



Research article

Influence of 20 years of anthropogenic disturbance, grazing, early fire, and selective cutting on aboveground biomass in savannah woodland of Burkina Faso, West Africa

Koala Jonas^{1*}, Zida Didier² and Louis Sawadogo²

¹Centre National de la Recherche Scientifique et Technologique/Institut de l'Environnement et de Recherches Agricoles/Direction Régionale des Recherches Environnementales et Agricoles du Centre. CNRST/INERA/DRREA Centre, BP 10 Koudougou, Burkina Faso

²Centre National de la Recherche Scientifique et Technologique/Institut de l'Environnement et de Recherches Agricoles/Département Environnement et Forêts. CNRST/INERA/DEF, 03 BP 7047, Ouagadougou 03, Burkina Faso

*Corresponding author email: koalajonas@gmail.com

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Abstract

Savanna ecosystems support low biomass per unit area, but they are more widespread than humid forests and could contribute substantially to carbon storage. The objective of this study was to measure biomass accumulation in savannah woodland subjected to disturbances such as grazing, early fire, and selective logging. Biomass was estimated indirectly using allometric equations. To this end, dendrometric variables measured sequentially since 1992 were used. For each measurement period, biomass was calculated for each individual tree. Then, the individual biomass was added together to find the total biomass for each 2,500 m² (50 x 50 m) subplot for each 5-year period. A repeated measures analysis of variance was applied to the data, and a two-tailed test was used to compare the means of the different treatments. Aboveground biomass increased from 50 to 67 t ha⁻¹, representing 35% increase over 20 years. This corresponds to an average annual increase of 0.8 t ha⁻¹ year⁻¹. The impact of early burning on root biomass varied by location: while it had no significant effect in one area, it led to a marked reduction in fine root biomass in the other. Aboveground, early burning consistently reduced wood density across both sites, though a negative impact on annual increment was localized to only one. Selective cutting negatively affected coarse roots in the more sensitive area and reduced aboveground biomass across both study sites. Similarly, grazing impacted both fine and coarse roots in only one location but showed no significant effect on aboveground biomass in either. Notably, the simultaneous application of early burning, grazing, and selective cutting resulted in a cumulative negative impact on aboveground biomass. The difference in the effects of disturbances between sites suggests that the biophysical conditions of the sites must be considered when using them as management tools.

Keywords: Aboveground biomass, Burkina Faso, Fodder, Grazing, Prescribed fire, Savanna, Selective tree cutting

Introduction

Discussions on the post-Kyoto Protocol have focused heavily on reducing atmospheric CO₂ levels by increasing Carbon (C) sequestration in terrestrial vegetation (Kumar and Nair, 2011). In recent decades, early fire has been prescribed as a management tool for savannah ecosystems in order to minimize serious ecological risks due to late fires and to improve grazing for wild and domestic animals (Bellefontaine *et al.*, 2000; Sawadogo *et al.*, 2005). In addition, grazing intensity is being assessed to support the sustainable integration of pastoral activities into the forest management plan, while selective tree cutting has been recommended on a rotational basis to support fuelwood production (Savadogo *et al.*, 2007b).

Extensive data on early fire, grazing and their effects on vegetation dynamics are now available. (Sawadogo *et al.*, 2002; Savadogo *et al.*, 2007a; Zida *et al.*, 2007; Savadogo *et al.*, 2008; Dayamba *et al.*, 2010; Savadogo *et al.* 2012; Doamba *et al.* 2014). Unfortunately, the direct influence of these disturbances on biomass accumulation in above- and belowground compartments in savannah ecosystems is insufficiently addressed (Sawadogo *et al.*, 2005; Bayala *et al.*, 2006; Berhanu *et al.*, 2007; Beringer *et al.*, 2007). Savanna woodlands are dynamic ecosystems shaped by complex interactions between fire, grazing, and selective tree harvesting. These disturbances significantly influence carbon sequestration and ecosystem structure, yet their effects remain variable and under-documented,

particularly regarding belowground carbon pools (Aynekulu *et al.*, 2021).

Fire acts as a primary consumer of biomass, litter, and soil organic matter, converting organic nutrients into inorganic forms (Wuyep *et al.*, 2024). In West African savannas, long-term frequent fire does not necessarily alter total aboveground herbaceous biomass, but annual early fires can reduce soil water infiltration by impacting soil organic matter (Aynekulu *et al.*, 2021).

Herbivory influences plant development through defoliation, trampling, and excretion. Moderate grazing can actually increase soil organic carbon (SOC) in certain habitats by redistributing aboveground carbon into belowground pools through dung deposition and trampling (Hyvarinen *et al.*, 2023). However, high-intensity grazing often reduces aboveground biomass and soil water infiltration (Aynekulu *et al.*, 2021). Partial or selective cutting alters forest structure by reducing stand basal area and aboveground biomass while simultaneously increasing understory carbon storage by up to 392% due to increased light and resource availability (Zou *et al.*, 2023).

Fire and grazing often exhibit a synergistic relationship known as pyric herbivory. Recently burned areas act as “magnets” for grazers attracted to nutrient-rich regrowth; these animals then reduce the fuel load, which lowers subsequent fire intensity and frequency (Johansson *et al.*, 2020; Venter *et al.*, 2017). This feedback loop is a critical management tool in the Sudanian savanna to maintain species richness and minimize the risk of severe late-season wildfires (Aynekulu *et al.*, 2021).

Research confirms that while tropical savannas support a lower biomass per unit area compared to rainforests, their extensive global distribution- covering approximately one-fifth of the land surface- allows them to contribute substantially to the global carbon cycle (Abreu *et al.*, 2017; Mbangilwa *et al.*, 2020). Standard assessment methodologies typically quantify carbon sequestration by evaluating variations in the biomass stocks of woody plants, which are capable of accumulating significant quantities of carbon- often reaching hundreds of tonnes per hectare over their lifespan (IPCC, 2006a). These methods frequently employ allometric equations to translate measurable tree dimensions, such as diameter at breast height (DBH) and height, into total biomass and subsequent carbon stock estimates (Lin *et al.*, 2016; Pechanec *et al.*, 2022). While traditional field inventories are labor-intensive, they remain the most accurate means of calibrating the predictive models used to scale these carbon measurements across diverse landscapes (Kuyah *et al.*, 2016; Pechanec *et al.*, 2022).

The aim of this study was to measure biomass accumulation in the woody stratum of savannah ecosystems subjected to disturbances such as grazing, early fire and selective logging. Specifically, the aim

was to measure the effect of disturbance on changes in (i) stump density and number of strands, (ii) total tree biomass (DBH > 3 cm) and (iii) annual biomass increment.

Materials and Methods

Study site: The biomass assessment was based on historical data collected in the Sudanian zone in Burkina Faso, West Africa, at two sites, Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) (Fig 1). The study areas are located within the transition zone between the northern and southern Sudanian sectors, characterized by aridity indices of 0.32 at Laba and 0.29 at Tiogo (Sawadogo *et al.*, 2005). Both sites experience a unimodal rainfall regime typically extending six months from May to October. Long-term meteorological data (1992-2012) indicate a mean annual rainfall of 916 ±158 mm at Laba and 837 ±158 mm at Tiogo, with significant inter-annual variability observed in both precipitation volume and the number of rainy days, which averaged 64 ± 16 and 62 ± 12, respectively (Koala *et al.*, 2017). Thermal conditions peak in April (mean daily min/max: 26°/40°C) and reach their minimum in January (16°/32°C).

Experimental design: The study took advantage of long-term experimental research trials (over 20 years) in which disturbances common in the West African region were tested. A factorial experiment was established in 1992 in each of the two sites to examine the effects of grazing, early fire, selective cutting and their interactions on woody and herbaceous vegetation dynamics (composition, abundance and diversity, biomass and regeneration).

Each of the two experimental designs, covering 50 ha, are statistical system with three levels of treatments and their combination with four (4) replicates.

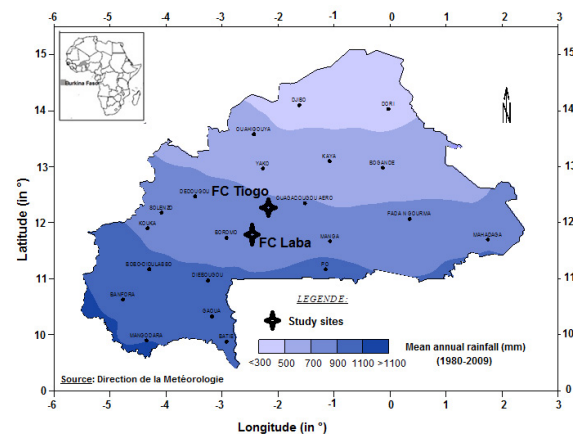


Fig 1. Location of the Tiogo (FC Tiogo) and Laba (FC Laba) classified forests, where the two experimental sites are located

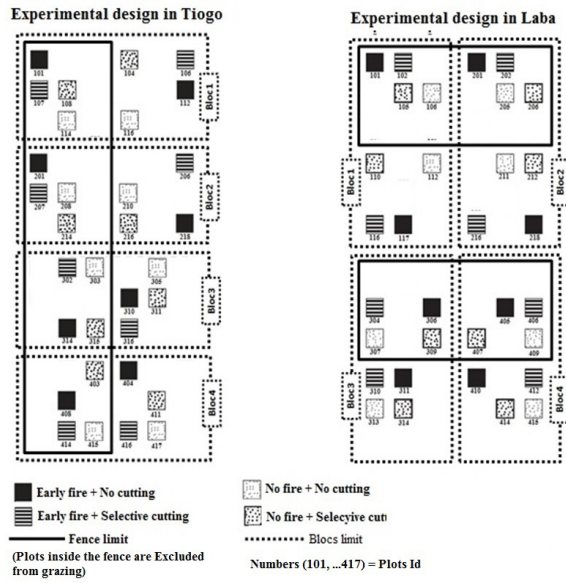


Fig 2. Schematic diagram of the experimental design

- Level 1: Effect of grazing: half of each block of the system is fenced and the other half is left open for grazing (freely roamed by livestock);
- Level 2: Effect of fire (no fire and early fire);
- Level 3: Effect of the type of silvicultural management (no cutting, selective cutting).

Each experimental design comprises 32 plots of 2.500 m² (50 x 50 m). The plots are subdivided into 25 m² (5 x 5 m) subplots marked by concrete markers. Perimeter and inter-plot firebreaks 20 to 30 m wide run through each plot. The layout of the plots is illustrated in Figure 2.

Soils in Laba are generally shallow (<45 cm depth) and the texture is 40% coarse sand, 17% clay, 17% fine sand, 16% coarse silt and 9% fine silt. In Tiogo, the soils are deep (>75 cm) and the texture is 25% coarse silt, 25% clay, 22% fine sand, 15% fine silt and 13% coarse sand (Sawadogo *et al.*, 2005). The vegetation is dominantly woodland and bushland savannah with a grass layer dominated by annual grasses *Andropogon pseudapricus* and *Loudetia togoensis* as well as perennial grass *Andropogon gayanus*. The main forb species are *Cochlospermum planchonii*, *Borreria* spp., and *Wissadula amplissima*. In terms of basal area, the main species are *Entada africana*, *Lannea acida*, *Anogeissus leicarpus*, *Vitellaria paradoxa*, *Detarium microcarpum*, *Combretum micranthum*, and *Acacia macrostachya*. The livestock carrying capacity in Laba State Forest was 1.0 tropical livestock unit ha⁻¹ (T.L.U. ha⁻¹) compared to 1.4 T.L.U. ha⁻¹ in Tiogo State Forest (Sawadogo, 1996) and the grazing pressure at both experimental sites was about half of this capacity.

Biomass measurement: Measuring carbon stock dynamics, according to the method recommended by the IPCC, requires the establishment of biomass carbon stock inventories for a particular area at two different points in

time. Annual variations in biomass are represented by the difference in biomass stock between time t2 and time t1, divided by the number of years between inventories (IPCC, 2006b). To do this, we used data from the temporal monitoring of the stand as a whole. This monitoring was carried out using forest inventory measurements in the study plots during the dry seasons from January to May in 1992, 1997, 2002, 2007 and 2012. Circumferences at 20 cm from the ground ($C_{0.2}$) and 130 cm ($C_{1.3}$) were measured, as well as the height (H) of the stems of all plants with a diameter at breast height >3 cm. Base diameter (D_b or $D_{0.2}$) and diameter at breast height (DBH or $D_{1.3}$) were deduced from the circumferences using the following formula:

$$D_i = \frac{C_i}{\pi} \quad (1)$$

With D_i the diameter at 20 cm or 130 cm and C_i , the circumference at 20 cm or 130 cm

For multicaulus feet, the circumferences and then the diameters of all the strands were measured. Average diameters (D) were calculated using the following formula:

$$D = \sqrt{\frac{\sum_{i=1}^n D_i^2}{n}} \quad (2)$$

The height of all strands was measured using a pole for stems less than 6 m high, and a clinometer for those over 6 m (Photo 3). The number of strands per stump was also noted. Species identification was carried out using the Berhaut (1967) identification key. Wood density is a critical parameter for estimating biomass and carbon stocks (Chave *et al.*, 2009). In this study, wood specific gravity was determined via incremental core sampling following the protocol established by Koala (2016). Samples were extracted at breast height (1.3 m) using a Pressler increment borer (40 cm length, 0.5 cm diameter). To account for radial density gradients common in tropical woody species (Nogueira *et al.*, 2005), the borer was inserted to a depth at least equal to the tree's radius, determined by prior diameter-at-breast-height (DBH) measurements. Each extracted core was immediately sealed in a labeled plastic bag to preserve moisture content, and its fresh length (L_{cf}) and fresh mass (M_f) were recorded using a precision electronic scale (accuracy: 0.1 g). To reach a constant dry mass (M_d), samples were oven-dried at 105°C for approximately 48 to 72 hours (Williamson & Wiemann, 2010). The fresh sample volume (V_f) was subsequently calculated using the following formula:

$$V (\text{cm}^3) = L_{cf} \times (R_t^2 \times \pi) \quad (3)$$

Where V (cm³) = sample volume; L_{cf} = sample length and R_t = auger radius.

The wood density (ρ) of each tree in g m⁻³ is calculated using the following formula:

$$\rho(g\text{ cm}^{-3}) = \frac{Ms \times 1\text{cm}^3}{V(\text{cm}^{-3})} \quad (4)$$

Where ρ (g cm^{-3}) = density of the wood; M_s = dry mass of the sample (in g) and V (cm^3) = volume of the sample. Biomass was estimated indirectly using allometric equations. The specific equations developed for this site for 11 species (Sawadogo et al., 2010) were used to calculate biomass of these species. For the others, the generic and general equation published by Chave et al., (2014) was used.

$$AGB = 0.0673 * (\rho * DBH^2 * h)^{0.976} \quad (5)$$

With AGB: Aboveground Biomass; ρ =Wood specific density; DBH= Diameter at Breast Height or Diameter at 1.3 m and h = Tree height.

To this end, dendrometric variables measured sequentially since 1992 were used. For each measurement period, biomass was calculated for each individual woody species. The individual biomass (B_{ind}) was then summed to find the total biomass for each plot (Bp) of 2,500 m^2 (50 x 50 m) for each 5-year period.–

$$Bp = \sum_{i=1}^n B_{ind}^i \quad (6)$$

We calculated the biomass per hectare (BH) using the following operation:

$$BH = Bp \times 4 \quad (7)$$

With 4, used to increase the area of the unit plot (2,500 m^2) to 1 hectare.

Finally, we calculated the average biomass accumulated in one year [annual increment (productivity)] in one hectare (Pa) for each plot using the following formula.

$$Pa = (BH_{t_{0+5}} - BH_{t_0})/5 \quad (8)$$

With 5, the number of years in the inventory period. These calculations were made for each plot and then subjected to statistical analysis.

Data analysis: All collected data were subjected to statistical analysis. Variable means were subjected to statistical analysis using a general linear model. A repeated-measures analysis of variance was applied to the data, and a two-tailed test was used to compare the means of the different treatments. The general linear model (GLM) had the following formula:

$$Y_{ijklm} = \mu + \beta_i + A_j + G_k + F_l + C_m + \beta A_{ij} + AG_{jk} + AF_{jl} + AC_{jm} + GFC_{klm} + AGFC_{jklm} + e_{ijklm}$$

where Y_{ijklm} is the explanatory variable, μ is the overall mean, β_i is the block effect i , A_j is the time effect j , G_k is the grazing effect k , F_l is the fire effect l , C_m is the cutting effect m . The parameters A_j , G_k , F_l , C_m and their interactions were considered fixed and the parameter β_i

random; e_{ijklm} is the measurement error. Spatial variation of vegetation, vegetation type and plots were considered as randomization effects.

Results and Discussion

This study investigated the long-term (20 years) effects of three common disturbances- early fire, grazing, and selective cutting- on plot-level changes in woody species density (diameter > 3 cm), total biomass, and annual biomass increment across the Laba and Tiogo sites. Overall, considering both sites, the standing density of woody plants (diameter at breast height > 3 cm) increased from 638 plants per hectare to 1 316 plants per hectare over the 20-year period. Total biomass rose from 50 to 67 t ha^{-1} , representing a 35% increase (17.3 t ha^{-1}) over the same period. Aboveground biomass increments remained consistent across both study areas from 1992 to 2012, with a mean annual rate of 0.8 $\text{t ha}^{-1} \text{ yr}^{-1}$ (Fig 3). Grazing applied alone at both sites, Tiogo and Laba, had no influence on the three variables (density of woody species, total biomass and annual biomass increment). The expectation, based on the documented negative impact of grazing on herbaceous biomass (Sawadogo et al., 2005; Savadogo et al., 2009; Dayamba et al., 2010), was that reduced herbaceous competition, coupled with nutrient inputs from ash and animal droppings (Jones et al., 2011), should have benefited the woody stratum. The absence of a significant effect can be explained by the way grazing is practiced at the two sites. As noted by Sawadogo et al. (2005) and Sawadogo (2009), the grazing regime does not critically impact the vital parts of the perennial herbaceous stratum. This allows the perennial grasses to quickly regenerate as soon as favorable conditions return, preventing a lasting competitive advantage for the woody species.

Selective cutting had a consistently negative effect on both tree density and total biomass. This observation aligns with established ecological principles and the findings of Djomo and Gravenhorst (2010), who reported similar negative trends following selective logging in the tropical rainforest of Cameroon. The immediate removal of standing woody stock through cutting directly

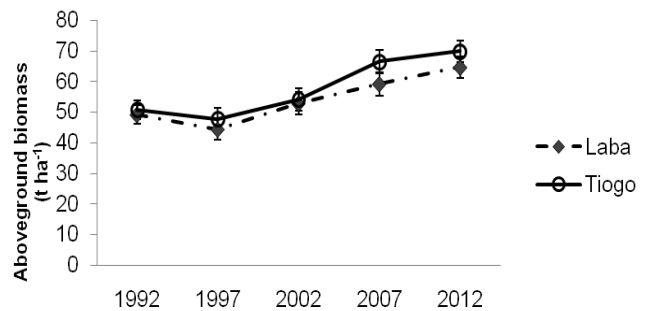


Fig 3. Biomass trends between 1992 and 2012 at the Laba and Tiogo sites in Burkina Faso, West Africa

reduces both the number of trees and the total standing biomass. However, the plots subjected to selective cutting demonstrated a remarkable capacity for recovery in terms of growth rate. The annual increment was $1.6 \text{ t ha}^{-1} \text{ yr}^{-1}$ in the five years immediately following the logging event. This post-logging surge in growth, which led to significant biomass accumulation, is likely attributable to the release from competition. Selective cutting, which removed approximately 50% of the standing woody plants (Sawadogo, 2009), creates canopy gaps that increase light availability and reduce belowground competition for resources among the remaining woody plants and new recruits. Despite this improved growth performance, the recovery was incomplete, and the plots subjected to cutting did not catch up to the total biomass levels of the uncut control plots over the study period.

Early fire applied alone and simultaneously with grazing (grazing + early fire) had a negative effect on annual increment and biomass at the Laba site. This negative impact is primarily linked to the effect of fire on the lowest stratum of vegetation (regeneration). Fire is a key factor in the abscission phenomenon (recurrent mortality of the aboveground part of seedlings and young shoots), as noted by Zida *et al.* (2007). This recurrent die-back limits the rate of development and recruitment from the regeneration layer into the adult (greater than 3 cm diameter) tree class, resulting in lower density in burnt plots compared to unburnt controls. This finding is corroborated by prior work on the same site (Zida *et al.*, 2007) and other managed forests (Ky-Dembélé *et al.*, 2007). Consequently, plots subjected to annual early fire favor the growth of only fire-tolerant species, and even these grow at a slower rate (Zida *et al.*, 2007; Sawadogo, 2009). In Tiogo, on the other hand, their effects were not significant. The results of the statistical analysis revealed heterogeneity between sites when considering the variation of parameters (tree density, total biomass and annual increment). This contrasting response is likely due to the difference in fire intensity between the two sites, which is driven by site-specific soil and herbaceous layer characteristics. The higher fire intensity at Laba leads to more severe damage and a greater reduction in annual growth and total biomass. This discrepancy highlights the importance of edaphic and fuel characteristics in mediating the ecological impact of fire (Zida *et al.*, 2007; Sawadogo, 2009)

In the Laba site, the density of woody species increased from 650 feet per hectare in 1992 to 1481 feet per hectare in 2012, an increase of 128% ($F_{[4,120]}=25.11$; $p < 0.001$). Among the treatments (grazing, annual early fire and selective cutting), only early fire had a significant effect on stand density in Laba ($F_{[1,120]}=76.65$; $p < 0.001$) (table 1). While density increased in both treatments, the gain in unburnt plots (172%) was more than double that of the burnt plots (82%). The significant difference (172 vs. 82%) confirms

that total protection against fire is the most powerful lever for rapid restoration of wood density. Early fires, although less intense than late fires, act as a “filter.” They kill some of the seedlings and, above all, “cut back” the young shoots, keeping them in what ecologists call the “fire trap.” Individuals remain stuck at the bush stage and are unable to reach a safe height (> 2–3 meters) to become mature trees (Savadogo *et al.*, 2007c; Dayamba, 2010). Livestock mainly consume the herbaceous layer. By reducing grass biomass, they paradoxically reduce the amount of fuel available for fire. Thus, moderate grazing can sometimes ‘help’ woody plants by limiting the intensity of fires (Savadogo *et al.*, 2005). In these ecosystems, cutting 50% of the basal area (the standard practice in Burkina Faso) does not necessarily reduce the number of trees in the long term, as each tree that is cut down often produces several shoots from the stump (multitemmed growth), which maintains or even increases the numerical density of stems.

Total biomass at the Laba site increased from 49 t ha^{-1} in 1992 to 65 t ha^{-1} in 2012, representing a total average accumulation of 15.5 t (31%; Fig 4). The treatments (Grazing, Early Fire and Selective Timber Harvesting and their interactions) applied during the period affected biomass differently. Early fire reduced biomass by 19 t ha^{-1} . Plots subjected to early fire accumulated an average total of 6 t over the 20 years, i.e., an increase of 11%. Results show fire ‘reduced’ potential biomass by 19 t ha^{-1} . Recent research by Bustamante *et al.* (2014) and Savadogo (2007c) suggests that frequent burning cycles not only destroy existing woody material but also volatilize nitrogen and carbon that would otherwise be incorporated into the soil and plant tissue. Plots not subjected to fire accumulated an average of 25 t of biomass, i.e., an increase of 52% over the period (Table1).

Selective cutting had a negative impact on biomass accumulation over the period. The rate of increase recorded in plots subjected to cutting (21% or 10 t of biomass over 20 years) was much lower than in plots without cutting, which was 41% (22 t). This can be explained by several factors. During cutting, every tree intentionally felled, significant collateral damage occurs to the surrounding stand, often leading to delayed growth in the remaining biomass (Pearson *et al.* 2023). Also, large-diameter trees, the ones usually targeted in selective cutting, can account for up to 50% of the stored carbon in certain forest patches. Removing even a few of these individuals drastically lowers the “ceiling” for biomass accumulation for decades (Mildrexler *et al.*, 2020). The early fire + selective cutting and grazing+early fire treatments also had a negative impact ($F_{[1,120]}=11.42$; $p < 0.001$ et $F_{[1,120]}=4.75$; $p = 0.031$, respectively) biomass accumulation. In plots subjected to the early fire+selective cutting treatment, biomass increased by 5 t over 20 years, equivalent to an 11% rate of increase, compared

Table 1. Results of the analysis of variance (ANOVA) of the variables stump density, total biomass and annual increment under the effect of time (A), grazing (P), early fire (F), selective logging (C) and their interactions in the Laba site in Burkina Faso, West Africa

Trait	Number of stumps (Nbre ha ⁻¹)			Biomass (t ha ⁻¹)			Increment (t ha ⁻¹ an ⁻¹)		
	ddl	F	P	ddl	F	P	ddl	F	P
P	1	0.78	0.378	1	1.96	0.165	1	0.09	0.763
F	1	76.65	0	1	2.37	0.126	1	8.78	0.004
C	1	0.42	0.517	1	16.98	0	1	2.71	0.103
P+F	1	3.74	0.056	1	4.75	0.031	1	0.25	0.618
P+C	1	1.7	0.195	1	0.39	0.534	1	0.03	0.868
F+C	1	0.63	0.43	1	11.42	0.001	1	0.4	0.529
P+F+C	1	2.95	0.089	1	0.57	0.453	1	0.33	0.565
A	4	25.11	0	4	4	0.004	3	12.83	0
A+P	4	0.02	0.999	4	0.06	0.993	3	0.58	0.628
A+F	4	5.32	0.001	4	1.5	0.206	3	4.26	0.007
A+C	4	0.14	0.969	4	0.78	0.543	3	9.16	0
A+P+F	4	0.19	0.945	4	0.24	0.917	3	4.52	0.005
A+P+C	4	0.23	0.923	4	0.06	0.993	3	0.75	0.528
A+F+C	4	0.02	0.999	4	0.09	0.985	3	1.58	0.199
A+P+F+C	4	0.24	0.918	4	0.16	0.958	3	1.59	0.198

with an accumulation of 30 t (73% rate of increase) for control plots. The drop from 30 t in control to 5 t in the plot subjected to Fire + Cutting suggests a synergistic rather than additive impact. Selective cutting opens the canopy, which increases the “fuel load” (logging slash) and lowers the relative humidity of the understory. This means that early fires in logged stands burn hotter and more thoroughly because of this drier, open-canopy microclimate (Zhu *et al.*, 2014). This destroys the saplings that would otherwise drive biomass recovery. A study by Bhatti *et al.* (2025) found that frequently disturbed stands by fire + logging have up to 38.5% less woody carbon stock compared to unburnt stands because the transition from sapling to adult is permanently suppressed. In plots subjected to the grazing+early fire treatments, the accumulated biomass was 15 t, equivalent to 33% growth rate. That was less detrimental than the fire + cutting treatment (5 t). Indeed, grazing mitigates the severity of fires by consuming the grasses that spread the fire (Pearson *et al.*, 2023; Archibald *et al.*, 2024) and sparing some woody biomass. Grazing alone did not significantly influence biomass accumulation (Fig 4).

At the Laba site, annual increment averaged 0.77 t ha⁻¹ yr⁻¹ over the 20 years. The annual increment was 0.29 t ha⁻¹ year⁻¹ in burnt plots, compared with 1.3 t ha⁻¹ year⁻¹ in unburnt plots. However, over the course of 20 years, there were annual fluctuations with two homogeneous periods (Fig 5): during the first ten years, the practice of early fire did not significantly influence the annual

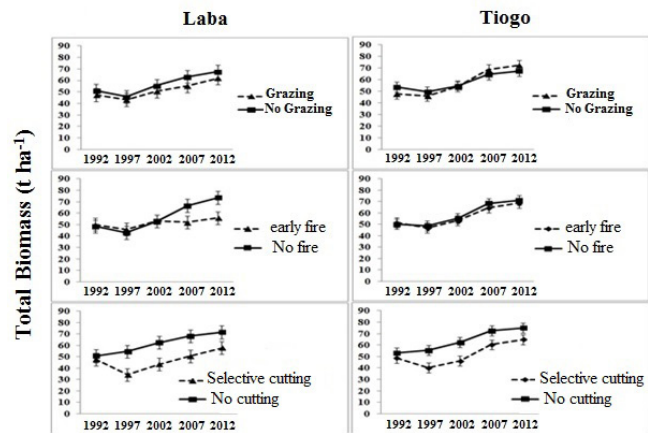


Fig 4. Total biomass trends in plots subjected to grazing, early fire and selective logging variation at the Laba and Tiogo sites in Burkina Faso, West Africa

biomass increment. It averaged 0.30 t ha⁻¹ yr⁻¹ in burnt plots versus 0.45 t ha⁻¹ yr⁻¹ in unburnt plots, giving an annual gap of 0.15 t ha⁻¹ yr⁻¹ (Fig 5). After ten years of practice, early fire contributed to a considerable drop in annual biomass increment. Biomass accumulated at a rate of 0.27 t ha⁻¹ yr⁻¹ in burnt plots, compared with 2.1 t ha⁻¹ yr⁻¹ in unburnt plots. This result in unburnt plot is less than typical values for ‘protected’ or ‘fenced’ Sudanian savannas, often reaching 3.0 to 4.5 t ha⁻¹ yr⁻¹ in the first 20 years of recovery (Zubkova *et al.*, 2019). In the long term, fire reduced biomass by 1.8 t ha⁻¹ yr⁻¹. The selective cutting

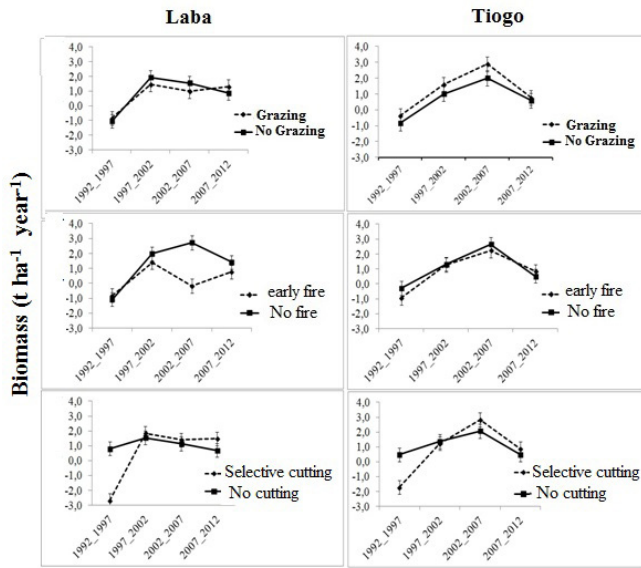


Fig 5. Annual biomass productivity trends in plots subject to grazing, early fires, and selective logging at the Laba and Tiogo sites in Burkina Faso, West Africa

and grazing + early fire treatments also contributed to a significant reduction in aboveground biomass over the study period ($F_{[3,96]}=9.16$; $p < 0.001$ et $F_{[3,96]}=4.51$; $p = 0.005$, respectively, in Tiogo and Laba).

The annual increment in plots subjected to selective cutting was $1.6 \text{ t ha}^{-1} \text{ year}^{-1}$ compared with $1.1 \text{ t ha}^{-1} \text{ year}^{-1}$ in plots without cutting. This corresponds to an improvement of $0.5 \text{ t ha}^{-1} \text{ year}^{-1}$. In the plots subjected to the grazing + early fire treatment, the increment was $0.49 \text{ t ha}^{-1} \text{ yr}^{-1}$ compared with $1.5 \text{ t ha}^{-1} \text{ yr}^{-1}$ for the control plots (Table 2).

In Tiogo site, stand density increased by 84%, from 626 feet per hectare in 1992 to 1152 feet per hectare in 2012. ($F_{[4,120]}=26.84$; $p < 0.001$). The practice of fire has ($F_{[1,120]}=26.97$; $p < 0.001$) reduced tree density (Table 3).

The rate of increase in burnt plots was 63%, compared with 105% in unburnt plots. The particularity of this site is that the cumulative effects of the treatments ('early fire + selective cutting' and 'grazing + early fire + selective cutting') had a negative influence on the increase in tree density (Table 3) (respectively $F_{[1,120]}=6.73$; $p = 0.011$ and $F_{[1,120]}=8.81$; $p = 0.004$). The rates of increase were 59 and 65%, respectively in the plots subjected to the 'early fire + selective cutting' and 'grazing + early fire + selective cutting' treatments, compared with an increase of 98% in the control.

Between 1992 and 2012, total biomass rose by 19 t (from 51–70 t), a total increase of 37%. Analysis of the effects of treatment application over this period showed that only selective cutting ($F_{[1,120]}=18.02$; $p < 0.001$) and early fire+selective cutting treatment ($F_{[1,120]}=6.60$; $p = 0.011$) significantly influenced biomass accumulation. Plots subjected to selective cutting had a growth rate of 31%, compared with 43% in plots without cutting. In plots treated with early fire + selective cutting, the rate of increase was 22%, compared with 43% in control plots (Table 4).

In Tiogo, the annual increment was $0.95 \text{ t ha}^{-1} \text{ yr}^{-1}$ over the 20-year period. Analysis of the effects of the treatments applied over 20 years showed that the separate and cumulative effects of the treatments had no significant influence ($p > 0.05$) on the annual biomass increment. Nevertheless, from one year to the next, selective cutting has had significant effects ($F_{[1,120]}=3.94$; $p = 0.011$) on the annual increment, from a negative increment ($-2.2 \text{ t ha}^{-1} \text{ yr}^{-1}$) in 1992 to $1.2 \text{ t ha}^{-1} \text{ yr}^{-1}$. In plots without cutting, the level of increment at year 20 is the same as in 1992, i.e., $0.6 \text{ t ha}^{-1} \text{ yr}^{-1}$ (Table 4). The average total biomass of 57 t ha^{-1} found in this study is comparable to other semi-arid savanna ecosystems, such as the $59 \pm 26.15 \text{ t ha}^{-1}$ reported by Ribeiro *et al.* (2013). Crucially, the observed contrasting response of disturbance effects on clay *versus* shallow sandy soils suggests that caution must be exercised

Table 2. Means and their confidence intervals (CI) of total standing biomass (t ha^{-1}), accumulated biomass (t ha^{-1}) between 1992 and 2012 (Biom acc.), Low limit (LL) and the Uer limit (UL) of CI, annual increment (Icr) ($\text{t ha}^{-1} \text{ yr}^{-1}$) and 20-year growth rate (Var.) (%) of plots subjected to grazing (P), early fire (F), selective logging (C) treatments and their interactions (+) in the Labaau site, Burkina Faso, West Africa

	Biomass (t ha^{-1})	CI (95%)		Biom acc.	CI (95%)		Icr	CI (95%)		Var (%)	CI (95%)	
		LL	UL		LL	UL		LL	UL		LL	UL
F	55.8	45.5	66.1	5.7	4.4	7.1	0.3	0.2	0.4	11.5	10.7	12.1
C	57.8	47.5	68.1	10.1	8.7	11.4	0.5	0.4	0.6	21.1	22.4	20.2
P	61.9	51.6	72.1	14.5	13.1	15.8	0.7	0.7	0.8	30.6	34.1	28.1
P+F	49.1	34.6	63.6	3.1	1.2	5.0	0.2	0.1	0.3	6.8	3.6	8.6
F+C	42.0	27.5	56.6	-1.7	-3.7	0.2	-0.1	-0.2	0.0	-4.0	-11.7	0.3
P+C	56.5	42.0	71.1	9.6	7.7	11.5	0.5	0.4	0.6	20.5	22.4	19.4
P+F+C	38.8	18.2	59.4	-5.7	-8.4	-3.0	-0.3	-0.4	-0.1	-12.8	-31.6	-4.8
Control	72.1	51.5	92.6	30.3	27.6	33.1	1.5	1.4	1.7	72.7	115.5	55.5

Table 3. Results of the analysis of variance (ANOVA) of the variables stump density, total biomass and annual increment under the effect of time (A), grazing (P), early fire (F), selective logging (C) and their interactions in the Tiogo site in Burkina Faso, West Africa

Source	Souches (Nbre ha ⁻¹)			Biomass (t ha ⁻¹)			Increment (t ha ⁻¹ an ⁻¹)		
	ddl	F	P	ddl	F	P	ddl	F	P
P	1	0.22	0.638	1	0	0.985	1	2.53	0.115
F	1	26.97	0	1	0.41	0.523	1	0.38	0.54
C	1	0.47	0.495	1	18.02	0	1	0.75	0.389
P+F	1	3.33	0.07	1	2.31	0.131	1	1.68	0.197
P+C	1	0.64	0.427	1	3.21	0.076	1	0.28	0.598
F+C	1	6.73	0.011	1	6.6	0.011	1	0.34	0.558
P+F+C	1	8.81	0.004	1	0	0.947	1	0.01	0.942
A	4	26.84	0	4	10.12	0	3	14.73	0
A+P	4	0.19	0.944	4	0.55	0.696	3	0.2	0.897
A+F	4	2.47	0.048	4	0.11	0.978	3	0.42	0.742
A+C	4	0.03	0.999	4	0.58	0.677	3	3.94	0.011
A+P+F	4	0.17	0.953	4	0.41	0.8	3	0.97	0.408
A+P+C	4	0.23	0.921	4	0.07	0.991	3	0.26	0.856
A+F+C	4	0.32	0.865	4	0.16	0.958	3	1.28	0.286
A+P+F+C	4	0.18	0.947	4	0.06	0.993	3	0.48	0.7

Table 4. Averages and their confidence intervals (CI) of total standing biomass (Biom), accumulated biomass between 1992 and 2012 (Biom acc.), Low limit (LL) and the Uer limit (UL) of CI, annual increment (Icr) over 20 years (Var.) of plots subjected to grazing (P), early fire (F), selective logging (C) treatments and their interactions (+) at the Tiogoau site Burkina Faso, West Africa

	Biom. (t ha ⁻¹)	CI (95%)		Biom acc.	CI (95%)		icr	CI (95%)		Var%	CI (95%)	
		LL	UL		LL	UL		LL	UL		LL	UL
F	68.6	58.3	78.9	17.0	15.6	18.4	0.8	0.8	0.9	32.9	36.6	30.3
C	64.8	54.5	75.1	16.2	14.8	17.5	0.8	0.7	0.9	33.3	37.3	30.5
P	72.4	62.1	82.6	24.3	23.0	25.7	1.2	1.1	1.3	50.7	58.8	45.1
P+F	70.2	55.7	84.7	26.6	24.7	28.5	1.3	1.2	1.4	61.0	79.6	50.8
F+C	67.1	52.6	81.7	12.2	10.2	14.1	0.6	0.5	0.7	22.1	24.2	20.9
P+C	66.2	51.7	80.8	23.2	21.3	25.1	1.2	1.1	1.3	54.0	70.1	45.2
P+F+C	67.1	46.5	87.6	23.3	20.6	26.0	1.2	1.0	1.3	53.2	79.3	42.2
Control	76.1	55.6	96.7	23.0	20.3	25.8	1.2	1.0	1.3	43.4	57.6	36.3

when generalizing results concerning the effects of disturbance on vegetation primary production across different ecological contexts. The local soil-moisture-fuel complex is a critical modulator of disturbance intensity, particularly fire, which dictates the resulting impact on woody vegetation dynamics.

Conclusion

The results of the study showed that the overall level of increase in aboveground biomass over the period 1992 to 2012 was statistically similar at both sites. Aboveground biomass rose from 50 t ha⁻¹ to 67 t ha⁻¹, an increase of 35%

over the said period. This corresponds to an average annual increment of 0.8 t ha⁻¹ yr⁻¹. Early fire negatively affected woody density and annual increment at Laba, while at Tiogo, it affected woody density only. Selective cutting had a negative impact on large roots only at Laba, and on aboveground biomass at both sites. Grazing affected both fine and coarse roots only at Laba. However, it did not significantly affect aboveground biomass at either site. Simultaneous application of treatments (early fire, grazing and selective cutting) adversely affected both root and aboveground biomass. The different effects of disturbance at different sites suggest that the biophysical

conditions of the sites must be taken into account when using them as management tools.

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