# Impact of Forest Management Regimes on Ligneous Regeneration in the Sudanian Savanna of Burkina Faso

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Cover: View of the savanna woodland at the beginning of the growing season (left) and fire disturbance (right) at the onset of the dry season (Photo: Didier Zida).

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# Abstract

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Annual early fire, selective tree cutting and grazing exclusion are currently used to manage the State forests of the Sudanian savanna of Burkina Faso, West Africa. Such prescriptions, however, are not based on experimental evidence. The long-term effects of such management on seedlings and saplings and the germination of selected tree species are discussed. Seedling quality attributes are also assessed. Studies over a 10-year period examined the effects of the three management regimes on species richness and population density. *Burkea africana* Kook, f., *Detarium microcarpum* Guill. et Perr., *Entada africana* Guill. et Perr., and *Pterocarpus erinaceus* Poir. seed germination was tested for different temperatures, light conditions, dry heat treatments and scarification methods. The quality of *Acacia macrostachya* Reichenb.ex DC. and *P. erinaceus* planting stock was evaluated in relation to nursery production period; field performance was assessed with and without watering.

Fire, grazing, and selective tree cutting acted independently on sapling and seedling population dynamics. Early fire reduced sapling recruitment; moderate grazing had no significant effect. Although the overall seedling population density was not affected by any of the treatments, fire and grazing had strong effects on single-stemmed seedling density. Ordination using Principal Component Analysis of the seedling population data revealed species-specific responses to treatments, in particular an increase of lianas compared to other species. *D. microcarpum* and *E. africana* seeds did not exhibit dormancy. Exposing *B. africana* seeds to 95-97% sulphuric acid for 15–20 minutes broke their physical dormancy. All seeds tested were neutrally photoblastic, with an optimal germination temperature of 25–35°C. *E. africana*, however, germinated over a wider temperature range. *P. erinaceus* seeds did not tolerate heat shock; while *D. microcarpum* and *E. africana* seeds responded positively at low intensity. Eighteen months after outplanting, survival and growth of *Acacia macrostachya* and *Pterocarpus erinaceus* seedlings were not affected by their initial size. Drought and non-drought factors affected seedling survival. Performance of *P. erinaceus* seedlings could be predicted from initial root collar diameter; more data will be required to build a reliable model.

This thesis recommends the use of annual early fire as a forest management tool to be continued if timing, weather conditions and other factors affecting fire intensity are given due consideration. Moderate level of grazing does not affect seedling and sapling recruitment. The current prohibition on grazing State forests may need revision to allow multiple-use management. The low seedling density of socio-economically valuable species indicates that natural regeneration could be supplemented by planting high quality seedlings.

Keywords: germination; seedling; saplings; lianas; seedling quality; woodland; dry forest; disturbance; West Africa

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# DEDICATION

To the memory of

My mother, Madeleine SAWADOGO,

My father, Michel ZIDA

And

My uncle, Emmanuel ZIDA

# Content

# Appendix

## Papers I – IV

The present thesis is based on the following papers, which will be referred to by their respective Roman numerals.

**I.** Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D. and Odén, P. C. 2007. Dynamics of sapling population in savanna woodland of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. Forest Ecology and Management, 243, 102-115.

**II.** Zida D., Tigabu M., Sawadogo L., Tiveau D., Odén P. C. Long-term effects of prescribed early fire, grazing and selective tree cutting on seedling population in Sudanian savanna of Burkina Faso (Manuscript).

**III.** Zida, D., Tigabu, M., Sawadogo, L., Odén, P. C. 2005. Germination requirements of seeds of four woody species from the Sudanian savanna in Burkina Faso, West Africa. Seed Science and Technology, 33, 581-593.

**IV.** Zida D., Tigabu M., Sawadogo L., Odén P. C. Initial seedling morphological characteristics and field performance of two Sudanian savanna species in relation to nursery production period and watering regimes (submitted).

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# Introduction

## African Savanna biome

The savanna biome comprises wooded grassland characterized by the presence of a xeromorphic, fire tolerant grass layer (Menaut, Lepage & Abbadie, 1995). The savanna is also defined as the transition between closed forest and grasslands or deserts (Breman & Kessler, 1995). Many classification systems for the African vegetation have been proposed (White, 1983), but the major categories range from rainforests to grasslands or steppes. The savanna areas are mainly classified as savanna woodlands, tree and shrub savannas, grasslands or steppes (Menaut, 1983; Scholes & Walker, 1993). In Africa, the savanna area is 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 Zambezian region) occupied by the miombo woodlands (Menaut, Lepage & Abbadie, 1995).

The Sudanian region lies between 6º and 13º N and covers an area of 5.25 million km$^2$ (Menaut, Lepage & Abbadie, 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, Lepage & Abbadie, 1995). The density and size of trees are higher in the savanna woodland formation than in the tree and shrub savannas, and the woody plants often have a distinct tree stature. The Sudanian savanna woodland is more open, less species rich and has smaller trees than the Zambezian woodlands (Menaut, 1983) owing to the higher ambient temperatures caused by lower altitudes and dry “harmattan” winds from the Sahara. Both the Sudanian and the Zambezian woodlands are typically burnt each year during the dry season and repeated burning has exerted a strong selective pressure in favour of fire resistant species (Scholes & Walker, 1993; Menaut, Lepage & Abbadie, 1995). The woody vegetation has tended to disappear as a result of climatic and anthropogenic impacts, and relatively small patches are left within the savanna biome (Menaut, Lepage & Abbadie, 1995). For example, estimates put the rate of deforestation in Burkina Faso at 0.2% per year (FAO, 2001). Because they are ecologically and socio-economically valuable, sustainable management of the savanna woodlands has become a growing global concern.

## Regeneration of woody species in Sudanian savanna

Regeneration is generally defined as a process by which plants replace or re-establish themselves through sexual (from seed) or/and asexual reproduction. Regeneration by seed encompasses an array of processes from seed germination and emergence to subsequent survival of seedlings (Bullock, 2000). The process requires there to be viable seeds at the regeneration site. Generally, there are two seed sources: seed rain (seeds recently dispersed to the site) and the soil seed bank (stored viable seeds on or in the soil). Seed germination is the protrusion of the radicle through the seed coat followed by elongation of the plumule (Fenner &

Thompson, 2005); this is governed by a number of factors, including dormancy (an evolutionary adaptation to delay germination after the seed has been shed from the plant) and suitable environmental conditions such as soil moisture, light and temperature. These germination-regulating factors exhibit a great inter-specific variation as shown in many studies (Teketay & Granström, 1997; Baskin & Baskin, 1998; Tigabu & Odén, 2001; Teketay, 2002). Seeds of the majority of savanna trees are dormant; physical dormancy is the most common type (Baskin & Baskin, 1998). Physical dormancy is the result of a hard and impermeable seed coat that acts as a barrier to the uptake of water and diffusion of oxygen into the embryo. Under natural conditions, this barrier is disrupted by high temperatures, abrasion by soil particles, fire and ingestion by herbivores and birds (Miller, 1995; Baskin & Baskin, 1998; Razanamandranto *et al.*, 2004). By simulating these natural phenomena, a variety of pre-sowing treatments such as hot water, sulphuric acid, and mechanical scarification have been used and have proved successful in overcoming physical dormancy (Bewley & Black, 1994; Teketay, 1996; Baskin & Baskin, 1998; Tigabu & Odén, 2001). The period between seed germination and establishment is the most vulnerable stage in the life cycle of plants, since the seedling is susceptible to damage as a result of unfavourable conditions such as drought (Kitajima & Fenner, 2000) or disturbance factors such as fire or grazing (Fenner & Thompson, 2005).

Most savanna tree species also regenerate vegetatively from dormant or newly formed buds on parent stumps, roots or other tissues (Olivier & Larson, 1996) following disturbances such as fire, herbivory and cutting (Bellefontaine, 1997; Gignoux, Clobert & Menaut, 1997; Bellefontaine *et al.*, 2000; Bationo, Ouédraogo & Guinko, 2001; Sawadogo, Nygård & Pallo, 2002; Ky-Dembele *et al.*, 2007). Several vegetative regeneration mechanisms have been identified among savanna species; namely seedling sprouting, epicormic sprouting or water sprouting, coppicing or stump sprouting, root suckering, and layering. The relative importance of each mechanism is different (Bellefontaine, 1997; Ky-Dembele *et al.*, 2007). Layering (propagation by forming roots on branches), for example is of very little importance (Ky-Dembele *et al.*, 2007); it is a rare regeneration mechanism within the savanna biome. Individuals of sexual and asexual origin differ in their survival and growth rates, dispersal distance, phenology of offspring production and establishment (Winkler & Fischer, 2002). Seeds can be dispersed over long distances, while clonal dispersal is rather limited but has a higher establishment rate than seedlings. Vegetative shoots of clonal recruits grow faster than newly established seed-derived plant because of their well-established root system (Hoffmann, 1998; Walter, 2003). As a whole, the population of woody recruits in the Sudanian savanna is a mosaic of juveniles originating from seeds and sprouts.

## Disturbances and their impacts on regeneration

Natural disturbance regimes are commonly touted as a good model for proper management of forest resources (Roberts, 2007). In Burkina Faso, for example, since 1986 the standard management regime of State forest in savanna woodlands has included the use of annual early fire, prohibition of grazing by livestock and selective tree cutting by harvesting 50% of the of the merchantable standing volume on a 20–year rotation (Bellefontaine, Gaston & Petrucci, 2000). Understanding the impacts of these disturbance regimes on the regeneration of woody species is essential for developing management prescriptions that touted natural disturbances. Disturbance is defined as a change in the structure of a system usually affecting its functioning (Frost *et al.*, 1986). Generally, after disturbances, some species may invade while others decline (Gibson & Brown, 1991). Such functional adaptations underlie two mechanisms of ecosystem response to disturbance: stability and resilience. Ecosystem stability refers to a system that changes little in response to disturbance while a resilient system is one that can change quite markedly as a result of disturbance but has the capacity to return to its original equilibrium condition (Walker & Noy-Meir, 1982; Frost *et al.*, 1986). Ecosystem resilience is an integral part of sustainable development, and understanding how disturbance affects ecosystem structure and function would facilitate making ecologically informed management decisions (Turner *et al.*, 2003). The most important anthropogenic disturbances that determine vegetation patterns in the Sudanian savanna are fire, grazing, browsing and tree cutting (Scholes & Walker, 1993; Breman & Kessler, 1995; Menaut, Lepage & Abbadie, 1995).

Between 25 and 50% of the Sudanian savanna burns annually (Delmas *et al.*, 1991); the entire zone burns every 2-3 years primarily because of human activities (Menaut & Solbrig, 1991). The effect of fire on the regeneration of woody species can be either positive or negative depending on the intensity of burning (Keeley & Fotheringham, 2000). Fires occurring earlier in the dry season tend to be of low intensity since the predominantly herbaceous fuel still holds moisture from the wet season (Liedloff *et al.*, 2001). Such fires, could therefore, enhance colonization processes by inducing a flush of germination. Heat shock during burning acts directly on the seed coat and/or the embryo of many species, thus stimulating seed germination (Teketay, 1996; Baskin & Baskin, 1998; Danthu *et al.*, 2003; Schelin *et al.*, 2003; 2004). Fire also generates smoke, which contains chemical compounds such as ethylene, ammonia, nitrogen oxide and ash that may trigger seed germination, as demonstrated in many studies on smoke-induced germination (De Lange & Boucher, 1990; Brown & van Staden, 1997; Keeley & Fotheringham, 1998; van Staden *et al.*, 2000; Brown & Botha, 2004; Razanamandranto *et al.*, 2005; Tigabu *et al.*, 2007). Burning may also trigger stem sprouting and root suckering in most savanna trees (Hoffmann, 1998) and may favour the development of multi-stemmed individuals of some species (Jacobs & Biggs, 2001).

Small seedlings do not generally tolerate fire and are killed (Kitajima & Fenner, 2000). High-intensity of fire may also create pH and osmotic conditions that are unfavourable for the germination of some species (Keeley & Fotheringham, 2000). Postfire gaps may be drought-prone, since the increased exposure may lead to elevated evaporation and thus reduced moisture availability at shallow soil depths where germination occurs; hence such gaps may contribute to higher rate of extinction. Intense fire may destroy unburied seeds (Razanamandranto 2003) since nearly all fires in West African savanna are surface fires (Menaut *et al.*, 1991), with the highest temperature being close to the soil surface and up to 20 cm above ground (Monnier, 1990; Nikiema, 2005). Fire prolongs the transition period from seedling to sapling as a result of killing the top part of the plants (Hoffmann & Solbrig, 2003). Recurrent fires could also cause a shift in species composition, favouring species capable of vegetative reproduction (Louppe, Ouattara & Coulibaly, 1995; Frost *et al.*, 1996; Hoffmann, 1998). Savanna tree species have evolved adaptive strategies to withstand the effects of fire; these include cryptogeal germination (Jackson, 1974), bark thickness, and wood basic density (Abbot & Lowore, 1999; Nygård & Elfving, 2000; Eriksson, Teketay & Granström, 2003).

Savannas constitute a habitat and/or food source for many herbivores including wildlife and livestock. Livestock is of economic importance in large parts of dryland Africa. For example in Burkina Faso, 85% of all households depend on livestock for some of their income (Gning, 2005). Despite attempts made by local authorities to prohibit livestock grazing from State forests, natural vegetation is the main food source for these animals. Herbivory therefore, constitutes another important disturbance agent with a potential effect on regeneration dynamics in the savanna. Herbivores enhance the colonization process by long distance dispersal of seeds (Miller, 1995; Jordano, 2000; Stiles, 2000), enhancement of seed germination through gut action (Traveset, 1998; Traveset & Verdu, 2002; Razanamandranto *et al.*, 2004) and regulation of tree-grass competition (Scholes & Archer, 1997). Woody plants and grasses interact through competition for light, water and nutrients or facilitation mechanisms (Scholes & Archer, 1997). Grasses may regulate woody plant recruitment directly through competition or indirectly through their effect on fuel load and thus fire intensity. Trees affect herbaceous production and biomass allocation as well as species composition (Scholes & Walker, 1993; Scholes & Archer, 1997). Herbivores can also hinder the regeneration process through seed and seedling consumption (Bationo, Ouedraogo & Boussim, 2000; Bullock, 2000; Bationo *et al.*, 2001; Drexhage & Colin, 2003; Fenner & Thompson, 2005). Depending on the stocking rate, livestock grazing can limit seedling recruitment by exacerbating drought as a result of soil compaction that, in turn, can reduce soil infiltration (Kozlowski, 1999; Savadogo, Sawadogo & Tiveau, 2007). Livestock can also impede seedling and sapling growth through over-browsing.

In most African countries, the woodlands provide both urban and rural populations not only with non-timber resources (fruit, medicines, fodder) but also with the greatest proportion of their fuel (Soto Flandez, 1995; Abbot & Lowore, 1999; Nygård, Sawadogo & Elfving, 2004). For example in Burkina Faso, wood account for 91% of energy consumption and selective tree cutting has been adopted as management tool for woodfuel production (Sawadogo, 2006). Selective tree cutting opens gaps in vegetation communities, reducing competition for resources such as light, nutrients and water, and inducing changes in soil temperature (Bullock, 2000). Depending on the level of reduction in competition and other factors influencing regeneration, the gaps created could be colonized by seedlings from soil seed banks, seed rains or seedling banks. Generally, the change in light intensity and quality (red: far-red ratio) as well as the level and fluctuations in temperature induce seed germination in many tree species (Teketay & Granström, 1997; Bullock, 2000; Yirdaw & Leinonen, 2002; Yirdaw & Luukkanen, 2004). It has been reported that emergence and survival of emerged seedlings increase with the number of canopy gaps (Bullock, Clear Hill & Silvertown, 1994; Bullock, 2000; Hutchinson, Sutherland & Yaussy, 2005) and gap size (Vandenberghe *et al.*, 2006) when light is the main limiting factor. However, in moisture-limited, open environments such as the Sudanian savanna, the beneficial effect on seedling establishment of gaps created by selective removal of trees could be reduced as a result of depletion of water resources. Moreover, in this savanna ecosystem the changes in resource availability and environmental conditions following selective tree cutting will affect not only woody species but also the herbaceous layer. Indeed, many trials carried out in southern African savannas and elsewhere have shown an immediate increase in grass production following removal of woody plants (Scholes & Walker, 1993; Gambiza *et al.*, 2000). This leads to more severe competition with ligneous regeneration. Colonization of post-cutting gaps can also result from asexual reproduction by, for example coppices and root suckers, since most savanna tree species are capable of regenerating vegetatively (Frost *et al.*, 1996; Bellefontaine, 1997; Bellefontaine *et al.*, 2000; Sawadogo, Nygård & Pallo, 2002).

Disturbance is common in plant communities and interactions may occur between disturbance types (Fenner & Thompson, 2005). For example, herbivores reduce grass biomass and hence the fuel load available for fires. The resulting low intensity fire can favour seedling and sapling recruitment (Scholes & Walker, 1993). The available evidence indicates that a strong grazer-browser-fire interaction exists; this in turn influences tree-grass mixtures (Scholes & Archer, 1997). In contrast, the increase in grass production following selective tree removal in savannas (Scholes & Walker, 1993; Gambiza *et al.*, 2000) may lead to more intense fires, adversely affecting seedling and sapling recruitment. Moreover abiotic factors such as soil characteristics and rainfall alone or in combination with these disturbances can also play key roles in the regeneration process (Frost *et al.*, 1986). These complex independent and/or interactive effects of disturbances on the regeneration of woody plants are highly variable and are not yet fully understood, despite continued research efforts. Therefore, understanding the impacts of fire, grazing, selective cutting of trees and their interactions is still needed in order to support sustainable management of savanna resources.

## Background to Forest Management in Burkina Faso

Management of forests and woodlands in West Africa has been influenced by the political and climatic histories of the region. In the 1930s a large part of the North Sudanian zone of West Africa was delimited and protected by the colonial administration as wildlife sanctuaries and to prevent the expansion of shifting cultivation (Shepard, 1992). After the Independence forests and woodlands have been preserved through the establishment of State forests for wood production and biodiversity conservation. In Burkina Faso, State forest reserves represent 25% of the total area of forests and woodlands, which covers 7.1 million ha or 26% of the country's land area (Kaboré, 2004). These State forests have continuously been used as sources of urban woodfuel and sometimes illegally as rangelands. After the severe drought years in the Sahelian region in the 1970s, large scale plantation projects using exotic species such as *Eucalyptus camaldulensis* Denh., *Gmelina arborea* Roxb., and *Tectona grandis* L. f. were initiated to meet the urban woodfuel needs and to control desertification; unfortunately these turned out to be costly (Jensen, 1997; Bellefontaine, Gaston & Petrucci, 2000; Nygård, 2000). From the 1980s, natural forest management emerged as a subject of interest in Burkina Faso, and participatory forest management (with wide responsibility and ownership assigned to the local population) has been implemented (Kaboré, 2004). Forest management action plans (programs, policies and acts) covering the technical, political or legal aspects of natural forest management, including regulation of disturbance factors such as fire, tree cutting and livestock grazing, have been drafted and implemented since the 1990s (Kaboré, 2004). Among other approaches, the application of annual early fire was formally adopted to minimize the risk of intense late fire and to improve pasture production for wildlife (Sawadogo, 1996; Sawadogo, 1998; Bellefontaine, Gaston & Petrucci, 2000). Selective tree cutting has been employed since 1986, harvesting 50% of the merchantable standing volume on a 20–year rotation (Bellefontaine, Gaston & Petrucci, 2000; Kaboré, 2004). Harvested plots are kept free from fire and grazing by livestock for 3 to 5 years and direct seeding with selected indigenous species is also undertaken with the intention of supplementing regeneration. Various issues have emerged as a result of these management practices. The lack of accurate volume functions has led to difficulties in assessing and controlling the stand volume (Kaboré, 2004). Furthermore, early fire following 3 years protection from grazing has shown a detrimental effect on ligneous regeneration at the experimental sites in Laba State forest (Manauté, 1996). This is due to the accumulation of grass biomass that favours intense fires. Direct seeding has produced unsatisfactory results, with low survival rates: 6% and 2% after 1 and 2 years, respectively, despite good germination rates of up to 80% (Kaboré, 2004; Sawadogo, 2006).

Although studies have been conducted on coppice growth (Renes, 1991; Nouvellet, 1993; Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004) and regeneration of a few selected species (Bationo, 2002), the long term effects of early fire, selective cutting and livestock grazing, on the dynamics of natural regeneration are not well known (Sawadogo, 2006). Thus, empirical evidence is still highly needed for an informed discussion on current woodland management strategies and to highlight possible improvements.

## Objectives

The general objective of this thesis was to gain knowledge that would support sustainable management of savanna-woodlands in Burkina Faso. The thesis presents data on the impacts of different management regimes (fire, grazing, selective tree cutting and their interactions) on ligneous regeneration and the need for assisting the natural regeneration process. The specific objectives were to:

1. Examine the dynamics of sapling populations in response to annual early fire, grazing and selective tree cutting by analyzing changes in species richness and sapling population density over a ten year period (Study-I);
2. Examine the effects of fire, grazing and selective cutting on seedling recruitment in the mid- and long-term by analyzing changes in seedling population density and species richness five and ten years after post treatment (Study-II);
3. Identify the seed germination requirements of selected savanna woodland species (Study-III); and
4. Identify seedling morphological attributes that ensure better field performance of two Sudanian woodland species (Study-IV).

# Materials and Methods

## Study areas

Study I was carried out at Tiogo (12°13' N, 2°42' W) and Laba (11°40' N, 2°50' W) State forests (forêts classées) while study II was conducted at Laba. Both experimental sites are in Burkina Faso, West Africa (Fig. 1) and located on flat areas at an altitude of 300 m a.s.l. Phyto-geographically the study sites are situated in the Sudanian regional centre of endemism (White, 1983) in the transition from the north to south Sudanian Zone (Fig. 1) (Fontes & Guinko, 1995). Laba and Tiogo State forests cover 17 000 and 30 000 ha, respectively.

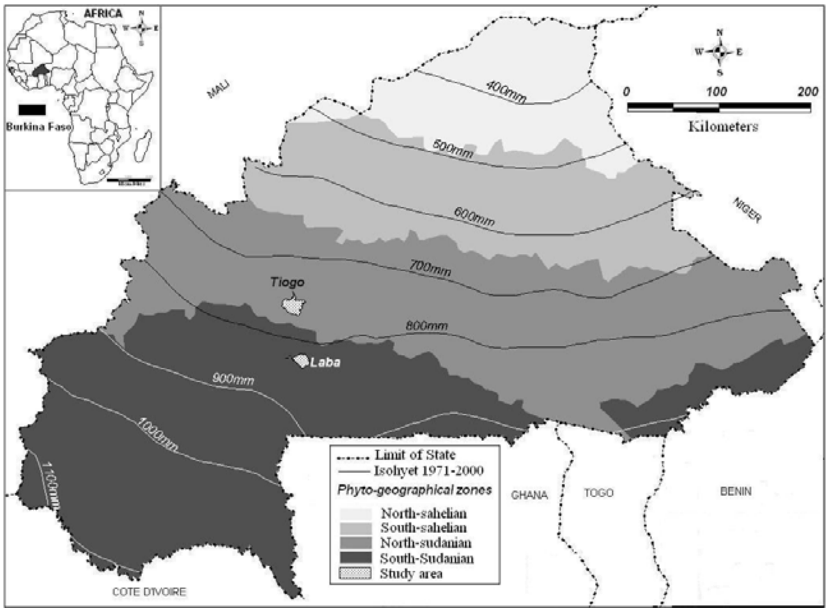

*Fig. 1.* Vegetation map of Burkina Faso with isohyets and location of the two study sites (Readapted April 2007 by CTIG/INERA, Burkina Faso after Fontes & Guinko 1995 and Direction of the National Meteorology).

The vegetation at both sites is a tree and bush savanna with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard and the perennial grasses *Andropogon gayanus* Kunth. (dominant in Tiogo) and *Andropogon ascinodis* C.B.Cl. (dominant in Laba). The main forb species are *Cochlospermum planchoni* Hook. F., *Borreria stachydea* (DC) Hutch. et Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Fries. The woody vegetation at both sites is dominated by Mimosaceae and Combretaceae. The main species in terms of basal area are *Detarium microcarpum* Guill. et Perr., *Combretum nigricans* Lepr. ex Guill. et Perr., *Acacia macrostachya* Reichenb. ex DC., *Entada africana* Guill. et Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpus* (D.C.) Guill. et Perr. and *Vitellaria paradoxa* Gaertn. f. Prior to the start of the experiment, trees at Laba had a mean basal area at stump level (20 cm above ground) and at breast height (130 cm above ground) of 10.7 and 6.3 $m^2$ $ha^{-1}$, respectively, and a stand density of 582 individuals $ha^{-1}$. Corresponding values at Tiogo were 10.9 $m^2$ $ha^{-1}$ and 6.1 $m^2$ $ha^{-1}$ at stump level and breast height, respectively, with a stand density of 542 individuals $ha^{-1}$ (Sawadogo, Nygård & Pallo, 2002).

The unimodal rainy season generally lasts about six months from May to October. The mean (± SD) annual rainfall for the period 1993 – 2001 was 910 ± 138 mm at Laba and 836 ± 219 mm at Tiogo. The number of rainy days per annum during the study period was 76 ± 13 and 70 ± 9 at Laba and Tiogo, respectively. There was large inter-annual variability in rainfall and number of rainy days per annum (Fig. 2). Mean daily minimum and maximum temperatures are 16 and 32°C in January (the coldest month) and 26 and 40°C in April (the hottest month) with an aridity index (Brown & Lugo, 1982) of 3.2 and 3.5 for Laba and Tiogo, respectively. According to the FAO's classification system (Dreissen, Deckers & Spaargaren, 2001), Lixisols are the most common soil type at both study sites; these soils occur over large tracts of the Sudanian zone in Burkina Faso (Pallo, 1998). Generally, the soils are shallow (<45 cm depth) silty-sand at Laba and mainly deep (>75 cm) silty-clay at Tiogo; some of their physical and chemical properties are :17.5% and 24.8% clay, 12.6% and 20.2% silt, 28.4% and 17.4% sand, 2.1% and 1.8% total organic matter, 0.1% and 0.1% total nitrogen, 1.3ppm and 1.4ppm available phosphorus for Laba and Tiogo, respectively (Sawadogo, Tiveau & Nygård, 2005).

## Methods

### *Studies I and II*

A split-plot experiment was established to examine the effects of fire (no fire / annual early fire), grazing (no grazing / grazing), cutting (no cutting / selective tree cutting) and their interactions on sapling (study I) and seedling (study II) populations. At Laba and Tiogo, each experimental site was split into two main plots, one of which was fenced at the beginning of the dry season in December 1992 to exclude grazing by livestock. Each main plot was further divided into 4 blocks of 2.25 ha, each containing four subplots of 0.25 ha (50 x 50 m), separated from each other by 20 – 30 m fire-breaks. The following treatments were randomly assigned to the four subplots within each block of the main plot, no cutting – no fire, no cutting – early fire, cutting – no fire, and cutting – early fire (Fig. 3).

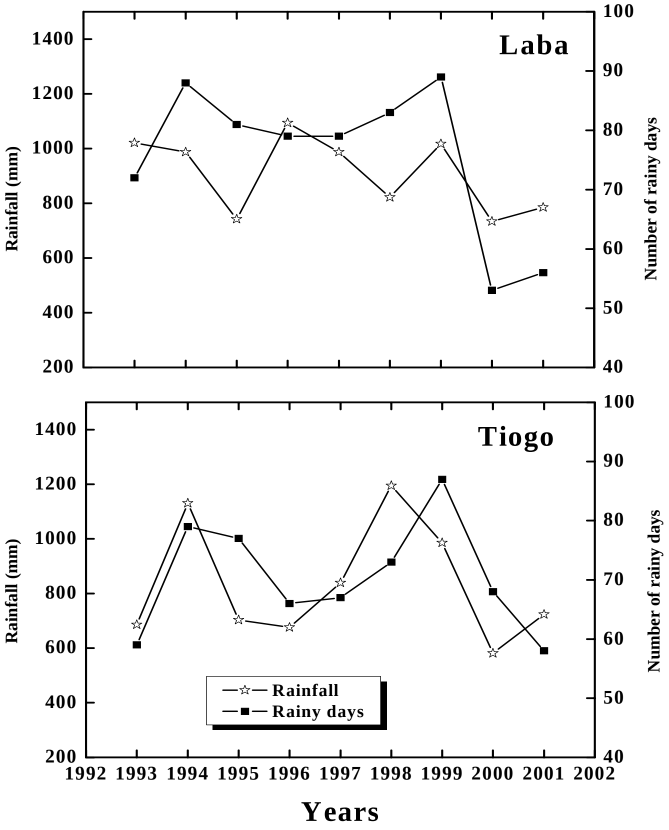

*Fig. 2.* Rainfall and number of rainy days for the study period (1993-2001) at Laba and Tiogo sites, Burkina Faso.

The selective cutting was conducted in December 1993 at Tiogo and 1 month later in January 1994 at Laba; 50% of the basal area at stump level was removed. In the savanna woodlands where trees are often multi-stemmed and existing volume functions often not applicable (Clement, 1982; Breman & Kessler, 1995; Kaboré, 2004; Nygård, Sawadogo & Elfving, 2004) it was easier to monitor removal of 50% of the basal area than the 50% of the merchantable volume as recommended in the management plan. Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and woodfuel, and woodfuel and other uses. Individuals in categories other than "protected species" were cut according to the following size criteria: > 30 cm diameter at stump level for timber species, > 14 cm diameter at stump level for poles and woodfuel species and > 8 cm diameter at stump level for woodfuel and other uses (Sawadogo, Nygård & Pallo, 2002). The prescribed early fire was applied at the end of the rainy season (October – November) each year beginning in 1992 when the grass layer humidity was approximately 40%. At both sites the main plot open for grazing was predominantly frequented by livestock, but wild animals also grazed there.

The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit $ha^{-1}$ (T.L.U. $ha^{-1}$) and in Tiogo it was 1.4 T.L.U. $ha^{-1}$ (Sawadogo, 1996); the grazing pressure at both sites was about half of this capacity (Sawadogo, Tiveau & Nygård, 2005). The presence of livestock in both forests varied spatially and temporally, mainly occurring during the rainy season when grasses were green and surrounding areas under cultivation.

At both experimental sites, the sapling inventories were carried out in 1992 (before applying the treatments) then ten years later in 2002. The seedlings were assessed in 1992, 1997 and 2002 at Laba. The following parameters were recorded in each 50 x 50 m subplot: species name, number of stems per individual, stem height, girth at stump level (for stems ≥ 10 cm girth), girth at breast height (for stems ≥ 10 cm girth). Changes in species richness and population density were calculated for both sapling and seedling populations and assessed by analysis of variance. Height class distribution and growth attributes were also investigated. The seedling data were also investigated using Principal Component Analysis (PCA) in order to explore the responses at the individual species level. Species identification and nomenclature followed Hutchinson et al. (1954) and Arbonnier (2002).

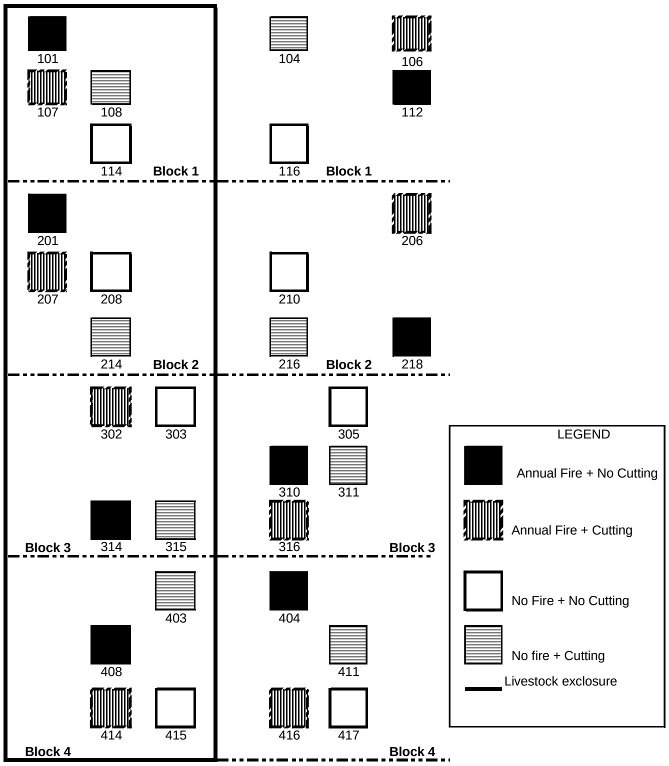

*Fig. 3*. Layout of the experimental design.

### Study III

This study was an investigation of the germination requirements of four leguminous species from the Sudanian savanna, namely *Burkea africana* Hook. f., *Detarium microcarpum*, *Entada africana*, and *Pterocarpus erinaceus* Poir. Information on the nature of dormancy in three of these species is scarce; *Pterocarpus erinaceus* seeds, however, are not dormant, so do not need pre-treatments (CNSF, 1995). The optimal germination temperature, light requirement and responses to heat shock for these species are not well known. Seeds of the four species were purchased from the National Tree Seed Centre in Ouagadougou, Burkina Faso and the germination trial conducted at Umeå, in the seed laboratory of the Faculty of Forest Sciences of SLU (Sweden). Seeds of *B. africana, D. microcarpum, E. africana* and *P. erinaceus* were collected in 2002, 2001, 1997 and 2002 from Sapouy, Ougarou, Koaré/Gourma and Nazinga in Burkina Faso, respectively. They were subjected to different scarification treatments (mechanical scarification, sulphuric acid and hot water). For the temperature experiment, seeds were placed in Petri dishes with filter paper and incubated on a thermo-gradient table set at 20, 25, 30, 35 and 40°C. Where appropriate, seeds were scarified to condition them for temperature response tests. The effect of light was investigated by sowing one set of scarified seeds (where necessary) in a dark room and the other set under constant light, 20 $\mu Em^{-2}s^{-1}$ (fluorescent lamp F40 W/33 RS cool white light) at room temperature. In the dry heat experiment, seeds were exposed to heat shock in a preheated oven at a range of different temperatures (70, 80, 90 and 100°C) and durations (20, 40 and 60 minutes).

A total of 100 seeds, four replicates of 25 seeds each, were used in each treatment for *B. africana*, *E. africana* and *P. erinaceus*. For *D. microcarpum*, 80 seeds (four replicates of 20 seeds each) were used in each treatment because of this species' large seed size. The germination process was monitored every day and germination was recorded when seeds had produced a 2 mm radicle of normal appearance. Germination capacity and mean germination time were calculated for each treatment and analyzed using a two-way ANOVA to test for significant differences among dry heat treatments and species, and one-way ANOVA to test the main effects of scarification treatments and temperature regimes. The effect of light conditions on seed germination for each species was compared using a t-test.

### *Study IV*

In this study, variations in initial seedling morphology and field performance of two economically valuable species, *Acacia macrostachya* and *Pterocarpus erinaceus*, were investigated. Seeds of *A. macrostachya* and *P. erinaceus* were purchased from the National Tree Seed Centre in Ouagadougou, Burkina Faso, and seedlings were raised in the nursery of the Institute of Environmental and Agricultural Research, Department of Forest Production in Ouagadougou from November 2003 to August 2004. Seedling production was designed in such a way that three seedling age groups (3-, 6- and 9- months old) were obtained by the time of outplanting. A 2 × 3 factorial experiment was designed to test the effects of watering regime (no watering / dry season watering) and nursery production period (3-, 6-, 9- months old seedlings) on survival, growth and biomass production of the seedlings. Seedlings were planted out at Saria Agricultural Research Station (12º 16′N – 2º 09′W; 300 m a.s.l.) in the Sudanian zone of Burkina Faso in August 2004 (during the rainy season). The planting site was divided into two blocks separated by 58 m, and each block was further divided into 6 plots of 18 × 8 m, these were separated from each other by 4 m (Fig. 4).

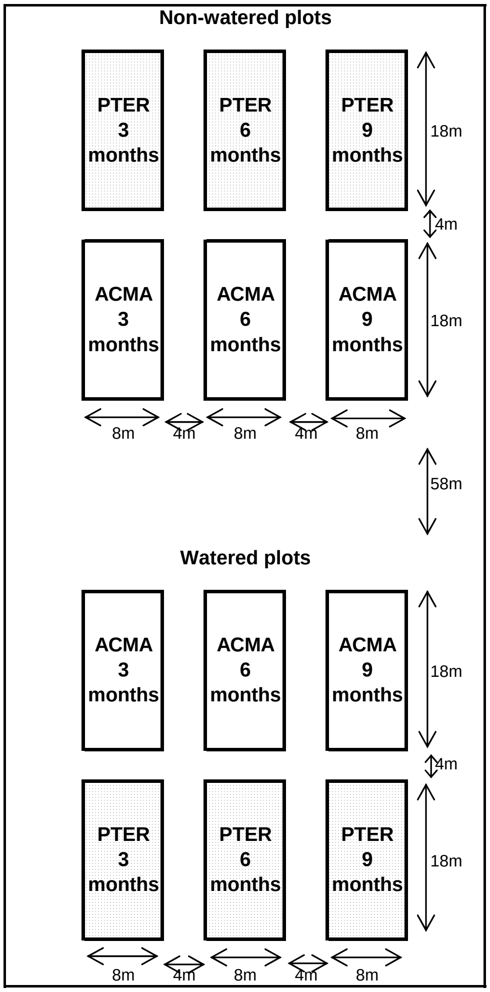

*Fig. 4.* Layout of the design for the planting experiment at Saria research station, Burkina Faso. ACMA = *Acacia macrostachya*; PTER = *Pterocarpus erinaceus*.

In each plot, 50 seedlings from one age group per species were planted. In one of the blocks, each planted seedling was watered with 5 litres of water twice a week during the dry season (October to May) while the other block was not watered. The planting site has a unimodal rainy season lasting for 6 months, from May to October. The experimental site was fenced to exclude large herbivores.

To quantify the variation in morphological characteristics of seedlings of different age, a sample of 30 seedlings per species and nursery age group was randomly selected prior to planting and measured for seedling height, root collar diameter and shoot and root dry mass. One month after planting out, the root collar diameter and total height of all seedlings in each treatment group were recorded; a second assessment was made 18 months after planting out. Relative growth rate (RGR) for root collar diameter and height were estimated based on 30 randomly selected individuals in each age group and species. In order to quantifying shoot and root dry masses after 18 months, five individuals of *A. macrostachya* from each watering regime and age group were randomly selected and harvested. For *P. erinaceus*, six individuals from each age group and watering regime were sampled to account for the observed variation in size within each age group. The shoot and root parts were separated and oven dried at 105ºC for 24 hours to determine the dry mass.

To examine the extent to which seedling death was caused by drought, the relative importance of drought as a cause of seedling mortality (*I*) and a drought performance parameter ($D_p$) were calculated following Engelbrecht, Thomas & Melvin (2005):

$$I = \frac{(M_D - M_W)}{M_D} = \frac{M_E}{(M_E + M_W)}$$

$$Dp = \frac{S_D}{S_W} \times 100 = 100 - \frac{S_W - S_D}{S_W} \times 100$$

Where $M_W$ = mortality in the watered plot, $M_D$ = mortality in the non-watered plot, $M_E$ = extra mortality in the non-watered plot ($M_D$ - $M_W$), $S_W$ and $S_D$ are the survival over 18 months in watered and non-watered plots, respectively. Since the calculation of *I* is based on two assumptions: (1) drought was not a cause of mortality in the watered plot, and (2) non-drought factors act equally on both treatments, it provides information on direct drought effects but may include mortality due to interactions between drought and other factors. To further assess whether initial seedling age had an effect on drought tolerance, the “proportional growth” for each age group was calculated as the ratio between the mean total biomass of seedlings in the drought stress treatment and that of the well-watered group. This followed Munns (2002), who proposed that stress tolerance should be assessed as the proportion of biomass production under stressed conditions in relation to that produced under control conditions. A two-Way ANOVA was performed to determine whether root collar diameter, height and biomass production were significantly affected by watering regime and initial seedling age. Each individual seedling was treated as a replicate during statistical analyses of the data and a stringent level of significance (0.01) and log- or square root-transformations were employed for data sets that violated the requirement for homoscedasticity and normality (Zar, 1996). Both simple and multiple linear regression analyses were performed to establish the relationship between initial shoot height, root collar diameter and or both at the time of planting and after 18 months of growth in the field.

# Results and Discussion

## Dynamics of sapling populations

The effects of fire, grazing and selective tree cutting on population dynamics of saplings in the Sudanian savanna woodlands are independent, as evidenced by the lack of significant interaction effects. Annual early fire had the strongest influence on the dynamics of the sapling population: it significantly reduced species richness, density of saplings and CAI in basal area at both study sites (Fig. 5). Recurrent burning probably limits species composition by favouring fire tolerant species and/or species adapted to resprouting after fire, since both fire tolerant and intolerant species grew well on unburnt plots. For example, we observed that *Anogeissus leiocarpus* was highly invasive in fire exclusion plots. The effect of fire on species richness is consistent with previous studies (Gignoux, Clobert & Menaut, 1997; Hoffmann, 1998; Hutchinson, Sutherland & Yaussy, 2005). The negative effect of fire on woody plant density has been reported previously by many authors (Gambiza *et al.*, 2005; Hutchinson, Sutherland & Yaussy, 2005; Albrecht & McCarthy, 2006). Nevertheless, in this study, the prescribed annual fire did not totally suppress recruitment of saplings, only slowed the rate of recruitment. This is consistent with previous studies in African savannas (Hochberg, Menaut & Gignoux, 1994; Menaut, Lepage & Abbadie, 1995). The delay in the rate of sapling recruitment could be responsible for the low basal area increment on burned subplots at both study sites, although basal area growth is related not only to number of individuals in the stand (density) but also to tree age, even in unburnt plots (West, 2004). A similar result was found in the miombo woodlands where basal area of woody plants was significantly reduced by frequent fires (Gambiza *et al.*, 2000).

Annual prescribed early fire favoured growth of multi-stemmed woody plants rather than the single-stemmed sapling population, as evidenced by the negative rate of change of the later, particularly at Laba (Fig. 5). This could be because fire destroys the aboveground biomass, inducing sprouting of newly formed and/or dormant buds that are present on the remaining stems and roots (Menaut, Lepage & Abbadie, 1995; Hoffmann & Solbrig, 2003; Kennedy & Potgieter, 2003) leading to a multi-stemmed morphology. Top-kill is also probably responsible for the observed effects on height class distribution and reduced annual increment in dominant height.

Grazing by livestock did not affect species richness, rate of change in population density or growth of saplings. Since the grazing intensity on the experimental plots was half of the carrying capacity, many species were able to survive this moderate level of grazing, allowing succession to proceed, but limiting the ability of highly competitive species to dominate the community. Belsky & Blumenthal (1997) provided evidence showing that low to moderate levels of herbivory sometimes have no measurable effect on species richness. Browsing can also turn a single stemmed individual into a multi-stemmed individual during the early stages of growth by removing the apical buds, as evidenced by the increasing tendency of the number of multi-stemmed individuals on grazed compared with ungrazed plots.

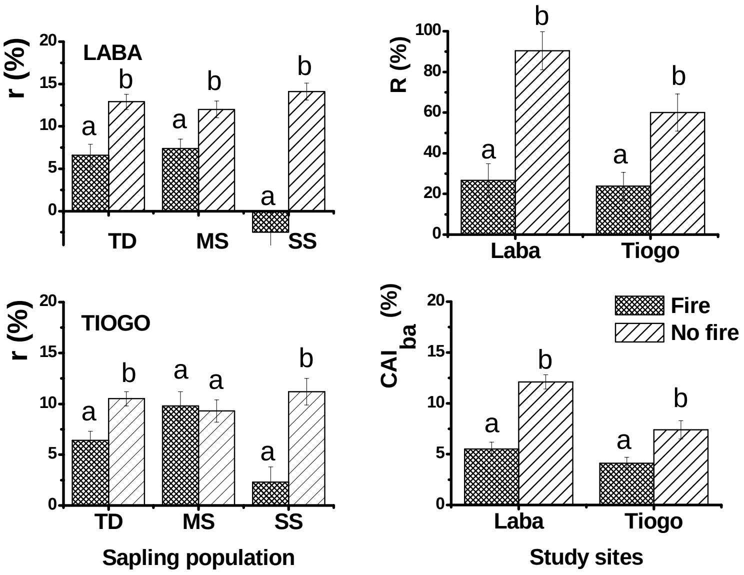

*Fig. 5.* Fire main effect on annualized rate of change in sapling population density (r), proportional increase in species richness (R) and current annual increment in basal area ($CAI_{ba}$). TD stands for Total population density, MS for multi-stemmed subpopulation density and SS for single-stemmed subpopulation density. Bars with same letters show non-significant difference in mean values.

Although selective removal of trees is expected to enhance the recruitment process by reducing competition for water and nutrients, opening up more growing spaces and increasing light quality and intensity in the understory (Frost *et al.*, 1986; Hutchinson, Sutherland & Yaussy, 2005), it did not affect sapling recruitment in these experiments on the Sudanian savanna woodlands. This may be related to the initial stock of trees. If tree density is high prior to cutting, selective cutting of trees reduces competition for resources and thus has a clear effect. However, savanna woodlands are not dense, so further opening of the canopy may create unfavourable thermal conditions in the understory, increasing soil evaporation and plant evapotranspiration, thus counterbalancing the expected positive effects of increased water and nutrient availability.

A number of factors influence the treatment effects; these include spatio-temporal heterogeneity in vegetation and rainfall, the presence of bush clumps, and differential sensitivity of species to treatments. The mosaic of annual (*Loudetia togoensis*) and perennial (*Andropogon gayanus*) grasses affects the distribution and availability of dry grass at the time of burning. The amount and distribution of annual rainfall over the study period (Fig. 2) had a great effect on species composition and biomass of the herbaceous layer (Breman & Kessler, 1995; Sawadogo, Tiveau & Nygård, 2005). This, in turn, affected fuel load. Bush clumps occur on termite mounds that are very resistant to fire even when exposed to extreme burning, thus fire generally skirts around the edges leaving the centre unburnt. The rate of recruitment of saplings is therefore influenced by such patchiness of the vegetation. Species growing on termite mounds, for example, like *Fertetia apodanthera* Del., *Tamarindus indica* Linn., *Combretum micranthum, Acacia erythrocalyx* Brenan and *Capparis sieperia* Lam., are seldom reached by fire and therefore grow faster (pers. obs.). Species that are sensitive or tolerant to fire and grazing exist in this savanna woodland in varying proportions. For example, the density of *Detarium microcarpum* was substantially higher on plots protected from burning, particularly at Laba. This species coppices vigorously but coppice shoots protected from fire and livestock during two consecutive years failed to survive burning in the third year (Manauté, 1996), indicating their sensitivity to fire. Species, such as *Crossopteryx febrifuga* (Afzel. Ex G. Don) Benth. and *Piliostigma thonningii* (Schumach.) Milne-Redhead, have greater fire resistance owing to their investment in thicker bark and higher aboveground growth rates (Gignoux, Clobert & Menaut, 1997).

## Dynamics of seedling populations

The overall species richness at the seedling stage is comparable to the whole stand species richness, but many species are represented by very few individuals (see appendix). The high proportion of tree species with few seedlings has already been reported as typical characteristics of many African savannas (Menaut, Lepage & Abbadie, 1995; Chidumayo & Frost, 1996; Luoga, Witkowski & Balkwill, 2004). Although the relative change in total seedling species richness was not significantly influenced by any of the treatments, the number of seedling species increased over the study period. This suggests that the management regimes played a minor role in the colonization process, which is governed by quality and quantity of dispersed seeds, soil seed banks, sprouts and suckers, and, the number of safe sites for establishment (Teketay & Granström, 1995; Teketay, 1997a; 1997b; Murray & Garcia, 2002; Luoga, Witkowski & Balkwill, 2004). On the experimental site, the soil seed bank probably plays a minor role in the recruitment of seedlings due to an overall paucity of viable soil-stored seeds of woody species (Zida, unpublished data). With respect to seedling morphology, the number of species with multi-stemmed individuals was higher on plots under the fire × cutting regime compared to the control. This can be related to the ability of most savanna trees to coppice and produce root suckers following disturbances like cutting and fire (Olivier & Larson, 1996; Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004). The number of species with single stem was much lower on burnt than unburnt plots. Fire kills the aboveground parts of plants, so may stimulate bud formation and activate dormant buds that produce root suckers or sprouts (Menaut, Lepage & Abbadie, 1995; Hoffmann & Solbrig, 2003). Recurrent or high intensity fires coupled with low seedling densities could increase the mortality rate of single-stemmed seedlings, since many seedling species were present at very low densities (see appendix).

Fire and grazing treatments substantially reduced the seedling density, particularly that of the single-stemmed sub-population. While herbivores kill seedlings by direct consumption or trampling (Braithwaite & Mayhead, 1996; Hester, Mitchell & Kirby, 1996; Drexhage & Colin, 2003), recurrent burning increases mortality by killing young succulent seedlings or exacerbating drought in post-burn environments (Gambiza *et al.*, 2005; Hutchinson, Sutherland & Yaussy, 2005; Albrecht & McCarthy, 2006). High intensity fire also limits seedling recruitment as a result of its destructive effect on unburied seed, as shown by several studies dealing with the effects of fire on seed germination (Teketay, 1996; Danthu *et al.*, 2003; Schelin *et al.*, 2003; 2004). Selective tree cutting tended to decrease seedling density, particularly that of single-stemmed individuals. This may be because cutting exacerbates drought by creating unfavourable thermal conditions in the understory (Frost *et al.*, 1986; Hutchinson, Sutherland & Yaussy, 2005), and increases the competitive exclusion of single-stemmed seedlings by suckers, sprouts and herbaceous species (Sawadogo, Nygård & Pallo, 2002; Nygård, Sawadogo & Elfving, 2004). In addition, cutting reduces the available seed source through decreased seed rain into the already impoverished soil seed bank. The effects of some treatments, such as fire on species richness interacted significantly with inventory time. This indicates inter-annual variation in fire intensity and severity, which in turn depends on life form, quantity of fuels, weather conditions and moisture content of fuels (Frost *et al.*, 1986). Temporal variation in grazing intensity, stocking rate and feeding behaviour is common in the Sahel (Hiernaux, 1998), and creates spatial and temporal heterogeneity in the fuel load and fire intensity.

The species level PCA ordination highlighted two important issues. First, the species that responded very well (i.e. having the largest change in total seedling density) to some treatments were lianas (woody vines). For example, *Baissea multiflora* A. DC. (code = BAMU) and *C. sepiaria* (code = CACO) were relatively more abundant in the fire × cutting plots while *Opilia celtidifolia* (Guill. Et Perr.) Endl. Es Walp. (code = OPCE) was relatively more abundant in grazing plots and grazing × fire plots (Fig. 6) than in the other plots. Species such as *B. multiflora* and *A. erythrocalyx* (code = ACPE) were even relatively more abundant in the control plot than the other plots. Lianas influence a number of essential forest processes, such as reducing tree growth and fecundity, increasing tree mortality and altering gap-phase regeneration (Schnitzer, Dalling & Carson, 2000; Schnitzer & Carson, 2001; Schnitzer, Kuzee & Bongers, 2005), thus their population size should be maintained at a level that does not adversely affect wood production and biodiversity conservation. It should, however, be noted that lianas play significant ecological and socio-economic roles in tropical forest vegetation: they contribute to the carbon budget and have ethno-botanical values. Thus, they deserve to be conserved in their ecosystem (Schnitzer & Bongers, 2002; Senbeta *et al.*, 2005).

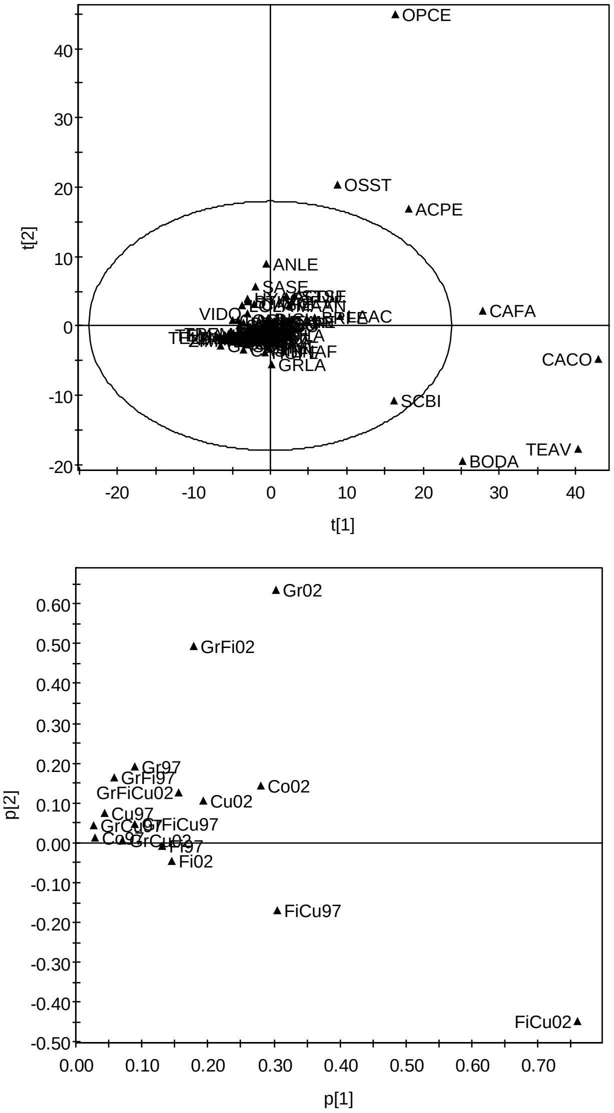

*Fig. 6.* Score (top panel) and loading (lower panel) plots from PCA ordination of species and treatments and year for the first two principal components for the overall seedling population. For species code, see appendix. Treatments were coded as followed: control (Co), grazing (Gr), fire (Fi), cutting (Cu) and their combinations.

The second important aspect is the relatively small change in total seedling density of socio-economically valuable species (e.g. *Burkea africana*, *Combretum nigricans*, *Acacia macrostachya* and *Entada africana*) irrespective of the management regimes applied. This accentuates the importance of supplementing the natural regeneration of these species through planting high quality seedlings as direct seeding has not been successful (Kaboré, 2004).

## Seed germination requirements

Seeds of the species tested in this study responded differently to the various scarification treatments. Both treated and untreated seeds of *D. microcarpum* and *E. africana* almost all germinated. Mechanical scarification and sulphuric acid treatments for 15 and 20 minutes resulted in higher germination of *B. africana* seeds (Fig. 7). Apparently, the hard seed coat acts as a physical barrier for the uptake of water, thus preventing germination of *B. africana* seeds. Mechanical scarification disrupts this barrier, allowing the uptake of water and oxygen by the seed and permits radicle emergence by weakening the seed coat. Sulphuric acid disintegrates the seed coat and the micropylar plug, thereby allowing increased imbibition and subsequent germination of seeds (Baskin and Baskin, 1998). Mechanical scarification and concentrated sulphuric acid have been widely used to improve germination of several species with hard seed-coat (Teketay, 1996; Sy, Grouzis & Danthu, 2001; Tigabu & Odén, 2001; Delachiave & De Pinho, 2003). The success of hot water treatment is not universal and species-specificity exists. For example, hot water treatments have been reported to enhance the germination of several legumes and species with a hard endocarp (Teketay, 1996; Tigabu & Odén, 2001; Schelin *et al.*, 2003), as reflected by the positive responses observed in the present study on seeds of *D. microcarpum* and *E. africana*. However, seeds sensitive to hot water treatments have also been reported (Teketay, 1996; Teketay & Tigabu, 1996; Tigabu & Odén, 2001). In this study, the seeds that did not germinate were all hard and intact, indicating that the hot water treatment was not sufficient to scarify the hard seed coat of *B. africana*.

The effect of dry heat treatment varied between species. Seeds of *D. microcarpum* and *E. africana* germinated well at low intensity heat shock (70 and 80°C). The stimulatory effect of dry heat treatment is often attributed to cracking of the seed coat or splitting of the palisade layer of the micropyle, thereby allowing imbibition, diffusion of oxygen and lowering mechanical resistance to the protrusion of the radicle (Baskin and Baskin, 1998). A number of studies have shown that dry heat treatments (60-100°C) break physical dormancy in the seeds of a range of species (Mucunguzi & Oryem Origa, 1996; Teketay, 1996; Schelin *et al.*, 2003; 2004). The germination of *B. africana* and *P. erinaceus* seeds was erratic and unsatisfactory after heat shock treatment compared with the control. The post germination assessment revealed that nearly all ungerminated seeds of *P. erinaceus* were dead. This indicates that seeds of this species are extremely sensitive to heat shock, so that fire, through its effect on the soil seed bank, could limit the regeneration by seed of this species in its natural habitat. It has been shown that the effect of heat shock on seeds without physical dormancy is related to their ability to withstand fire (Danthu *et al.*, 2003; Razanamandranto, 2003). This effect depends, however, on the intensity of fire, which can vary between 40 and 140°C in the Sudanian savanna (Razanamandranto, 2003) where *P. erinaceus* grows naturally. Seeds of *B. africana* that remained ungerminated were still hard and intact, indicating that either high intensity heat shock or extended time of exposure to dry heat treatments is required to scarify the hard seed coat. Physical dormancy and the erratic nature of germination of *B. africana* seeds could explain the species' poor natural regeneration in the Sudanian savanna in Burkina Faso (See Study-II).

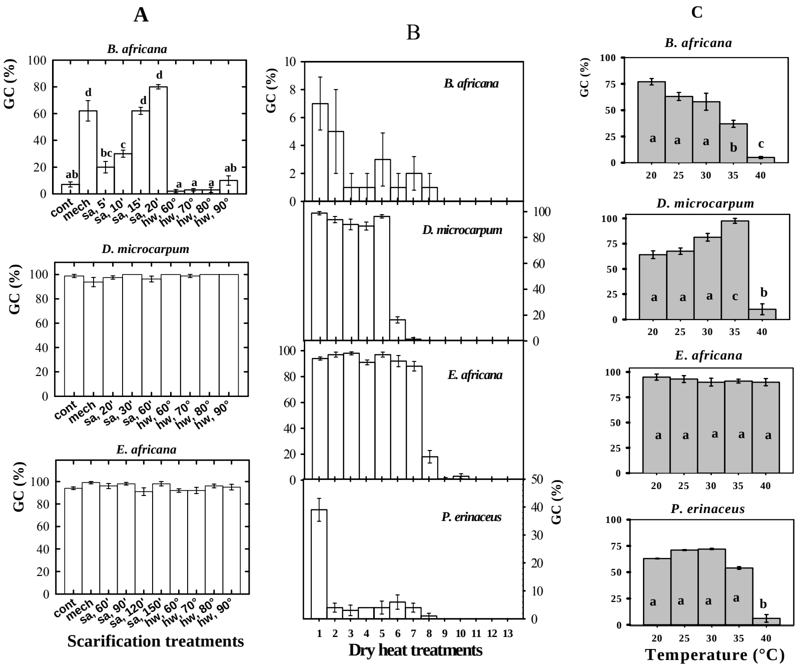

***Fig. 7.*** Germination capacity of seeds of Sudanian woody species in response to scarification treatments (A), dry heat treatments (B) and different constant temperature regimes (C). Scarification treatments were as followed; mechanical scarification (mech), sulphuric acid (sa), hot water (hw), and control (cont). Dry heat treatments were; treatment no. 1, control; 2-4, dry heat at 70°C for 20, 40 and 60 min; 5-7, dry heat at 80°C for 20, 40 and 60 min; 8-10 dry heat at 90°C for 20, 40 and 60 min; and 11-13, dry heat at 100°C for 20, 40 and 60 min, respectively. Values are mean ± SE and bars with the same letter (s) are not significantly different using Tukey's test (p = 0.05).

Seeds of the species tested exhibited different responses when incubated at different constant temperature. The germination of *B. africana* seeds was high when incubated between 20 and 30°C while the optimal temperature for germination of *D. microcarpum* was 35°C. Seeds of *P. erinaceus* germinated well across the temperature range of 20-35°C and *E. africana* seeds also germinated rapidly and in a large number at all temperature. These results are consistent with previous studies on several legumes and other woody species (Teketay, 1996; Teketay & Tigabu, 1996; Tigabu & Odén, 2001). The high degree of thermo-plasticity displayed by seeds of *E. africana* enables the species to germinate and establish readily in the Sudanian savanna ecosystem, which is characterized by high temperatures, 16-40°C, and relatively long dry periods, 5-7 months, with an aridity index of 3.7 (Sawadogo, Nygård & Pallo, 2002). Seeds of all four species germinated equally well in light and dark conditions, suggesting that germination of these species is not light-dependent (neutral-photoblastic). This result is consistent with previous studies of other woody species from similar dry ecosystems (Teketay & Tigabu, 1996; Teketay, 1998).

## Assessment of Seedling quality

For *P. erinaceus,* nearly all morphological attributes were significantly lower for younger seedlings than older ones. Only the root collar diameter of *A. macrostachya* seedlings exhibited significant differences in relation to nursery production period (Fig. 8).The actual mean values of the various morphological attributes differed slightly among age groups, which might be associated with depletion of nutrients over time as fertilizer was not applied during seedling production. In fact, the growth of containerized seedlings in the nursery is affected not only by the length of the production period but also by various nursery practices, such as the type of substrate, container size and type, watering and fertilization regime (Bayley & Kietzka, 1996; Wightman, Shear & Goldfrab, 2001; Aphalo & Rikala, 2003). Apparently, nursery farming practices other than production period should be manipulated in order to produce seedlings with a wide range of morphological attributes. This would allow seedling quality to be evaluated on the basis of the morphological characteristics of seedlings prior to planting.

Survival of seedlings in the field was considerably high (more than 70%) for both species irrespective of initial age at nursery and dry season watering treatment. This could be related to the intact root system of container-grown seedlings, which resulted in lower resistance to water flow through the soil-plant-atmosphere continuum (Grossnickle, 2005). Since the degree of disturbance to the root system during lifting, transporting and planting is much lower for container-grown seedlings, these seedlings experience lower plant water stress after planting out and achieve better survival in the field than bare rooted seedlings. This finding is consistent with the results reported by Engelbrecht and Kursar (2003) where both dry season irrigation and seedling size at the onset of drought had no significant effect on survival of potted seedlings of 12 out of the 28 tropical woody species they investigated. The high survival rate of both small and large seedlings could also be explained by the favourable root to shoot dry mass ratio (> 1.0 g/g) at the time of planting, which was also maintained in the field. Despite the higher field survival, seedling mortality as high as 30% was recorded. Drought accounted for 75% of the observed mortality in 3- and 9-month old seedlings of *A. macrostachya* while non-drought factors were the major cause of death in 6-month old seedlings.

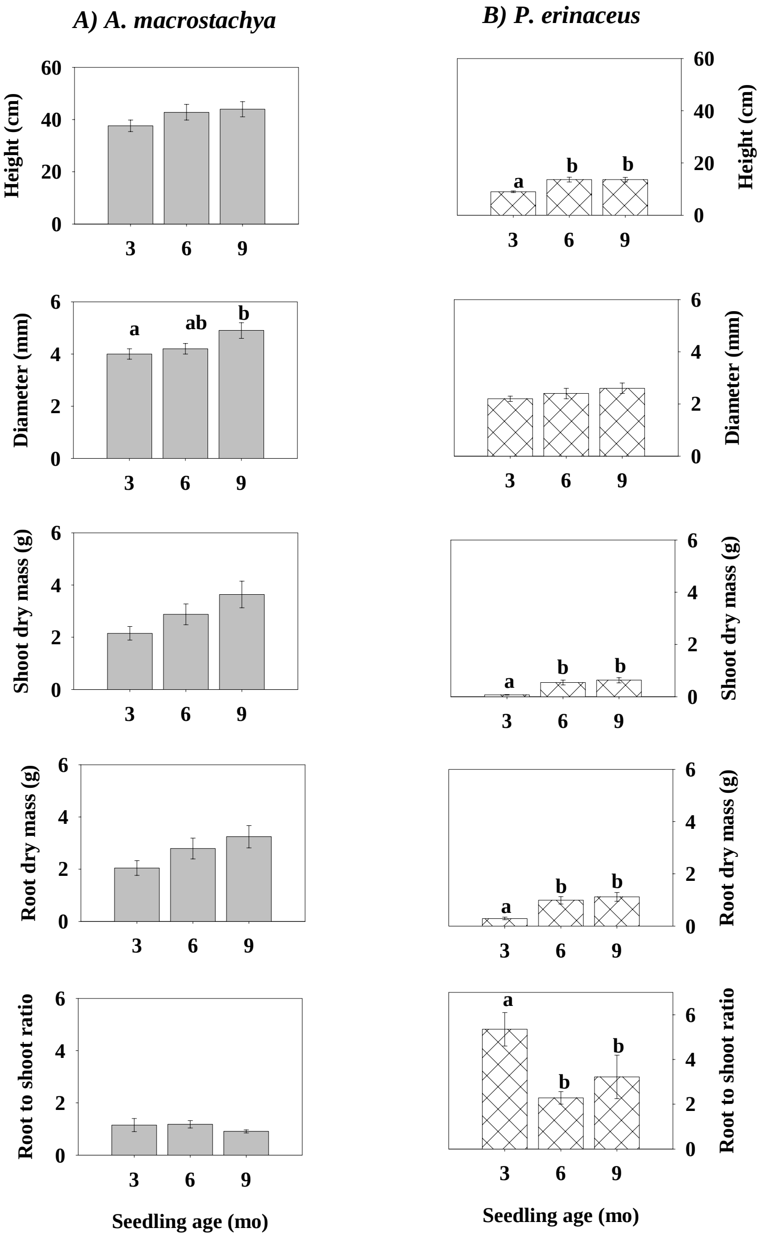

*Fig. 8.* Seedling sizes of *A. macrostachya* (A) and *P. erinaceus* (B) differing in nursery age prior to outplanting (Mean ± SE). Bars with the same letter are not significantly different.

In the case of *P. erinaceus*, non-drought stressors were the major causes of seedling mortality, particularly for 3- and 9-month old seedlings as evidenced by the higher mortality in watered than non-watered plots (Fig. 9).

Seedling mortality can occur as a direct result of drought stress or non-drought stressors, such as herbivores, pathogens or competition exacerbated by drought (Gerhardt, 1996; 1998; Engelbrecht, Thomas & Melvin, 2005). Mortality of watered seedlings of *P. erinaceus* was mainly the result of herbivory (pers. obs.). Indeed, during the dry season when most of the plants have shed their leaves, the watered *P. erinaceus* seedlings attracted herbivores such as rodents, ants, and grasshoppers, which eat the green leaves and shoots. This situation could be one of the factors responsible for the delay in transition of seedlings to sapling stage, resulting in limited sapling population density in the study area (see study - I). Defoliation by insects has been suggested as one of the causes of seedling mortality in dry Afromontane forest species (Teketay, 1997b), in two Neotropical secondary forest species (Gerhardt, 1998), and in *Andira inermis* (W. Wright) Kunth ex. DC seedlings in both wet and dry plots (Engelbrecht, Thomas & Melvin, 2005). The results suggest that the importance of drought as a causal agent of seedling mortality (particularly for *P. erinaceus*) has been overestimated.

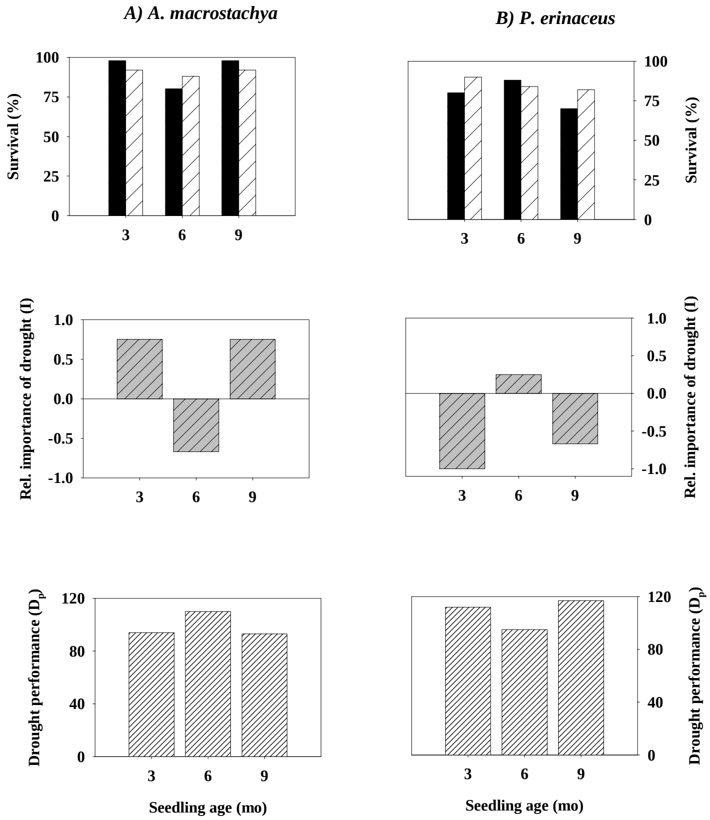

*Fig. 9.* Survival of *A. macrostachya* (A) and *P. erinaceus* (B) seedlings in watered (black bar) and dry plots (striped bar) after 18 months of outplanting, and the relative importance of drought as causes of seedling mortality (I) and drought performance ($D_p$).

Young and old seedlings of *P. erinaceus* were morphologically distinct at the time of planting. In contrast, *A. macrostachya* seedlings differed significantly only with respect to collar diameter. However, younger and older seedlings of both species had favourable root to shoot dry mass ratios (> 1.0 g/g) at the time of planting, and continued to maintain the same pattern in the field regardless of their initial age. Patterns of biomass allocation between shoot and root systems are the result of species environmental conditions, age, season, soil type and abiotic pressure as well as growth form and phenology (Snyman, 2005). Plants are also capable of adjusting the relative sizes and distribution of organs (e.g. shoot canopies, root systems) in response to changes in the supply of resources (Paz, 2003); these eventually determine plant growth rate. In general, when the availability of soil nutrients and water increases, plants allocate relatively less to their root system – the so called "resource optimization hypothesis". The high biomass allocation to roots, which is a common strategy for species in dry sites, could be driven by drought stress and/or low soil nutrient availability. This high allocation to roots regardless of seedling initial age resulted in reduced aboveground growth, which explains the lack of significant differences in height growth for both species in this study.

It is interesting to note that allocation to roots differs between species investigated; i.e. the root to shoot dry mass ratio was much higher for *P. erinaceus* than *A. macrostachya* seedlings in both watered and non-watered plots. This might be an important component of adaptive strategies for recruitment of *P. erinaceus* following disturbances. *Pterocarpus erinaceus* has a lingo-tuber type of tap root, typical of species adapted to resprouting following shoot dieback. The available evidence indicates that savanna trees have higher root to shoot ratios and a high level of total non-structural carbohydrate (TNC) reserves in their roots (Dembele, 2004; Hoffmann, Orthen & Franco, 2004). This results in greater resprouting ability following burning while rendering seedlings more tolerant to fire (Hoffmann, 2000). The relatively high root to shoot ratio of *P. erinaceus* seedlings compared with that of *A. macrostachya* could also be partly related to shoot damage induced by defoliators in the former species.

Seedling shoot height and root collar diameter alone or in combination with other seedling attributes have been used to relate planting stock quality to future field success (Thompson & Schultz, 1995; Bayley & Kietzka, 1996; Dey & Parker, 1997; Jacobs, Salifu & Seifert, 2005). In this study, the usefulness of initial shoot height in predicting future growth performance in the field appeared to be marginal, accounting for 6.2% and 7.2% of the variation in field height and diameter, respectively. This could be, in part, because, the initial variation in shoot height of individual seedlings was very low. On the other hand, repeated seedling shoot dieback in response to high temperature stress might render height a poor indicator of field performance. Root collar diameter prior to planting, however, appeared to be a potential predictor of future diameter growth of *P. erinaceus* in the field, as evidenced from the relatively high coefficient of determination (25%). Similar results have been reported for red oak seedlings, where the best predictive model was based on initial root collar diameter and predicted as high as 23% to 51% of the variation in second-year field diameter (Dey & Parker, 1997; Jacobs, Salifu & Seifert, 2005). There is evidence of a strong and significant correlation between root collar diameter and many root characteristics (such as root volume, tap root dry mass, total root dry mass, and first order lateral roots) that influence seedling performance in the field (Dey & Parker, 1997; Jacobs, Salifu & Seifert, 2005). The large unexplained variation in both single- and multiple-trait models might be attributed to several uncontrolled factors such as genetics, root to shoot ratio and/or amount of stored reserves. These were not incorporated into the model.

# Concluding remarks and practical implications

Results of these studies provide little evidence of significant additive effects of fire, grazing and selective tree cutting on the regeneration of woody species in the Sudanian savanna. The two components of woody species regeneration (seedling and sapling populations) reacted differently to the management regimes. Fire was the most detrimental with respect to sapling recruitment and affected the seedling population mainly by reducing the density of single-stemmed individuals without significantly impacting on the overall seedling recruitment. It should be noted that early fire did not completely halt sapling recruitment but simply slowed down the rate. Therefore, provided that due care is taken with regard to the timing of burning, weather conditions and other possible factors that increase fire intensity, the use of early fire as a management tool in Sudanian savanna, is a good compromise between the utopian aim of total protection and the occurrence of more damaging late fires. Grazing had the same effects as fire on the seedling population but had no effect on the sapling population. Moderate level of livestock grazing did not hinder overall seedling recruitment, although it did reduce the density of the more vulnerable single-stemmed seedlings. Therefore prohibition of livestock grazing from State forests, which is intended to protect ligneous regeneration, may need to be reconsidered especially when a lack of resources makes it difficult for the State to enforce the policy. In addition, there is an increasing demand from local communities for livestock feed. Empowering the local population could help to control grazing intensity. Selective tree cutting did not significantly affect sapling or seedling recruitment. Cutting intensities other than 50% of the basal area may need to be evaluated to achieve the expected beneficial effects of selective cutting on regeneration. At the seedling stage, the population of lianas increased relatively more across the study period in both treated and control plots than the other socio-economically valuable species. The existing management strategies may need to incorporate cleaning operations to regulate the liana populations, thereby preventing them from hampering tree growth without sacrificing their diversity.

The investigation on germination requirements concluded that *Burkea africana* seeds need mechanical scarification or acid treatment to effectively break their physical dormancy. Seeds of *Detarium microcarpum* and *Entada africana* do not need scarification, but scarified seeds germinate more rapidly. Seeds of *P. erinaceus* did not tolerate heat shock while those of *D. microcarpum* and *E.*

*africana* responded positively to low intensity heat shock. Seeds of all species investigated in this study germinated well at 25-35°C, and in both light and dark conditions. Seeds of *E. africana* showed exceptionally high germination performance over all temperature regimes tested.

The results of the seedling quality assessment experiment suggest that nursery practices other than length of production period should be considered to produce seedlings with the required morphological and physiological attributes for enhanced field performance. Survival of outplanted seedlings was high irrespective of dry season watering and initial seedling size as a result of high root to shoot ratio. Drought tolerance was not related to initial size and the importance of non-drought stressors on seedling mortality was observed. Root collar diameter at the time of planting had a potential for being used as predictor of the field performance of *P. erinaceus* seedlings. This could be further improved by using a wide range of initial root collar diameters during the development of a predictive model.

# Appendix

A complete list of species in the seedling population together with their growth form and density (average number of individuals per ha) in 1992, 1997 and 2002 at Laba. Species were grouped per local use following Nouvellet et al. (1995) and Sawadogo et al. (2002). Growth form (GF) description was translated from Guinko (1984): lTr = large tree, mTr = medium-sized tree, sTr = small tree, Bu = bush, Sh = shrub, sSh = sub-shrub, Li = liana.

| | Code | GF | 1992 | 1997 | 2002 |
|---|---|---|---|---|---|
| **Protected species** | | | | | |
| *Afzelia africana* Smith ex Pers. | ALAF | mTr | 1 | 4 | 1 |
| *Albizia chevalieri* Harms | ALCH | sTr | 17 | 3 | 3 |
| *Albizia malacophylla* (A. Rich.) Walp. | ALBO* | mTr | 2 | 9 | 7 |
| *Balanites aegyptiaca* (L.) Del. | BAAE | Bu | 19 | 49 | 69 |
| *Bombax costatum* Pellegr. et Vuillet | BOCO | sTr | 21 | 56 | 62 |
| *Khaya senegalensis* (Dersr.) A. Juss. | KHSE | lTr | - | - | 58 |
| *Lannea acida* A. Rich. | LAAC | sTr | 4 | 37 | 19 |
| *Lannea microcarpa* Engl. et K. Krause | LAMI | sTr | 2 | 4 | 2 |
| *Lannea velutina* A. Rich. | LAVE | Bu | 7 | 26 | 14 |
| *Parkia biglobosa* (Jacq.) Benth. | PABI | mTr | 2 | 2 | 3 |
| *Prosopis africana* (Guill. et Perr.) Taub. | PRAF | sTr | 4 | 5 | 3 |
| *Pterocarpus erinaceus* Poir. | PTER | sTr | 42 | 124 | 80 |
| *Saba senegalensis* (A. DC.) Pichon | SASE | Li | 3 | 2 | 3 |
| *Sclerocarya birrea* (A. Rich.) Hochst. | SCBI | sTr | 4 | 11 | 7 |
| *Sterculia setigera* Del. | STSE | sTr | 2 | 9 | 6 |
| *Stereospermum kunthianum* Cham. | STKU | sTr | 29 | 35 | 34 |
| *Tamarindus indica* Linn. | TAIN | mTr | 9 | 23 | 33 |
| *Terminalia laxiflora* Engl. | TELA | sTr | 66 | 79 | 4 |

# Appendix (continued)

| | Code | GF | 1992 | 1997 | 2002 |
|---|---|---|---|---|---|
| *Vitellaria paradoxa* Gaertn. f. | BUPA* | sTr | 81 | 162 | 201 |
| *Vitex doniana* Sweet | VIDO | sTr | 2 | 3 | 2 |
| **Timber** | | | | | |
| *Burkea africana* Hook. f. | BUAF | mTr | 46 | 81 | 63 |
| *Isoberlinia doka* Craib et Stapf | ISDO | mTr | 1 | - | - |
| *Mitragyna inermis* (Willd.) O. Kuntze | MIIN | sTr | - | - | 6 |
| *Terminalia avicennioides* Guill. et Perr. | TEAV | Bu | 15 | 85 | 151 |
| *Terminalia macroptera* Guill.et Perr. | TEMA | sTr | 1 | 5 | 1 |
| *Xeroderris stulhmannii* (Taub.) Mendonça&E.P. Sousa | OSST | sTr | 5 | 23 | 19 |
| **Pole and fuelwood** | | | | | |
| *Acacia polyacantha* Willd. | ACPO | sTr | - | - | - |
| *Anogeissus leiocarpus* (DC.) Guill. et Perr. | ANLE | mTr | 72 | 126 | 106 |
| *Combretum nigricans* Lepr. ex Guill. et Perr. | CONI | Bu | 62 | 72 | 103 |
| *Crossopteryx febrifuga* (Afzel. Ex G. Don) Benth. | CRFE | sTr | 75 | 103 | 113 |
| *Detarium microcarpum* Guill. et Perr. | DEMI | Bu | 525 | 1428 | 857 |
| *Diospyros mespiliformis* Hochst. ex A. Rich. | DIME | sTr | 3 | 7 | 6 |
| *Pseudocedrela kotschyi* (Schweinf.) Harms | PSKO | mTr | 19 | 27 | 13 |
| *Ziziphus mauritiana* Lam. | ZIMA | Sh | - | - | 1 |
| **Fuelwood and others** | | | | | |
| *Acacia dudgeoni* Craib. ex Hall. | ACDU | Bu | 133 | 667 | 383 |
| *Acacia erythrocalyx* Brenan | ACPE* | Li | 35 | 133 | 316 |
| *Acacia macrostachya* Reichenb.ex DC. | ACMA | Sh | 89 | 201 | 124 |
| *Acacia nilotica* (L.) Willd. ex Del. | ACNI | Bu | 1 | - | - |
| *Acacia seyal* Del. | ACSE | Bu | 3 | 5 | 3 |
| *Acacia sieberiana* DC. | ACSIE | sTr | - | - | 2 |
| *Allophyllus africanus* P. Beauv. | ALAF | Sh | - | 12 | 20 |
| *Annona senegalensis* Pers. | ANSE | sSh | 211 | 316 | 242 |
| *Baissea multiflora* A. DC. | BAMU | Li | - | 2 | 33 |
| *Boscia senegalensis (*Pers.) Lam ex Poir. | BOSE | Sh | - | - | 1 |
| *Boswellia dalzielii* Hutch. | BODA | sTr | - | 1 | - |
| *Bridelia ferruginea* Benth. | BRFE | Bu | 5 | 6 | 9 |
| *Cadaba farinosa* Forssk. | CAFA | sSh | 2 | 8 | 12 |
| *Capparis sepiaria* L. | CACO* | Li | 3 | 17 | 39 |
| *Cassia sieberiana* DC. | CASIE | Bu | 3 | 6 | 5 |
| *Senna singueana* (Del.) Lock | CASIN | sSh | 9 | 9 | 8 |
| *Combretum fragrans* F. Hoffm | COFR | Bu | 225 | 380 | 276 |
| *Combretum glutinosum* Perr. ex DC. | COGL | Bu | 1 | 2 | 2 |
| *Combretum micranthum* G. Don. | COMI | Sh | 3 | - | - |
| *Combretum molle* R. Br. ex G. Don | COMO | Bu | 39 | 41 | 32 |
| *Dichrostachys cinerea* (L.) Wight et Arn. | DICI | Sh | 59 | 201 | 159 |
| *Entada africana* Guill. et Perr. | ENAF | Sh | 6 | 14 | 11 |
| *Feretia apodanthera* Del. | FEAP | sSh | 36 | 75 | 113 |
| *Gardenia erubescens* Stapf et Hutch. | GAER | sSh | - | 8 | - |
| *Gardenia sokotensis* Hutch. | GASO | sSh | 8 | - | 1 |
| *Gardenia ternifolia* Schum et Thonn. | GATE | sSh | 159 | 184 | 133 |
| *Grewia bicolor* Juss. | GEBI | Bu | 23 | 38 | 41 |

# Appendix (continued)

| | Code | GF | 1992 | 1997 | 2002 |
|---|---|---|---|---|---|
| *Grewia flavescens* Juss. | GRFL | Sh | 3 | 2 | - |
| *Grewia lasiodiscus* K. Schum. | GRLA | Sh | 3 | 1 | 3 |
| *Grewia venusta* Fresen. | GRMO* | Sh | 52 | 75 | 68 |
| *Guiera senegalensis* J. F. Gmel. | GUSE | Sh | 2 | 1 | 1 |
| *Ozoroa insignis Del.* | HEIN* | *Sh* | *3* | *2* | *1* |
| *Holarrhena floribunda* (G. Don) Dur et Schinz | HOFL | Bu | 3 | 1 | 3 |
| *Hymenocardia acida*Tul. | HYAC | Bu | 5 | 12 | 9 |
| *Lonchocarpus laxiflorus* Guill. et Perr. | LOLA | sTr | 4 | 16 | 3 |
| *Maerua angolensis* DC. | MAAN | Sh | 3 | 3 | 4 |
| *Maytenus senegalensis* (Lam.) Exell | MASE | Sh | 4 | 7 | 6 |
| *Opilia celtidifolia* (Guill. et Perr.) Endl. ex Walp. | OPCE | Li | - | 2 | 18 |
| *Pericopsis laxiflora* (Benth.) van Meeuwen | AFLA* | sTr | 15 | 23 | 25 |
| *Piliostigma reticulatum* (DC.) Hochst. | PIRE | Sh | 2 | 2 | 1 |
| *Piliostigma thonningii* (Schumach.) Milne-Redh. | PITH | Sh | 66 | 111 | 98 |
| *Pteleopsis suberosa* Engl. et Diels | PTSU | Bu | 126 | 276 | 278 |
| *Securidaca longepedunculata* Fres. | SELO | Bu | 1 | 1 | 5 |
| *Securinega virosa* (Roxb. ex Willd.) Baill. | SEVI | Sh | 17 | 60 | 59 |
| *Strychnos innocua* Del. | STIN | Sh | - | - | 8 |
| *Strychnos spinosa* Lam. | STSP | Sh | 238 | 391 | 342 |
| *Trichilia emetica* Vahl | TREM | sTr | - | 5 | 1 |
| *Ximenia americana* L. | XIAM | sSh | 2 | 1 | 1 |
| *Ziziphus mucronata* Willd. | ZIMU | Sh | 1 | 5 | 2 |

* Code adopted from species synonym

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# French summary (Résumé en Français)

## Impact des mesures d’aménagement forestier sur la régénération ligneuse dans la savane soudanienne du Burkina Faso

Le feu précoce annuel, la coupe sélective de bois et l’interdiction du pâturage sont actuellement les principales prescriptions utilisées dans l’aménagement des forêts classées dans la zone soudanienne du Burkina Faso. Cependant, ces prescriptions ne sont pas basées sur des données scientifiques. Le présent travail se veut alors une contribution à l’étude des effets à long terme de ces pratiques d’aménagement sur les jeunes arbres, les plantules et la germination des semences de certains ligneux. Les critères de qualité des plantules produites en pépinière ont été de même évalués. Sur une période de 10 ans il a été examiné les effets de ces trois outils d’aménagement sur la régénération des ligneux notamment la richesse spécifique et la densité de la population. La germination des graines de *Burkea africana* Kook, f., *Detarium microcarpum* Guill. et Perr., *Entada africana* Guill. et Perr. et *Pterocarpus erinaceus* Poir a été testée après les traitements suivants: température, éclairage, chaleur sèche et scarification. La qualité des plantules d’*Acacia macrostachya* Reichenb.ex DC. et *Pterocarpus erinaceus* Poir. a été évaluée en fonction du temps de production en pépinière ; leurs performances après plantation ont été évaluées sous des conditions d’arrosage et de stress hydrique.

Le feu, le pâturage et la coupe sélective ont influencé de façon indépendante la dynamique de la population des plantules et des jeunes arbres. Le feu précoce a réduit le recrutement des jeunes arbres tandis que le pâturage modéré n’a pas eu d’effet significatif. Bien qu’aucun traitement n’ait influencé la densité de la population des plantules, le feu et le pâturage ont influencé fortement la densité des plantules monocaules. Une Analyse en Composante Principale (ACP) a montré que la réponse des plantules aux traitements dépend de l’espèce. Elle a révélé en particulier une augmentation de la population des lianes par rapport aux autres espèces. Les semences de *D. microcarpum* et *E. africana* n’ont pas montré de dormance alors qu’un trempage des graines de *B. africana* dans l’acide sulfurique pendant 15-20 mn a permis de lever leur dormance physique. Les graines de toutes les espèces étudiées ont été indifférentes à l’éclairage. Les températures optimales de germination étaient de 25-35 $^{o}$C pour toutes les graines excepté celles d’*E. africana* qui ont bien germé à toutes les températures testées. Les semences de *P. erinaceus* n’ont pas supporté le choc thermique tandis que celles de *D. microcarpum* et d’*E. africana* ont répondu positivement à ce traitement appliqué à basse intensité. La survie et la croissance des plantules d’*A. macrostachya* et de *P. erinaceus* évaluées après 18 mois de plantation n’ont pas été influencées par leur taille initiale. La survie des plantules a été influencée par des facteurs hydriques et non hydriques. La croissance des plantules de *P. erinaceus* pourrait être prédite à partir du diamètre initial du collet ; néanmoins, une plus grande base de données serait nécessaire pour construire un modèle plus fiable.

A partir des résultats obtenus, il est recommandé de continuer d’utiliser le feu précoce comme outil d’aménagement des forêts en tenant compte du temps de mise à feu, des conditions atmosphériques et d’autres facteurs qui influenceraient l’intensité du feu. Le pâturage modéré n’a pas influencé le recrutement des plantules et des jeunes arbres. Un pâturage modéré pourrait alors être autorisé dans les forêts classées afin de permettre un aménagement multi-usages des ressources forestières. La faible densité des plantules des espèces à grande valeur socio-économique pourrait être améliorée par une plantation de plantules de grande qualité.

Mots clés: germination, plantules, jeunes arbres, lianes, semis, qualité de plantules, savane arborée, forêt sèche, perturbation, Afrique de l’Ouest.