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Grass competition is more important than seed ingestion by livestock for *Acacia* recruitment in South Africa

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Abstract Although grazing livestock may have direct negative effects on woody species through herbivory and trampling, (heavy-)grazing is often associated with woody plant encroachment. Two main mechanisms can explain the positive effects of grazers on woody cover: (1) Grazers reduce the interspecific competition with trees and may reduce fuel load, and (2) gut passage through livestock increases seedling establishment by scarification (increased germination) and fertilization by dung (higher survival and growth of seedlings). We tested the effects of fire, grass, cattle ingestion (transit) and dung on germination, seedling height and survival as well as on recruitment of *Acacia sieberiana* in a sub-humid grassland of South Africa. About 8,000 seeds were planted in the field in a randomized block design. The removal of grass by grazing and/or fire had the most important effect on *Acacia* recruitment in savanna. Our findings highlight the hierarchy of the main factors affecting *Acacia* recruitment, which provides new insights to the understanding of woody plant encroachment.

Keywords Dung · Encroachment · Fire · Grassland · Savanna · Tree–grass competition

Introduction

Woody plant encroachment is widespread in most savannas (Archer et al. 1995; Bond 2008). Trees can decrease the biomass of the grass layer (Kraaij and Ward 2006; Wigley et al. 2009), which decreases livestock yield (Burkinshaw and Bork 2009). Effective management requires understanding of the causes of woody plant encroachment. There is consensus that water (rainfall), fire, herbivory and nutrients are key variables of tree–grass balance in grasslands (Sankaran et al. 2004; Ward 2005; Wiegand et al. 2006). Other factors have also been recorded to influence tree populations, such as seed gut transit (Or and Ward 2003), rodents (Goheen et al. 2004; Maclean et al. 2011) and bruchid beetles (Coe and Coe 1987; Rohner and Ward 1999; Or and Ward 2007) that feed on *Acacia* seeds and may destroy most of them.

Sankaran et al. (2005) suggested a global model for African savannas where mean annual precipitation (MAP) is the main determinant of woody plant density up to MAP $= 650$ mm. In mesic areas (MAP $>$ 650 mm), tree densities are not limited by water and

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are mainly driven by fire and herbivory. In mesic areas, inter-annual climatic variability, fire and herbivory limit germination, seedling survival and sapling growth and thus, the transition to mature trees (Sankaran et al. 2004; Prior et al. 2009). However, the respective influence of these disturbances and their interactions is not well understood because of the scarcity of field data and the complexity of the interactions. There is, thus, little consensus on the relative influence of the factors involved with woody encroachment processes.

Multi-factorial experiments, taking fire and herbivores into account, have been emphasized as the only way to study the causes of woody encroachment (Ward 2005; Kraaij and Ward 2006), especially on tree seed and seedling stages that are a prerequisite for maintaining or increasing adult tree abundance and are very influential in the process of woody encroachment (Kraaij and Ward 2006; Gignoux et al. 2009). Although herbivores may have direct negative effects on woody species through herbivory and trampling, grazing is often associated with tree encroachment. Herbivores, often studied for their grazing activities (Mbatha and Ward 2010), may reduce the ability of grasses to compete with trees (Kraaij and Ward 2006; Riginos 2009; Goheen et al. 2010). However, they may also increase seed germination and survival and subsequent recruitment of woody species through gut passage and scarification of seeds and through dung fertilization (Halevy 1974; Miller and Coe 1993; Or and Ward 2003; Bodmer and Ward 2006). To better understand and clarify the mechanisms involved, as well as to identify the hierarchy of these factors, we studied seedling establishment of *Acacia sieberiana*, an encroaching tree common in sub-humid grasslands in KwaZulu-Natal (South Africa). We manipulated passage through grazing livestock (hereafter called *Transit*), presence or absence of animal faeces (*Dung*), competition with grasses (*Grass*), and *Fire* and tested their effects on seed germination, seedling height, seedling survival and recruitment. We especially focus on recruitment after one complete year of experiment that is the most important for determining the global effect of all factors and their interactions on *A. sieberiana* recruitment from the seed to the seedling stage (Ward and Esler 2010).

We, thus, tested these main hypotheses: (1) Germination is favored by transit, dung and fire, while germination is limited by grass because of competition for resources. (2) Seedling survival and height are increased by dung as a nutrient input, while they are decreased by grass and fire. (3) As an effect of the first two hypotheses, recruitment should be favored by transit and dung, but disadvantaged by grass. We expect fire to show a neutral effect on recruitment because of its combined direct effect (heat and burnt effect) on *A. sieberiana* and its indirect effect reducing the grass layer.

Materials and methods

Study site

The study site is located in a commercial grassland 8 km south–east of Bergville, South Africa (28°47′14″S; 29°22′38″E). The altitude of the site is 1,235 m and is representative of the grassland biome present in the KwaZulu-Natal Drakensberg foothills. The vegetation is classified as Northern KwaZulu-Natal moist grassland (Mucina and Rutherford 2006). The climate is sub-humid sub-tropical with a rainy summer (October–April) and dry winter (May–September). The mean annual precipitation calculated for the last 65 years was 745 mm, and it was 690 mm for the year of the experiment. The mean annual temperature is 13 °C (Schulze 1997), and it was 16.7 °C for the year of the experiment. Potential evaporation is between 1,600 and 2,000 mm (Guy and Smith 1995). Encroachment by *A. sieberiana* var. *woodii* (Burtt Davy) Keay and Brenan is occurring in the valley, especially in the adjacent communal grassland (Grellier 2011). The main grass species on the site were *Hyparrhenia hirta* (L.) Stapf., *Cymbopogon excavatus* (Hochst.) Stapf. ex Burtt Davy, *Eragrotis curvula* (Schrad.) Nees, *Eragrotis plana* Nees and *Sporobolus africanus* (Poir.) Robyns and Tournay. The general soil type is a luvisol (World Reference Base 1998) with two well-delimited main horizons. Cattle are the only large mammalian herbivores in this grassland with a stocking rate of 1 animal per 2.5 ha, grazing only in the summer.

Experimental design

The experimental design comprised 48 plots of 1 × 2 m. All plots were separated from each other by a 1-m-wide buffer zone. We planted 160 seeds per plot in parallel lines, 10 cm apart from each other, at 1-cm depth in the soil to ensure contact between soil and seed testa (Brown and de Booysen 1967), making a total of 7,680 seeds. We divided and installed these 48 plots into two identical, large fenced plots 20 × 20 m with two different fire histories but the same cattle management: 24 plots were located on an area burnt every year during the dry season for at least 12 years (burnt plots) and the other 24 plots were located on an area not burnt for at least 5 years (unburnt plots). To exclude cattle and all other animals at least as large as rabbits and to avoid the destruction of seedlings, the two large plots were fenced. These two plots were 20 m apart. This constitutes our first treatment (1) *Fire* versus *No-Fire*. Because of their different fire histories, these two plots had different soil surface features as visually estimated by expert judgment 3 months after the beginning of the experiment. Percentages of vegetation cover, structural soil crust, dung patch and micro-aggregates were determined for the 48 plots based on the classification of Valentin and Bresson (1992).

With this experimental design, we were able to test for an indirect long-term effect of fire through its effects on soil surface features (growing season, October 2009–June 2010), as well as to test for both the direct and the indirect short-term effects of fire on germination, seedling survival, seedling height and recruitment (survey in November 2010 after the dry season and after a fire was applied on the burnt plots).

Within each large plot (nested design), we studied three other treatments according to a completely crossed randomized block design with three replicates per treatment: (2) *Grass* versus *No-Grass*, (3) *Dung* versus *No-Dung* and (4) *Transit* seeds versus *No-Transit* as follows:

Grass versus *No-Grass*

To simulate an indirect effect of grazing, we manually cut the 24 plots before planting and then re-cut these plots every month to keep the grass at ground level during the experiment. Attention was made to conserve all seedlings and cut the grass around them.

Dung versus *No-Dung*

We used cattle dung collected from the Ukulinga research farm of the University of KwaZulu-Natal in Pietermaritzburg to ensure the absence of *A. sieberiana* seeds in the dung as this farm was not encroached. We applied 60 cm^3 of homogenised fresh dung to each seed in *Dung* plots just after planting to simulate the effect of dung as nutrient input.

Transit versus *No-Transit*

We collected *Transit* seeds in the adjacent grassland encroached by *A. sieberiana* in an area where cattle rest and deposit dung. Molar teeth marks observed on seeds confirmed that all seeds were ingested by cattle. *No-Transit* seeds were collected in the same grassland directly from pods that were lying on the ground under trees (to ensure maturity of seeds). We opened pods and removed seeds. We sorted all *Transit* and *No-Transit* seeds in the laboratory to exclude seeds that were either infested by bruchid beetles, germinated or mechanically damaged. As we harvested both types of seeds in June 2009, once sorted, we kept them in the refrigerator at 4 °C until planting in October 2009. To confirm the viability of *Transit* and *No-Transit* seeds, we conducted viability tests of sub-samples (150 *Transit* seeds and 150 *No-Transit* seeds) in the laboratory. After clipping of one of the seed extremity, we cultivated seeds in petri dishes on agar gel at 25 °C for 10 days.

Monitoring of experiment

The experiment lasted for one year. We planted seeds in October 2009 at the beginning of the wet season. We monitored all seeds every week at the beginning of the experiment and then every month to record germinated seeds, seedling height and seedling survival until June 2010. Thereafter, we recorded plants in November 2010 at the beginning of the following wet season after the dry season and one burning event in July (for the burnt plots). In June 2010 and in November 2010, recruitment was calculated from the difference between the number of germinated seeds and the number of seedlings that died since the beginning of the experiment.

Statistical analyses

We did all statistical analyses with R version 2.12.1 (http://www.R-project.org). We analysed the effects of the four treatments on the probability of seed germination, seedling survival and recruitment at the end of the growing season (June 2010) and after the dry season (November 2010) by Nested ANOVA with a mixed effects model (binomial model for binary response variables) with a random term for plots nested within *Fire* (large plots).

We tested the height of seedlings after the dry season (November 2010) by a similar Nested ANOVA after a Box-Cox transformation ($\lambda = 0.44$) with normal residuals and homogeneity of variance.

During the growing season (from October 2009 to June 2010), seedlings died, lost height or grew. As we measured heights of each *A. sieberiana* seedling every month, we decided to work only on the maximal height reached by each seedling during the growing season to avoid pseudoreplication. Because of non-normal residuals and heterogeneity of variance, we tested the effects of the four treatments on maximal height reached by each seedling during the growing season by Kruskal–Wallis non-parametric tests. Because of the nesting of treatments within the *Fire* treatment, we first tested for the *Fire* effect with a Kruskal–Wallis test and then tested the three other factors separately for each large plot (*Fire* and *No-Fire*) with further Kruskal–Wallis tests. Kruskal–Wallis non-parametric tests were also applied to test for the effect of *Fire* on soil surface features (proportion data). Results were considered significant with *P* value <0.05. Where we performed multiple tests (in June 2010 and in November 2010) on dependent variables, we applied a Bonferroni correction for each *P* value.

Results

Soil surface features

Percentage of structural soil crusts (*Fire*: 26.3 ± 15.9 %, *No-Fire*: 3.9 ± 6.1 %) and percentage of vegetation cover (*Fire*: 67.6 ± 11.9 %, *No-Fire*: 92.6 ± 7.4 %) were significantly different between *Fire* and *No-Fire* ($\chi^2 = 24.69$, df = 1, $P < 0.001$ for structural soil crusts and $\chi^2 = 31.16$, df = 1, $P < 0.001$ for vegetation cover). Percent cover of dung (*Fire*: 4.3 ± 4.7 %, *No-Fire*: 1.0 ± 1.5 %) and of soil micro-aggregates (*Fire*: 1.7 ± 3.2 %, *No-Fire*: 2.5 ± 3.5 %) did not differ significantly between *Fire* and *No-Fire* ($\chi^2 = 3.34$, df = 1, $P = 0.067$ for dung and $\chi^2 = 1.84$, df = 1, $P = 0.17$ for soil micro-aggregates).

Seed germination, seedling survival, seedling height and recruitment during the growing season (October 2009–June 2010)

The viability test for *Transit* seeds of *A. sieberiana* was significantly higher than for *No-Transit* seeds. There was 98.7 % germination for *Transit* seeds and 79.0 % germination for *No-Transit* seeds ($\chi^2 = 17.5$, $P \leq 0.001$).

The mean germination for all treatments at the end of the growing season was 10.3 % (790 seeds); 78.1 % (617 seeds) of the germinated seeds survived until June 2010. All four treatments significantly affected germination of *A. sieberiana* seeds over the season (Fig. 1). Across all other treatments, germination was higher under *Fire,* increasing from 8.5 to 12.1 %, whereas germination was lower under *Grass*, *Transit* and *Dung* decreasing from 15.0 to 5.6 %, from 14.3 to 6.3 % and from 12.3 to 8.3 %, respectively (Table 1). One interaction was significant (Table 1): *Grass* versus *Transit* showed that grass had a stronger (negative) impact on germination for *Transit* seeds (Fig. 1).

During the growing season, seedling survival was significantly affected by *Fire* and *Transit* treatments (Table 1). Survival was lower with *Fire* than *No-Fire* and increased from 73.5 to 84.6 %, whereas survival was higher with *Transit* than *No-Transit* and decreased from 87.7 to 76.5 % (Fig. 2). Three nested factors were significant (Table 1): *Fire*{*Grass}*, *Fire*{*Transit}* and *Fire*{*Dung}*. Survival was significantly higher with *No-Grass* but only in unburnt plots, whereas survival was significantly higher with *Transit* only in burnt plots and survival was significantly higher with *Dung* only in unburnt plots (Fig. 2).

At the end of the growing season (June 2010), recruitment was not significantly affected by the indirect long-term effect of *Fire* (Table 1). However, recruitment was significantly lower with *Grass* (3.9 % of seeds became seedlings and were still alive in June 2010 with *Grass* versus 12.1 % with *No-Grass*), *Transit* (5.1 versus 10.9 % with *No-Transit*) and *Dung* (6.5 versus 9.6 % with *No-Dung*) (Table 1, data not shown in figure). The nested *Fire*{*Transit}* effect was significant (Table 1) and showed that recruitment decreased more with *Transit* in unburnt plots (from 11.1 % for *No-Transit* seeds to 3.2 % for *Transit* seeds) than in burnt plots (from 10.8 % for *No-Transit* seeds to 7.1 % for *Transit* seeds). The

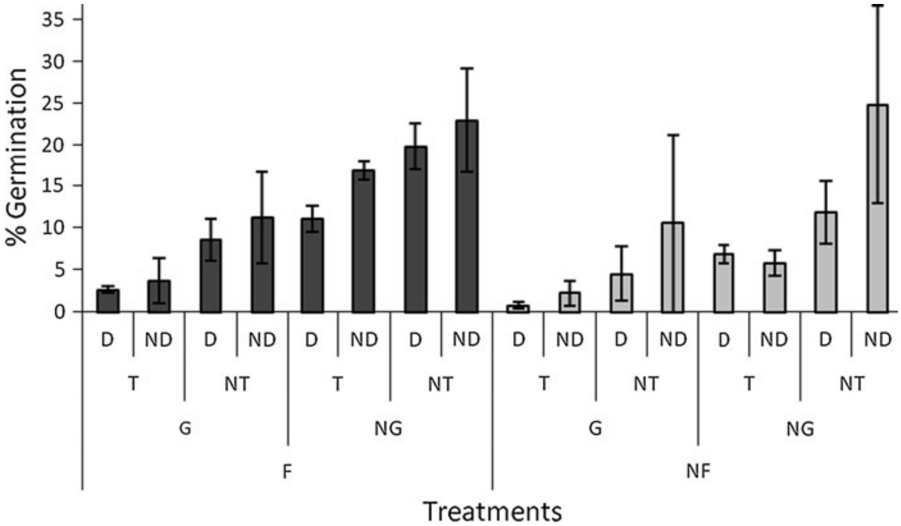

Fig. 1 Comparison of *A. sieberiana* seed germination among the four treatments for the growing season (test on 7,680 planted seeds/480 seeds per treatment combination). All treatments had significant effects (cf. Table 1 for statistical results). *F* fire, *NF* no fire, *G* grass, *NG* no grass, *T* transit, *NT* no transit, *D* dung, *ND* no dung. Standard deviations of the mean of the three replicates (3 × 160 seeds) per treatment are displayed using *error bars*

Table 1 Statistical results (Nested ANOVA) and associated *P* values for the effects of the four treatments and their interactions on germination, seedling survival and recruitment at the end of the growing season (June 2010) and after the dry season (November 2010)

Treatments	End of the growing season (June 2010)						After the dry season (Nov. 2010)			
	Germination		Survival		Recruitment		Survival		Recruitment	
Fire	$z = -4.01$	<0.001	$z = -2.9$	0.006	–	–	$z = -5.24$	<0.001	$z = 3.61$	<0.001
Grass	$z = 6.63$	<0.001	–	–	$z = 7.17$	<0.001	$z = -2.85$	<0.001	$z = 4.64$	<0.001
Transit	$z = -6.22$	<0.001	$z = -2.73$	0.012	$z = -4.15$	<0.001	–	–	$z = -4.34$	<0.001
Dung	$z = 3.28$	0.002	–	–	$z = 3.69$	<0.001	–	–	–	–
Fire{grass}	–	–	$z = -2.5$	0.024	–	–	$z = 2.77$	0.01	$z = -2.31$	0.041
Fire{transit}	–	–	$z = 2.76$	0.005	$z = -4.24$	0.004	–	–	–	–
Fire{dung}	–	–	$z = 2.28$	0.044	–	–	–	–	–	–
Grass versus Transit	$z = 2.72$	0.012	–	–	$z = 2.40$	0.032	–	–	–	–
Grass versus Dung	–	–	–	–	–	–	$z = -3.23$	0.002	–	–

Absence of value "–" indicates non-significant terms and were thus withdrawn from the statistical model

*Grass*X*Transit* interaction was also significant (Table 1) and showed that recruitment decreased more under *Grass* for *Transit* seeds (from 8.4 % for *No-Grass* to 1.8 % for *Grass*) than for *No-Transit* seeds (from 15.8 % for *No-Grass* to 6.0 % for *Grass*).

Maximal height reached by each seedling during the growing season was significantly affected by three of the four factors (data not shown in figure), *Fire* (372/315 observations for *Fire* versus *No-Fire*, $\chi^2 = 16.64$, df = 1, $P < 0.001$), *Transit* (*Fire*:147/225 observations for *Fire-Transit* versus *Fire-No-Transit,* $\chi^2 = 27.12$, df = 1, $P < 0.001$; *No-Fire*: 75/240 observations for *No-Fire-Transit versus No-Fire-No-Transit,* $\chi^2 = 5.00$, df = 1, $P = 0.025$) and *Grass* (*Fire*: 96/276 observations for *Fire-Grass* versus *Fire-No-Grass,* $\chi^2 = 22.88$, df = 1, $P < 0.001$; *No-Fire*: 84/231 observations for *No-Fire-Grass versus No-Fire-No-Grass,* $\chi^2 = 52.28$, df = 1, $P < 0.001$). Seedling height (±SD) was significantly lower on burnt plots (*Fire* = 11.6 ± 5.0 cm, *No-Fire* = 13.7 ± 6.5 cm)

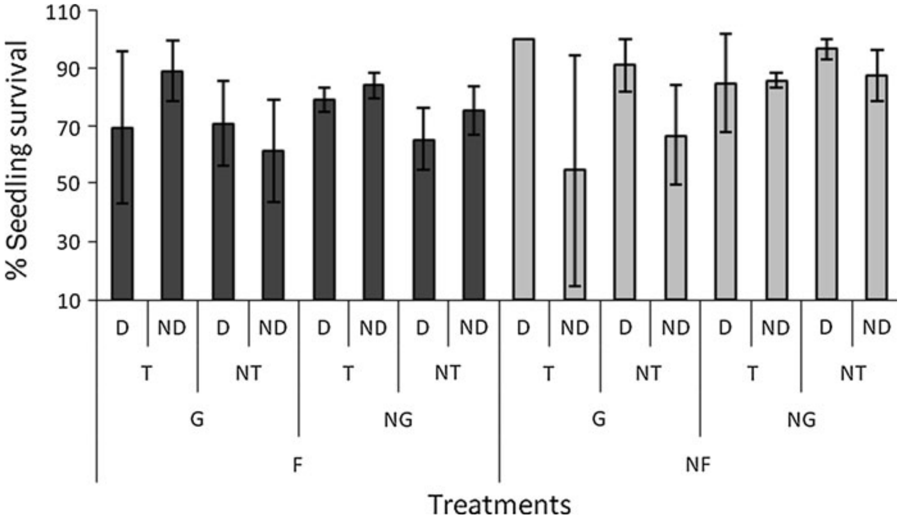

Fig. 2 Comparison of *A. sieberiana* seedling survival among the four treatments for the growing season (test on the 790 germinated seeds) (cf. Table 1 for statistical results). *G* grass, *NG* no grass, *T* transit, *NT* no transit, *D* dung, *ND* no dung. Standard deviations of the three replicates (3 × 160 seeds) per treatment are displayed using *error bars*

and for *Transit* (*Transit* = 10.6 ± 5.3 cm, *No-Transit* = 13.5 ± 5.8 cm) while it was higher under *Grass* (*Grass* = 15.6 ± 6.3 cm, *No-Grass* = 11.5 ± 5.2 cm).

Results after the dry season (November 2010)

In November 2010, after one dry season and a fire (burnt plots only), only 16 seeds had germinated (since June 2010) out of 6,890 ungerminated seeds. There was no significant effect of treatments because of the low number of germinated seeds. During the dry season, 45.5 % (281 out of 617) of the seedlings that were still alive at the end of the preceding growing season (June 2010) survived. Seedling survival decreased significantly with *Fire* (*Fire*: 26.3 %, *No-Fire*: 63.6 %) and with *Grass* (*Grass*: 24.5 %, *No-Grass*: 48.9 %) and the significant *Fire*{*Grass*} nested factor indicated that *Grass* decreased survival more strongly with *Fire* (decrease from 33.7 % with *No-Grass* to 4.6 % with *Grass*) than *No-Fire* (decrease from 67.3 % with *No-Grass* to 51.6 % with *Grass*) (Table 1, data not shown in figure). The *GrassXDung* interaction was also significant (Table 1) and showed that survival decreased significantly with *Dung* associated with *No-Grass* only.

We focus here on the results of recruitment after one complete year of experiment (including survival through the crucial dry season). *Fire*, *Grass* and *Transit* treatments significantly negatively affected recruitment (Table 1; Fig. 3). Recruitment was lower with *Fire* (decreasing from 4.9 to 2.4 %), with *Grass* (decreasing from 6.2 to 1.1 %) and with *Transit* (decreasing from 5.6 to 1.7 %). The most important result was the highest value of recruitment for the control treatment (*No-fire, No-grass*, *No-transit*, *No-dung*) (Fig. 3). The significant *Fire*{*Grass}* nested factor (Table 1) showed that the presence of grass had a greater negative effect on recruitment in burnt plots (decreasing recruitment from 4.6 to 0.2 %) than in unburnt plots (decreasing from 7.9 to 2.0 %).

Between June and November 2010, height of seedlings was significantly affected by *Fire* only ($F = 13.46$, $P = 0.001$, data not shown in figure). Mean height (±SD) of seedlings was lower on burnt plots (5.2 ± 4.0 cm) than on unburnt plots (7.29 ± 5.4 cm). The nested *Fire{Grass}* factor was also significant ($F = 8.25$, $P = 0.007$) and the mean height of seedlings was shorter under *Grass* (1.64 ± 2.2 cm) than on *No-Grass* (5.4 ± 4.0 cm) in burnt plots while seedlings' mean height was taller under *Grass* (9.5 ± 6.0 cm) than *No-Grass* (6.8 ± 5.1 cm) in unburnt plots.

Discussion

Germination

The acid in the digestive tracts of cattle attacks seed coats and favors germination (Rohner and Ward 1999). Indeed, Bodmer and Ward (2006) have shown that the larger the animal ingesting the seeds, the greater the likelihood of germination. The higher

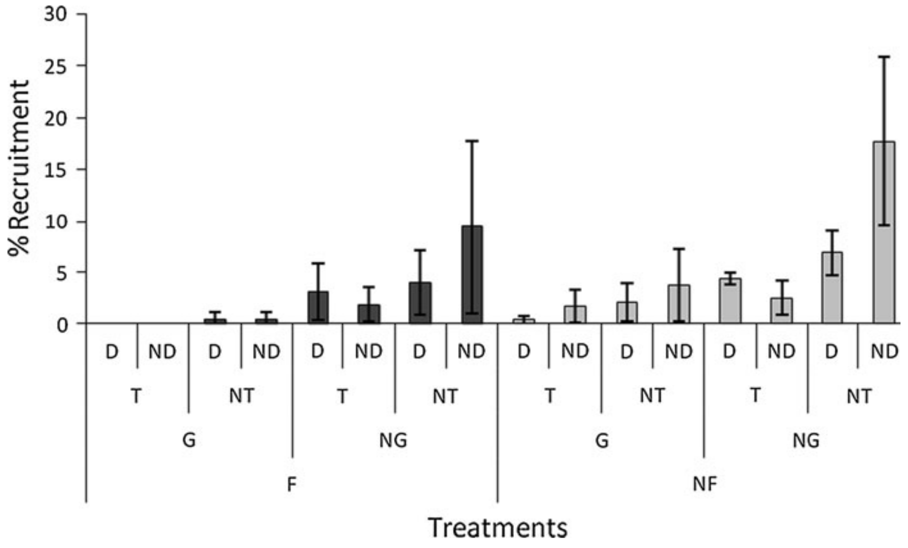

Fig. 3 Comparison of *A. sieberiana* recruitment among the four treatments after one full year in November 2010 (test on 7,680 planted seeds/480 seeds per treatment combination) (cf. Table 1 for statistical results). *F* fire, *NF* no fire, *G* grass, *NG* no grass, *T* transit, *NT* no transit, *D* dung, *ND* no dung. Standard deviations of the three replicates (3 × 160 seeds) per treatment are displayed using *error bars*

viability of *Transit* seeds than *No-Transit* seeds in the experiment should have confirmed and reinforced a higher germination for *Transit* seeds. However, results led to the opposite conclusion in contradiction of hypothesis 1 (see "Introduction" section).

Germination in the growing season decreased with *Grass* and *Dung*, whereas germination increased with the indirect long-term *Fire* effect [high fire frequency reduces grass cover and thus grass competition, as was shown by Oluwole et al. (2008) for grass biomass], which was only partially consistent with hypothesis 1. Grass and *Acacia* seeds compete for the same resources, namely, space, light, water and nutrients (Wilson 1988). At the seed stage, *Acacia* may be disadvantaged by germinating among grass plants (Cramer et al. 2007) because of reduced space (Coffin and Lauenroth 1990), as well as reduced water and light availability (Bush and Van Auken 1995; Jeltsch et al. 1996). In the field, in the presence of decomposers, dung should decompose (Brown et al. 2010) and nutrients quickly incorporated into the soil (Guillard 1967; Edwards and Aschenborn 1987). However, dung decomposition was incomplete as we observed dry dung patches on the plots after a few months. Germination may be limited by dry dung because of the hard dung layer (Coe and Coe 1987). The positive indirect long-term effect of fire on germination during the growing season may be because of the less dense grass cover of regularly burnt plots, reducing the competition between grass and tree seeds for space, water (O'Connor 1995) and light (Campbell and Clarke 2006), which has been shown by the above-mentioned authors to increase germination.

Seedling survival and height

The indirect long-term effect of fire (12 years of annual fire) reduced vegetation cover and resulted in higher structural crust percentages on the soil surface, as was also found by Hilty et al. (2003). Low vegetation cover increased soil detachment by increasing the kinetic energy of raindrops compared with a higher vegetation cover, resulting in the formation of soil crusts (Neave and Rayburg 2007; Podwojewski et al. 2011). These soil crusts are known to increase runoff and limit water infiltration (Casenave and Valentin 1992; Podwojewski et al. 2011) which may limit water availability for seedlings. This process may explain the lower seedling survival in burnt plots during the growing season. Contrastingly, the dense vegetation cover on *Grass*-unburnt plots induced lower survival than on *No-Grass*-unburnt plots (seen in the significant nested factor *Fire*{*Grass}*) probably because of competition for light (Kanz 2001; Campbell and Clarke 2006) and for water as seedlings have to develop their root systems in the established dense root system of grasses. The above-mentioned light competition may also be the process that explains the increase of seedling height under grass during the growing season in contrast to hypothesis 2. While other studies usually mentioned a decrease in size or biomass of tree seedlings with grass because of competition for water and nutrients (Wilson 1988; Kraaij and Ward 2006; Ward and Esler 2010), etiolation has also been observed (O'Connor 1995) and may be the mechanism occurring in this study. Indeed, we observed a clear etiolation process under grass on the unburnt plots.

The negative effect of fire measured in November 2010 is partially because of the direct effect of heat and intensity of fire that killed tree seedlings and reduced height (e.g. Trollope 1980; Roques et al. 2001), which is consistent with hypothesis 2. This effect was greatly enhanced when grass was present. Grass served as fuel that increased heat and fire intensity (Van Auken 2009). Grass also had the most negative effect on seedling survival that is probably because of strong competition between *Acacia* seedlings and grass during the dry season when water was scarce.

Recruitment

Recruitment results, especially in November 2010 after a complete year of experiment, are the most important of this study as they are the consequence of all the processes we have studied. The long-term indirect effect of *Fire* on recruitment appeared to be neutral in June 2010, indicating that the positive effect on germination was suppressed by a negative effect on seedling survival. However, the addition of the direct effect of *Fire* (heat and burnt effect) in the survey of November 2010 induced a global negative effect of *Fire* on recruitment of *A. sieberiana* contrary to the hypothesis 3 in the "Introduction" section. Nevertheless, grass cover had the most important negative effect on *A. sieberiana* recruitment compared with the three other treatments, consistent with Ward and Esler (2010). This is a consequence of the negative effect of grass on tree germination and on tree seedling survival.

Surprisingly, the control (*No-Dung*) had the highest recruitment percentage after the dry season (Fig. 3) when there was no competition with grass and *No-Transit*, regardless of whether there was fire or not. This suggests that a positive effect of livestock may be to disperse seeds away from the mother tree rather than the passage through the animal's gut *per se* or dung fertilization. This favors spreading of seeds in the grassland where competition with adult trees is reduced (Miriti 2006; Kambatuku et al. 2011). Furthermore, livestock, through their grazing activity, reduces grass biomass and may thus promote the recruitment of *A. sieberiana*. This grazing effect, i.e., limiting grass competition, was the most important effect of livestock on recruitment. Similarly, fire reduced grass biomass.

Conclusions

This multifactorial field experiment on germination of *Acacia sieberiana* seeds in grassland was set up to study the interactions of the main factors that play a role in the establishment of *A. sieberiana* seedlings. We showed that grass competition was the most important factor for the establishment of *A. sieberiana* seedlings. We also emphasize the importance of grazing by livestock and fire as affecting the herbaceous layer and thus grass competition. Our study, as well as other multifactorial studies (Kraaij and Ward 2006; Sankaran et al. 2008; Ward and Esler 2010; Maclean et al. 2011), suggests that interactions between the various factors and their direct and indirect effects may lead to the general conclusion that removal of grass, either by grazing or fire, is of primary importance for savanna tree seedling recruitment.

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