

# Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade

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## Abstract

Fire, grazing, browsing and tree cutting are major anthropogenic determinants of vegetation patterns in African savannas. In Burkina Faso forest management policies prohibit grazing while recommending annual early fire and selective tree cutting of 50% of the merchantable standing volume on a 20-year rotation period. These management prescriptions are not based on long-term experimental evidence, particularly the responses of saplings to these management regimes are not well known. A factorial experiment with two levels was designed to examine the effects of moderate level of grazing, early fire and selective tree cutting on the dynamics of sapling populations on two sites, Laba and Tiogo, in the savanna woodland of Burkina Faso and assessed for 10 years from 1992 to 2002. Species richness, sapling population density, structure and growth were analysed. The results provide evidence that fire, grazing and selective cutting acted independently to influence the population dynamics of saplings. Annual early fire significantly reduced species richness ( $p = 0.037$  in Laba and  $p = 0.016$  in Tiogo), population density ( $p < 0.001$  in Laba and  $p = 0.003$  in Tiogo) and current annual increment (CAI) in basal area ( $p < 0.001$  in Laba and  $p = 0.016$  in Tiogo). Grazing and fire affected sapling morphology but the response was site specific. Selective removal of trees did not affect any of the parameters studied, except the CAI in dominant height at the Tiogo site which was significantly ( $p = 0.028$ ) reduced by the cutting treatment. Early fire also significantly reduced the CAI in dominant height at Laba. The height class distribution revealed that more than 93% of the saplings recorded were less than 400 cm tall, and fire significantly reduced the rate of change in density of saplings in the 200–400 cm height class. It can be concluded that annual early fire was the factor that most affected sapling recruitment. The sapling response to these management regimes was species specific.

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## 1. Introduction

The Sudanian savanna forms a belt right across the African continent from Senegal in the west to the Ethiopian highlands in the east that is characterised by 6–7 months of dry season and a

mean annual rainfall between 700 and 1200 mm (Bremen and Kessler, 1995; Menaut et al., 1995). In this tropical savanna, fire, grazing, browsing and tree cutting are the most important anthropogenic disturbances (Scholes and Walker, 1993; Bremen and Kessler, 1995; Menaut et al., 1995) that determine vegetation patterns (Kennedy and Potgieter, 2003). Fire is a crucial ecological factor in all savannas (Scholes and Walker, 1993) and in the Sudanian zone, 25–50% of the area burns annually (Delmas et al., 1991) and every 2–3 years all areas burn primarily due to anthropogenic causes (Menaut and Solbrig, 1991). Fire increases light availability in the understory by reducing tree density and canopy cover. Low intensity and less frequent fire in the savannas lead to an increase in woody plant density and biomass, and fire may accelerate short-term mineralization of nitrogen thereby

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boosting grass layer production the following year (Scholes and Walker, 1993). Recurrent fires affect species composition by favouring species with potential for vegetative reproduction (Gignoux et al., 1997; Hoffmann, 1998), which most savanna tree species have (Bellefontaine, 1997; Bationo et al., 2001). Fire can also result in the development of multi-stemmed morphology for some species (Jacobs and Biggs, 2001). Most savanna tree species go through a prolonged period of die back or shoots at the juvenile stage of their development (Menaut et al., 1995; Chidumayo, 1997; Bationo et al., 2001; Luoga et al., 2004) and recurrent fires maintain this process until the shoots reach a free-to-grow stage above the fuel bed (Sawadogo et al., 2002). Since seedlings suffer from repeated shoot die back (Ky-Dembélé et al., 2007), saplings are assumed to be the first stable stage during the growth of trees in dry savannas and could therefore be used to predict the productivity. Trees in savanna ecosystems have developed resistance strategies in response to fire including bark thickness, wood basic density (Abbot and Lowore, 1999; Nygard and Elfving, 2000) and rapid initial growth rate.

The geographic spread of fires in the savanna woodlands and their consequences on natural vegetation depend on time of occurrence. Late fire, occurring at the end of the dry season when the herbaceous biomass is dry, is more intense than early fire that occurs just after the end of the rainy season when vegetation moisture content is still high (Sawadogo et al., 2002). The effects of fire are characterized by spatial heterogeneity, especially early fire, due to spatial variability of moisture content in vegetation, distribution and types of biomass—tall perennial grasses, short annual grasses or trees (Sawadogo et al., 2002). Annual early fire has been adopted as a management tool in the State forests of Burkina Faso to minimize the risk of intense late fire spreading due to natural and/or anthropogenic causes and to improve pasture production for wildlife (Sawadogo, 1996, 1998; Bellefontaine et al., 2000). Therefore, assessing the effect of early fire and its interactions with other disturbances like grazing and selective tree cutting on forest dynamics and especially on ligneous regeneration is essential for better use of fire as a forest management tool.

Ligneous regeneration is also exposed to animal damages (Braithwaite and Mayhead, 1996) and exclusion of grazing is reported to decrease its mortality rate (Fenner, 1987). Browsing damage on ligneous juvenile plants depends on its intensity and frequency as well as plant development stage (Drexhage and Colin, 2003). Heavy browsing and grazing by mammals can inhibit the development of woody vegetation (Luoga et al., 2002, 2004) while zero-grazing is often assumed to improve regeneration of woody species. By reducing herbaceous biomass, grazing can, however, reduce competition from the herbaceous layer and also the intensity and frequency of fire, thereby increasing wood production (Peltier and Eyog-Matig, 1989) and regeneration (Sawadogo et al., 2002). Moreover, livestock can play an important role in long distance dispersal of seeds (Miller, 1995; Stiles, 2000; Razanamandranto et al., 2004) thus enhancing species richness at a given site. The effects of livestock grazing and trampling vary with rainfall, slope, soil stability and vegetation type, as

well as with animal density, season of use, duration of use and animal distribution (Belsky and Blumenthal, 1997). Grazing impact on regeneration in savanna woodlands is a balancing act between positive and negative effects and these have to be assessed experimentally.

Woodfuel is the main source of energy in large parts of Africa (Nygard et al., 2004) where harvesting has evolved from dead wood collection to cutting of live trees due to increased scarcity of dead wood (Flandez, 1995; Peltier et al., 1995). User preferences determine what species are to be cut. Intense cutting pressure on few locally preferred species could therefore influence the remaining species dynamics and decrease the biodiversity of the forest. Most savanna tree species have vegetative regeneration strategies (Chidumayo and Frost, 1996; Frost et al., 1996; Bellefontaine, 1997). They react to cutting by producing more coppice and root suckers. Furthermore, juvenile development may be improved due to increasing light in the understory (Hutchinson et al., 2005). Many trials carried out in southern African savannas and elsewhere have however shown an immediate increase in grass production following removal of woody plants (Scholes and Walker, 1993; Gambiza et al., 2000) leading to more competition with ligneous regeneration. Hence, the effects of selective tree removal on stand renewal are important for forest managers.

In addition to prescribed annual early fire, the state forest management policies in Burkina Faso prohibit grazing by livestock while recommending selective tree cutting by harvesting 50% of the of the merchantable standing volume on a 20-year rotation period since 1986 (Bellefontaine et al., 2000; Kaboré, 2004). Trees are mainly cut for commercial woodfuel and poles by local people organized in cooperatives in both forests (Sawadogo, 2006). Studies have been conducted on coppice growth (Renes, 1991; Nouvellet, 1993; Nygard et al., 2004) but much remains to be unveiled regarding the effects of fire, grazing and selective tree cutting, as well as combinations thereof over a longer time period on all forms of ligneous regeneration including coppice and sexually reproduced saplings. In order to address this issue, this study was performed as a split plot experiment using combinations of three management regimes: grazing by livestock, annual early fire and selective tree cutting for 10 years (1992–2002). The objective of the study was to determine how implementing these management regimes, independently or additively, affect sapling species composition, population density and structure as well as growth parameters after a decade.

## 2. Materials and methods

### 2.1. Study area

The experimental sites are located on flat areas in Laba (11°40'N and 2°50'W) and Tiogo (12°13'N, 2°42'W) State Forests (forêts classées), both at an altitude of 300 m a.s.l. in Burkina Faso, West Africa. 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 (Guinko, 1984). Laba and Tiogo State Forests cover 17,000 and 30,000 ha, respectively. The unimodal rainy season generally lasts about 6 months, from May to October. The mean annual rainfall for the period 1993–2001 was  $910 \pm 138$  mm at Laba and  $836 \pm 219$  mm at Tiogo. The number of rainy days per annum during the study period was  $76 \pm 13$  and  $70 \pm 9$  at Laba and Tiogo, respectively. Rainfall and number of rainy days per annum showed large inter-annual variability (Fig. 1). Mean daily minimum and maximum temperatures are 16 and  $32^\circ\text{C}$  in January (the coldest month) and  $26$  and  $40^\circ\text{C}$  in April (the hottest month) with an aridity index (Brown and Lugo, 1982) of 3.2 and 3.5 for Laba and Tiogo, respectively. According to FAO's classification system (Dreissen et al., 2001), Lixisols are the most encountered soil type at both study sites, which are also representative of 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, and their physical and chemical characteristics are described in Sawadogo et al. (2005).

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 asciodis* C.B.Cl.

(dominant in Laba). The main forbs species are *Cochlospermum planchonii* Hook. F., *Borreria stachydea* (DC) Hutch. and Dalz., *Borreria radiata* DC. and *Wissadula amplissima* Fries. The woody vegetation is dominated by Mimosaceae and Combretaceae at both sites. The main species in terms of basal area are *Detarium microcarpum* Guill. and Perr., *Combretum nigricans* Lepr. ex Guill. and Perr., *Acacia macrostachya* Reichenb. ex Benth., *Entada africana* Guill. and Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpus* (D.C.) Guill. and Perr. and *Vitellaria paradoxa* C.F. Gaertn. 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  $6.3\text{ m}^2\text{ ha}^{-1}$ , respectively, with a stand density of  $582\text{ individuals ha}^{-1}$ , and the corresponding values at Tiogo were  $10.9$  and  $6.1\text{ m}^2\text{ ha}^{-1}$  at stump level and breast height, respectively, with a stand density of  $542\text{ individuals ha}^{-1}$  (Sawadogo et al., 2002).

## 2.2. Experimental design

This study was part of a larger split plot experiment with four replicates, widely described in Sawadogo et al. (2002). In this study, three factors with two levels each were tested: grazing by livestock as a main factor (no grazing/grazing); fire (no fire/annual early fire); cutting (no cutting/selective tree cutting). Each experimental site (in Laba and Tiogo) was split into two contiguous main plots of which one was fenced off at the beginning of the dry season in December 1992 as to exclude livestock. Each main plot was further divided into four blocks of  $2.25\text{ ha}$ , each containing four subplots of  $0.25\text{ ha}$  ( $50\text{ m} \times 50\text{ m}$ ), separated from each other by  $20\text{--}30\text{ m}$  fire-breaks. To the four subplots within each block of the main plot, the following treatments were randomly assigned: no cutting–no fire, no cutting–early fire, cutting–no fire and cutting–early fire (Table 1). The selective cutting was made in December 1993 at Tiogo and 1 month later in January 1994 at Laba by removing 50% of the basal area at stump level. In the savanna woodlands where trees are often multi-stemmed and where existing volume functions are not precise (Clement, 1982; Breman and Kessler, 1995; Nygard et al., 2004) it was easier to monitor removal of 50% of the basal area than 50% of the volume. Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and

Table 1  
Summary of the experimental design

Livestock	Fire	Cutting	Number of replicates
No grazing	No Fire	No cutting	4
		Cutting	4
	Fire	No cutting	4
		Cutting	4
Grazing	No Fire	No cutting	4
		Cutting	4
	Fire	No cutting	4
		Cutting	4

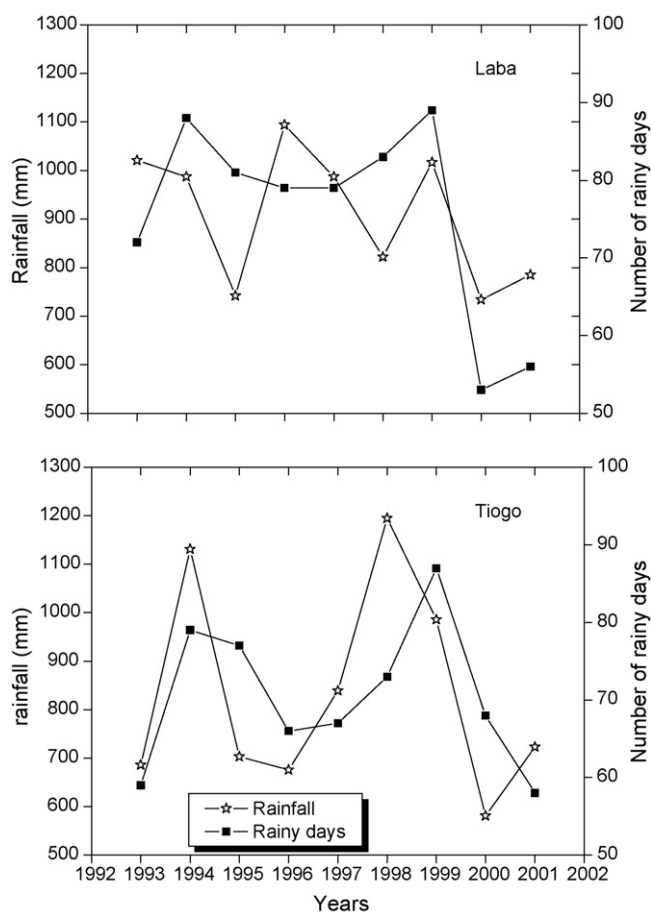


Fig. 1. Rainfall and number of rainy days for the study period (1993–2001) at Laba and Tiogo sites.

fuelwood, and fuelwood and others. Except protected species, individuals of other categories were cut according to the following size criterion: >30 cm diameter at stump level for timber species, >14 cm diameter at stump level for poles and fuelwood species and >8 cm diameter at stump level for fuelwood and others (Sawadogo et al., 2002). The prescribed early fire was applied at the end of the rainy season (October–November) each year beginning 1992 when the grass layer humidity was approximately 40%. At both sites the main plot open for grazing was visited by livestock mainly but also wild animals. The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit ha<sup>-1</sup> (T.L.U. ha<sup>-1</sup>) and that of Tiogo was 1.4 T.L.U. ha<sup>-1</sup> (Sawadogo, 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo et al., 2005). The presence of the livestock in the two forests varied spatially and temporally, mainly occurring during the rainy season when grasses were green and surrounding area cultivated.

### 2.3. Data collection and analysis

Different definitions of the term sapling have been employed in various regeneration studies (Carson and Abbiw, 1990; Sabogal, 1992; Felfili, 1997; Hutchinson et al., 2005). In this paper, the term ‘sapling’ refers to a woody plant less than 10 cm girth at breast height and either more than 150 cm in height or more than 10 cm girth at stump level. These criteria enabled us to take species having a bushy stature into account. A sapling individual was considered as multi-stemmed when it had more than one stem that fulfilled the above size criteria, otherwise it was considered single-stemmed. It was not possible, however, to distinguish whether saplings were originated from true seedlings (regenerated from seeds), root suckers or coppice.

The inventories were carried out in 1992 (before applying the treatments) and in 2002 (10 years after applying the treatments). The following parameters were recorded in each 50 m × 50 m subplot: species name, number of stems per individual, stem height, girth at stump level (for stems ≥ 10 cm) and girth at breast height (for stems ≥ 10 cm). Species identification and nomenclature followed Hutchinson et al. (1954) and Arbonnier (2002). The proportional increase in species richness was computed as followed:

$$R_I = \left[ \frac{R_{02} - R_{92}}{R_{92}} \right] \times 100$$

$R_I$  is proportional increase in species richness, and  $R_{02}$  and  $R_{92}$  are species richness in 2002 and 1992 inventories. Sapling density (number of individuals per hectare) was calculated for each inventory, and the rate of population change was computed using the standard logarithmic growth model (Lieberman and Lieberman, 1987; Condit et al., 1996; Gonzalez-Rivas, 2005) as followed:

$$r = \frac{\ln N_{02} - \ln N_{92}}{\Delta t}$$

$r$  is the annualized rate of population change,  $\ln$  the natural logarithm,  $N_{02}$  and  $N_{92}$  the sapling density recorded in 2002 and

1992, respectively, and  $\Delta t$  is the time interval between the two assessments. Before computing annualized rate of change, we added 1.0 to the density of each species to account for zero in some of the treatment subplots (Tabachnick and Fidell, 1996). The height of individuals was measured using a graduate pole, and individuals were grouped into three height classes of 200 cm interval, i.e., <200, 200–400 and ≥400 cm. Annualized rate of population change was also computed for the two first height classes, as the last height class contained less than 7% of the saplings. Dominant height was calculated for each subplot as the arithmetic mean of the 100 tallest individuals ha<sup>-1</sup> (West, 2004). Current annual increment (CAI) in dominant height was calculated for the study period. Girth at stump level was measured in centimeter with a tailor-tape and the basal area and its CAI were calculated per subplot.

The proportional increase in species richness, annualized rate of population change and CAI were subjected to analysis of variance using the following split plot design model:

$$Y_{ijkl} = \mu + \beta_i + G_j + F_k + C_l + \beta G_{ij} + GF_{jk} + GC_{jl} + FC_{kl} + GFC_{jkl} + e_{ijkl}$$

$Y_{ijk}$  is the response variable,  $\mu$  the overall mean,  $\beta_i$  the block effect (replication)  $i$ ,  $G_j$  the effect of grazing by livestock (main plot)  $j$ ,  $F_k$  the effect of fire  $k$  and  $C_l$  is the effect of the cutting  $l$ . The parameters  $G_j$ ,  $F_k$  and  $C_l$  and their interactions were regarded as fixed effects and the parameter  $\beta_i$  as random;  $e_{ijkl}$  was the error term. Data on proportional increase in species richness were arcsine transformed to meet the normality assumption for analysis of variance and differences between treatments were judged based on 5% significance level (Zar, 1996). All statistical analyses were performed with SPSS 14 software package (Copyright SPSS for Windows, Release 2005, SPSS Inc., Chicago). The analyses were performed for each site separately.

## 3. Results

### 3.1. Species richness

Across all subplots, a total of 43 and 59 species at sapling stage was recorded in 1992 and 2002, respectively, at Laba, and the corresponding figures at Tiogo were 49 and 64 species, respectively (see Appendix A). On average, the number of species recorded per treatment subplot in 1992 and 2002 was 18 and 27, respectively, at Laba site and 21 and 29 at Tiogo. The main effects of grazing, annual early fire and selective cutting on species richness of saplings is shown in Table 2. Species richness increased on both grazed and ungrazed subplots from 1992 to 2002 at Laba and Tiogo, however, the proportional increase in species richness did not differ significantly. The main effect of fire on species richness was significant at both study sites. After 10 years of annual early fire, the proportional increase in sapling species richness was at least three times higher in the unburnt than burnt subplots at both Laba and Tiogo. Species richness did not vary significantly between cut and uncut subplots at both study sites. First and second order



Table 2  
Main effect of livestock grazing, annual prescribed early fire and selective tree cutting on proportional increase in species richness (R1) of saplings at Laba and Tiogo (mean  $\pm$  S.E.)

Factors	Species number in Laba			Species number in Tiogo		
	1992	2002	R1 (%)	1992	2002	R1 (%)
Grazing	17 $\pm$ 1	26 $\pm$ 2	58.2 $\pm$ 12.0	21 $\pm$ 1	28 $\pm$ 2	34.6 $\pm$ 09.8
No grazing	18 $\pm$ 1	28 $\pm$ 2	58.8 $\pm$ 12.0	20 $\pm$ 1	30 $\pm$ 1	49.2 $\pm$ 08.3
<i>p</i> -Value			0.058			0.646
Fire	18 $\pm$ 1	22 $\pm$ 2	26.7 $\pm$ 08.2	21 $\pm$ 1	26 $\pm$ 1	23.8 $\pm$ 06.8
No fire	17 $\pm$ 1	32 $\pm$ 1	90.4 $\pm$ 09.4	21 $\pm$ 1	32 $\pm$ 1	60.0 $\pm$ 09.1
<i>p</i> -Value			0.037			0.016
Cutting	17 $\pm$ 1	25 $\pm$ 2	58.1 $\pm$ 11.7	21 $\pm$ 1	28 $\pm$ 1	38.8 $\pm$ 08.6
No cutting	18 $\pm$ 1	28 $\pm$ 2	58.9 $\pm$ 12.4	21 $\pm$ 1	29 $\pm$ 2	45.0 $\pm$ 09.8
<i>p</i> -Value			0.636			0.727

interaction effects of grazing, fire and selective cutting on species richness were not significant.

### 3.2. Changes in sapling population density

The main effects of grazing, fire and selective cutting treatments on rate of change in total population density as well as densities of single-stemmed and multi-stemmed saplings are shown in Table 3. The total sapling density at Tiogo was not affected by grazing, but the density of single-stemmed individuals increased significantly over the study period on ungrazed compared to grazed subplots while the density of multi-stemmed individuals tended ( $p = 0.087$ ) to increase on grazed compared to ungrazed subplots. At Laba, grazing did not affect the rates of change in total density and the density of multi-stemmed or single-stemmed individuals. The main effect of fire

on rate of change in population density of saplings was significant at both experimental sites, except the population of multi-stemmed individuals at Tiogo (Table 3). The rates of change in total density and density of single-stemmed individuals were significantly lower on burned compared to unburned subplots at both study sites. Particularly, fire reduced the density of single-stemmed individuals at Laba, as shown by negative annualized rate of change ( $-2.5\%$ ). The change in density of multi-stemmed individuals was significantly lower on burnt than unburnt subplot at Laba, no significant difference was observed at Tiogo. Selective tree cutting did not influence the change in sapling density over the study period at both experimental sites (Table 3). Nevertheless, the change in density of single-stemmed individuals tended ( $p = 0.084$ ) to be lower on subplots subjected to selective cutting than uncut subplots. None of the treatments showed significant interaction effects.

Table 3  
Main effects of livestock grazing, annual prescribed early fire and selective tree cutting on the annualized rate of population change ( $r\%$ ) of multi-stem (MS), single-stem (SS) and total sapling density, TD (number of individuals per hectare) at Laba and Tiogo (mean  $\pm$  S.E.)

Sites	Parameters	Treatments								
		Gazing	No grazing	<i>p</i> -Value	Fire	No fire	<i>p</i> -Value	Cutting	No cutting	<i>p</i> -Value
Laba	MS 1992	212 $\pm$ 24	175 $\pm$ 20		212 $\pm$ 26	7.4 $\pm$ 1.1		190 $\pm$ 25	197 $\pm$ 20	
	MS 2002	509 $\pm$ 60	480 $\pm$ 40		439 $\pm$ 56	550 $\pm$ 43		472 $\pm$ 46	516 $\pm$ 56	
	<i>r</i>	8.9 $\pm$ 1.3	10.5 $\pm$ 1.0	0.431	175 $\pm$ 19	12.0 $\pm$ 1.0	0.005	9.8 $\pm$ 1.4	9.5 $\pm$ 0.9	0.864
	SS 1992	208 $\pm$ 39	210 $\pm$ 27		237 $\pm$ 35	182 $\pm$ 30		189 $\pm$ 31	230 $\pm$ 35	
	SS 2002	385 $\pm$ 73	517 $\pm$ 114		206 $\pm$ 50	696 $\pm$ 92		423 $\pm$ 110	479 $\pm$ 82	
	<i>r</i>	5.1 $\pm$ 3.0	6.5 $\pm$ 2.6	0.363	$-2.5 \pm 2.3$	14.1 $\pm$ 1.0	<0.001	6.2 $\pm$ 2.9	5.4 $\pm$ 2.6	0.778
	TD 1992	420 $\pm$ 57	7.5 $\pm$ 1.8		449 $\pm$ 54	357 $\pm$ 41		379 $\pm$ 51	427 $\pm$ 47	
	TD 2002	893 $\pm$ 122	385 $\pm$ 40		645 $\pm$ 100	1246 $\pm$ 115		896 $\pm$ 139	995 $\pm$ 125	
	<i>r</i>	997 $\pm$ 142	9.0 $\pm$ 1.4	0.301	3.6 $\pm$ 1.3	12.9 $\pm$ 0.9	<0.001	8.6 $\pm$ 1.8	7.9 $\pm$ 1.5	0.721
Tiogo	MS 1992	162 $\pm$ 28	221 $\pm$ 38		194 $\pm$ 36	188 $\pm$ 33		203 $\pm$ 32	180 $\pm$ 36	
	MS 2002	463 $\pm$ 63	464 $\pm$ 71		477 $\pm$ 56	450 $\pm$ 77		484 $\pm$ 72	443 $\pm$ 62	
	<i>r</i>	11.1 $\pm$ 1.4	7.9 $\pm$ 0.9	0.087	9.8 $\pm$ 1.4	9.3 $\pm$ 1.1	0.781	9.4 $\pm$ 1.1	9.6 $\pm$ 1.4	0.902
	SS 1992	191 $\pm$ 31	177 $\pm$ 27		193 $\pm$ 31	175 $\pm$ 26		180 $\pm$ 27	188 $\pm$ 31	
	SS 2002	357 $\pm$ 62	476 $\pm$ 108		258 $\pm$ 46	574 $\pm$ 103		387 $\pm$ 114	445 $\pm$ 54	
	<i>r</i>	4.8 $\pm$ 1.8	8.8 $\pm$ 1.6	0.014	2.3 $\pm$ 1.5	11.2 $\pm$ 1.3	<0.001	5.0 $\pm$ 1.7	8.5 $\pm$ 1.8	0.084
	TD 1992	353 $\pm$ 53	398 $\pm$ 58		387 $\pm$ 54	363 $\pm$ 57		383 $\pm$ 56	368 $\pm$ 55	
	TD 2002	819 $\pm$ 118	940 $\pm$ 167		735 $\pm$ 98	1024 $\pm$ 172		871 $\pm$ 180	888 $\pm$ 99	
	<i>r</i>	8.3 $\pm$ 1.0	8.6 $\pm$ 1.0	0.639	6.4 $\pm$ 0.9	10.5 $\pm$ 0.7	0.003	7.8 $\pm$ 1.0	9.1 $\pm$ 1.0	0.293

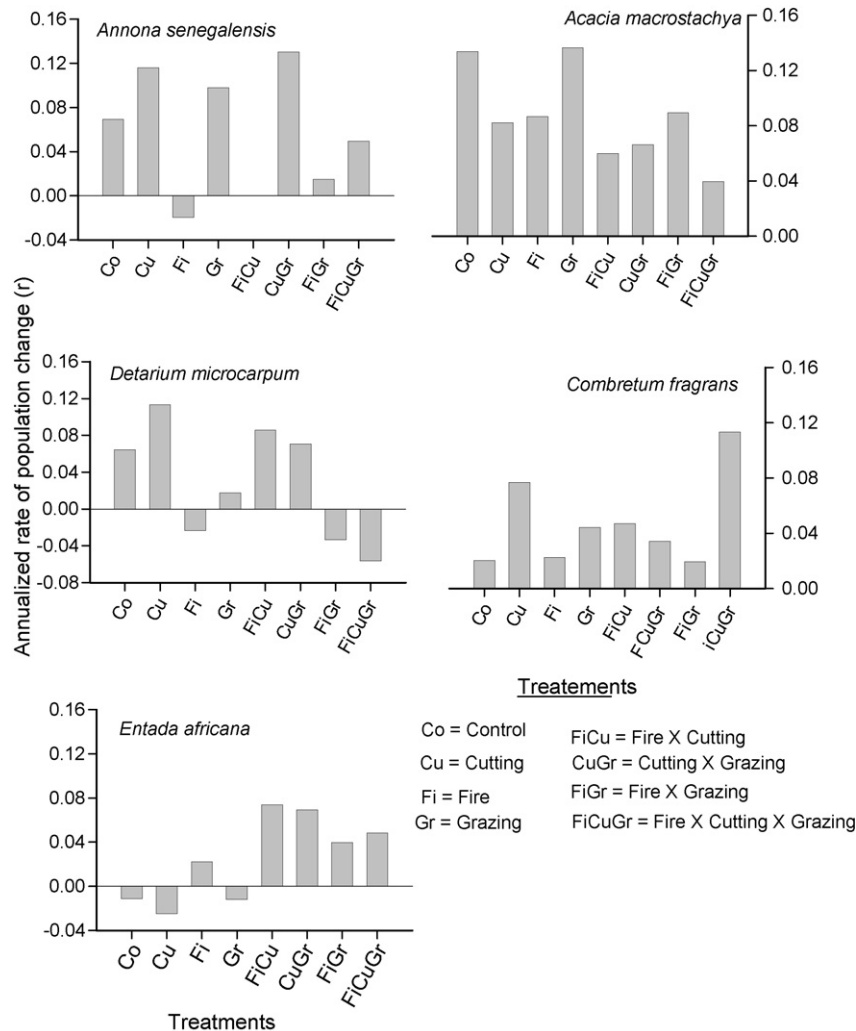


Fig. 2. Annualized rate of change in sapling population density of selected species.

Three species at Laba (*Annona senegalensis* Pers., *Combretum fragrans* F. Hoffm., Beitr. Kenntn. and *D. microcarpum*) and two at Tiogo (*A. macrostachya* and *E. africana*) were abundant enough to allow rate of population change analysis. As a whole, sapling density of these species tended to vary across treatment subplots during the study period (Fig. 2). *C. fragrans* and *E. africana* had lower sapling density and less variability in almost all treatment subplots except the former species that had the highest sapling density in 2002 on the subplots subjected to grazing × fire × cutting treatment. It was only fire that significantly decreased the rate of change in sapling populations of *A. senegalensis* ( $p = 0.001$ ) and *D. microcarpum* ( $p < 0.001$ ). No significant interaction effect was observed for any of the species.

### 3.3. Height class distribution

The height class distribution of sapling individuals showed a similar pattern at both Laba (Fig. 3a) and Tiogo (Fig. 3b). Of the total number of sapling individuals recorded during the study period, 97–98% at Laba and 93–94% at Tiogo were represented in the two first classes (<200 and 200–400 cm). Analysis of

variance by height class showed that fire significantly decreased the rate of sapling population change at Laba (Table 4). At Tiogo, the population density of saplings in 200–400 cm height class was twice as high on unburnt compared to burnt subplots while no significant effect was observed in the lower class (Table 4). Grazing by livestock and selective tree cutting did not significantly affect the rate of change in population density of saplings in either height classes (Table 4). There was no significant interaction effect of the three factors.

### 3.4. Growth of sapling

The current annual increment in sapling dominant height was significantly decreased by prescribed early fire at Laba ( $p < 0.001$ ) but not at Tiogo ( $p = 0.193$ ). At Laba, the CAI in dominant height was three times higher on the unburnt than burnt subplots (Fig. 4). Grazing did not significantly affect dominant height CAI at either site ( $p = 0.949$  for Laba and  $p = 0.219$  for Tiogo). Selective tree cutting significantly decreased CAI in Tiogo ( $p = 0.028$ ) but not in Laba ( $p = 0.504$ ). At Tiogo, the CAI in dominant height was three times higher on the uncut than cut subplots (Fig. 4). The current

Table 4  
Main effects of livestock grazing, annual prescribed early fire and selective tree cutting on annualized rate of change ( $r\%$ ) in sapling density by height class for Laba and Tiogo (mean  $\pm$  S.E.)

Factors	$r$ , Laba		$r$ , Tiogo	
	<2 m	2–4 m	<2 m	2–4 m
Grazing	5.2 $\pm$ 1.7	10.9 $\pm$ 2.4	7.2 $\pm$ 0.8	8.9 $\pm$ 1.5
No grazing	5.6 $\pm$ 1.3	13.1 $\pm$ 1.6	8.4 $\pm$ 1.1	9.0 $\pm$ 1.0
$p$ -Value	0.856	0.130	0.255	0.922
Fire	1.9 $\pm$ 1.3	6.7 $\pm$ 1.9	6.5 $\pm$ 0.9	5.9 $\pm$ 1.2
No fire	8.9 $\pm$ 1.1	17.3 $\pm$ 1.0	9.1 $\pm$ 0.9	12.1 $\pm$ 0.8
$p$ -Value	0.001	<0.001	0.095	<0.001
Cutting	5.7 $\pm$ 1.6	11.9 $\pm$ 2.1	7.4 $\pm$ 1.0	8.6 $\pm$ 1.3
No cutting	5.1 $\pm$ 1.4	12.1 $\pm$ 2.0	8.2 $\pm$ 0.9	9.4 $\pm$ 1.3
$p$ -Value	0.745	0.946	0.612	0.578

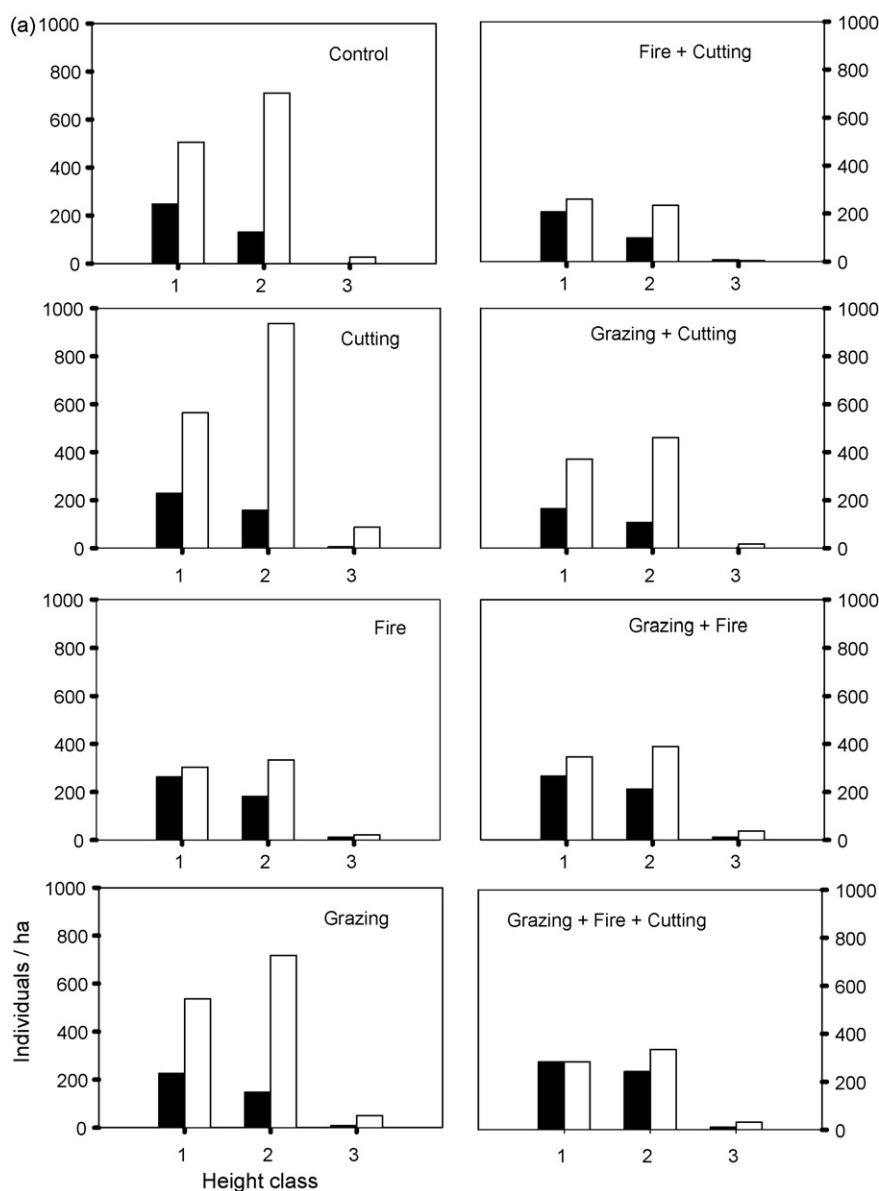


Fig. 3. Height class (1 = <200 cm; 2 = 200–400 cm; 3 =  $\geq$ 400 cm) distribution for saplings at: (a) Laba forest and (b) Tiogo forest in 1992 (shaded bars) and 2002 (open bars).

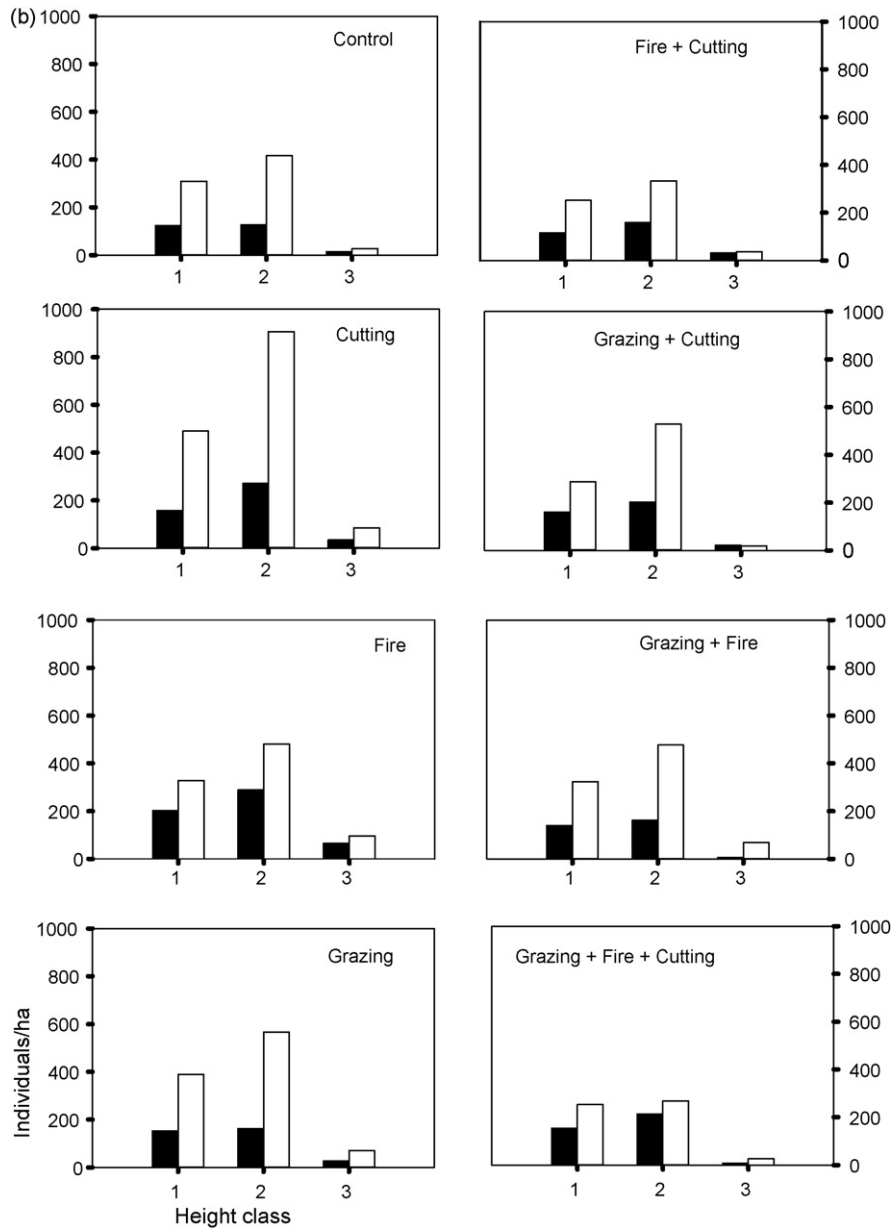


Fig. 3. (Continued).

annual increment in sapling basal area was significantly decreased by fire at both Laba and Tiogo but not affected by either grazing or selective tree cutting (Table 5). The current annual increment in sapling basal area was more than double on the unburnt than burnt subplots at Laba while at Tiogo it was almost double. The interaction effects of grazing, fire and selective cutting were not significant for both CAI in dominant height and basal area of saplings.

#### 4. Discussion

The effects of fire, grazing and selective cutting on population dynamics of saplings in the Sudanian savanna woodlands are independent, as evidenced from lack of significant interaction effects. Annual early fire had the strongest influence on dynamics of sapling population; i.e., it significantly reduced species

richness, density of sapling and CAI in basal area at both study sites. The available evidences suggest that environmental conditions such as flooding, fire or drought favour the establishment and growth of plants with strategies ensuring successful post-disturbance regeneration (Aubréville, 1950; Deiller et al., 2003). Thus, the recurrent burning might have limited the species composition by favouring fire tolerant species and/or species adapted to sprouting following fire disturbance while both fire tolerant and intolerant species grew sufficiently on unburnt plots. For example, we observed that *A. leiocarpus* was highly invading in fire exclusion plots. Our result of fire effect on species richness is consistent with previous studies (Gignoux et al., 1997; Hoffmann, 1998; Hutchinson et al., 2005).

Frequent burning has been reported to prevent development of a sapling layer and canopy in-growth (Peterson and Reich, 2001). Depending on intensity and duration, fire can kill seeds



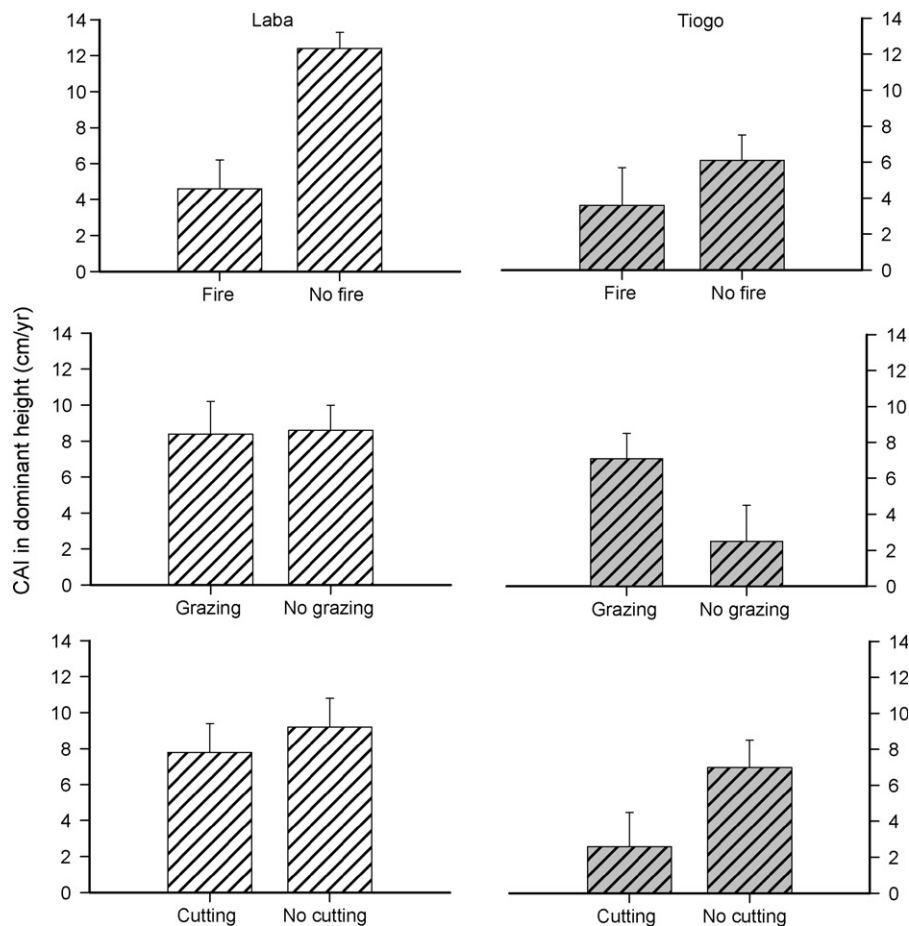


Fig. 4. Main effects of grazing, early fire and selective cutting on current annual increment (CAI) in dominant height of saplings at Laba and Tiogo (mean  $\pm$  S.E.).

within the litter layer or superficially buried in the soil. Indeed many experimental studies made on dry heat effect on seed germination have shown that intensity and duration of fire are determining factors for the positive or negative role of fire on seed germination (Teketay, 1996; Danthu et al., 2003; Schelin et al., 2003, 2004; Zida et al., 2005). Moreover, fire is partly responsible for the shoot die back exhibited by many savanna tree species (Menaut et al., 1995; Chidumayo, 1997; Bationo et al., 2001; Luoga et al., 2004). The negative effect of fire on

woody plant density has been previously reported by many authors (Hoffmann and Solbrig, 2003; Gambiza et al., 2005; Hutchinson et al., 2005; Albrecht and McCarthy, 2006). Nevertheless, in this study, the prescribed annual fire did not suppress the recruitment of saplings; it only slowed the rate of recruitment down. This finding is consistent with previous studies in African savannas (Hochberg et al., 1994; Menaut et al., 1995). The delay in the rate of sapling recruitment could be accounted for the low basal area increment on burned

Table 5  
Main effects of livestock grazing, annual prescribed early fire and selective tree cutting on current annual increment in basal area (CAI<sub>ba</sub>, m<sup>2</sup>/ha) of saplings at Laba and Tiogo sites (mean  $\pm$  S.E.)

Factors	Laba			Tiogo		
	1992	2002	CAI <sub>ba</sub>	1992	2002	CAI <sub>ba</sub>
Gazing	0.161 $\pm$ 0.041	1.060 $\pm$ 0.108	0.090 $\pm$ 0.012	0.240 $\pm$ 0.031	0.752 $\pm$ 0.078	0.051 $\pm$ 0.008
No grazing	0.238 $\pm$ 0.052	1.098 $\pm$ 0.099	0.086 $\pm$ 0.011	0.250 $\pm$ 0.047	0.892 $\pm$ 0.094	0.064 $\pm$ 0.009
<i>p</i> -Value			0.753			0.357
Fire	0.247 $\pm$ 0.058	0.792 $\pm$ 0.067	0.055 $\pm$ 0.007	0.268 $\pm$ 0.032	0.678 $\pm$ 0.055	0.041 $\pm$ 0.006
No fire	0.153 $\pm$ 0.031	1.366 $\pm$ 0.078	0.121 $\pm$ 0.007	0.222 $\pm$ 0.046	0.966 $\pm$ 0.099	0.074 $\pm$ 0.009
<i>p</i> -Value			<0.001			0.016
Cutting	0.211 $\pm$ 0.049	1.047 $\pm$ 0.095	0.084 $\pm$ 0.010	0.294 $\pm$ 0.045	0.807 $\pm$ 0.107	0.051 $\pm$ 0.011
No cutting	0.188 $\pm$ 0.046	1.111 $\pm$ 0.111	0.092 $\pm$ 0.012	0.197 $\pm$ 0.029	0.837 $\pm$ 0.064	0.064 $\pm$ 0.007
<i>p</i> -Value			0.427			0.321

subplot 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). Our result is consistent with a study made on the miombo woodlands where the basal area of woody plants was significantly reduced by frequent fires (Gambiza et al., 2000). Annual prescribed early fire relatively favoured multi-stemmed woody population compared with the negative effect on rate of change of single-stemmed sapling populations, particularly at Laba site. This could be related to its top-killing effect (i.e., death of the aerial biomass), which might activate dormant buds to produce more root suckers or sprouts (Menaut et al., 1995; Hoffmann, 1998; Kennedy and Potgieter, 2003) that could lead to multi-stemmed morphology. Top-kill is also accounted for the observed fire effect on height class distribution and increment in dominant height.

The effect of grazing by livestock on tree regeneration and subsequent growth is generally related to spatial and temporal variations in grazing intensity, stocking rate and feeding behaviour, as well as plant phenophase and differential responses of species to browsing and trampling (Walker, 1981; Milchunas et al., 1988; Braithwaite and Mayhead, 1996; Hester et al., 1996; O'Connor, 1996; Drexhage and Colin, 2003). Temporal variation in grazing intensity, stocking rate and feeding behaviour is common in the Sahel (Hiernaux, 1998) where free grazing by mixed herds—cattle, sheep and goats, is practiced (which is also the case on our sites). In the present study, grazing by livestock did not affect species richness, rate of change in population density or growth of saplings. Since the grazing intensity on our plots was half the carrying capacity (50% of the potential), many species could survive moderate levels of grazing, which allow succession to proceed but limit the ability of few highly competitive species to dominate the community. Belsky (1987) has provided evidence showing that low to moderate levels of herbivory sometimes has no measurable effect on species richness. Browsing can also turn a single-stemmed individual into a multi-stemmed individual at early stage of growth by cutting the apical buds, as evidenced from an increasing tendency of multi-stemmed individuals on grazed than ungrazed plots.

Selective removal of trees is expected to enhance the recruitment process by reducing competition for water and nutrients, opening up more growing space and by increasing the availability of light in the understory (Frost et al., 1986; Hutchinson et al., 2005). This was not the case in our study. The selective cutting treatment was applied once by extracting 50% of the basal area of all trees; therefore, the competition for light, water and nutrients might have been determined by initial stocking of trees. For instance, if tree density was high before cutting, selective cutting of trees might reduce the competition for resources and thus have a clear effect. However, savanna woodlands are less dense, thus further opening of the canopy can create unfavourable thermal condition in the understory that increases soil evaporation and plant evapotranspiration, thereby counterbalancing the initial positive effect of increased water and nutrient availability due to selective removal of trees. Since most savanna species have profound resprouting and

suckering ability following cutting disturbance (Sawadogo et al., 2002; Nygard et al., 2004; Ky-Dembélé et al., 2007) and since the sprouts and suckers depend on already well-established root systems of the original tree for accessing water and soil nutrients, they can easily out-compete seedlings regenerated by seeds that would have contributed to increased species diversity. Selective removal of mature trees could also result in decreased seed rain to the already poor soil seed bank (unpublished data), thereby constraining the recruitment process. The probable reason why the selective cutting treatment did not significantly influence the change in population density might be a shift from sapling to adult size of sprouts and suckers that are known to grow faster (Hoffmann, 1998; Walter, 2003). Selective cutting slowed down the increment in height at Tiogo, most likely due to its effect on herbaceous biomass. Indeed during the study period, selective cutting significantly increased the mean biomass of annual grasses at Tiogo (Sawadogo et al., 2005) that might have led to increased competition for water and soil nutrients with saplings. The poor height growth in a dense grass vegetation has been previously reported elsewhere (Renes, 1991).

One major factor influencing the treatment effects was the spatio-temporal heterogeneity of vegetation and climate (rainfall). For instance, the mosaic of annual (*L. togoensis*) and perennial (*A. gayanus*) grasses with different life cycles affected the spatial variability of dry grass at the time of burning. Amount and distribution of annual rainfall over the study period have large effect on species composition and biomass of the herbaceous layer (Bremen and Kessler, 1995; Sawadogo et al., 2005), which in turn has an impact on fuel load. Another factor affecting the spatial heterogeneity was the occurrence of bush clumps on termite mounds. Since the bush clumps are very resistant to fire even under extreme burning conditions, fire generally skirts around the edges, leaving the centre unburnt. The rate of recruitment of saplings is therefore influenced by this patchiness of the vegetation. For instance, species growing on termite mounds like *Fertetia apodanthera* Del., *Tamarindus indica* Linn., *Combretum micranthum*, *Acacia erythrocalyx* and *Capparis sieperia* Lam., have seldom be reached by fire and may grow faster (personal observation). Third, the impact of the treatments on the dynamics of sapling population is species dependent (Fig. 2), as fire sensitive and fire tolerant species could exist in this savanna woodland. For example, the density of *D. microcarpum* was substantial high on plots protected from burning, particularly at Laba. This species coppices vigorously but its coppices protected from fire and livestock during 2 consecutive years fail to survive burning the third year (Manaute, 1996). Species such as *Crossopteryx febrifuga* (Afzel. Ex G. Don) Benth. and *Piliostigma thonningii* (Schum.) Milne-Redhead have greater fire resistance owing to their investment in the form of thicker bark and greater aboveground growth rates (Gignoux et al., 1997).

## 5. Management implications

Results from the present study provide evidence that the effects of early fire, grazing and selective cutting are independent

and no evidence of additive effect on the dynamics of sapling population in the savanna woodlands. These treatments could be a compromise between total protection (which is utopian) and uncontrolled use of the forest products. Nevertheless, they should be modulated to get a suitable balance of the different forest products (wood, forage, non-timber forest product, etc.) for sustainable multiple-use of the state forests, which is an envisaged management objective. Annual early fire is the factor that most affected the rate of sapling recruitment at both study sites after a decade, thus its use as management tool should be made with due caution to the timing of burning, weather conditions and other possible factors that increase fire intensity. Provided that grazing is kept at moderate intensities, the current policy that prohibits grazing in state forests may need revision so that the management of savanna woodlands could be integrated with livestock husbandry, as it is the main source of livelihoods for local people. One way of

monitoring the grazing intensity would be to organize the villagers into user groups and empower them with management responsibilities, as in the case of wood harvesting. Although the current cutting intensity (50% of the basal area) has no negative effect on regeneration, testing different cutting intensities may be required to achieve the expected beneficial results of selective cutting, thereby expediting advance regeneration.

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### Appendix A

Sapling species composition, life form and abundance (average number of individuals per hectare) at Laba and Tiogo. Species were grouped per local use following Nouvellet et al. (1995) and Sawadogo et al. (2002). Growth form description was translated from Guinko (1984)—lTr: large tree (>30 m height), mTr: medium-sized tree (15–30 m height), sTr: small tree (7–15 m height), Bu: bush (4–7 m height), Sh: shrub (4–7 m height), sSh: sub-shrub (0.5–4 m height), Li: liana.

Species	Life forms	Laba		Tiogo	
		1992	2002	1992	2002
Protected species					
<i>Albizia chevalieri</i> Harms	sTr	–	–	2	3
<i>Albizia malacophylla</i> (A. Rich.) Walp.	mTr	–	2	–	–
<i>Balanites aegyptiaca</i> (L.) Del.	Bu	4	6	3	5
<i>Bombax costatum</i> Pellegr. et Vuillet	sTr	3	16	–	2
<i>Khaya senegalensis</i> (Dersr.) A. Juss.	lTr	–	1	–	–
<i>Lannea acida</i> A. Rich.	sTr	2	6	5	12
<i>Lannea microcarpa</i> Engl. et K. Krause	sTr	1	–	–	1
<i>Lannea velutina</i> A. Rich.	Bu	2	6	1	2
<i>Parkia biglobosa</i> (Jacq.) Benth.	mTr	–	1	–	2
<i>Prosopis africana</i> (Guill. et Perr.) Taub.	sTr	–	1	1	3
<i>Pterocarpus erinaceus</i> Poir.	sTr	1	1	2	3
<i>Saba senegalensis</i> (A. DC.) Pichon	Li	1	1	1	1
<i>Sclerocarya birrea</i> (A. Rich.) Hochst.	sTr	1	3	3	8
<i>Sterculia setigera</i> Del.	sTr	–	1	1	1
<i>Stereospermum kunthianum</i> Cham.	sTr	1	3	1	7
<i>Tamarindus indica</i> Linn.	mTr	1	4	2	6
<i>Terminalia laxiflora</i> Engl.	sTr	2	1	7	1
<i>Vitellaria paradoxa</i> C.F.Gaertn.	sTr	3	11	8	19
<i>Vitex doniana</i> Sweet	sTr	–	–	1	1
Timber					
<i>Burkea africana</i> Hook. f.	mTr	4	9	–	–
<i>Mitragyna inermis</i> (Willd.) Kuntze	sTr	–	–	1	1
<i>Terminalia avicennioides</i> Guill. et Perr.	Bu	1	12	5	13
<i>Terminalia macroptera</i> Guill. et Perr.	sTr	–	–	7	18
<i>Xeroderris stuhlmannii</i> (Taub.) Mendonça et E.P. Sousa	sTr	–	2	–	1
Pole and fuelwood					
<i>Acacia polyacantha</i> Willd.	sTr	–	1	–	–
<i>Anogeissus leiocarpus</i> (DC.) Guill. et Perr.	mTr	13	66	31	79
<i>Combretum nigricans</i> Lepr. ex Guill. et Perr.	Bu	8	19	16	30
<i>Crossopteryx febrifuga</i> (Afzel. Ex G. Don) Benth.	sTr	7	20	2	3
<i>Detarium microcarpum</i> Guill. et Perr.	Bu	109	147	7	12
<i>Diospyros mespiliformis</i> Hochst. ex A. Rich.	sTr	1	3	2	4
<i>Pseudocedrela kotschy</i> (Schweinf.) Harms	mTr	–	–	1	1
<i>Ziziphus mauritiana</i> Lam.	Sh	–	1	–	1

## Appendix A (Continued)

Species	Life forms	Laba		Tiogo	
		1992	2002	1992	2002
Fuelwood and others					
<i>Acacia dudgeoni</i> Craib. ex Hall.	Bu	3	21	–	10
<i>Acacia erythrocalyx</i> Brenan	Li	11	60	16	22
<i>Acacia macrostachya</i> Reichenb. ex DC.	Sh	39	52	28	62
<i>Acacia seyal</i> Del.	Bu	–	–	1	1
<i>Allophyllus africanus</i> P. Beauv.	Sh	–	7	–	8
<i>Anona senegalensis</i> Pers.	sSh	52	106	11	16
<i>Baissea multiflora</i> A. DC.	Li	–	2	–	2
<i>Boscia senegalensis</i> (Pers.) Lam ex Poir.	Sh	–	–	–	–
<i>Boswellia dalzielii</i> Hutch.	sTr	–	–	1	2
<i>Bridelia ferruginea</i> Benth	Bu	1	2	–	1
<i>Cadaba farinosa</i> Forsk.	sSh	–	2	–	3
<i>Capparis sepiaria</i> L.	Li	3	12	12	25
<i>Cassia sieberiana</i> DC.	Bu	–	1	1	3
<i>Senna singueana</i> (Del.) Lock	sSh	2	1	2	1
<i>Combretum fragrans</i> F. Hoffm.	Bu	29	43	9	10
<i>Combretum glutinosum</i> Perr. ex DC.	Bu	–	–	5	12
<i>Combretum micranthum</i> G. Don.	Sh	1	–	35	82
<i>Combretum molle</i> R. Br. ex G. Don	Bu	8	9	–	–
<i>Dichrostachys cinerea</i> (L.) Wight et Arn.	Sh	11	47	11	63
<i>Entada africana</i> Guill. et Perr.	Sh	2	4	29	37
<i>Feretia apodanthera</i> Del.	sSh	6	33	42	116
<i>Gardenia erubescens</i> Stapf et Hutch.	sSh	1	–	–	1
<i>Gardenia sokotensis</i> Hutch.	sSh	–	–	–	2
<i>Gardenia ternifolia</i> Schum et Thonn.	sSh	1	4	2	4
<i>Grewia bicolor</i> Juss.	Bu	7	20	11	26
<i>Grewia flavescens</i> Juss.	Sh	–	–	5	24
<i>Grewia lasiodiscus</i> K. Schum.	Sh	–	1	1	–
<i>Grewia venusta</i> Fresen.	Sh	12	39	6	11
<i>Guiera senegalensis</i> J.F. Gmel.	Sh	–	–	2	11
<i>Ozoroa insignis</i> Del.	Sh	–	1	–	–
<i>Holarrhena floribunda</i> (G. Don) Dur et Schinz	Bu	–	1	–	1
<i>Hymenocardia acida</i> Tul.	Bu	–	2	–	1
<i>Lonchocarpus laxiflorus</i> Guill. et Perr.	sTr	–	–	–	–
<i>Maerua angolensis</i> DC.	Sh	–	2	1	3
<i>Maytenus senegalensis</i> (Lam.) Exell	Sh	1	2	–	1
<i>Opilia celtidifolia</i> (Guill. et Perr.) Endl. ex Walp.	Li	–	2	–	2
<i>Pericopsis laxiflora</i> (Benth.) van Meeuwen	sTr	1	3	–	–
<i>Piliostigma reticulatum</i> (DC.) Hochst.	Sh	–	–	1	3
<i>Piliostigma thonningii</i> (Schumach.) Milne-Redh	Sh	12	18	10	7
<i>Pteleopsis suberosa</i> Engl. et Diels	Bu	7	13	2	3
<i>Securinega virosa</i> (Roxb. ex Willd.) Baill.	Sh	8	42	8	13
<i>Strychnos innocua</i> Del.	Sh	–	4	–	–
<i>Strychnos spinosa</i> Lam.	Sh	12	55	–	–
<i>Ximenia americana</i> L.	sSh	–	–	18	54
<i>Ziziphus mucronata</i> Willd.	Sh	1	1	–	–

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