Dominant species' resprout biomass dynamics after cutting in the Sudanian savanna-woodlands of West Africa: long term effects of annual early fire and grazing

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ORIGINAL PAPER

Dominant species' resprout biomass dynamics after cutting in the Sudanian savanna-woodlands of West Africa: long term effects of annual early fire and grazing

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Abstract

• ***Background*** The potential of forest to regenerate after harvesting is a key element for sustainability of the ecosystem. For semi-arid tropical savanna environments, managing resprouts after tree cutting is ideally suited because of the natural ability of many indigenous species to regenerate vegetatively. Regeneration in this ecosystem is, however, prone to many disturbance factors such as fire and grazing by livestock.

• ***Methods*** In this paper, we used a factorial experiment to examine the long-term effects of annual early burning and grazing on dominant species' resprout biomass dynamics after selective cutting in the Sudanian savanna-woodlands of Burkina Faso, West Africa

• ***Results*** Burning decreased shoot mortality of *Crossopteryx febrifuga* while grazing increased that of *Detarium microcarpum*. Burning, in later measurement years, reduced resprouts' size of *Acacia macrostachya*, *C. febrifuga* and *D. microcarpum* while an increased basal area was observed for *Combretum glutinosum*. There was no significant evidence of grazing hampering growth.

• ***Conclusions*** Moderate livestock grazing could be integrated in the forest management prescriptions in Burkina Faso for the sake of multi-purpose uses, while more attention should be paid to burning practices to lower fire severity, as complete fire exclusion is utopian in this savanna ecosystem.

Keywords Disturbance · Forest regeneration · Sustainable forest management · Tropical ecosystems

1 Introduction

Harvesting of forests is essential for rural livelihoods in tropical dry forests, as it provides employment, income as well as consumption goods and services. In West Africa, firewood is the major source of energy used for cooking, heating, and other domestic purposes, and woodfuel, including fuelwood and charcoal, accounts for about 90% of the total energy consumption (Brocard et al. 1998; Nygard et al. 2004). The main vegetation cover used by the households to produce woodfuel is obtained from natural forests, and management strategies are expected to make this ecosystem sustainable by ensuring good regeneration after harvesting.

Most tropical dry forest species have the ability to regenerate vegetatively (Murphy and Lugo 1986; Ky-Dembele et al. 2007), and coppice growth is an important species-specific trait that strongly influences fuelwood production and regeneration (Kaschula et al. 2005). Coppice management for fuelwood and charcoal is perhaps ideally suited for semi-arid tropical savanna

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environments due to the natural ability of many indigenous species to regenerate vegetatively, as well as the resilience of resultant coppice regrowth to anthropogenic disturbance, drought, nutrient poor soils, pests, and disease (Kennedy 1998). This form of post-harvest regeneration is also far more rapid than seedling regeneration, owing to the swift development of leaf area index and the associated greater interception of solar radiation (Harrington and Fownes 1995; Luoga et al. 2004).

Forest regeneration in tropical savanna ecosystems is subject to many disturbance factors. In the Sudanian zone, fire is a prominent feature, and it is estimated that 25 to 50% of the area is burnt annually (Delmas et al. 1991), and all areas burn every 2–3 years primarily due to anthropogenic causes (Menaut et al. 1991). Burning, especially late in the dry season when herbaceous biomass is dry, is fierce and can be devastating for woody shoots. Also, post-fire environment may be drought-prone as a result of increased soil exposure to direct radiation (Zida et al. 2008). Fire may, however, increase light availability and accelerate short-term mineralization of nitrogen which might be beneficial for shoots.

Livestock grazing is one of the main causes of soil and vegetation degradation (Warren et al. 2001). Depending on the stocking rate, livestock grazing can limit seedling recruitment by exacerbating drought (Kozlowski 1999) through its soil compaction effects, which in turn reduces soil infiltration (Savadogo et al. 2007). Browsing may prevent seedlings from establishing and reduce height growth of coppice stems, thus suppressing their recruitment into the adult stage (Gignoux et al. 1997). By reducing herbaceous biomass, grazing can, however, reduce the competition from the herbaceous layer, thereby increasing wood production (Peltier and Eyog-Matig 1989) and regeneration (Sawadogo et al. 2002).

The co-occurrence of fire and grazing is expected to have a synergistic effect on plant communities both in time and space. Many grazers are attracted to recently burnt ground to feed on the post-fire regrowth of grasses. Grazers in turn, reduce the fuel load by consumption and trampling, and therefore lower the intensity and frequency of fire (Savadogo et al. 2008). According to Dembélé (1996), regeneration through coppicing is favored by the synergistic effect of fire and grazing but those shoots are prone to die-back.

Current policies for sustainable management of savanna-woodlands in Burkina Faso focus on woody vegetation and entail prohibition of grazing, setting annual early fires, and selective tree cutting of 50% of the basal area over a 20-year rotation (Bellefontaine et al. 2000). This approach is not based on scientific evidence. To generate scientific information for use in development of appropriate management strategies, long-term experimental plots were established in 1992 to examine the ecological effect of repeated burning, grazing and selective tree cutting on both the woody and herbaceous components of the Sudanian savanna-woodlands (Sawadogo et al. 2005).

Studies have reported the relationship between number of coppice shoots and stump characteristics (Shackleton 2000), and the influence of stump diameter and stump height on a range of coppice response variables for selected species (Boivin-Chabot et al. 2004; Kaschula et al. 2005). The effects of forest disturbances on resprout biomass dynamics, which is essential for designing sustainable management strategies is, however, not well-documented, especially in the West African context. We hypothesized that forest biomass reconstitution after cutting (resprouts biomass) is affected by disturbances such as fire and grazing. Because coppicing effectiveness is variable among species (Luoga et al. 2004) we selected six species (*Combretum ghazalense* F. Hoffm., *Crossopteryx febrifuga* (Afz. ex G. Don) Benth., *Detarium microcarpum* Guill. et Perr., *Acacia macrostachya* Rchb. ex DC., *Combretum glutinosum* Perr. ex DC. and *Entada africana* Guill. et Perr.) that were the most common on nearly all experimental plots for analysis of the effect of fire and grazing treatments on resprout biomass dynamics at individual species level, using 13 years of data.

2 Material and methods

2.1 Site description

The experimental sites are located on flat areas in Laba (11°40′N, 2°50′W) and Tiogo (12°13′N, 2°42′W) State forests, both at an altitude of 300 m above sea level in Burkina Faso, West Africa. Both forests are located along the only permanent river (Mouhoun, formerly known as Black Volta) in the country. The unimodal rainy season lasts for about 6 months, from May to October. Based on data collected from in situ mini-weather station at each site, the mean annual rainfall during the study period (1994–2006) was 857±143 mm for Laba and 860±185 mm for Tiogo, and the number of rainy days per annum was 68±18 and 66±10 for Laba and Tiogo respectively. Mean daily minimum and maximum temperatures ranged from 16 to 32°C in January (the coldest month) and from 26 to 40°C in April (the hottest month). Most frequently encountered soils are Lixisols, and the soil at Laba is shallow (<45 cm depth) silty-sand, while it is mainly deep (>75 cm) silty-clay at Tiogo. These soils are representative of large tracts of the Sudanian Zone in Burkina Faso (Pallo 1998). Phyto-geographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to south Sudanian Zone

(Fontès and Guinko 1995). The Sudanian savanna is an area stretching across the African continent from Senegal in the west to the Ethiopian highlands in the east, and is characterized by 6–7 months of dry season and a mean annual rainfall between 700 and 1200 mm (Breman and Kessler 1995; Menaut et al. 1995). The vegetation type at both sites is a tree/bush savanna, with a grass layer dominated by the annual grasses *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilg.) C.E. Hubb., as well as the perennial grasses *Andropogon gayanus* Kunth (dominant in Tiogo) and *Andropogon ascinodis* C.B. Clarke (dominant in Laba). The main forb species are *Cochlospermum planchonii* Hook. ex Planch., *Borreria stachydea* (DC.) Hutch. and Dalziel, *Borreria radiata* DC., and *Wissadula amplissima* Linn. Species of the families Mimosaceae and Combretaceae dominate the woody vegetation component at both sites. In terms of basal area, the main woody species are *Detarium microcarpum* Guill. & Perr., *Combretum nigricans* Leprieur ex Guill. & Perr., *Acacia macrostachya* Rchb. ex DC., *Entada africana* Guill. & Perr., *Lannea acida* A. Rich., *Anogeissus leiocarpa* Guill. & Perr., and *Vitellaria paradoxa* C.F. Gaertn. Prior to the start of the experiments, the mean basal area of woody species at Laba was 10.7 and 6.3 m^2 ha^{-1} at stump level (20 cm) and breast height (130 cm) respectively, with the stand density of 582 individuals ha^{-1} having at least one stem ≥10 cm GBH (girth at breast height). At Tiogo, the equivalent values were 10.9 m^2 ha^{-1} at stump level, 6.1 m^2 ha^{-1} at breast height and 542 individuals ha^{-1}. Both sites were frequently grazed by livestock and wild animals and burnt almost every year during the dry season (November–May) long before the start of the experiment. The presence of livestock in the two State forests varies spatially and temporally, occurring mainly during the rainy season (June–October) when the grass is green and the surrounding areas are cultivated. During the dry season, they graze on straws in the bush clumps that have escaped the fire, as well as on the young shoots of perennial grass species and young woody foliage induced by the fire.

2.2 Experimental design and treatments

A factorial experiment was established in each of the two State forests to examine the effects of grazing, early fire, and selective cutting and their interaction on the ecology and productivity of the Sudanian savanna-woodlands. Each experimental site (18 ha) was divided into eight blocks (2.25 ha), four of which were fenced to exclude livestock (hereafter referred to as ungrazed plots) and the other four were open for grazing (hereafter referred to as grazed plots). Each block contained 9 plots of 0.25 ha (50×50 m) separated by a 20–30 m fire break. To the nine plots within each block, three treatments were randomly assigned as no cutting, selective cutting, and selective cutting followed by direct seeding of tree species. To each plot that had received the same cutting treatment, one of three fire treatments was applied: fire protection, 2-year fire protection after cutting followed by early annual fire, and early annual fire since the establishment of the trials. In the present paper only cut plots were considered, and we assessed the effect of early fire and grazing on resprout dynamics. We did not assess "2-year fire protection", as this treatment was not strictly followed later on. Also, as the direct seeding was not successful, the two logging modalities "selective cutting" and "selective cutting followed by direct seeding of tree species" were both considered to be a "selective cutting treatment". Each fire × grazing combination resulted in eight replications. The selective cutting was done in December 1993 at Tiogo, and a month later in January 1994 at Laba by removing 50% of the basal area of stem >10 cm girth. Prior to cutting, all species were categorized according to their local uses as protected species, timber, poles and fuelwood, and others (Sawadogo 1996). Except protected species, individuals of other categories were cut at about 15 cm above ground (Sawadogo et al. 2002). The structural characteristics at each site for the six studied species (Table 1) indicated that *D. microcarpum* had the highest relative dominance (36%), followed by *C. febrifuga* at Laba site. At the Tiogo site,

Table 1 Sample size of stump and average value of diameter and height of trees with stem ≥10 cm girth at breast height together with the relative dominance of the selected species

	N	H (cm)	Dbase (cm)	Dbh (cm)	RD (%)
Laba					
All species	13,405	457±3	14.81±0.12	10.54±0.10	
C. ghasalense	1,632	365±5	11.98±0.20	7.65±0.15	8.29
C. febrifuga	1,200	566±10	21.07±0.47	15.36±0.36	12.17
D. microcarpum	5,373	481±4	16.23±0.13	11.41±0.11	35.64
Tiogo					
All species	17,639	411±3	11.36±0.10	7.72±0.09	
A. macrostachya	1,657	357±5	8.80±0.14	5.67±0.10	6.45
C. glutinosum	630	458±13	12.38±0.50	8.36±0.31	3.31
E. africana	6,888	452±5	12.21±0.13	8.63±0.11	26.20

N = number of stump; H = mean height; Dbase = mean diameter at 20 cm above ground; Dbh = diameter at breast height; RD = Relative dominance [= (total basal area for a species/ total basal area of all species) × 100]

E. africana stood out as the most dominant, followed by *A. macrostachya*. The prescribed early fire was applied at the end of the rainy season (October–November) each year, beginning in 1993 when the grass layer humidity was approximately 40%. The grazed plots at both study sites were open for grazing by livestock (a mixed herd of cattle, sheep and goats). The livestock carrying capacity in Laba forest was 1.0 tropical livestock unit ha^{-1} (T.L.U. ha^{-1}), and that of Tiogo was 1.4 T.L.U. ha^{-1} (Sawadogo 1996) and the grazing pressure at both sites was about half of this capacity (Sawadogo et al. 2005).

2.3 Data collection

Every cut stump was surveyed annually at the end of the dry season in May over a period of 13 years (1994–2006), and the following variables were recorded:

- Shoot mortality, determined by counting the number of dead shoots for a species in a plot and dividing by the total number of shoots of this species recorded during the survey in that plot.
- Height (cm) (or length along the stem if the shoot is leaning) of all coppice shoots, measured with a graded pole.
- Girth (cm) of coppice shoots at stump height and at breast height. Girth was measured with a tailor tape and was used to calculate basal area at stump and at breast height.

2.4 Statistical analyses

A single treatment plot comprised many cut stumps, and we sought to investigate shoot biomass dynamics per species as affected by fire and grazing treatments by pooling resprout biomass per species at plot level. Basal area at stump level, basal area at breast height, and tree height were computed and analyzed with linear mixed-effect models. Year was treated as a continuous factor, grazing and fire as categorical fixed factors, and plot as a random factor. To account for the temporal autocorrelation of the data, we included in the models an auto-regressive correlation structure of order 1, which assumes that observations made close to each other in time are more related than those separated further in time (Pinheiro and Bates 2000). We avoided data transformation as a solution to heterogeneity (unequal variance), as heterogeneity is interesting ecological information that should not be thrown away just because it is statistically inconvenient (Zuur et al. 2009). Instead, we modeled the heterogeneity within the data (shown by preliminary analyses) by allowing each indicated stratum (in the data) to have its own residuals spread. Shoot mortality was analyzed with generalized linear mixed-effect models, using penalized quasi-likelihood with binomial errors in order to account for the non-normal errors and the non-constant variances that are associated with proportional data. Year was used as a continuous factor, and the same categorical fixed factors and random factor as above. All models were checked for meeting the assumptions, and 95% confidence intervals were produced and checked to ensure that the models' estimates were adequate.

For practical reasons the inventory was not conducted at Laba State forest in 1998. Also, a plot at Tiogo State forest had missing values in 1999. Values for these years and plots were declared missing during the analyses. The type of missing value we had in the data sets could be considered as dropout completely at random (DCAR) according to Everitt (2007), as the probability of these data being missing did not depend on the observed or missing values of the responses; in other words, these data were not missing (discarded) because of knowledge of their values. This kind of missing values cause the least problem for data analyses, and the mixed-effect models give valid results (Davis 2002; Everitt 2007). All statistical analyses were performed within the R statistical package (Zuur et al. 2009). The nlme package was used to calculate the linear mixed-effect models. The MASS package was used to calculate the generalized linear mixed-effect models using penalized quasi-likelihood estimates. Results of the statistical analyses were considered significant if P-value<0.05, and to show tendencies if 0.05 <P<0.1.

3 Results

3.1 Resprout mortality

Fire and fire × year significantly affected mortality of *C. febrifuga* (Table 2, Fig. 1); for this species, at a later stage of the experiment (after 4 years), burnt plots had lowest mortality, while the reverse was the case at early stage. For *D. microcarpum*, mortality was significantly higher for grazed plots as compared to ungrazed ones (2.50±0.15% and 1.64±0.12% respectively). Grazing and grazing × fire significantly affected mortality of *E. africana* (Table 2); burning markedly reduced mortality within ungrazed treatment (0.67±0.09% and 1.15±0.17% for burnt and unburnt plots respectively), while in grazed treatment the difference between the two fire treatments was low (0.94± 0.12% and 1.17±0.18% for burnt and unburnt plots respectively). For *C. ghazalense* (Fig. 1); except for the first 2 years where ungrazed and burnt plots showed the highest mortality, in general, mortality was highest for grazed and burnt plots. None of the treatments affected mortality of *A. macrostachya* and *C. glutinosum*.

Table 2 Effects of fire (F) and grazing (G) on dominant species' resprout size parameters in Laba and Tiogo State forests in Burkina Faso. Significant ($p<0.05$) differences are in italics

	Basal area at base			Basal area at breast height		Average height		Maximum height		Mortality	
	d.f.	t	*P*	t	*P*	t	*P*	t	*P*	t	*P*
Acacia macrostachya											
Grazing	26	−0.15	0.883	−0.10	0.924	−1.03	0.315	−1.41	0.170	0.34	0.739
Fire	26	0.07	0.948	0.15	0.881	0.63	0.533	0.77	0.449	−1.28	0.213
Year	355	3.74	*<0.001*	3.77	*<0.001*	4.77	<0.001	8.16	*<0.001*	0.29	0.770
G × F	26	0.15	0.883	0.04	0.970	0.85	0.401	1.14	0.264	0.89	0.384
G × Y	355	−1.61	0.108	−1.89	*0.059*	−0.38	0.701	−0.74	0.457	−0.31	0.754
F × Y	355	−1.22	0.222	−1.21	0.226	0.02	0.981	−2.36	*0.019*	0.57	0.568
G × F × Y	355	1.50	0.134	1.69	*0.092*	0.01	0.990	1.08	0.283	−0.59	0.555
Combretum ghazalense											
Grazing	25	0.35	0.730	0.27	0.787	−0.17	0.867	−1.05	0.304	0.53	0.601
Fire	25	0.30	0.769	0.19	0.849	0.53	0.603	−0.14	0.887	0.29	0.772
Year	315	5.33	*<0.001*	4.69	*<0.001*	5.31	*<0.001*	5.00	*<0.001*	2.33	0.020
G × F	25	-0.23	0.817	−0.04	0.971	0.23	0.821	0.37	0.718	−1.07	0.295
G × Y	315	−1.85	*0.065*	−1.73	*0.084*	0.27	0.790	0.47	0.641	−1.71	0.089
F × Y	315	0.05	0.959	0.64	0.525	1.13	0.260	0.57	0.572	−1.72	0.086
G × F × Y	315	−0.03	0.978	−0.49	0.625	−1.40	0.164	−0.37	0.712	2.63	0.009
Combretum glutinosum											
Grazing	12	0.27	0.793	1.59	0.138	−0.03	0.979	−0.09	0.931	0.71	0.493
Fire	12	0.45	0.662	3.16	*0.008*	0.32	0.755	0.30	0.766	0.75	0.466
Year	188	6.37	*<0.001*	3.90	*<0.001*	3.83	*<0.001*	10.18	*<0.001*	1.01	0.316
G × F	12	-0.28	0.787	−1.59	0.138	−0.09	0.931	0.07	0.943	−0.39	0.704
G × Y	188	−0.13	0.900	−0.59	0.558	−0.64	0.522	−0.39	0.694	−0.25	0.800
F × Y	188	−2.19	*0.030*	−1.54	0.126	0.86	0.390	−1.43	0.153	−0.69	0.491
G × F × Y	188	1.00	0.319	0.80	0.425	−0.33	0.739	2.10	0.037	0.34	0.734
Crossopteryx febrifuga											
Grazing	22	0.08	0.934	0.02	0.984	0.35	0.730	0.17	0.863	1.03	0.313
Fire	22	−0.30	0.765	−0.32	0.752	−0.13	0.901	−0.11	0.911	2.10	*0.048*
Year	282	1.67	*0.096*	1.43	0.155	4.15	*<0.001*	6.79	*<0.001*	3.50	*<0.001*
G × F	22	−0.01	0.991	−0.02	0.986	−0.17	0.864	0.11	0.911	−1.73	0.098
G × Y	282	0.21	0.835	0.48	0.632	0.32	0.751	1.10	0.272	−1.54	0.124
F × Y	282	2.17	*0.031*	2.38	0.018	1.70	*0.090*	2.66	*0.008*	−2.95	*0.004*
G × F × Y	282	0.36	0.722	0.34	0.735	0.35	0.725	-0.52	0.601	1.62	0.107
Detarium microcarpum											
Grazing	28	0.56	0.579	0.38	0.709	0.38	0.705	−0.54	0.593	−2.29	*0.030*
Fire	28	0.31	0.757	0.39	0.700	0.71	0.486	−0.47	0.642	0.71	0.485
Year	348	3.52	*<0.001*	2.66	*0.008*	2.90	*0.004*	8.15	*<0.001*	2.04	*0.043*
G × F	28	−1.83	0.078	-1.72	*0.096*	−0.75	0.461	−0.02	0.985	0.20	0.843
G × Y	348	0.25	0.801	0.33	0.738	1.09	0.275	1.16	0.247	0.04	0.965
F × Y	348	2.46	*0.015*	2.76	*0.006*	4.64	*<0.001*	3.00	*0.003*	−1.51	0.133
G × F × Y	348	−0.62	0.539	-0.44	0.662	1.87	*0.062*	0.03	0.980	0.50	0.616
Entada africana											
Grazing	23	−1.15	0.260	−0.87	0.396	0.71	0.486	−0.69	0.497	−2.16	*0.042*
Fire	23	−0.71	0.484	−0.43	0.672	1.37	0.185	−0.85	0.405	−0.60	0.554
Year	319	5.51	*<0.001*	4.65	*<0.001*	0.90	0.366	11.52	*<0.001*	2.31	*0.021*
G × F	23	0.83	0.414	0.48	0.633	−0.58	0.567	0.76	0.457	2.50	*0.020*
G × Y	319	−1.66	*0.097*	−1.22	0.223	−1.03	0.305	1.52	0.130	0.39	0.696
F × Y	319	−1.12	0.262	−0.19	0.847	−0.29	0.774	1.39	0.165	−0.37	0.714
G × F × Y	319	0.82	0.416	0.53	0.600	−0.31	0.755	−1.24	0.216	−1.88	*0.062*

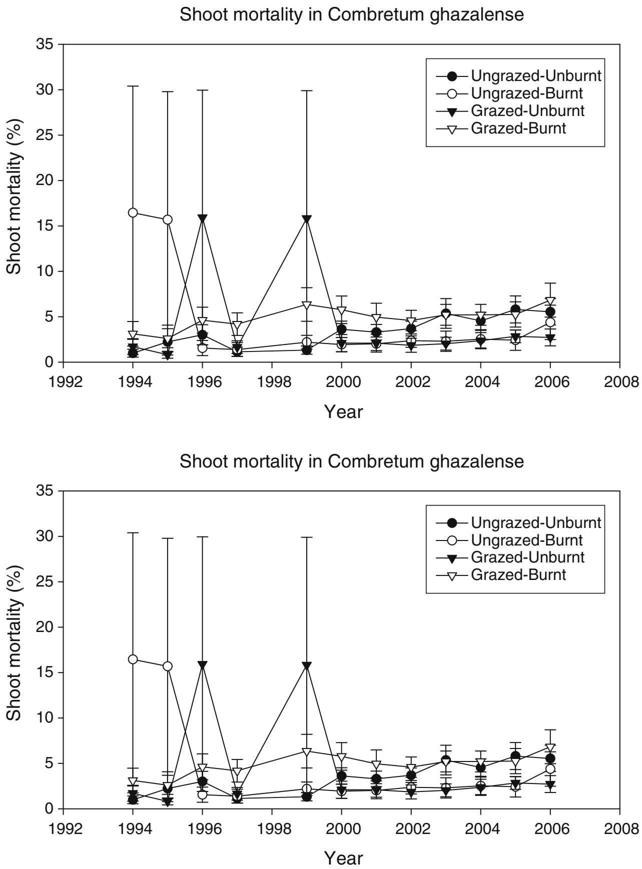


Fig. 1 Inter-annual variations in fire, grazing and their interaction effects on dominant species' resprout mortality in the Sudanian savanna-woodlands of Burkina Faso. Graphs are presented for significant results only for the sake of conciseness

3.2 Biomass of dominant species' resprout

Among the most common species it was only for *C. glutinosum*, and on basal area at breast height, that the main effect of fire treatment was significant (561±42 cm^2 ha^{-1} and 476±41 cm^2 ha^{-1} respectively, for burnt and unburnt plots). The interaction between grazing and fire tended to be significant for basal area of *D. microcarpum*; in grazed plots, burning markedly decreased the basal area at stump level (4485±373 cm^2 ha^{-1} and 8221±577 cm^2 ha^{-1} respectively for burnt and unburnt), while in ungrazed plots the difference between fire treatments was not marked (5195±412 cm^2 ha^{-1} and 6068±455 cm^2 ha^{-1} respectively for burnt and unburnt plots). A similar trend was observed for basal area at breast height (Table 2). For all species except *E. africana* and *C. febrifuga*, the annual variation in all resprout size parameters was significant ($p<0.01$ in all cases). For *E. africana*, the annual variation did not reach significance for only average height, while for *C. febrifuga* we observed a marginal time (year) effect on basal area at stump level. In addition, some of the treatments interacted significantly with the within-subject factor, year. Grazing × year tended to

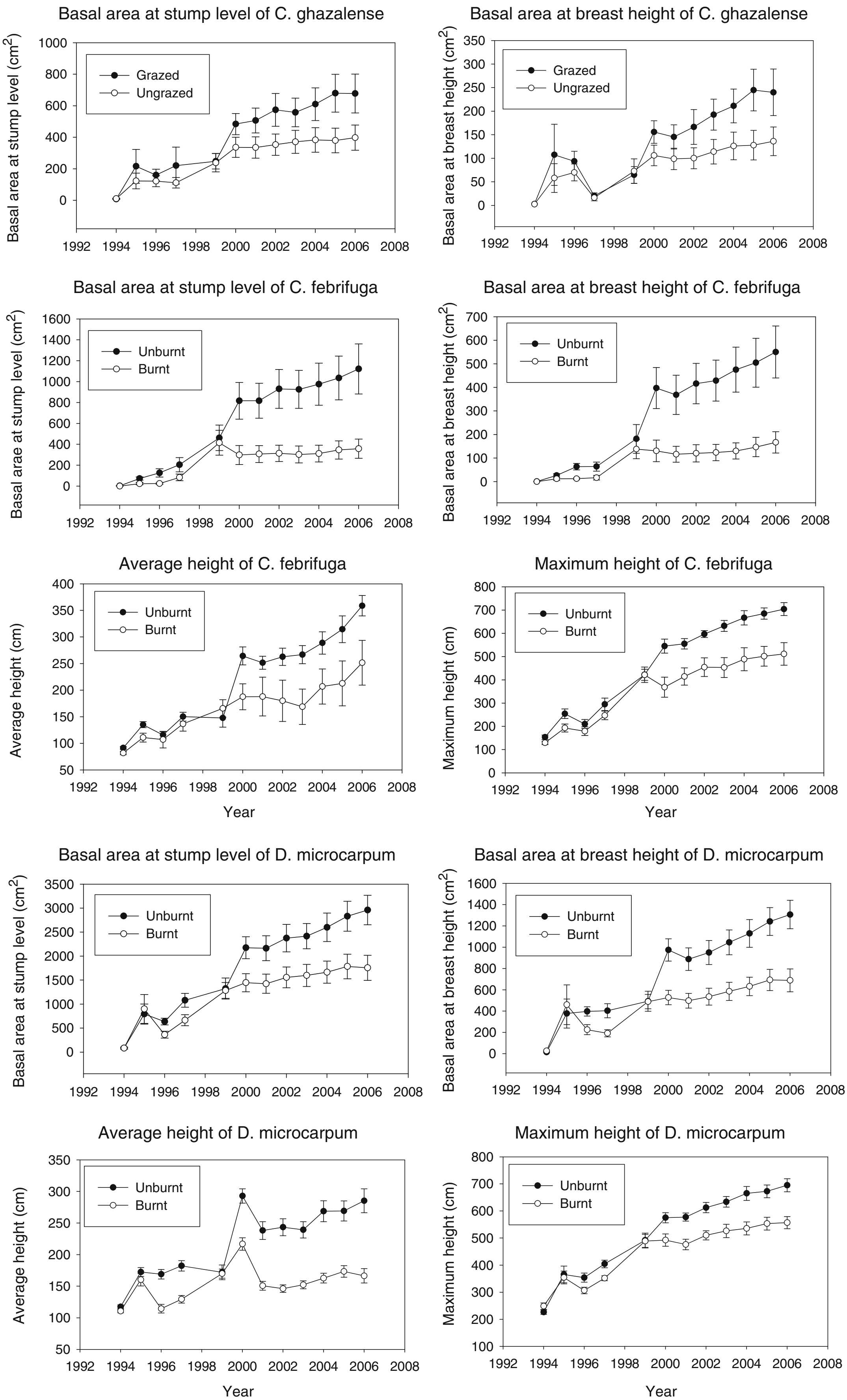
Fig. 2 Inter-annual variations in fire, grazing and their interaction effects on dominant species' resprout size parameters in the Sudanian savanna-woodlands of Burkina Faso. Graphs are presented for significant results only for the sake of conciseness ▶

affect *C. ghazalense*, with grazing increasing the basal area both at stump level and breast height (Table 2, Fig. 2) throughout the years, except in few cases where the difference was not marked. For *C. febrifuga* and *D. microcarpum*, the interaction between fire and year was significant, with burning decreasing the basal area (at stump level and breast height) and tree height (average height and maximum height) mostly starting from the 7th year of measurement, while the difference was often not marked at the early stage of the experiment (Table 2, Fig. 2). For *A. macrostachya*, burning significantly reduced the maximum height in most of the measurement years (interaction fire × year). For this species, we observed higher values of basal area at breast height for grazed individuals, especially within burnt plots, while the lowest values were for ungrazed and burnt plots. For *C. glutinosum*, fire × year affected the basal area at stump level, with higher values being for burnt plots in most of the years. But maximum height was the highest for ungrazed and unburnt plots throughout the study period. For *E. africana*, no significant treatment or treatment interaction effect with year was observed, but there was a tendency of higher values of basal area at stump level for grazed individuals (especially in later years of the measurements) (Table 2, Fig. 2).

4 Discussion

4.1 Resprout mortality

Dominant species responded differently to the fire, grazing and their interaction effects. Differences in bark thickness produce large difference in fire resistance ability, and fire will tend to prey selectively on thinner barked species within a community (Nefabas and Gambiza 2007). Some woody species are well-adapted to fire, and show no major effect on their mortality (Williams et al. 1999). The treatment regimes did not affect mortality of *A. macrostachya* and *C. glutinosum*. For the latter species, Thiombiano and Kere (1999) reported that its young individuals lignify early, and are more resistant to environmental factors such as fire. Unburnt plots showed higher mortality at later years for *C. febrifuga*, and it appears that the accumulating litter in those plots, throughout the years, becomes more detrimental to shoot survival compared to burning effect. In *C. ghazalense*, fire in combination with grazing increased mortality. The establishment of plants may be prevented


Basal area at stump level of C. ghazalense
Basal area at stump level (cm^2)
Grazed
Ungrazed
Basal area at breast height of C. ghazalense
Basal area at breast height (cm^2)
Grazed
Ungrazed
Basal area at stump level of C. febrifuga
Basal arae at stump level (cm^2)
Unburnt
Burnt
Basal area at breast height of C. febrifuga
Basal area at breast height (cm^2)
Unburnt
Burnt
Average height of C. febrifuga
Average height (cm)
Unburnt
Burnt
Year
Maximum height of C. febrifuga
Maximum height (cm)
Unburnt
Burnt
Year
Basal area at stump level of D. microcarpum
Basal area at stump level (cm^2)
Unburnt
Burnt
Basal area at breast height of D. microcarpum
Basal area at breast height (cm^2)
Unburnt
Burnt
Average height of D. microcarpum
Average height (cm)
Unburnt
Burnt
Year
Maximum height of D. microcarpum
Maximum height (cm)
Unburnt
Burnt
Year

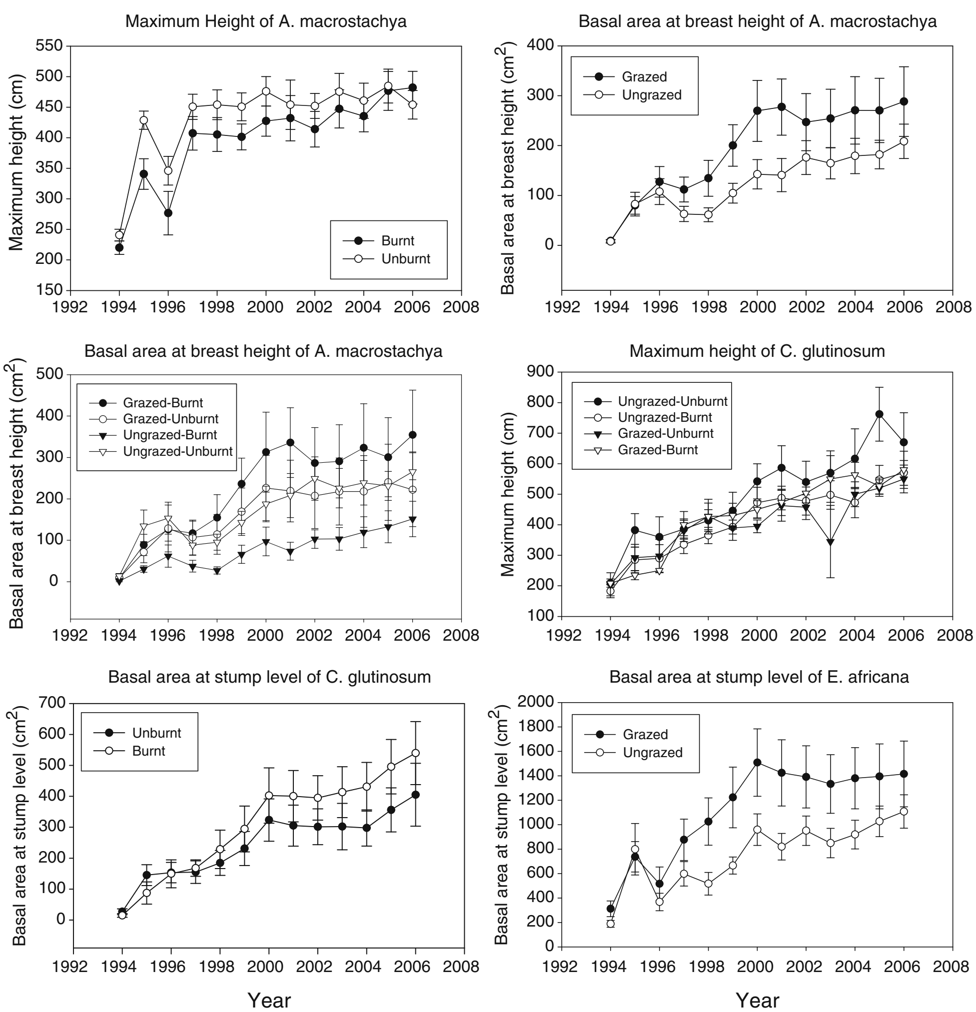


Fig. 2 (continued)

by several factors such as herbivory and water availability, but fire is particularly important in African savannas (Wilson and Witkowski 2003). Burning exacerbates the recurrent die-back of shoots at the juvenile stage (Sawadogo et al. 2002; Hoffmann et al. 2009) and those shoots that do not die outright in a fire may suffer fire-induced shoot die-back due to water stress following heat damage of the xylem (Balfour and Midgley 2006). In addition, post-fire gaps may be drought-prone, as increased exposure may lead to elevated evaporation, and thus to reduced moisture availability (Elberse and Breman 1990). In ungrazed plots, burning reduced mortality of *E. africana*, presumably due to the fact that fire reduces the otherwise elevated herbaceous/sprout competition in such plots. Livestock may have deleterious effects on plant young individuals, due to browsing and trampling. We observed higher mortality in grazed plots for *D. microcarpum* and *E. africana*. Increased resprout mortality as observed in our burnt and grazed plots for *C. ghazalense* could be explained by increased herbivore activity in burnt area; indeed, some grazers are attracted by plants growing in such environments. This also lends credence to Midgley et al. (2010) that fire and herbivory together are a lethal combination for woody plants. The interaction of the treatments with year could be due to the fact that fire and grazing exacerbate worse climatic conditions in particular years.

4.2 Biomass of dominant species' resprout

For all dominant species examined the main effect of burning did not significantly impact resprout size parameters except *C. glutinosum* which showed an increasing basal area. This is in agreement with previous studies that most savanna tree species are sometimes described as fire-tolerant and that there is a differential effect of the fire treatments on tree growth (Guinto et al. 1999; Kaschula et al. 2005). It might be that in addition to some species resistance ability (e.g. *C. glutinosum*), they have developed nutritional mechanisms to cope with disturbances such as fires (e.g., within-plant recycling of nutrients) (Guinto et al.

2002). Iin addition, repeated prescribed burning might have increased "available" P in the long term by possibly raising soil pH and thereby increasing the solubility of phosphate ions; this is a beneficial effect of burning on plant P nutrition, although not all species reflect it in their biomass production (Guinto et al. 2002). The tolerance response of plants can, however, be weakened through repeated defoliation by fire, as evidenced by the significant decreasing effect of the interaction between fire and year on some size parameters for *C. febrifuga* and *D. microcarpum*. In the long run, frequent burning might decrease the topsoil total N, mineralizable N and cumulative N mineralization, which could in turn lead to a long-term reduction in tree growth (Guinto et al. 1999). The adverse effect of early dry season fires on these species may also be due to the fact that fire may decrease both the number and the biomass of resprouts (due to stems being killed and replaced by small stems), implying that carbohydrates are stored underground to produce basal sprouting from the lower part of the stem as the wet season approaches. Thus, the allocation of resource for the development of lateral shoots could reduce the increment in the basal area; fire also removes leading shoots and reduces the apical dominance, resulting in the development of lateral shoots which reduce the height of the plant.

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 to plant phenophase and differential responses of species to browsing and trampling (Braithwaite and Mayhead 1996; Hester et al. 1996; O'Connor 1996; Drexhage and Colin 2003). In plots receiving repeated grazing over 13 years, there was a tendency of increased basal area for *C. ghasalense* and *E. africana*. Some woody plants are known to use stem and branches for storage of nutrient that can later be mobilized to support biosynthesis for growth or other functions as a browsing tolerance strategy, which could explain the slight beneficial effect of grazing on basal area (Gordon and Prins 2008). Moreover, *C. ghazalense* has been shown to be well-adapted to disturbances such as fire and grazing (Dembélé 1996). Ungrazed plots that were left unburnt produced taller individuals of *C. glutinosum* in most of the measurement years, corroborating the fact that individuals grow freely in the absence of disturbance.

The results from the present study show the variability, depending on species, of resprout response to common forest disturbance regimes in tropical dry area. Early burning significantly decreased all size parameters for dominant species tested except *C. glutinosum*. There was no significant evidence of grazing hampering growth. Most of the treatment effect was marked at the later stage of the experiment, confirming the need for such long-term experiments to study forest management regimes. Moderate livestock grazing could be integrated into the forest management prescriptions in Burkina Faso for the sake of multi-purpose uses, while more attention should be paid to burning practices to lower fire severity, as complete fire exclusion is utopian in this savanna ecosystem.

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