cutting in the Sudanian savanna-woodlands of West Africa: long-term effects of annual early fire and grazing. (Submitted manuscript).

V. Sidzabda Djibril Dayamba, Patrice Savadogo, Louis Sawadogo, Didier Zida, Mulualem Tigabu, Daniel Tiveau, Per Christer Oden (2010).

Community dynamics and productivity of herbaceous species in the Sudanian savanna-woodlands of Burkina Faso: short term impact of burning season. *African Journal of Range and Forage Science (in Press).*

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The contribution of Sidzabda Djibril Dayamba to the papers included in this thesis amounted to ca. 80% of the total work load.

1 Introduction

1.1 Savanna

The term savanna has been widely used and variously defined. The prevailing ecological usage denotes tropical or near-tropical seasonal ecosystems with a continuous herbaceous layer, usually dominated by grasses or sedges, and a discontinuous layer of trees and/or shrubs (Frost et al., 1986; Skarpe, 1992; Scholes and Archer, 1997; Andersen et al., 1998). The savannas of the world all occur in hot regions with a highly seasonal rainfall distribution. This results in a warm dry season that lasts three to eight months, and a hot, wet season for the remainder of the year. The mixture of contrasting life-forms, coupled with strong alternation of wet and dry seasons in tropical and subtropical regions, distinguishes savanna structurally and functionally from forest, grassland and desert biomes (Scholes and Archer, 1997).

Savannas cover approximately half of the African land surface and a fifth of the land surface of the world (Scholes and Walker, 1993). They are one of the most important, but least understood, terrestrial ecosystems. In Africa, savanna areas are divided into two distinct regions: the northern hemisphere (also known as the Sudanian region) with humid and arid woodlands and the southern hemisphere (also known as the Zambezian region) mainly occupied by the miombo woodlands (Menaut *et al.*, 1995). The Sudanian region lies between 6° and 13° N and covers an area of 5.25 million km^2 (Menaut *et al.*, 1995). The Sudanian savanna stretches across the African continent from Senegal in the west to the Ethiopian highlands in the east, and is characterized by a dry season lasting 6-7 months and a mean annual rainfall between 700 and 1200 mm (Menaut *et al.*, 1995).

Diverse environmental and biotic factors (including geomorphology, climate, soils, vegetation, fauna, and fire) correlate with the distribution of savannas (Cole, 1986; Scholes and Walker, 1993). In addition, the structure and function of savanna are strongly influenced by factors such as water and nutrient availability, fire and herbivory (Scholes and Archer, 1997). Water availability controls the duration of the period in which processes such as primary production and nutrient mineralization occur, thus influencing height and density of trees and the relative proportion of trees and grasses (Scholes and Walker, 1993). These, in turn, influence the type and extent of herbivory and associated animal effects, as well as the frequency and intensity of fire (Savadogo, 2007). Fire influences the density, height, canopy volume and biomass of woody plants, and the composition and biomass of the herbaceous layer. Both woody and herbaceous components of savanna woodland in West Africa have wide ecological importance and are harvested to meet socio-economic needs of local people (Sawadogo *et al.*, 2005; Zida, 2007; Savadogo *et al.*, 2008). The challenge is thus to find optimal management strategies that ensure the sustainability of the ecosystem, while continuing to meet the needs of the local people.

1.2 Natural regeneration in savanna

Tropical dry forests including savannas are the most threatened tropical terrestrial ecosystems. However, their restoration through natural regeneration (the natural process whereby plants replace or reestablish themselves) needs continued investigations (Vieira and Scariot, 2006). Most savanna species regenerate both sexually and asexually, especially following disturbances, such as fire and selective cutting (Bellefontaine *et al.*, 2000; Bationo *et al.*, 2001a; Luoga *et al.*, 2004; Zida *et al.*, 2007).

1.2.1 Vegetative (asexual) regeneration

Vegetative regeneration from dormant or newly formed buds on parent stumps, roots or other organs is prevalent in many savanna species, especially following disturbance (Bellefontaine, 1997; Gignoux *et al.*, 1997; Hoffmann, 1998; Sawadogo *et al.*, 2002; Ky-Dembele *et al.*, 2007; Bognounou *et al.*, 2010). Several vegetative regeneration mechanisms have been identified among savanna species, including seedling sprouting, epicormic sprouting or water sprouting, coppicing or stump sprouting, root suckering, and layering. The relative importance of these mechanisms varies among species (Bellefontaine, 1997; Ky-Dembele *et al.*, 2007; Zida, 2007). Coppicing, the emergence of shoots from the base of stumps (cut stems) or from the stumps themselves, is an important species-specific trait that strongly influences fuelwood production and regeneration (Kaschula *et al.*, 2005). Coppice management for fuelwood and charcoal is ideally suited for semi-arid tropical savanna environments due to the natural ability of many indigenous species to regenerate vegetatively and the tolerance of the resultant coppice regrowth to anthropogenic disturbance, drought, nutrient-poor soils, pests and disease (Kennedy, 1998). This form of post-harvest regeneration is also far more rapid than seedling regeneration owing to the swift development of leaves and associated increases in interception of solar radiation (Harrington and Fownes, 1995). Frequent disturbances such as fires may influence the relative abundance of species that are able to reproduce vegetatively, causing a shift in species composition, favoring species capable of vegetative reproduction (Hoffmann, 1998; Setterfield, 2002). However, vegetative regeneration has the drawback of reducing genetic variability which may, in the long term, render plants unable to adapt to changes in selective pressures (Fenner and Thompson, 2005). Thus, in conservation efforts it is also important to promote concomitant regeneration from seeds.

1.2.2 Sexual regeneration (germination)

Sexual regeneration plays a major role in the maintenance of plant populations. In a disturbed savanna-woodland in Burkina Faso, Ky-Dembele *et al.* (2007) found that sexual reproduction was the dominant mechanism of woody seedling recruitment. This finding is consistent with studies of tropical dry forests in Ghana, and the Sahel and Sudanian zones in West Africa (Lieberman and Li, 1992; Bellefontaine, 1997). In field conditions, one of the crucial stages of sexual regeneration is seed germination, the definition of which differs in agronomy and seed science. In agronomic terms, germination is marked by the emergence of a young seedling with cotyledons. However, in seed science, germination, *sensu stricto*, is the process that starts with the uptake of water by the dry seed and ends with the protrusion of an embryo root (the radicle) through the surrounding tissues; e.g. endosperm and testa (Spoelstra, 2002; Fenner and Thompson, 2005). For a seed to germinate and the time at which it does so depends on a number of factors including those present in the seed's environment. The chemical environment must be appropriate; water must be available, oxygen must be present because the seed must respire, and noxious or inhibitory chemicals should be absent. The physical environment, too, must be favorable; the temperature and, in many cases, the quality and quantity of light, must be suitable. However, in many cases, a seed may fail to germinate even if all of these conditions are satisfied (Bewley and Black, 1994). This brings about the notion of dormancy which can be defined as the inability of a viable seed to germinate under conditions that are favorable for germination (Baskin and Baskin, 1998; Spoelstra, 2002). Dormancy may be imposed by the seed's surrounding tissues (coat-imposed dormancy) or an inherent feature of the embryo itself (embryo dormancy). Seeds of the majority of savanna trees are dormant; physical dormancy is the most common type (Baskin and Baskin, 1998). Dormancy needs to be broken before the seed can give rise to a new plant.

In general, although the endosperm thickness varies among species, the occurrence of radicle protrusion in endospermic seeds is determined by a balance between the growth potential of the embryo and the mechanical resistance of the endosperm. For the radicle to protrude, the growth potential of the embryo must exceed the mechanical resistance of the endosperm (Müller *et al.*, 2006). Either an increase in the embryo growth potential, a decrease in the mechanical resistance of the endosperm, or both have to occur to change the balance (Nonogaki, 2006). Biological processes influence both the embryo growth potential and the mechanical resistance of the endosperm to regulate the dormancy and dormancy release. From biological point of view, there is a hormonal theory governing germination and dormancy; the transition of a seed from dormancy to germination is controlled aside from external environmental cues, by the internal growth regulators (hormones), mainly gibberellin acid (GA) and abscisic acid (ABA) (Peng and Harberd, 2002). The hormonal theory states that dormancy is maintained by inhibitors such as ABA, and it can be terminated only when the inhibitor is removed or when promoters (e.g. gibberellins) overcome it (Bewley and Black, 1994). These hormones affect either the growth potential of the embryo or the mechanical resistance of the embryo surrounding structures to maintain (ABA) or release (GA) dormancy.

From an ecological perspective, plant establishment in field conditions is affected by diverse environmental factors, and the most important in savanna being herbivory, fire and fire-related cues.

1.3 Factors influencing regeneration in savanna ecosystem

1.3.1 Herbivory

African savannas are famous for the diversity and abundance of large mammalian herbivores that they support. Nowadays, over large parts of Africa the wild herbivores have been replaced by cattle, sheep and goats.

Livestock and wildlife form the basis of the present-day economic use of savannas (Scholes and Walker, 1993). Herbivores exert diverse effects on ecosystem and particularly on vegetation succession. The effects of livestock grazing arise from three processes: plant defoliation due to animal foraging, dunging (deposition of faeces and urine), soil and litter trampling and compaction (Hiernaux *et al.*, 1999). Dunging constitutes a potential source of soil nutrients and improves the physical and chemical properties of soil (Harris, 2002; Cumming and Cumming, 2003; Rufino *et al.*, 2006; Savadogo, 2007). By selective biomass removal, grazing and browsing regulate the interaction and competition between plants; by reducing herbaceous biomass, grazing can reduce competition from the herbaceous layer, thereby increasing tree production (Peltier and Eyog-Matig, 1989) and regeneration (Sawadogo *et al.*, 2002). Herbivores may specially be important for regeneration through enhancing both colonization process by long-distance dispersal of seeds (Miller, 1995; Stiles, 2000) and seed germination through gut action (Traveset, 1998; Razanamandranto *et al.*, 2004). On the other hand, soil and litter trampling and compaction may reduce soil water infiltration rates in savanna-woodlands, depending on the stocking rate (Savadogo *et al.*, 2007a). In addition, gaps created by trampling lead to unfavorable thermal conditions, thus increasing soil evaporation and plant transpiration (Savadogo *et al.*, 2007a). High level of herbivory can, thus, degrade soil and vegetation (Warren *et al.*, 2001) and limit seedling recruitment by exacerbating drought (Gignoux *et al.*, 1997; Kozlowski, 1999) or through seed and seedling consumption (Bationo *et al.*, 2000; Drexhage and Colin, 2003; Fenner and Thompson, 2005).

1.3.2 Fire

Grass fires are an inevitable consequence of the annual cycle of profuse herbaceous production (in the wet season) followed by seasonal drought (in the dry season), and savannas have experienced frequent fires throughout their evolutionary history (Scholes and Archer, 1997; Andersen *et al.*, 1998). Most savannas, particularly African savannas, are believed to owe their existence more to the impact of fire and large herbivores than to climate, and these factors seem largely to determine the boundary between savanna and forest (Skarpe, 1992). Fire is thought to be important for the maintenance and conservation of African savanna ecosystems (Govender *et al.*, 2006). Without fire, considerable areas of African savannas could potentially develop into closed woodlands under the current climate, and the occurrence of fires over the past *c.* 8 million years has also seen the evolution of a fire-tolerant and fire-dependent flora (Bond *et al.*, 2005). Fire provides a unique opportunity for habitat management at the landscape scale (Andersen *et al.*, 1998). This has led to widespread use of fire for savanna management, and in most protected Sudanian savanna-woodlands, prescribed early fire has been adopted as an ecosystem management tool (Bellefontaine *et al.*, 2000; Sawadogo *et al.*, 2005).

Fire contributes strongly to changes in the composition of vegetation communities (Danthu *et al.*, 2003) and affects various aspects of plant growth and development, such as flowering, seed dispersal, germination, seedling establishment, plant mortality and biomass production (Walters *et al.*, 2004; De Luis *et al.*, 2005). It is recognized that fire plays an important role in savanna ecology, although this role appears unclear due to several conflicting studies that exist on the effects of fire on savanna vegetation (Higgins *et al.*, 2000; Russell-Smith *et al.*, 2003). The effects of fire on savanna ecosystems, especially their plant components is heavily dependent on the nature of the fire regime (Bond and Van Wilgen, 1996). It has been suggested that if human disturbances, such as fire, mimic the patterns and processes of natural disturbances, they might enhance biological diversity (Mitchell *et al.*, 2002). However, biological resilience varies both across and within landscapes, and between different plant groups, so the application of fire will always remain a key management challenge because no single fire regime can optimize all biodiversity outcomes; different elements are differentially sensitive to different components of fire regimes, different taxa require different fire regimes, and indeed the same species may require a mix of fire regimes (Williams *et al.*, 2003).

Fire affects the establishment of plant species through both direct and indirect effects. Post-fire conditions have many advantages for regeneration (seeds and seedlings); the post-fire environment is characterized by high light, temperature and water availability (as a result of reduction in transpiring leaf surface area) and high levels of nutrients (DeBano *et al.*, 1998). The post-fire decline in granivorous rodents and ants is of special significance for plant species that recruit by seed after fire. Some species have an obligate dependence on fire for reproduction and can be driven to extinction if fires are suppressed (Bond and Van Wilgen, 1996). Frequent burning, however, can be a major constraint for reproduction, especially sexual reproduction (Hoffmann, 1998). The abundance of seedlings establishing after fire will be controlled by the degree of soil heating during the passage of the fire, the distribution of seeds in the soil profile, and soil moisture availability in the post-fire environment (Auld and O'Connell, 1991). Since fire characteristics vary with seasons of occurrence (Gillon, 1983), the effects of fire on plant reproduction will also vary with the time of the year at which fire occurs. Moreover, the fire season in savanna is a key determinant of grass/tree balance; repeated annual late dry season burning may convert woodland to near-grassland, while early dry season burning may lead to denser woodland due to extensive tree recruitment (Bond and Van Wilgen, 1996). Thus, plant demographic studies which ignore fire season effects could fail to predict major shifts in community composition. The effects of fire on vegetation are often due to the independent or combined effects of fire-related cues, the immediate and obvious cues being heat and smoke.

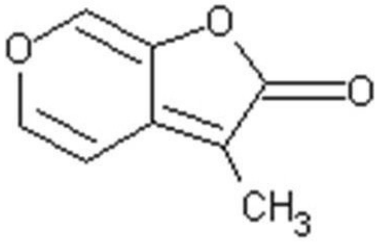
1.3.3 Heat

The direct effect of fire is the release of heat to the vicinity. For fire-prone environments, dry heat has long been recognized as an effective cue for breaking dormancy in seeds of a number of species (Baskin and Baskin, 1998; Light and van Staden, 2004). It mainly acts on seeds with physical dormancy by cracking the seed coat or splitting the palisade layer of the micropyle, although some physiological effects on seed embryo have been documented. Indeed, heat has been suggested to regulate germination in some seeds, through the release or induction of physiological dormancy (Baskin and Baskin, 1998). This has been further corroborated by many experimental studies (Clarke *et al.*, 2000; Gashaw and Michelsen, 2002; Schelin *et al.*, 2003). The effect of heat on seed germination is highly dependent on temperature and different species have different minimum temperature requirements and different thresholds at which heat may become lethal to them. Moreover, studies on germination responses to heat shock (Herranz *et al.*, 1998; Valbuena and Vera, 2002; Zida *et al.*, 2005) have revealed that not only the amount of heat reaching the seeds, but also the duration of seeds' exposure to a given temperature is important. Heat-stimulated germination of fire may fail if fires are of low intensity (Bond and Van Wilgen, 1996).

1.3.4 Smoke

Smoke generated by burning is widely recognized as affecting plant species dynamics. After the discovery by De Lange and Boucher (1990) that seeds of *Audouinia capitata* Brongn. germinate well at sites with smoke-fumigated soils, but not at smoke-free (control) sites, numerous studies have revealed the potential of plant-derived smoke in many aspects of plant biology such as seed germination, seedling growth (Dixon *et al.*, 1995; Razanamandranto *et al.*, 2005; Sparg *et al.*, 2005; Kulkarni *et al.*, 2006), plant flowering (Keeley, 1993) and somatic embryogenesis (Senaratna *et al.*, 1999). In some fire-prone environments (Fynbos of South Africa, Californian chaparral and Australian rangelands and woodlands), smoke has been shown to be an important factor for the understanding of vegetation dynamics, and has a potential uses in horticulture, agriculture, ecological management and rehabilitation of disturbed areas (Light and van Staden, 2004). The adaptation of plants to this fire-related cue is particularly true for seeds and smoke-stimulated germination is very widespread (Brown and van Staden, 1997; van Staden *et al.*, 2000). The mechanism of smoke-stimulated germination is not elucidated. First investigations led to the theory of chemical scarification of the seed coat (Egerton-Warburton, 1998). Because the germination of decoated seeds of *Grevillea wilsonii* A.Cunn. was stimulated by smoke (Morris *et al.*, 2000), it was suggested that smoke may act on the embryo as well. Smoke has also been postulated to affect plant processes through interaction, in some way, with endogenous plant growth regulators (van Staden *et al.*, 2000). For instance, Gardner et *al.* (2001) found that smoke-promoted germination can be effectively prevented by far-red light treatment, suggesting that at least part of the mechanism of smoke action is phytochrome-dependent. Smoke can also substitute for the light requirement in the germination of some seeds (e.g. *Shoenia filifolia* subsp. *Subulifolia*) (Plummer *et al.*, 2001; Todorovic *et al.*, 2005). Moreover, the level of gibberellins in smoke-treated seeds has been found to remain low initially, but to rise concurrently with the start of germination (Gardner *et al.*, 2001). In addition, paclobutrazol and AMO 1618, inhibitors of gibberellin biosynthesis, were found to decrease the germination of smoke-treated seeds significantly. Gibberellin synthesis was thus thought to be a likely component of the mechanism underlying smoke-induced germination. Van Staden et *al.* (2000) concluded that smoke may: activate the phytochrome system; influence the biosynthesis / metabolism of gibberellins and / or other plant hormones, thus increasing the amount of active phytohormones that can respond to the phytochrome system; change membrane permeability, thereby enhancing transport of phytohormones to active sites; interact with hormone receptors, thus changing their sensitivity; and activate enzymes required for the initiation of reserve mobilization and the commencement of germination.

The active germination stimulant in smoke, now known as karrikinolide (Nelson *et al.*, 2009), was identified to be the butenolide 3-methyl-2H-furo[2,3-c]pyran-2-one (Flematti *et al.*, 2004; van Staden *et al.*, 2004). The compound has been chemically characterized (Flematti *et al.*, 2008) and is known to be active at very low concentrations (<1 ppb, 10^{-9}M), stable at high temperatures (melting point, 118° to 119°C), water-soluble, neutral and to have a UV absorbance maximum at 330 mm. Its chemical representation is shown below.



Karrikinolide could be involved in early induction of the cell cycle activities, thus accelerating radicle emergence in germinating seeds (Jain and Van Staden, 2006). It has also been suggested to increase the expression levels of expansins (Jain *et al.*, 2008a), proteins mainly involved in cell wall loosening activity, required during the process of seed germination to reduce the physical restriction that the endosperm causes to the embryo expansion. The stimulating effect of smoke is often reversed, becoming inhibitory if smoke is applied at high concentrations. It has recently been found that smoke also contains another butenolide compound, 3,4,5-trimethylfuran-2(5H)-one, which inhibits germination and significantly reduces the effects of the related promotive compound (Light *et al.*, 2010). With respect to post-germination smoke effects such as increasing seedling vigor, karrikinolide has been shown to have both cytokinin- and auxin-like activities when applied at low concentrations (Jain *et al.*, 2008b). These findings demonstrate the increasing potential of smoke in a variety of applications related to seed technology.

1.4 Relevance of the study in Burkina Faso

Despite the importance of natural forests for the daily needs (fuelwood, food, fodder, medicinal plants and many other products and environmental services) of local populations in semiarid Africa in general, and Burkina Faso in particular, the decline of these forests has long been an obvious fact (Fries and Heermans, 1992). In Burkina Faso, firewood is the major source of energy for cooking, heating and other domestic purposes, and woodfuel including fuelwood and charcoal accounts for about 90% of the total energy consumption (Brocard *et al.*, 1998; Nygard *et al.*, 2004). For centuries, livestock production in the savanna-woodlands of Burkina Faso has been one of the main sources of livelihood. It is the second biggest sector after agriculture (mainly cotton production), which supports both local communities and the national economy (MARA, 1996; Gning, 2005;

Savadogo, 2007). Livestock production, especially under extensive systems, is based on the use of natural pastures. Livestock grazing, fire and wood-cutting are the main anthropogenic factors influencing natural forests in the Sudanian zone (Fries and Heermans, 1992; Zida, 2007; Sawadogo, 2009).

Currently, natural forests in Burkina Faso cover approximately 7 million ha and these forests are being preserved through the establishment of "State forest" reserves (representing 26% of the total land area) for wood as well as biodiversity conservation (Savadogo, 2007; Zida, 2007). In order to reverse the tendency of degradation of natural resources, the country also embarked on a program of sustainable management of natural forests in the 1980s. This management is based on the following prescriptions: selective wood cutting of 50 % of the merchantable standing volume on a 20-year rotation period; annual prescribed early burning; and prohibition of livestock in State forests, national parks and wild life reserves (Bellefontaine *et al.*, 2000). Unfortunately, these management prescriptions were not supported by empirical evidence due to insufficient knowledge regarding the biology and ecology of indigenous species and the effects of biotic and anthropogenic factors on the dynamics of natural forests (Sawadogo, 2009).

Nowadays, there is an increasing body of literature on the ecology and dynamics of both ligneous and herbaceous components of this ecosystem under disturbance factors (Sawadogo *et al.*, 2002; Sawadogo *et al.*, 2005; Zida *et al.*, 2007; Savadogo *et al.*, 2008; Zida *et al.*, 2008b; Savadogo *et al.*, 2009), but there are still knowledge gaps. For instance, natural regeneration and establishment of plant species in Burkina Faso is a recognized concern but, to date, only tree species regeneration has attracted the attention of researchers (Bationo *et al.*, 2001a; Bationo *et al.*, 2001b; Zida *et al.*, 2005; Zida *et al.*, 2007; Zida *et al.*, 2008a; Zida *et al.*, 2008b). The regeneration of herbaceous species, which constitute the greater proportion of the aboveground biomass in this ecosystem, has received less attention. There is, however, evidence that the population and distribution of some herbaceous species, generally the socio-economically most important species, are declining (Dayamba, 2005). Therefore, there is a need to identify strategies for managing and assisting the reestablishment of the herbaceous species. These strategies should be based on sound understanding of the regeneration dynamics of herbaceous species under disturbance factors. Moreover, disturbance effects on vegetation are often attributable to the independent or combined effects of individual cues related to this disturbance; for instance, smoke generated by burning and heat account for much of the effects of fire on vegetation. To date, these individual disturbance-related cues have not been intensively studied in the Sudanian savanna-woodlands. In addition, some aspects of the disturbances, such as the season of occurrence (of fire, for instance) have received little attention, although their importance is recognized (Bond and Van Wilgen, 1996).

2 Objectives

The overall objective of the studies this thesis is based upon was to generate knowledge supporting the management of natural forests in Burkina Faso. The studies assessed the effects of fire, fire-related cues and grazing on the regeneration, productivity and diversity in the Sudanian savanna-woodlands of Burkina Faso. More specifically, the following aspects were examined:

1. Differences in fire temperature and temperature residence time with respect to season of burning and their implications for the germination of seeds buried in the soil (Study I).

2. The occurrence of smoke-responsive species and extent of smoke-responsiveness in the Sudanian savanna-woodlands of Burkina Faso and possible interactive effects of smoke and heat on seed germination (Studies II, III).

3. Dominant species resprouts' biomass dynamics after selective cutting in Sudanian savanna-woodlands subjected to repeated annual early burning and grazing (Study IV).

4. The effects of different seasons of burning on the dynamics and productivity of herbaceous species (Study V).

The overall hypothesis underlying the studies was that disturbance by fire and herbivory affect plant species regeneration, productivity and dynamics in the Sudanian savanna-woodlands.

3 Materials and Methods

3.1 Research sites

Studies I and V were carried out in Laba State forest while study IV was undertaken in both Laba and Tiogo State forests. Herbaceous seeds for studies II and III were collected in the two forests. The experimental sites (studies I, IV, V) are located on flat areas in Laba (11°40'N, 2°50'W) and Tiogo (12°13'N, 2°42'W) State forests, both at an altitude of 300 m a.s.l. in Burkina Faso, West Africa (Fig. 1). The Laba and Tiogo State forests were delimited by the colonial French administration in 1936 and 1940 and cover 17,000 and 30,000 ha, respectively. Both forests are located along the only permanent river (Mouhoun, formerly known as Black Volta) in the country. The unimodal rainy season lasts for about six months, from May to October. Based on data collected from *in situ* mini-weather station at each site, the mean annual rainfall since the establishment of the experiment (1992–2009) was 900 ± 158 mm at Laba and 839 ± 165 mm at Tiogo, and the number of rainy days per annum was 66 ± 16 and 64 ± 11 at Laba and Tiogo, respectively. Mean daily minimum and maximum temperatures ranged from 16 to 32 °C in January (the coldest month) and from 26 to 40 °C in April (the hottest month). Most frequently encountered soils are Lixisols (Driessen *et al.*, 2001) and the soil at Laba is shallow (< 45 cm depth) silty-sand, while it is mainly deep (> 75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo, 1998). Phytogeographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone (Fontès and Guinko, 1995).

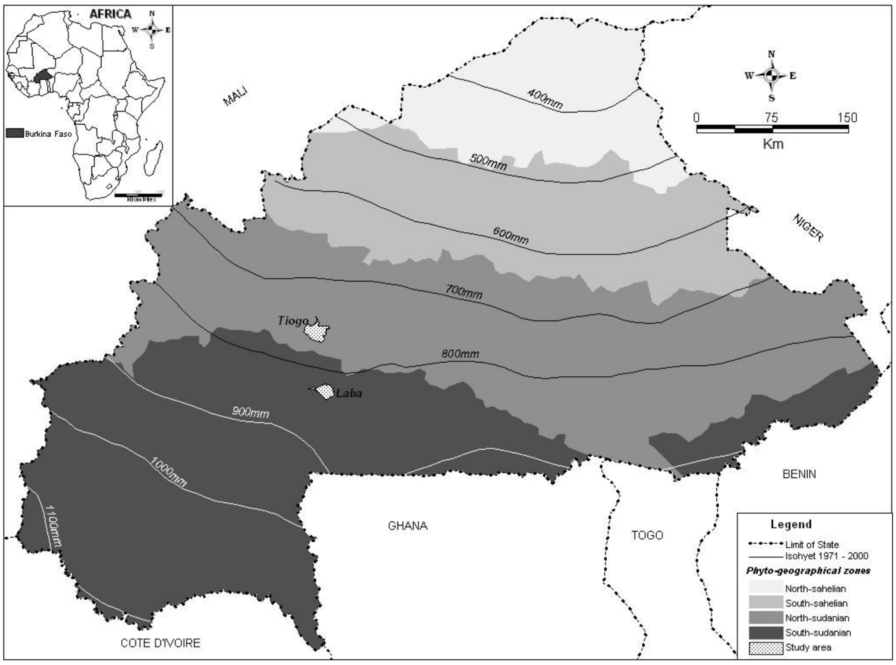


Figure 1. Vegetation map of Burkina Faso with isohyets and location of the two study sites (Adapted by CTIG/INERA/Burkina Faso April 2007 from Fontes & Guinko 1995 and Direction of the National Meteorology).

The vegetation type at both sites is a tree/bush savanna with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilg.) C.E. Hubb. and the perennial grasses *Andropogon gayanus* Kunth (dominant in Tiogo) and *Andropogon ascinodis* C.B. Clarke (dominant in Laba). The main forb species are *Cochlospermum planchonii* Hook. ex Planch., *Borreria stachydea* (DC.) Hutch. and Dalziel, *Borreria radiata* DC. and *Wissadula amplissima* Linn. Species of the families Mimosaceae and Combretaceae dominate the woody vegetation component at both sites. In terms of basal area, the main woody species are *Detarium microcarpum* Guill. & Perr., *Combretum nigricans* Leprieur ex Guill. & Perr., *Acacia macrostachya* Rchb. ex DC., *Entada africana* Guill. & Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpa* Guill. & Perr. and *Vitellaria paradoxa* C.F. Gaertn. Prior to the start of the experiments, the mean basal area of woody species at Laba was 10.7 and 6.3 m^2 ha^{-1} at stump level (20 cm) and breast height (130 cm), respectively, with the stand density of 582 individuals ha^{-1} having at least one stem ≥ 10 cm GBH (girth at breast height). At Tiogo, the corresponding values were 10.9 m^2 ha^{-1} at stump level, 6.1 m^2 ha^{-1} at breast height and 542 individuals ha^{-1}. Both sites had been frequently grazed by livestock and wild animals, and burnt almost every year during the dry season (November–May) long before the start of the experiment. The presence of livestock in the two State forests varies spatially and temporally, occurring mainly during the rainy season (June–October) when the grass is green and the surrounding areas are cultivated. During the dry season, they graze on straws in the bush clumps that have escaped the fires, and the young shoots of perennial grass species and young woody foliage induced by the fire.

3.2 Methods

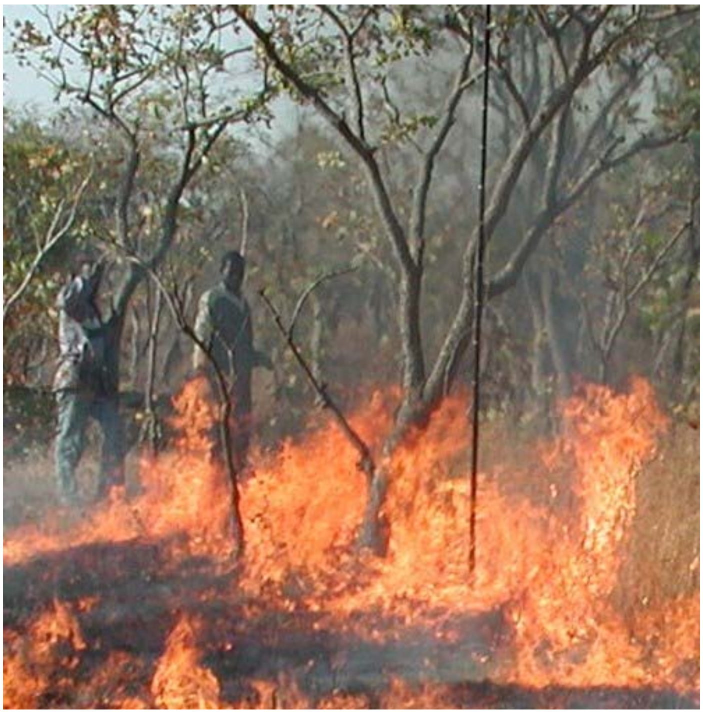
3.2.1 Study I

This study assessed the effects of season of burning on fire temperature and temperature residence time (above 60 °C) as well as their implications for the germination of seeds buried at different soil depths. A permanent experimental site, with 16 plots (50 × 50 m), was established in Laba forest in September 2006. The following fire treatments, each with four replicates, were randomly assigned to the 16 plots: no fire, control plots; early season fire, fire set at the beginning of the dry season in December; mid-season fire, fire set at the peak of the dry season in mid-January; and late season fire, fire set at the end of the dry season and just before the next rainy season at the end of March. Fire was initiated early in the morning by igniting the vegetation with a drip torch along one side of each plot at a time to rapidly establish a fire line and to ensure linear ignition. For the sake of uniformity, in all plots fire was lit following the wind direction (head fires).

Fire temperatures were registered following the procedure described by Savadogo *et al.* (2007b). MiniCube dataloggers with 10 thermo elements type-K and probes placed at -10, -5, -2, 0, 20, 50, 150, 300, 500 cm from ground level, were used. For each burnt plot, the maximum temperature at each probe position was considered during data analysis. The series of temperatures recorded at each probe position were used to calculate the temperature residence time above 60°C, which is considered lethal for plant tissues (Daniell *et al.*, 1969). Residence time was defined as the time elapsed before the maximum fire temperature declines to less than 60°C.

Seeds of three socio-economically valuable tree species *D. microcarpum*, *E. africana* (purchased from the National Tree Seed Centre and originally collected in 2002 and 1997, respectively) and *Combretum glutinosum* (collected from the Tiogo State forest in February 2008) were used to investigate the effects of different fire seasons on the germination of buried seeds. All studied species have no physical dormancy (Zida *et al.*, 2005; Dayamba *et al.*, 2008).

Prior to burning at each fire season, seeds of the above species were buried at different soil depths (0, 2 and 5 cm), in accordance with the nature of the soil seed bank in the study area, which is restricted to the first few cm in the soil (Zida, pers. obs.). The fire treatments were applied after burial of seeds as described above and the burnt soil was left to cool to ambient temperature after the fires were extinguished. Seeds from the same species and the same soil depth in each plot were pooled in a single paper bag and constituted a replicate. The germination parameters of the treated seeds were then assessed in a 30-day germination trial as follows. A total of 100 seeds per species and treatment, with 25 seeds per replicate, were sown in trays containing sterilized sand (sand heated in an oven set at 120°C for two hours). For each species, untreated (unburied and unburnt) seeds were also sown (4 × 25 seeds) as controls. The seeds were exposed to in-coming sunlight during the daytime and to darkness during the night and watered daily. All other conditions (temperature) were ambient as it would naturally be in field conditions. Germination was monitored every day and seeds showing a radicle at least 2 mm long were considered as germinated, were recorded and discarded from the trays. Germination trials for seeds burnt during early and mid-season fires were not successful due to unsuitable ambient environmental conditions (low temperatures) at the time of the trials. Therefore, only seeds germination in relation to depth of burial in the soil during late fire is reported.



Metallic stick with probes (of the MiniCube datalogger) attached at different heights to measure fire temperature

MiniCube datalogger held by a field worker

3.2.2 Studies II and III

Germination responses of some of the most dominant and socio-economically important species in the savanna-woodlands of Burkina Faso to cold aerosol smoke (Study II), smoke water at a range of dilutions (Study III) and heat shock treatments (II and III) were assessed. Species investigated in each study are presented in Table 1, together with their ecological characteristics in relation to fire. In study II, seeds of the woody species were purchased from the National Tree Seed Centre in Ouagadougou, Burkina Faso. Information regarding the dormancy status of the studied tree seeds is scarce, except for *Prosopis africana* and *Burkea africana*, which are known to possess physical dormancy (Razanamandranto *et al.*, 2005; Zida *et al.*, 2005). The National Tree Seed Centre recommends acid pretreatment for *Afzelia africana* and *Terminalia avicennioides* seeds, implying that they also have physical dormancy. *C. glutinosum, C. nigricans, A. leiocarpa* and *Pteleopsis suberosa* seeds do not need any pretreatment to germinate, according to the Seed Centre. Seeds of the herbaceous species (Studies II and III) were collected from the Laba and Tiogo State forests, directly from plants at the time of natural dispersal of each species (Baskin and Baskin, 1998; Overbeck *et al.*, 2006). All structures enclosing the caryopsis were removed (Clarke *et al.*, 2000; Clarke and French, 2005) to ensure that no empty dispersal unit was used in the germination test.

Five levels of heat shock - no heat, incubating seeds at 40, 80, 120°C (Studies II and III) or 140°C (Study III), two levels of smoke treatment - no smoke or exposure to cold aerosol smoke (Study II), and six dilutions of smoke water - 100% smoke solution, 75%, 50%, 25% and 5% and 0% concentrations of smoke solutions (v/v) (Study III) were used with 4 replications; each replicate consisted of 25 seeds. For the smoke treatment in Study II, seeds were placed on aluminum paper, which was placed on the ground. The seeds were enclosed within a metallic chamber and fumigated for 1 h with smoke derived from the combustion of a mixture of the most dominant herbaceous and ligneous species in the Tiogo State forest. For study III, the smoke generation procedure was similar to that applied in study II, except that the smoke derived from the combustion was forced to bubble into a bottle of water for about 10 h to trap substantial amounts of the active compound. The smoke treatment involved soaking seeds of each species in each smoke solution for 24 h while de-ionized water was used as control. For the heat shock treatment, seeds were placed in a preheated kiln for 2 min 30 s. The heat treatment levels in this experiment were chosen considering the range of temperatures occurring at the soil surface and in the first few centimeters below ground during burning in savanna, while the exposure time was based on the mean fire residence time in the Sudanian savanna-woodland (Savadogo *et al.*, 2007b).

For the germination test, seeds were placed on filter papers moistened with distilled water, covered with bell jars with a hole at the top to allow air circulation. The test was performed at a constant temperature of 25 °C, day and night, with permanent illumination of about 20 $\mu Em^{-2}s^{-1}$ (fluorescent lamp F 40 W/33 RS cool white light). The experiment ran for 30 days for all species. Before sowing, the tree seeds were soaked in 1% sodium hypochlorite solution for 10 min and rinsed with distilled water to avoid fungal attack. To avoid possible damage to the grass seeds (which were small, with soft seed coats) by additional manipulation before sowing, these seeds were not subjected to hypochlorite cleaning. Germination was monitored every day. Seeds showing a radicle at least 2 mm long were considered as germinated and were recorded and discarded.

Table 1. Main ecological characteristics (related to fire) of species investigated in studies I, II and III

Species	Life form	Family	Main ecological characteristic in relation to fire	STUDY
Andropogon ascinodis C. B. Clarke.	Perennial grass	Poaceae	SENSITIVE; abundance disfavoured by fire (Savadogo *et al.*, 2008)	II, III
Andropogon gayanus Kunth	Perennial grass	Poaceae	SENSITIVE; abundance and biomass disfavoured by fire (Sawadogo *et al.*, 2005; Savadogo *et al.*, 2008)	II, III
Borreria radiata DC.	Forb	Rubiaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Borreria scabra K. Schum.	Forb	Rubiaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Brachiaria distichophylla Stapf	Annual grass	Poaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Brachiaria lata (Schumach.) C.E. Hubb.	Annual grass	Poaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Cassia mimosoides L.	Forb	Caesalpiniaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Chasmopodium caudatum Stapf	Annual grass	Poaceae	ADAPTED; As an annual grass it tends to be favored by fire; number of annual grasses was higher on burnt plot (Savadogo, 2007)	II
Cochlospermum planchonii Hook. *f.* ex Planch.	Forb	Cochlospermaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Cymbopogon schoenanthus Spreng.	Perennial grass	Poaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III

Table 1 (continued).

Species	Life form	Family	Main ecological characteristic in relation to fire	STUDY
Diheteropogon amplectens (Nees) Clayton	Perennial grass	Poaceae	SENSITIVE; Abundance of perennial grasses was higher on unburnt plots (Savadogo, 2007)	II
Euclasta condylotricha Stapf	Annual grass	Poaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Loudetia togoensis (Pilg.) C.E. Hubb.	Annual grass	Poaceae	ADAPTED; biomass increased by fire (Sawadogo *et al.*, 2005; Savadogo *et al.*, 2008)	III
Rottboellia exaltata L. f.	Annual grass	Poaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	II, III
Tephrosia pedicellata Baker	Forb	Fabaceae	TOLERANT; abundance insensitive to fire treatment (Savadogo *et al.*, 2008)	III
Combretum glutinosum Perr. ex DC.	Bush (4 - 7 m)	Combretaceae	TOLERANT; Its seedlings, lignifying early, are more resistant to environmental factors such as fire (Thiombiano and Kere, 1999).	I, II
Combretum nigricans Lepr. ex Guill. et Perr.	Bush (4 - 7 m)	Combretaceae	TOLERANT; Relatively small change in seedling density irrespective of management regime (notably, fire) (Zida, 2007)	II
Anogeissus leiocarpa Guill. et Perr.	Medium-sized tree (15 – 30 m)	Combretaceae	SENSITIVE; Highly invading in unburnt plot; Very sensitive to bush fire (Sacande and Sanogo, 2007; Zida *et al.*, 2007)	II
Terminalia avicennioides Guill. et Perr.	Bush (4 - 7 m)	Combretaceae	ADAPTED; Relatively abundant in fire treatment plots (Zida, 2007)	II

Table 1 (continued).

Species	Life form	Family	Main ecological characteristic in relation to fire	STUDY
Pteleopsis suberosa Engl. et Diels.	Bush (4 – 7 m)	Combretaceae	ADAPTED; Large seedling establishment after the passage of fire (Dayamba, personal observation)	II
Afzelia africana Sm.	Medium-sized tree (15 – 30 m)	Leguminoseae	SENSITIVE; Seedlings very sensitive to fire and need to be protected against this constraint (Bationo *et al.*, 2001).	II
Entada africana Guill. et Perr.	Shrub (4 – 7 m)	Leguminoseae	---	I
Detarium microcarpum Guill. et Perr.	Bush (4 – 7 m)	Leguminoseae	SENSITIVE; Substantially high density on plots protected from burning (Zida *et al.*, 2007).	I
Burkea africana Hook.	Medium-sized tree (15 – 30 m)	Leguminoseae	TOLERANT; Relatively small change in seedling density irrespective of management regime (notably, fire); also classified as semi fire-tolerant (Cauldwell and Zieger, 2000; Zida, 2007).	II
Prosopis africana Taub.	Small tree (7 – 15 m)	Leguminoseae	TOLERANT; hard and dormant seeds, withstanding fire (Razanamandranto, 2003)	II

3.2.3 Study IV

This study assessed the effects of annual early burning and grazing on dominant species' resprouts dynamics after selective cutting in the two State forests of Tiogo and Laba. The experimental site in each forest (18 ha) was divided into eight blocks (2.25 ha); four of which were fenced to exclude livestock (hereafter referred to as ungrazed plots), while the other four were open for grazing (hereafter referred to as grazed plots). Each block contained 9 plots of 0.25 ha (50 × 50 m) separated by 20 – 30 m fire breaks. To the nine plots within each block, three treatments were randomly assigned as no cutting, selective cutting and selective cutting followed by direct seeding of tree species. To each plot that had received the same cutting treatment, one of three fire treatments was applied: fire protection, 2-year fire protection after cutting followed by early annual fire and early annual fire since the establishment of the trials. Only cut plots were considered and the effect of early fire and grazing on resprouts' dynamics was assessed. The "2-year fire protection" treatment was not assessed as this treatment was not strictly followed later on. In addition, as the direct seeding was not successful, the two logging modalities "selective cutting" and "selective cutting followed by direct seeding of tree species" were both considered to be a "selective cutting treatment". The selective cutting was done in December 1993 at Tiogo and a month later in January 1994 at Laba by removing 50% of the basal area of stems with > 10 cm girth. Individuals were cut at about 15 cm above ground. The structural characteristics at each site indicated that *D. microcarpum* had the highest relative dominance (36%) followed by *Crossopteryx febrifuga* (Afz. ex G. Don) Benth. at the Laba site. At the Tiogo site, *E. africana* stood out as the most dominant followed by *A. macrostachya*. The prescribed early fire was applied at the end of the rainy season each year from 1993 when the grass layer humidity was approximately 40%. The grazed plots at both study sites were open for grazing by livestock (a mixed herd of cattle, sheep and goats). The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit ha^{-1} (T.L.U. ha^{-1}) and that of Tiogo was 1.4 T.L.U. ha^{-1} (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo *et al.*, 2005).

At the two experimental sites, every cut stump was surveyed annually at the end of the dry season in May for 13 years (1994- 2006) and the following variables were recorded:

– Shoot mortality, determined by counting the number of dead shoots of each species in each plot and dividing by the total number of shoots of this species recorded during the survey in that plot.

– Height (cm) (or length along the stem if the shoot was leaning) of all shoots, measured with a graded pole.

– Girth (cm) of shoots at stump height and breast height, which was measured with a tailor's tape and used to calculate basal area at both stump and breast height.

Six species - *Combretum ghazalense* F. Hoffm., *C. febrifuga, D. microcarpum*, *A. macrostachya*, *C. glutinosum* and *E. africana* - that were common on nearly all treatment plots, were selected to assess the treatments' effects.

3.2.4 Study V

This study assessed herbaceous species dynamics and productivity under fires burning at three different times during the dry season. The experimental design was the same as in study I. The abundance of herbaceous vegetation was assessed every year from 2006 to 2009 at the end of the rainy season (September–October), when most of the species were flowering and fruiting, which allowed easy species identification. The point-intercept sampling procedure (Levy and Madden, 1933) was used to gather species-cover data. The presence of species was recorded along a 20 m permanent line laid in each plot at an interval of 20 cm, giving a total of 100 sampling points. At each of these points, a 5 mm diameter pin taller than the maximum height of the vegetation was projected from above, and all contacts were recorded if the pin hit any of the live parts of a grass species. The positions of the transect lines were permanently marked to be able to localize them every year. Identification of species and families of plants followed the International Plant Names Index (www.ipni.org).

The richness, diversity and biomass of herbaceous species were computed for each replicate in each treatment. Species richness was defined as total number of species. Species diversity was assessed using Shannon's diversity index (H'), calculated using the following equation:

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

where p_i is the relative abundance of species i in a plot (Magurran, 2004). Biomass was assessed every year at the end of the rainy season by harvesting the herbaceous vegetation within six quadrats (1 m^2 each) randomly located in each plot. The biomass was sorted by species and weighed in the field using a spring balance. Samples were then taken to the laboratory for dry weight assessment after air-drying to constant mass. Abundance was expressed as percentage cover and was computed for the species *A. ascinodis* which was encountered in all treatment plots.

20 m line laid on top of the vegetation for the inventory of herbaceous species (Levy and Madden's procedure)

3.3 Data analysis

In studies I, II and III the germination capacity (GC) and mean germination time (MGT) were calculated for each species and treatment (Bewley and Black, 1994). GC, MGT, the fire temperature and temperature residence time data were transformed as deemed necessary to meet normality and homogeneity assumptions (Gomez and Gomez, 1976; Zar, 1999) and

ANOVA was performed to test for significant differences in main and interaction effects of the treatments. When a significant difference was found between treatments, a pairwise comparison was made using Tukey's test at the 5% level of significance.

In study IV, basal area at stump level, basal area at breast height and tree height were analyzed with linear mixed effect models. Year was treated as a continuous factor; grazing and fire as categorical fixed factors; and plot as a random factor. To account for the temporal autocorrelation of the data, we included in the models an autoregressive correlation structure of order 1, which assumes that observations made close to each other in time are more related than those separated further in time (Pinheiro and Bates, 2000). We modeled the heterogeneity within the data (shown by preliminary analyses) by allowing each indicated stratum (in the data) to have its own residuals' spread. Shoot mortality was analyzed with generalized linear mixed effects models using penalized quasi likelihood with binomial errors in order to account for the non-normal errors and the non-constant variances that are associated with proportional data. Year was used as continuous factor and the same categorical fixed factor and random factor as above. All models were checked for meeting the assumptions and 95% confidence intervals were produced and checked to ensure that the models' estimates were adequate. All statistical analyses were performed within the R statistical package (R Development Core Team 2009). The nlme package was used to calculate the linear mixed effect models. The MASS package was used to calculate the generalized linear mixed effect models using penalized quasi-likelihood estimates. Results of the statistical analyses were considered significant if P-values < 0.05 and to show tendencies if $0.05 < P < 0.1$.

In study V, prior to statistical analyses, abundance, species richness, diversity and biomass data were checked for normality. We used repeated-measures analysis of variance (Davis, 2002) to determine whether abundance, species richness, diversity and biomass were affected by year, fire seasons and their interactions. The homogeneity of variance assumption was checked using Mauchly's test of sphericity and was not violated. All statistical analyses were performed with SPSS 18 software package (Copyright SPSS for Windows, Release 2009 Chicago: SPSS Inc.).

The whole species community was further explored using multivariate ordination techniques. Initial data exploration to investigate the range of variation in the dataset was carried out using detrended correspondence analysis (DCA), a method of indirect gradient analysis (Ter Braak and

Smilauer, 2002). Then, Canonical Correspondence Analysis (CCA) was applied on the species and the fire treatments data matrices. The statistical significance of the CCA axes was evaluated using Monte Carlo permutation test ($p = 0.05$ after 499 permutations under split-plot constraints) by permuting freely data from the whole treatments within each year. The analyses were performed using the software package CANOCO 4.5 and the ordination diagram drawn in CANODRAW (Ter Braak and Smilauer, 2002)

4 Results and Discussion

4.1 Assessment of fire-related cues – temperature and its residence time

The effects of season of burning on fire temperature and its residence time was assessed. Fire temperatures were found to be significantly lower during early fire compared to mid-season and late fires ($p < 0.001$), but the last two fires did not differ significantly ($p = 0.98$) (Fig. 2). This may be explained by differences in the level of desiccation of the fuel (Govender *et al.*, 2006; Savadogo *et al.*, 2007b), because as the dry season advances, the vegetation continuously dries due to long exposure to the sun. Residence time was also longer during late fires (Fig. 2) since a longer time is required for temperature to fall below 60°C if the initial temperature is higher. In addition, heat transfer to the atmosphere is slower during late fires when the weather is naturally warmer (Whelan, 1995). As found in previous studies (Bradstock and Auld, 1995; Savadogo *et al.*, 2007b), fire temperatures and residence times were higher above the soil surface than below the soil surface, with a decreasing tendency with increasing soil depth. This is related to the thermal conductivity across the soil profile (Valette *et al.*, 1994).

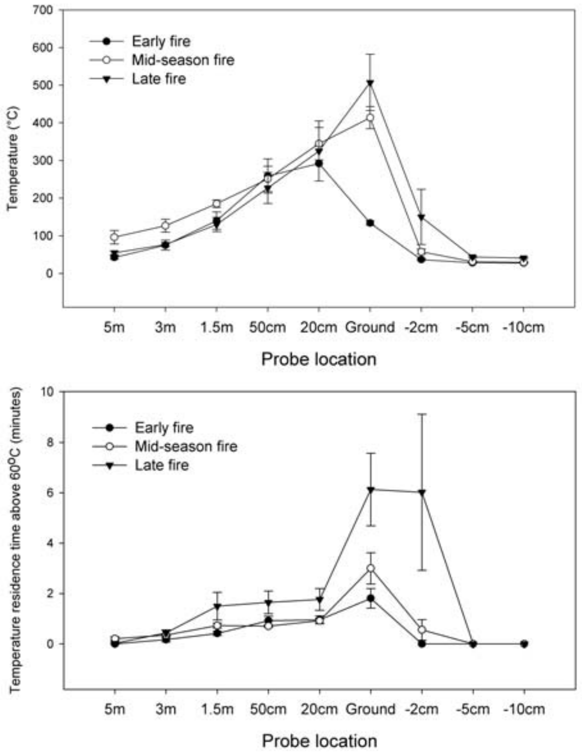


Figure 2. Main effect of fire season on temperature and temperature residence time above 60 °C (mean ± s.e.) at different probe locations.

4.2 Seed germination responses to fire, smoke and heat

4.2.1 Fire

Seed germination responses to fire and depth of seed burial in the soil profile were assessed. For all species studied, seeds placed on the soil surface during late fires did not germinate and were visibly rotten at the end of the germination trial. The temperature data suggest that these seeds experienced temperatures exceeding 500°C during the passage of fire, which certainly killed them. Zida *et al.* (2007) previously observed that the seedling density of one of our study species, *D. microcarpum*, was substantially higher on fire-protected plots than on burnt plots, suggesting that seeds at the soil surface were killed by extreme temperatures. The substantially higher temperature (150°C on average) recorded at 2 cm below ground did not result in any difference in germination capacity compared to seeds in the control and 5 cm below ground in the two leguminous species tested (*D. microcarpum* and *E. africana*). This suggests that these two species have similar temperature sensitivity and can withstand heat shocks up to 150°C. Gashaw and Michelsen (2002) also reported a species from the genus *Entada*, resisting temperature of up to 200°C. 150°C was, however, sufficient to reduce germination of *C. glutinosum* seeds (88% of germination at 2 cm below ground compared to 98 and 99% for controls and seeds buried 5 cm below the ground, respectively). These findings suggest that there are inter-species variations in responses to fire treatment that might be due to differences in the ability of the seeds' integument to protect them against high temperatures (Bond and Van Wilgen, 1996). The length or mass of seeds may also affect their resistance to high temperature (Gashaw and Michelsen, 2002), as embryos in large seeds (such as *D. microcarpum*) are exposed to high temperatures for shorter times than embryos in small seeds.

Seeds of *C. glutinosum* buried at 2 cm below the soil surface also took longer to germinate (18 days) compared to control seeds (nine days) and seeds at 5 cm below the soil surface (eight days). This suggests a need to recover from a temporary heat-induced physiological dormancy (Baskin and Baskin, 1998) before germination could proceed. In field conditions, this could be an adaptive strategy that synchronizes germination with the availability of sufficient moisture in the soil (Gashaw and Michelsen, 2002). However, delayed germination was not observed in seeds of the leguminous species, in contrast to results reported by Zida *et al.* (2005), who found that increases in temperature and exposure time delayed germination of *D. microcarpum* and *E. africana* seeds. A possible explanation for this discrepancy is that, as shown by the observed residence times in this study (Fig. 2), in real field conditions seeds do not experience such long exposures to heat shock as those (20, 40 and 60 min) applied by Zida *et al.* (2005).

The observed temperatures at the different soil depths during early and mid-season fires (Fig. 2), and the responses of seeds in relation to temperatures observed during late fires, indicate that lower proportions of seeds at the soil surface may be killed during the passage of early fires than during mid-season and late fires; and hence fairly high proportions of superficially buried seeds or unburied seeds on the surface of the forest floor may germinate.

4.2.2 Smoke

The smoke responsiveness of 15 herbaceous species (four perennial grasses, six annual grasses and five forbs) and eight ligneous species was tested, in total. The results confirmed and extended previous findings (Brown *et al.*, 1994; Dixon *et al.*, 1995; Roche *et al.*, 1998; Morris, 2000; Thomas *et al.*, 2003; Merritt *et al.*, 2006; Norman *et al.*, 2006) by showing that the degree of smoke responsiveness is a species-specific attribute; in total, seeds of two herbaceous species (*B. scabra* and *E. condylotricha*) (Fig. 3) and two tree species (*T. avicennioides* and *P. suberosa*) responded significantly to smoke treatment. Responses to smoke were independent of taxon (Adkins and Peters, 2001; Crosti *et al.*, 2006); the germination capacity of smoke-treated *B. scabra* seeds was at least 3-fold higher than that of untreated seeds of this species, while the results were not significantly different for *B. radiata* seeds. The study also revealed that the type of smoke used is of great importance; for instance, smoke water did not affect germination parameters of *A. gayanus* while aerosol smoke delayed its germination. In addition, as found in previous studies (Light *et al.*, 2002; Sparg *et al.*, 2005), increasing the smoke concentration had inhibitory effects, decreasing or delaying the germination of responsive species (Fig. 3, *E. condylotricha*). The mechanism whereby smoke inhibits germination is unclear, but Clarke and French (2005) suggested that it could be due to a toxic effect of specific compounds present in smoke at high concentrations. There is now evidence that, apart from the stimulant compound, smoke also contains a butenolide, 3,4,5-trimethylfuran-2(5H)-one, that inhibits germination and significantly reduces the effect of the stimulant compound when applied simultaneously (Light *et al.*, 2010). It has also been shown that washing can eliminate the toxic effect of smoke, allowing seeds to germinate thereafter (Gilmour *et al.*, 2000; Light *et al.*, 2002; Sparg *et al.*, 2005). In burnt areas, smoke could therefore be a limiting factor for the rapid establishment of *A. gayanus* and *E. condylotricha* seedlings. This could, in turn, partly explain the reduction of biomass of *A. gayanus* in prescribed early fire plots at our study site (Sawadogo *et al.*, 2005).

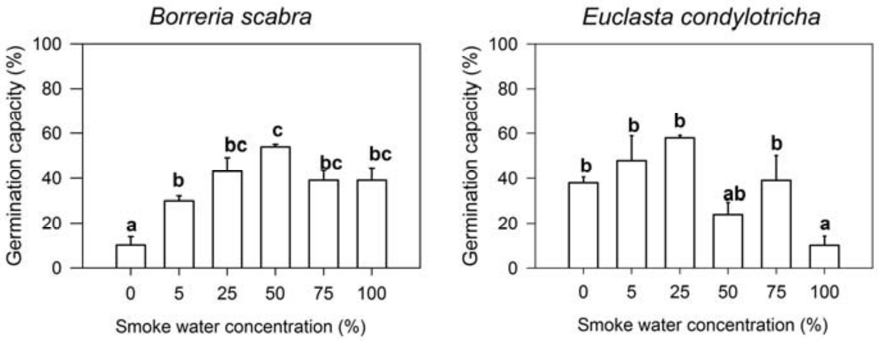


Figure 3. Effects of different concentrations of smoke solution on the germination capacity of two responsive herbaceous seeds from a Sudanian savanna-woodland of West Africa. Bars with different letters are significantly different at the 5% level using Tukey's HSD test.

For some species, we observed similarities between smoke responsiveness and field responses to fire; for instance, despite the very low germination rates of *T. avicennioides* and *P. suberosa* seeds, the positive smoke effect observed is consistent with their observed fire responses in the field (Table 1). Our observations for the two fire-tolerant *Borreria* species (Savadogo *et al.*, 2009) indicate that they may be favored by fire. However, the responses to smoke of other species could not explain their field responses to fire, for instance the observation that smoke depresses the germination of *E. condylotricha* seeds does not corroborate the observation of Savadogo *et al.* (2009) that the species seemed to be insensitive to fire treatment. This could be related to the exposure time and dosage of smoke produced under field conditions, which may substantially differ from that in the simulated laboratory experiment, as well as the species-specific requirements for varying levels of smoke treatment. Moreover, previous studies have shown that smoke responsiveness transcends plant species' ecological characteristics, notably their fire response categories (Roche *et al.*, 1997a; Roche *et al.*, 1997b; Norman *et al.*, 2006).

Smoke treatment, under laboratory conditions, has so far failed to stimulate germination in seeds with physical dormancy (Razanamandranto *et al.*, 2005). This could account for the non-responsiveness of some of our tested species (*C. planchonii*, *C. mimosoides* and *T. pedicellata*). The other species tested with no response to the treatment may be insensitive to this cue, although not all cases conform to the species' field responses to fire (Table 1). Seeds (even physically dormant) may, however, become responsive to smoke after some period of storage or soil burial (Roche *et al.*, 1997a, 1998; Tieu *et al.*, 2001b). There could also be discrepancies between laboratory results and field responses because smoke may act as a deterrent against predation (Roche *et al.*, 1997b), that is, untreated seeds in control plots may be more palatable to predators than smoke-treated seeds.

The ability of smoke treatment to shorten germination time was reported in previous studies (Razanamandranto *et al.*, 2005; Sparg *et al.*, 2005; Crosti *et al.*, 2006; Daws *et al.*, 2007). Smoke slightly shortened the overall germination time of seeds of *C. glutinosum* and *C. nigricans*. It has been proposed that smoke induces early germination interactively with plant growth hormones (van Staden *et al.*, 2000). Evidence also shows that the stimulant compound in smoke could be involved in early induction of the cell cycle activities, and thus accelerate radicle emergence in germinating seeds (Jain and Van Staden, 2006). Smoke-treated seeds would therefore germinate more quickly than untreated seeds. A shorter mean germination time results in more vigorous seedlings with higher survival rates, and enhances the ability of seedlings to compete in a post-fire environment (Brown and van Staden, 1997). This might explain why *C. glutinosum* has shown good regeneration in habitats prone to annual fire (Thiombiano and Kere, 1999). Germination of *B. radiata* seeds was, however, delayed following treatment with 75% smoke solution, compared to all other treatments (9 days vs. <3 days). This could be due to different compounds being active at different concentrations (Boucher and Meets, 2004).

4.2.3 Heat

Seed germination responses to heat shock under laboratory conditions were also tested. No effect of the treatment on germination parameters of grass species was observed, as noted for some of the grass species tested by Overbeck *et al.* (2006). However, all studied species germinated after exposure to high temperature (120 °C), which is an indication of adaptation to fire (Clarke and French, 2005; Overbeck *et al.*, 2006). Thus, seeds of these species should be able to germinate after a fire event and colonize the field, unless they are situated at ground level where lethal temperatures can be reached. Seeds of the forb species *B. radiata* and *B. scabra* and the tree species *A. leiocarpa* failed to germinate at higher temperatures tested, possibly because their integument could not provide protection against the effects of such high temperatures. Lethal effects of high temperature shock on seeds of some species have previously been documented (Auld and O'Connell, 1991; Teketay, 1996; Herranz *et al.*, 1998; Zida *et al.*, 2005). The negative effects of high temperature and the production of empty dispersal units (Kambou and Guinko, 1995) could account for the low regeneration of *A. leiocarpa* in the field. Zida *et al.* (2007) confirmed the negative effect of fire on this species by observing that it was highly invasive in unburnt plots. Seeds of *B. radiata* and *B. scabra*, under lower temperatures (40 and 80 °C), imbibed water, were not killed but failed or took more time to germinate, implying that they have some heat-induced physiological dormancy (Baskin and Baskin, 1998; Clarke *et al.*, 2000). For *C. mimosoides* seeds, although the physical dormancy was apparently broken, physiological dormancy seemed to be induced by treatment with heat shocks at 120 and 140 °C. For all leguminous tree species tested, the Combretaceae *T. avicennioides* and the forbs *C. planchonii* and *T. pedicellata* the heat level applied was inefficient to break the seed coat-imposed dormancy, whereas acid scarification of the forb species for two hours substantially promoted germination within a few days. These species which are common in the study area and can resist temperatures up to 140 °C, could be considered adapted to fire (Clarke and French, 2005; Overbeck *et al.*, 2006) and would require higher temperatures and/or other cues before they germinate. In contrast to previous findings regarding some species in our study area (Schelin *et al.*, 2004; Zida *et al.*, 2005), heat accelerated the germination of *C. nigricans* and *C. glutinosum* seeds.

4.2.4 Interactions between smoke and heat

Smoke and heat did not interactively influence seed germination of the grass species investigated, suggesting that these species are adapted to the independent effects of these fire-related cues. Some taxa may, however, require a synergistic action of the physical effects of temperature (heat) and chemical properties (smoke) of fire to produce maximal germination responses (Dixon *et al.*, 1995; Crosti *et al.*, 2006). For example, for the tree species *T. avicennioides*, germination capacity was highest when seeds were treated with “smoke and heat shock at 120 °C”. This also shows that a combination of smoke and heat could be required to draw conclusions regarding the fire response of a species (Tieu *et al.*, 2001a; Thomas *et al.*, 2003). Knowledge of responsive species to individual cues has, however, practical importance in site rehabilitation and restoration with native species (Roche *et al.*, 1997b; Rokich *et al.*, 2002). The germination of seeds of some common species in the study area was promoted by neither smoke nor heat. This finding highlights the importance of the indirect effects of fire (through its modification of the light regime, exposure of bare mineral soil, and prolonged higher temperatures from solar radiation) and other environmental factors, such as fluctuating temperatures and microbial action, on vegetation communities in fire-prone environments, as documented by Baskin and Baskin (1998). In addition, seeds of all tested herbaceous species except *A. gayanus* and *C. schoenanthus*, showed low germination (< 50%) irrespective of the treatment applied. The legume species (*C. mimosoides* and *T. pedicellata*), the Cochlospermaceae (*C. planchonii*) and the Poaceae *B. lata* would need some treatment releasing their physical dormancy (sulfuric acid, mechanical scarification or optimum heat treatment) to increase their germination rates. The rest of the species, which visually imbibed water but failed to germinate, showed evidence of embryo dormancy. All seeds tested in this study were collected in the preceding season; some may perhaps need a longer after-ripening period or other dormancy-releasing treatments.

4.3 Resprouts' responses to fire and grazing

4.3.1 Mortality

The effects of grazing and fire on resprouts' dynamics after selective cutting of dominant species were examined, and inter-species differences in responses to the treatments were observed (Table 2). Accordingly, it is known that differences in bark thickness result in major differences in trees' ability to resist fire, and fire will tend to prey selectively on thinner barked species within a community (Nefabas and Gambiza, 2007). It is also known that some woody species are well adapted to fire and that it has no major effects on their mortality (Williams *et al.*, 1999). The treatment regimes did not affect the mortality of either *A. macrostachya* or *C. glutinosum*, in accordance with previous observations, for the latter, that young individuals lignify early and are highly resistant to environmental factors such as fire (Thiombiano and Kere, 1999). In later years of the experiment, fire reduced the mortality of *C. febrifuga* (Fig. 4) and it appears that the accumulating litter in unburnt plots, throughout the years, becomes more detrimental to shoot survival due to competition for resources. The mortality-reducing effect of fire is more pronounced in ungrazed plots (fire × grazing interaction) in the case of *E. africana*, presumably because fire reduces the otherwise elevated herbaceous/sprout competition in such plots. In contrast to fire, grazing increased the mortality of species such as *D. microcarpum* and *E. africana* due to browsing and trampling. In grazed plots, however, fire increased the mortality of *C. ghazalense* (Fig. 4), lending credence to the observation by Midgley *et al.* (2010) that fire and herbivory together are a lethal combination for woody plants. Increased mortality of *C. ghazalense* resprouts in burnt and grazed plots could be due to higher herbivore activity in burnt areas, since grazers are attracted by the more nutritious regrowth of perennial grasses and new leaves of trees induced by fire.

Table 2. Effects of fire and grazing on dominant species' resprouts size parameters in Laba and Tiogo State forests in Burkina Faso.

	Basal area at base			Basal area at breast height		Average height		Maximum height		Mortality	
	d.f.	t	P	t	P	t	P	t	P	t	P
Acacia macrostachya											
Grazing	26	–0.15	0.883	–0.10	0.924	-1.03	0.315	-1.41	0.170	0.34	0.739
Fire	26	0.07	0.948	0.15	0.881	0.63	0.533	0.77	0.449	-1.28	0.213
Year	355	3.74	**<0.001**	3.77	**<0.001**	4.77	**<0.001**	8.16	**<0.001**	0.29	0.770
G × F	26	0.15	0.883	0.04	0.970	0.85	0.401	1.14	0.264	0.89	0.384
G × Y	355	-1.61	0.108	-1.89	**0.059**	–0.38	0.701	–0.74	0.457	–0.31	0.754
F × Y	355	-1.22	0.222	-1.21	0.226	0.02	0.981	-2.36	**0.019**	0.57	0.568
G × F × Y	355	1.50	0.134	1.69	**0.092**	0.01	0.990	1.08	0.283	–0.59	0.555
Combretum ghazalense											
Grazing	25	0.35	0.730	0.27	0.787	–0.17	0.867	-1.05	0.304	0.53	0.601
Fire	25	0.30	0.769	0.19	0.849	0.53	0.603	–0.14	0.887	0.29	0.772
Year	315	5.33	**<0.001**	4.69	**<0.001**	5.31	**<0.001**	5.00	**<0.001**	2.33	**0.020**
G × F	25	–0.23	0.817	–0.04	0.971	0.23	0.821	0.37	0.718	-1.07	0.295
G × Y	315	-1.85	**0.065**	-1.73	**0.084**	0.27	0.790	0.47	0.641	-1.71	**0.089**
F × Y	315	0.05	0.959	0.64	0.525	1.13	0.260	0.57	0.572	-1.72	**0.086**
G × F × Y	315	–0.03	0.978	–0.49	0.625	-1.40	0.164	–0.37	0.712	2.63	**0.009**

Table 2 (continued)

Combretum glutinosum										
	Basal area at base			Basal area at breast		Average height		Maximum height		Mortality	
	d.f.	t	P	t	P	t	P	t	P	t	P
Grazing	12	0.27	0.793	1.59	0.138	–0.03	0.979	–0.09	0.931	0.71	0.493
Fire	12	0.45	0.662	3.16	0.008	0.32	0.755	0.30	0.766	0.75	0.466
Year	188	6.37	<0.001	3.90	<0.001	3.83	<0.001	10.18	<0.001	1.01	0.316
G × F	12	-0.28	0.787	-1.59	0.138	–0.09	0.931	0.07	0.943	-0.39	0.704
G × Y	188	-0.13	0.900	–0.59	0.558	–0.64	0.522	-0.39	0.694	-0.25	0.800
F × Y	188	-2.19	0.030	-1.54	0.126	0.86	0.390	-1.43	0.153	-0.69	0.491
G × F × Y	188	1.00	0.319	0.80	0.425	–0.33	0.739	2.10	0.037	0.34	0.734
Crossopteryx febrifuga											
Grazing	22	0.08	0.934	0.02	0.984	0.35	0.730	0.17	0.863	1.03	0.313
Fire	22	-0.30	0.765	-0.32	0.752	-0.13	0.901	-0.11	0.911	2.10	0.048
Year	282	1.67	0.096	1.43	0.155	4.15	<0.001	6.79	<0.001	3.50	<0.001
G × F	22	-0.01	0.991	-0.02	0.986	-0.17	0.864	0.11	0.911	-1.73	0.098
G × Y	282	0.21	0.835	0.48	0.632	0.32	0.751	1.10	0.272	-1.54	0.124
F × Y	282	2.17	0.031	2.38	0.018	1.70	0.090	2.66	0.008	-2.95	0.004
G × F × Y	282	0.36	0.722	0.34	0.735	0.35	0.725	-0.52	0.601	1.62	0.107

Table 2 (continued)

Detarium microcarpum	Basal area at base			Basal area at breast		Average height		Maximum height		Mortality	
	d.f.	t	P	t	P	t	P	t	P	t	P
Grazing	28	0.56	0.579	0.38	0.709	0.38	0.705	–0.54	0.593	-2.29	**0.030**
Fire	28	0.31	0.757	0.39	0.700	0.71	0.486	–0.47	0.642	0.71	0.485
Year	348	3.52	**<0.001**	2.66	**0.008**	2.90	**0.004**	8.15	**<0.001**	2.04	**0.043**
G × F	28	-1.83	**0.078**	-1.72	**0.096**	-0.75	0.461	-0.02	0.985	0.20	0.843
G × Y	348	0.25	0.801	0.33	0.738	1.09	0.275	1.16	0.247	0.04	0.965
F × Y	348	2.46	**0.015**	2.76	**0.006**	4.64	**<0.001**	3.00	**0.003**	-1.51	0.133
G × F × Y	348	-0.62	0.539	-0.44	0.662	1.87	**0.062**	0.03	0.980	0.50	0.616
Entada africana											
Grazing	23	-1.15	0.260	–0.87	0.396	0.71	0.486	–0.69	0.497	-2.16	**0.042**
Fire	23	-0.71	0.484	-0.43	0.672	1.37	0.185	-0.85	0.405	-0.60	0.554
Year	319	5.51	**<0.001**	4.65	**<0.001**	0.90	0.366	11.52	**<0.001**	2.31	**0.021**
G × F	23	0.83	0.414	0.48	0.633	-0.58	0.567	0.76	0.457	2.50	**0.020**
G × Y	319	-1.66	**0.097**	-1.22	0.223	-1.03	0.305	1.52	0.130	0.39	0.696
F × Y	319	-1.12	0.262	-0.19	0.847	-0.29	0.774	1.39	0.165	-0.37	0.714
G × F × Y	319	0.82	0.416	0.53	0.600	-0.31	0.755	-1.24	0.216	-1.88	**0.062**

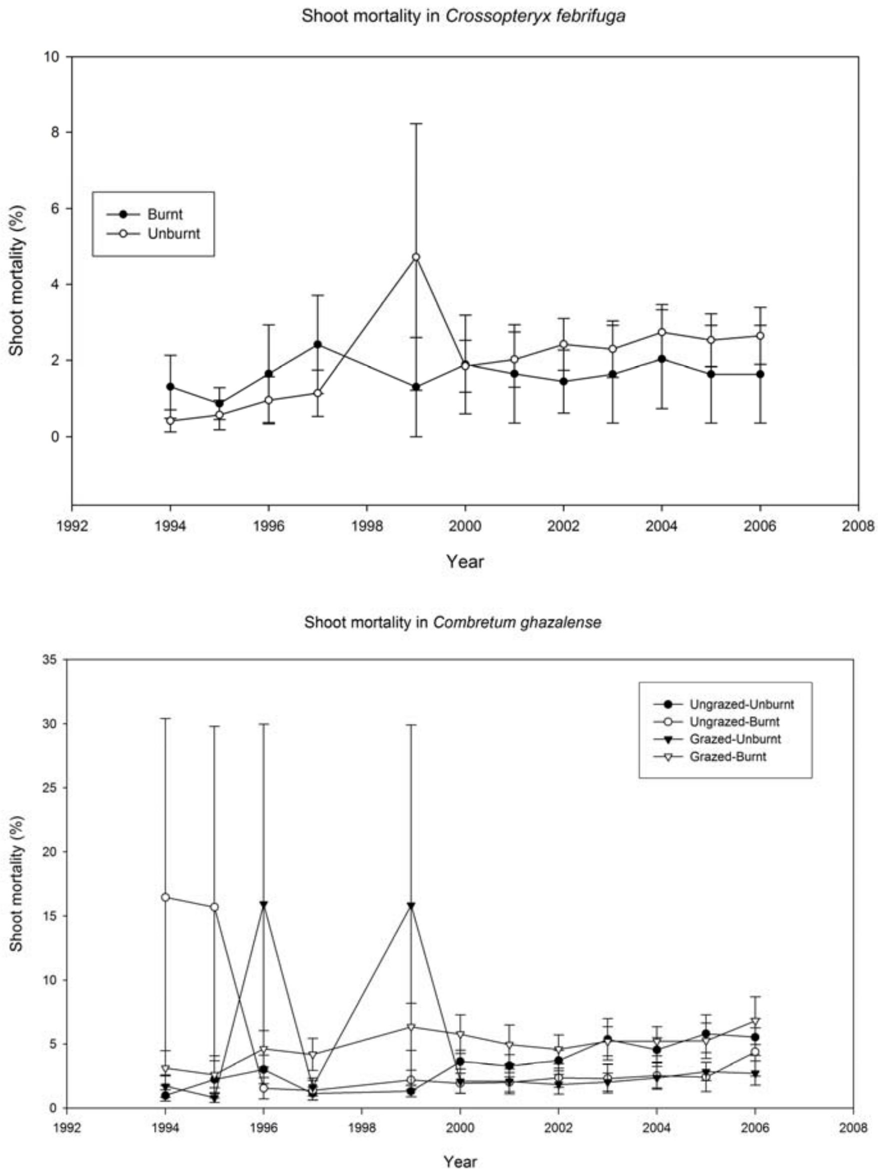


Figure 4: Inter-annual variations in fire, grazing and their interaction effects on dominant species' resprout mortality in the Sudanian savanna-woodlands of Burkina Faso. Graphs are presented for significant results only for the sake of conciseness.

4.3.2 Biomass of dominant species' resprouts

Plant leaf area explains a substantial amount of the variation in the increment of individual tree stem volume (Dean, 2004). By burning off the leaves, fire could therefore be expected to reduce tree growth. Indeed, according to Chidumayo (2007), after fire, subsequent allocation of resources will be directed to crown regrowth, thus negatively affecting stem growth. For the dominant species examined in this study, the main effect of burning did not significantly impact on resprouts' size parameters, except *C. glutinosum* which, on the contrary, showed an increasing basal area. This is in agreement with previous studies that most savanna tree species are sometimes described as fire-tolerant and that there is a differential effect of the fire treatments on tree growth (Guinto *et al.*, 1999; Kaschula *et al.*, 2005). It might be that in addition to some species resistance ability (e.g. *C. glutinosum*), they have developed nutritional mechanisms to cope with disturbances such as fire (e.g. within-plant recycling of nutrients). Also repeated prescribed burning might have increased "available" P in the long-term by possibly raising soil pH and thereby increasing the solubility of phosphate ions; this is a beneficial effect of burning on plant P nutrition although not all species reflect it in their biomass production (Guinto *et al.*, 2002). The tolerance of plants can however, be weakened by repeated defoliation by fire, as observed for *C. febrifuga* and *D. microcarpum* (Fig. 5), for which fire reduced resprouts' size parameters in later stages of the experiment. In the long term frequent burning might also decrease topsoil total N and mineralizable N, as well as cumulative N mineralization, which could in turn lead to long-term reductions in tree growth (Guinto *et al.*, 1999). The interaction of the treatments with year could be partly explained by the variability between and within years of environmental factors such as rainfall; fire treatment could have exacerbated the effects of the most adverse climatic conditions in particular years.

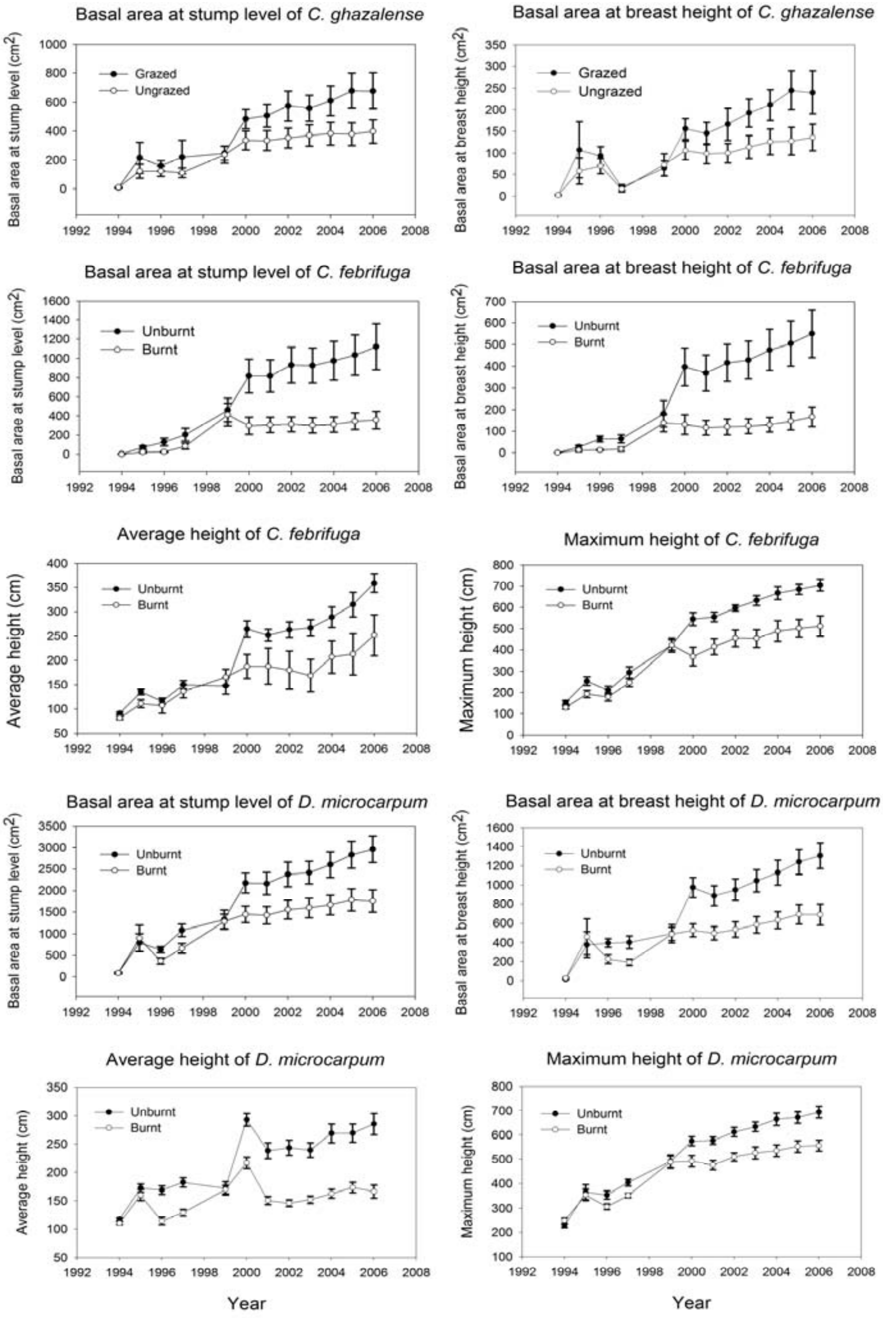


Figure 5. Inter-annual variations in fire and grazing effects on resprouts' size parameters of dominant species in Laba State forest in the Sudanian savanna-woodlands of Burkina Faso. Graphs are presented for significant results only for the sake of conciseness.

There was no negative effect of grazing on dominant species resprouts' size parameters, perhaps due to the moderate grazing intensity (50% of the potential intensity) on the plots. There was, instead, a tendency of increased basal area for *C. ghasalense* and *E. africana* in plots subject to repeated grazing over 13 years (Figs. 5 and 6). Some woody plants are known to use stem and branches for storage of nutrients that can be mobilized later to support biosynthesis for growth, or other functions as a browsing tolerance strategies, which could explain the slightly beneficial effect of grazing on basal area (Gordon and Prins, 2008). In addition, grazing and trampling can favor tree regeneration by decreasing grass biomass. Moreover, *C. ghazalense* has been shown to be well adapted to disturbances such as fire and grazing (Dembélé, 1996).

Ungrazed plots that were left unburnt produced taller individuals of *C. glutinosum* in most of the measurement years, corroborating the fact that individuals grow freely in the absence of disturbance. However, grazing in combination with burning had a slightly beneficial effect on the basal area of *A. macrostachya*.

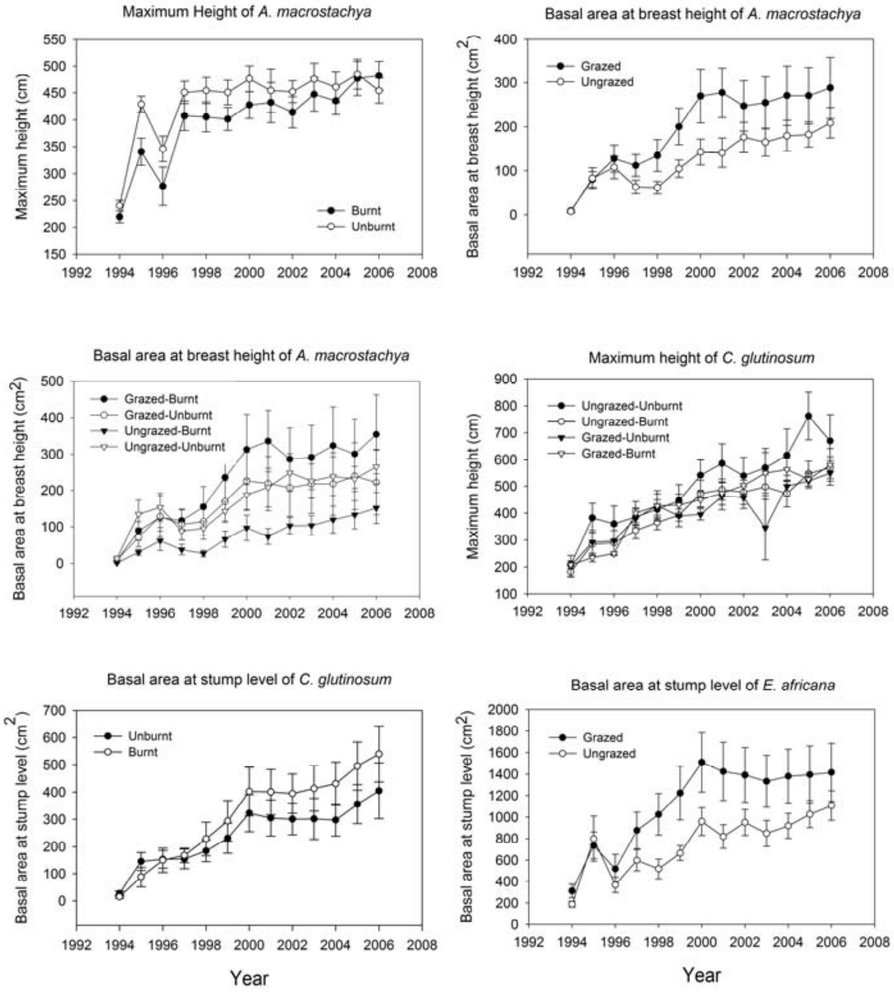


Figure 6. Inter-annual variations in fire, grazing and their interaction effects on resprouts' size parameters of dominant species in Tiogo State forest in the Sudanian savanna-woodlands of Burkina Faso. Graphs are presented for significant results only for the sake of conciseness.

4.4 Community dynamics and productivity of herbaceous species as influenced by fire season

The effects of season of burning on herbaceous species richness, diversity, biomass and abundance were examined. In total, 93 herbaceous species belonging to 25 families and 64 genera were identified at the site during the four years (Appendix 1). Prior to applying the treatments in 2006, the pool of herbaceous species included 10 perennial grasses, 19 annual grasses and 31 forbs. The differences in effects of fires in different seasons is often attributable to the fact that, due to greater heat penetration into the top soil during late fires, they release a greater proportion of seeds from dormancy and, thus promote greater seedling density than do early fires (Williams *et al.*, 2005). Moreover, the germination of seeds (wet or dry, in the soil) is known to be one of the key attributes of season of burn effects (Bond and Van Wilgen, 1996). Records from our study site showed that fire temperature and residence time in the first few cm (2 cm) belowground were substantially higher during late fires than during early fires (Study I). However, no significant difference in herbaceous species' attributes between fire seasons was observed, probably due to the paucity of seed banks at the site (Zida, unpublished data). Moreover our results corroborate those of Sawadogo *et al.* (2005), who did not find significant differences in herbaceous biomass production (at plot level) between prescribed early fire and no fire treatments.

There was, however, inter-annual variation in herbaceous species attributes. Williams *et al.* (2003) reported that fire may have relatively little influence on grass-layer composition in the short to medium term, with inter-annual variation in composition and diversity determined primarily by rainfall. The inter-annual variation in herbaceous species richness, diversity and biomass observed in study V may have been partly due to the differences in precipitation patterns between and within years, since it has been suggested that the dynamics of the herbaceous stratum in dry savannas are affected primarily by intra- and inter-annual variations in rainfall and seasonal drought stress (Seghieri *et al.*, 1994; Nippert *et al.*, 2006; Savadogo, 2007). Moreover, colonization and extinction agents (wind, ants, termites etc.) that could also vary from year to year may have contributed to the variation observed in the dynamics of the herbaceous community. The abundance of the dominant species, *A. ascinodis*, did not vary over time during the study period, probably because this species is well adapted to the area and annual variation in climatic conditions would need to be of wider amplitude and more persistent before its abundance can be affected.

The multivariate analysis (CCA) also showed that fire season could not explain the distribution of species (Fig. 7); the different fire seasons appeared close to each other in the CCA diagram and no clustering of species around a particular fire treatment was observed. This is probably due to the short time scale of the study. Savadogo *et al.* (2009) found that early fire influences the abundance of herbaceous species, but treatment regimes had a significant effect only after a longer period of time (seven years) than the scale tested in our study. Thus, the time scale appears to be a key determinant of the effects of disturbance on the herbaceous species community, and the late fire treatment might have greater effects after some years. It is also possible that the species distribution in this ecosystem is governed by other environmental factors (e.g. small-scale edaphic variables and interactions between ground layer vegetation and trees) that were not assessed in this study. Although fire season was not significant for the species distribution, some species with physical dormancy (*C. planchonii* and *C. mimosoides*) appeared close to mid-season and late-season fire treatments in the CCA ordination diagram, lending credence to the findings of Dayamba *et al.* (2010) that they require high heat temperature from such fire treatments to increase their germination and thus their cover.

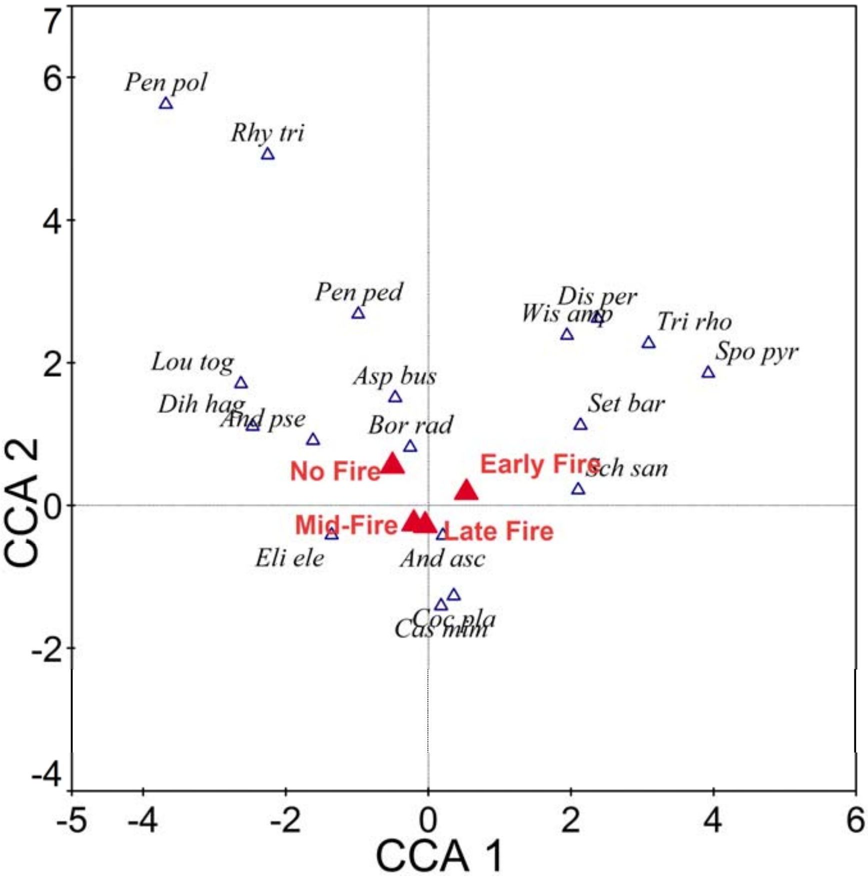


Figure 7. Canonical Correspondence Analysis ordination diagram presenting 18 of the 93 species. Full names of species are presented in Appendix 1.

5 Conclusions and Recommendations

The investigations described in this thesis provide evidence of substantial differences in fire temperature and temperature residence time with respect to season of burning and soil depth, which, in turn, affect the germination of seeds buried in the soil. Early fire, burning from October to December, appeared a good compromise between late fire and no-fire which is utopian in savanna ecosystem. Seed germination responses to fire-related cues confirmed that the degree of smoke responsiveness is a species-specific attribute and that the type (smoke water or aerosol smoke) and concentration of smoke used is of great importance. In addition, smoke responsiveness transcends plant species' ecological characteristics, notably their fire response categories. Heat shock treatment was lethal to certain seeds while temporary heat-induced physiological dormancy was observed in others. The heat level applied in this study failed to break the physical dormancy of all leguminous tree species tested, the Combretaceae *T. avicennioides* and the forbs *C. planchonii* and *T. pedicellata*. Combining smoke and heat is required to draw conclusions regarding the fire response of a species. For instance, the germination of *B. scabra* seeds was promoted by smoke but, as shown by the heat treatments, seeds would first need to survive high heat temperatures during fire. Specific levels of smoke and heat induce maximal germination responses, for instance germination of *T. avicennioides* was maximal following the smoke × heat shock at 120°C treatment. Moreover, all of the tested herbaceous species except *A. gayanus* and *C. schoenanthus* showed low germination (< 50%) irrespective of the treatment applied. The legume trees (*B. africana* and *P. africana*) and herb species (*C. mimosoides* and *T. pedicellata*), the Combretaceae *T. avicennioides*, the Cochlospermaceae (*C. planchonii*) and the Poaceae *B. lata* would need some physical dormancy-releasing treatment (sulfuric acid, mechanical scarification or optimum heat treatment) to increase their germination percentage. The rest of the species, which visually imbibed water but failed to germinate show some embryo dormancy and thus might require a longer after-ripening period or other dormancy-releasing treatments.

After cutting, tree resprouts responded differently to fire and grazing. Fire did not affect the mortality of dominant species such as *A. macrostachya* and *C. glutinosum*, and reduced the mortality of *C febrifuga*. However, grazing increased the mortality of *D. microcarpum* and *E. africana*. The additive effects of fire and grazing result in higher mortality for some species, e.g. *C. ghazalense*. With regards to biomass production, fire effects were not consistent; increases in basal area in burnt plots were observed for some species, such as *C. glutinosum* but decreases for *C. febrifuga* and *D. microcarpum*. Grazing tended to increase basal area of *C. ghazalense* and *E. africana*. Combining grazing and burning results in short individuals. Most of the treatments' effects were more pronounced in later stages of the experiment, confirming the need for long-term experiments to evaluate forest management regimes.

The community dynamics of herbaceous species was not affected by the season of burning, but inter-annual variations in species richness, diversity and biomass were observed, which could be primarily determined by rainfall. The multivariate analysis showed that fire season could not explain the distribution of species and no species had affinity for a particular season of burning. This is probably due to the short time scale of the experiment (4 years) and a longer study period may be required to gain a complete picture.

Overall, moderate livestock grazing could be integrated in the management prescriptions to promote multi-purpose uses of the ecosystem but more attention should be paid to burning conditions to reduce fire severity. Further, assuming optimal dosage levels are identified, fire-related cues (smoke and heat) could have potential uses in reforestation with native species.

Appendix 1. Names and growth forms (PG = perennial grass, AG = annual grass, FO = forbs) of the species encountered at the site during study V.

Species	Code	Life fm	Family
Ageratum conyzoides L.	Age con	FO	Asteraceae
Alysicarpus ovalifolius (Schum.) J. Léonard	Aly ova	FO	Fabaceae
Ampelocissus grantii (Bak.) Planch.	Amp gra	FO	Vitaceae
Anchomanes difformis Engl.	Anc dif	FO	Araceae
Andropogon ascinodis C. B. Clarke	And asc	PG	Poaceae
Andropogon fastigiatus Sw.	And fas	AG	Poaceae
Andropogon gayanus Kunth	And gay	PG	Poaceae
Andropogon pseudapricus Stapf	And pse	AG	Poaceae
Aspilia bussei O. Hoffm. & Muschl.	Asp bus	FO	Compositae
Aspilia rudis Oliv. & Hiern	Asp rud	FO	Compositae
Bidens pilosa L.	Bid pil	FO	Compositae
Biophytum petersianum Klotzsch	Bio pet	FO	Oxalidaceae
Blepharis maderaspatensis Heyne ex Roth	Ble mad	FO	Acanthaceae
Borreria radiata DC.	Bor rad	FO	Rubiaceae
Borreria scabra K. Schum	Bor sca	FO	Rubiaceae
Borreria stachydea (DC.) Hutch. et Dalz.	Bor sta	FO	Rubiaceae
Brachiaria distichophylla Stapf	Bra dis	AG	Poaceae
Brachiaria jubata Stapf	Bra jub	AG	Poaceae
Cassia mimosoides L.	Cas mim	FO	Caesalpiniaceae
Cassia nigricans Vahl	Cas nig	FO	Caesalpiniaceae
Chasmopodium caudatum Stapf	Cha cau	AG	Poaceae
Cissus gracilis Guill. & Perr.	Cis gra	FO	Vitaceae
Cochlospermum planchonii Hook. f. ex Planch.	Coc pla	FO	Cochlospermaceae
Cochlospermum tinctorium Perr.	Coc tin	FO	Cochlospermaceae
Commelina nudiflora L.	Com nud	FO	Commelinaceae
Coreopsis borianiana Sch. Bip. ex Schweinf.	Cor bor	FO	Compositae
Crinum ornatum (L.f.) Herb.	Cri orn	FO	Amaryllidaceae
Crotalaria sp	Cro sp	FO	Fabaceae
Crotalaria vogelii Benth.	Cro vog	FO	Fabaceae
Curculigo pilosa (Schumach. & Thonn.) Engl.	Cur pil	FO	Hypoxidaceae
Cyanotis lanata Benth.	Cya lan	FO	Commelinaceae
Desmodium dicotomum DC.	Des dic	FO	Fabaceae

Appendix 1 (continued)

Species	Code	Life fm	Family
Desmodium sp	Des sp	FO	Fabaceae
Digitaria gayana (Kunth) A. Chev.	Dig gay	AG	Poaceae
Digitaria horizontalis Willd.	Dig hor	AG	Poaceae
Diheteropogon hagerupii Hitchc.	Dih hag	PG	Poaceae
Dyschoriste perrottetii (Nees) O. Ktze.	Dis per	FO	Acanthaceae
Elionurus elegans Kunth	Eli ele	AG	Poaceae
Englerastrum gracillimum T.C.E.Fr.	Eng gra	FO	Lamiaceae
Euclasta condylotricha Stapf	Euc con	AG	Poaceae
Euphorbia hyssopifolia L.	Eup hys	FO	Euphorbiaceae
Euphorbia polycnemoides Hochst. ex Boiss.	Eup pol	FO	Euphorbiaceae
Fimbristylis hispidula Kunth	Fim his	FO	Cyperaceae
Fimbristylis littoralis Gaudich.	Fim lit	FO	Cyperaceae
Hackelochloa granularis (L.) Kuntze.	Hac gra	AG	Poaceae
Hibiscus asper Hook. f.	Hib asp	FO	Malvaceae
Hyparrhenia cyanescens Stapf	Hyp cya	PG	Poaceae
Hyparrhenia diplandra (Hack.) Stapf	Hyp dip	PG	Poaceae
Hyptis spicigera Lam.	Hyp spe	FO	Lamiaceae
Indigofera colutea (Burm. f.) Merrill	Ind col	FO	Fabaceae
Indigofera leprieurii Bak. f.	Ind lep	FO	Fabaceae
Indigofera macrocalyx Guill. & Perr.	Ind mac	FO	Fabaceae
Indigofera pulchra Willd.	Ind pul	FO	Fabaceae
Kaempferia aethiopica Solms ex Engl.	Kae aet	FO	Gimgiberaceae
Kohautia senegalensis Cham. & Schltdl.	Koh sen	FO	Rubiaceae
Lepidagathis anobrya Nees	Lep ano	FO	Acanthaceae
Loudetia togoensis (Pilg.) C.E. Hubb.	Lou tog	AG	Poaceae
Melanthera elliptica O. Hoffm.	Mel ell	FO	Asteraceae
Microchloa indica (L. f.) P. Beauv.	Mic ind	AG	Poaceae
Monocymbium ceresiiforme Stapf	Mon cer	AG	Poaceae
Oldenlandia corymbosa L.	Old cor	FO	Rubiaceae
Pandiaka heudelotii (Moq.) Hiern.	Pan heu	FO	Amaranthaceae
Panicum phragmitoides Stapf	Pan phr	PG	Poaceae
Paspalum orbiculare G.Forst.	Pas orb	AG	Poaceae
Pennisetum pedicellatum Trin.	Pen ped	AG	Poaceae
Pennisetum polystachyon (L.) Schult.	Pen pol	PG	Poaceae
Phyllanthus amarus Schumach	Phy ama	FO	Euphorbiaceae

Appendix 1 (continued)

Species	Code	Life fm	Family
Polycarpaea corymbosa (L.) Lam.	Pol cor	FO	Polycarpaceae
Polycarpaea eriantha Hochst. ex A. Rich.	Pol eri	FO	Polycarpaceae
Polycarpaea linearifolia DC.	Pol lin	FO	Polycarpaceae
Polygala arenaria Willd.	Pol are	FO	Polygalaceae
Polygala multiflora Poir.	Pol mul	FO	Polygalaceae
Pupalia lappacea Juss.	Pop lap	FO	Amaranthaceae
Rhytachne triaristata Stapf	Rhy tri	AG	Poaceae
Rottboelia exaltata L. F.	Rot exa	AG	Poaceae
Sapium grahamii Prain.	Sap gra	FO	Euphorbiaceae
Schizachyrium exile Stapf	Sch exi	AG	Poaceae
Schizachyrium platyphyllum Stapf	Sch pla	AG	Poaceae
Schizachyrium sanguineum (Retz.) Alston	Sch san	PG	Poaceae
Setaria barbata (Lam.) Kunth	Set bar	AG	Poaceae
Setaria parviflora (Poir.) Kerguélen	Set par	PG	Poaceae
Sida alba L.	Sid alb	FO	Malvaceae
Sida urens L.	Sid ure	FO	Malvaceae
Sporobolus microprotus Stapf	Spo mic	AG	Poaceae
Sporobolus pyramidalis P. Beauv.	Spo pyr	PG	Poaceae
Sporobolus sp.	Spo spe	AG	Poaceae
Striga asiatica (L.) Kuntze	Str asi	FO	Scrophulariaceae
Stylochaeton hypogaeus Lepr.	Sty hyp	FO	Araceae
Tephrosia pedicellata Baker	Tep ped	FO	Fabaceae
Tripogon minimus Hochst. ex Steud.	Tri min	AG	Poaceae
Triumfetta rhomboidea Jacq.	Tri rho	FO	Tiliaceae
Waltheria indica L.	Wal ind	FO	Sterculiaceae
Wissadula amplissima R.E.Fr.	Wis amp	FO	Malvaceae

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Résumé en Français (French summary)

La régénération des plantes, leur dynamique et leur productivité est soumise à plusieurs facteurs environnementaux et parmi les plus importants dans les écosystèmes savanicoles, on cite le pâturage, le feu et ses constituants (fumée et chaleur). La présente étude a évalué l'effet des facteurs ci-dessus cités sur la régénération, la productivité et la diversité des strates ligneuse et herbacée dans la savane Soudanienne du Burkina Faso.

La saison des brûlis affecte la température des feux et la durée de la température létale, ce qui affecte la germination des semences du sol. La germination des semences enfumées (de façon expérimentale) est spécifique à chaque espèce et cela est indépendant de la caractéristique écologique de l'espèce notamment sa réaction au feu en milieu réel. Le type et le dosage de la fumée sont des critères à prendre en compte pour une germination maximale. Aussi pour certaines espèces, la combinaison de la fumée et de la chaleur produit les meilleurs taux de germination. La chaleur, à certains degrés, induit chez certaines espèces une dormance physiologique qui peut avoir pour avantage, en milieu réel, de retarder la germination jusqu'à une saison favorable. La pâture et le feu ont par ailleurs été testés pour leur effet sur la dynamique des rejets de souches après coupe de bois. L'effet sur les rejets de souche était spécifique à chaque espèce mais d'une façon général, le feu produit des effets négatifs tandis qu'aucun effet significatif n'a été observé pour la pâture. Pour la strate herbacée, la saison des brûlis n'a affecté ni la richesse spécifique, la diversité, la production en biomasse, ni l'abondance.

En conclusion, les brûlis précoces tels que pratiqués de nos jours pourraient continuer comme compromis entre les feux tardifs et l'utopique protection absolue; mais beaucoup plus dispositions devraient être prises pour réduire autant que possible la sévérité de ces feux. La pâture pourrait être intégrée dans les prescriptions pour promouvoir un usage multiple des forêts. Avec des doses optimales, les facteurs liés au feu (fumée et chaleur) ont une utilisation potentielle dans la reforestation avec les espèces locales.

Mots clés: Feu, fumée, chaleur, pâture, germination, rejets de souche, biomasse, diversité, Burkina Faso, Afrique de l'Ouest.