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ABSTRACT

Questions: Perennial tussock grasses represent the principal fuel source for savanna fires, however basic information about the impact of fire on their demography remains scarce. Do dominant perennial grass species differ in their demographic parameters? What is the overall impact of tussock circumference and fire regimes on grass demographic parameters? Do grass species differ in the sensitivity of their demographic parameters to fire regimes and tussock circumference?

Location: The study site is located in the savanna of the Lamto reserve, in the center of Ivory Coast (6˚ 9 to 6° 18 N; 5˚ 15 to 4° 57 E).

Methods: Data on the nine dominant species of tussock grasses were sampled over one year under four fire treatments (early fire, mid-season fire, late fire and no fire). We studied the impact of these fire treatments and tussock circumference on five demographic parameters: mortality, fragmentation (the division of a tussock into several smaller ones), growth, retrogression (the decrease in tussock size) and fecundity.

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Results: All demographic parameters varied among species and across the fire regimes. The late fire had the largest negative effect on all parameters except fecundity. *Schizachyrium platyphyllum* was the most disadvantaged species by fire in terms of mortality, retrogression and growth, whilst *Andropogon ascinodis* was the most prone to fragmentation. *Hyparrhenia smithiana* and *Sorghastrum bipennatum* produced the most seeds and *Brachiaria brachylopha* produced the most new tussocks. The circumference of perennial grasses impacted all demographic parameters. Small individuals had the highest mortality and growth rates, while large individuals showed the highest fragmentation and retrogression rates, and produced the most seeds.

Conclusions: This study showed that perennial grass species differed in their sensitivity to fire treatments. Nevertheless, the mid-season fire could be advised to managers for the sustainable management of the Lamto savanna.

Key words: demographic parameter, fecundity, fire regime, humid savanna, Lamto, mortality, perennial tussock grass, tussock circumference, tussock fragmentation, tussock retrogression.

INTRODUCTION

Fires are critical to the functioning of savannas (Abbadie, Gignoux, Lepage, & Roux, 2006; Bond, Woodward, & Midgley, 2005). In particular, fires are used to conserve and sustainably manage savannas by stopping tree encroachment (Case & Staver, 2017; Stevens, Lehmann, Murphy, & Durigan, 2017), which is a common phenomenon occurring world-wide in savannas (Archer, Schimel, & Holland, 1995; Moleele, Ringrose, Matheson, & Vanderpost, 2002) and could lead to the disappearance of these ecosystems (Gillson, 2015). In this perspective, different fire regimes are studied to compare their impact on savanna functioning

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to find the most appropriate regime (Case & Staver, 2017; Stevens et al., 2017). These studies mostly focus on trees (February, Higgins, Bond, & Swemmer, 2013; Gignoux, Lahoreau, Julliard, & Barot, 2009; Smit, Asner, Govender, Vaughn, & van Wilgen, 2016) with few studies focusing on fire impacts on perennial grasses for which basic demographic information is scarce, especially in West Africa (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011; O'Connor, 1994).

Perennial tussock grasses generally dominate the herbaceous layer of humid savannas that is the main source of fire fuel (Williams, Müller, Wahren, Setterfield, & Cusack, 2003). These grasses are adapted to fires. Indeed, their aboveground biomass burns while belowground biomass tends to stay alive (Monnier, 1968; Sarmiento, 1992), which allows the quick regrowth of tussocks after fire (Abbadie et al., 2006; Moore, Camac, & Morgan, 2019; Sarmiento, 1992). Nevertheless, fires and fire regimes likely impact the demographic parameters of grass tussocks: mortality (Zimmermann, Higgins, Grimm, Hoffmann, & Linstädter, 2010), retrogression i.e. decrease in tussock size (Canales, Trevisan, Silva, & Caswell, 1994), growth i.e. increase in tussock size (Yuan, Liang, & Zhang, 2016), fragmentation i.e. the division of a tussock into several smaller tussocks which leads to a form of clonal reproduction (Fair, Lauenroth, & Coffin, 1999; Hartnett & Bazzaz, 1985), and fecundity (Brys, Jacquemyn, & De Blust, 2005). Our first goal is to document for perennial grasses the impact of contrasted fire regimes and the absence of fire on these demographic parameters. These parameters are hypothesized to vary with grass species, fire regimes and the interaction between the two, if species have different sensitivities to fire regimes. Testing this broad hypothesis is an important step to choose the best fire regime for the sustainable management of savannas.

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The demographic parameters of tussock grasses also likely depend on tussock circumference, since plant demographic parameters are highly dependent on plant size (Caswell, 1989) and tussock circumference is considered as a good proxy of their size (Garnier & Dajoz, 2001; Lata, 1999). We therefore studied the impact of tussock circumference on the five demographic parameters (see above) and tested interactions between the circumference, fire regimes and species, because tussock circumference might have different demographic impacts in different species and under different fire regimes.

In West African humid savannas, three fire regimes are generally described (Bruzon, 1994; N'Dri et al., 2018): (1) Early fires occur at the beginning of the dry season when vegetation is not fully dry, (2) Mid-season fires occur in the middle of the dry season when grass biomass is dry and neither grasses nor trees are growing, (3) Late fires occur at the end of the dry season when trees and grasses have resumed their growth. We analyzed over one year the impact of these three fire regimes and the absence of fire on five demographic parameters (see above) of the nine dominant perennial grass species of the Lamto savanna (Abbadie, Gignoux, Le Roux, & Lepage, 2006) in Ivory Coast. This savanna is a natural reserve and has been managed since 1962 using the mid-season fire. This fire regime negatively impacts the demography of trees in this savanna (Gignoux, Dajoz, Durand, Garnier, & Veuille, 2006; Gignoux et al., 2009) and is critical to maintain a savanna ecosystem, i.e. to maintain areas deprived of trees. In turn, this is important to preserve the whole biodiversity of Lamto savanna, which includes forbs growing in the herbaceous layer, and a range of animals (insects, small mammals and larger mammals such as the kob antelope) that all depend on the presence of a grass layer (Mishra & Young, 2014; Ritchie, Tilman, & Knops, 1998). For almost thirty years, some bush encroachment has nevertheless been observed in Lamto savanna, with areas transformed into savanna woodland (Dauget & Menaut, 1992; Gautier, 1990). This justifies testing the impact of the different possible fire regimes on the tree

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community of Lamto savanna but it is also important to test whether these fire regimes are not detrimental to the whole grass layer, or to some grass species, therefore threatening grass diversity. We specifically addressed the following questions: (1) How does tussock circumference affect grass demographic parameters? (2) What is the overall impact of fire regimes on grass demographic parameters? (3) Do grass species differ in the sensitivity of their demographic parameters to fire regimes and tussock circumference? (4) What is the fire regime that better maintains grass diversity and abundances?

MATERIAL AND METHODS

Study site description

The study site is located in the savanna of the Lamto reserve (Abbadie et al., 2006), in the center of Ivory Coast (6˚ 9 to 6° 18 N; 5˚ 15 to 4° 57 E) where the vegetation is a forest-savanna mosaic, with a tropical humid climate. The average annual rainfall is 1200 mm and the mean annual temperature is 27°C. Mid-season fire has been used for the management of the reserve since 1962. The grass stratum is mostly composed of nine perennial grass species: *Andropogon ascinodis* C. B. Cl., *Andropogon canaliculatus* (Schumach.), *Andropogon schirensis* (Hochst. ex A. Rich), *Brachiaria brachylopha* Stapf (now *Urochloa serrata*, Soreng et al., 2015; Sosef, 2016), *Hyparrhenia diplandra* (Hack.) Stapf, *Hyparrhenia smithiana* (Hook. f.) Stapf, *Loudetia simplex* (Nees) C.E. Hubbard, *Sorghastrum bipennatum* (Hack.) Pilg. and *Schizachyrium platyphyllum* (Franch.) Stapf (Menaut & Abbadie, 2006).

Study plots

Three separate blocks of 3.72 ha each were identified in the shrubby savanna zone. In each block, four plots were established in September 2013 to implement four fire treatments (N'Dri et al., 2018): early fire (in November), mid-season fire (in January), late fire (in March) and no fire (unburned plot). In each of these plots, a plot was delimited to monitor

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grass demography. This results in a total of 12 plots (3 blocks × 4 plots) on which data were collected. These plots were 5 x 5-m for early fire, late fire and no fire treatments, and 5 x 10-m for the mid-season fire.

Data collection

The first sampling of perennial grasses took place in April and May of 2015 after 2 yrs of implementation of the different fire regimes. All tussocks with more than five tillers were labelled with a fire-proof metal label tied to a metal peg. Pegs were placed at the base of each tussock in the same direction to avoid confusing neighboring tussocks, skipping a tussock or repeatedly counting the same tussock. Grass species were identified using the herbarium of the Ecology Station of the Lamto Reserve. The circumference of each tussock was measured at the soil surface using a measuring tape.

In May and June 2016, all labelled tussocks were retrieved to determine their status, i.e. dead or alive. When a tussock was alive, it was determined whether it was fragmented or not, i.e. whether the tussock was divided in at least two independent tussocks because of the death of groups of tillers. In cases of fragmentation, the number of fragment was recorded, the old peg was given to the principal fragment (i.e. the fragment with the largest circumference) and the other fragments were each labelled with a new peg. New tussocks arising from seed germination were also labeled. These new tussocks were distinguished from fragments of old tussocks due to their very small sizes and the absence of mark of fire at the base of the tussocks (remains of burnt stems). The circumference (cm) of all live tussocks (old live tussocks, tussock fragments and new tussocks) was measured. The difference between the new circumference (in 2016) and the former one (in 2015) was calculated to determine tussocks that had grown (difference > 5 cm), tussocks that had retrogressed (difference < -5 cm) and tussock that had not change in size (-5 cm < difference < 5 cm). The 5 cm threshold was chosen due to the uncertainty in the precise circumference measurement. Finally, fifteen

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tussocks of various circumferences were chosen for each species on each plot to count the number of seeds produced from mid-November to mid-March 2016 before each fire regime (depending on the maturation of seeds for each species and plot). The number of new tussocks (deriving from seed germination, as proved by the absence of marks of fire) and the number of seeds produced per tussock were used to estimate fecundity. The fecundity in new tussocks was calculated as the number of new tussocks per adult of the same species in a plot, assuming that all individuals have the same fecundity regardless of their circumference.

Data analyses

All statistical analyses were performed using the 3.1.1 version of the R software. Mixed linear models with the block as random effect were used to account for the dependence of measurements within the same block for variables measured at the tussock scale, i.e. for all variables except the fecundity (measured as a number of seeds). The glmer procedure of the *lme4* package was used to test the effects of fire treatments, species, circumference and all interactions between them on tussock probability to die, to become fragmented, to grow (increase in circumference > 5 cm) and to retrogress (decrease in circumference > 5 cm), using a binary logistic regression model. Linear models using lm procedure were used to analyse: (1) the effect of fire treatments and species on the average fecundity measured as the number of new tussocks per adult; (2) the effect of fire treatments, grass species and tussock circumference on the number of seeds produced by tussock (in this case no random effect was used because there was no significant block). The Tukey Honest Significant Difference (HSD) post-hoc test was used to compare the different modalities of factors (fire treatments and species) with a significant effect, using the glht procedure of the *multcomp* package. The cld procedure was used following Tukey HSD post-hoc tests to group non-significantly different modalities. All tests were achieved with a significance level $\alpha = 0.05$.

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RESULTS

During the first sampling year (i.e. 2015) 5116 tussocks were found on all plots. During the second year (i.e. June 2016) a total of 5355 tussocks were recorded with 797 new tussocks (Table 1). One hundred and ninety tussocks (4% of the tussocks) had become fragmented and 558 tussocks (11% of the tussocks) had died. Fifty percent of the new tussocks were fragments coming from old tussocks, 43% had arisen from seed germination and 6% were small tussocks that had not been tagged the first year. About 34% of alive tussocks had not changed in size (decrease or increase in circumference > 5 cm), 43% had grown (increase in circumference > 5 cm) and 23% had retrogressed (decrease in circumference > 5 cm).

Mortality

Grass mortality decreased with increased tussock circumference (Table 2, circumference effect) from about 30% for the smallest circumferences (3 – 10 cm circumference) to 0% for the highest circumferences (about 150 cm) irrespective of fire treatment (Figure 1c) and grass species (Figure 1d). Overall, mortality differed significantly between fire treatments and species (Table 2, Fire treatment x Species). This mortality was significantly higher in the late fire treatment compared to other fire treatments. Mortality was significantly lower for the early and mid-season fire treatments than for the no fire treatment (Tukey HSD test, $p < 0.01$. Figure 1a). Mortality of *S. platiphylum* was significantly higher than that of any of the other species (Tukey HSD test, $p < 0.001$. Figure 1b). *Andropogon schirensis*, *H. diplandra* and *H. smithiana* had higher mortality than *L. simplex* (Tukey HSD test, $p < 0.001$, $p = 0.016$ and $p = 0.018$ respectively. Figure 1b) and *A. canaliculatus* had lower mortality than *A. schirensis* (Tukey HSD test, $p = 0.002$. Figure 1b).

The significant effect of the "Fire treatment x Species" interaction on mortality (Table 2) revealed by the glmer suggests that species differed in their sensitivity to fire treatment. The impact of circumference differed between fire treatments (Table 2, significant interaction

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between fire treatment and circumference. Figure 1c) and species (Table 2, significant interaction between species and circumference. Figure 1d). Tussock mortality decreased slower with circumference for the late fire and the no fire treatments than for the early and mid-season fire treatments (Tukey HSD test, $p < 0.01$). Tussock of *S. platiphylum* revealed more rapid mortality when compared to the tussocks of *A. canaliculatus*, *H. diplandra* and *H. smithiana* (Tukey HSD test, $p = 0.048$; $p < 0.001$ and $p = 0.005$). The mortality decreased slower with circumference for *A. schirensis* than for *H. diplandra* (Tukey HSD test, $p = 0.032$).

Tussock fragmentation

Overall, the probability of fragmentation increased with tussock circumference from 0.2 for the smallest circumferences to about 0.8 for the highest circumferences (Table 2, circumference effect) regardless of fire treatment (Figure 2c) and species (Figure 2d). This probability varied with the fire treatment (Table 2, fire treatment effect) and the grass species (Table 2, species effect) and was significantly higher for the late fire (Tukey HSD test, $p < 0.01$. Figure 2a). The probability was higher for *A. ascinodis* than for *A. schirensis*, *H. diplandra* and *L. simplex* (Tukey HSD test, $p = 0.032$, $p = 0.014$ and $p = 0.001$ respectively). *Andropogon canaliculatus* had a higher probability of fragmentation than *H. diplandra* and *L. simplex* (Tukey HSD test, $p = 0.046$ and $p = 0.005$ respectively. Figure 2b).

Tussock growth

The probability of tussock growth decreased with tussock circumference (Table 2, circumference effect) from approximately 0.6 for the smallest circumferences to about 0.2 for the highest circumferences (logistic regression, $p < 0.05$) for all fire treatments (Figure 3c) and all species (Figure 3d). Generally, regardless of the circumference, this probability differed significantly between fire treatments and species. It was higher for the mid-season than for the late fire (Tukey HSD test, $p < 0.001$. Figure 3a). *Schizachyrium platiphylum* had

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a lower growth probability than all other species (Tukey HSD test, $p < 0.01$) but *B. brachylopha* that had a lower growth probability than *H. diplandra* (Tukey HSD test, $p = 0.02$. Figure 3b).

The "Fire treatment x Species" interaction had a significant effect on the growth probability (Table 2) showing that species differed in the sensitivity of their growth to the fire treatment. The impact of circumference differed between fire treatments (Table 2, significant interaction between fire treatment and circumference, Figure 3c) and species (Table 2, significant interaction between species and circumference, Figure 3d). Tussock probability to grow decreased quicker with circumference for the late fire than for the early fire treatment (Tukey HSD test, $p = 0.022$). This probability decreased with circumference slower for the early fire and no fire treatments than for the mid-season fire (Tukey HSD test, $p < 0.001$). Tussock growth probability decreased with circumference slower for *S. platiphylum* than for *H. diplandra*, *H. smithiana*, *L. simplex* and *S. bipennatum* (Tukey HSD test, $p < 0.01$) and slower for *A. ascinodis* and *A. canaliculatus* than for *H. smithiana* (Tukey HSD test, $p = 0.032$ and $p = 0.031$ respectively).

Tussock retrogression

The probability of tussock retrogression increased with tussock circumference (Table 2, circumference effect) from about 0.1 for the smallest circumference to about 0.9 for highest circumference (logistic regression, $p < 0.01$) whatever the fire treatment (Figure 4c) and whatever the species (Figure 4d). Overall, this probability differed significantly between fire treatments and species. It was significantly higher for the late fire than for the other fire treatments (Tukey HSD test, $p < 0.001$. Figure 4a) and was higher for the no fire treatment than for the mid-season fire (Tukey HSD test, $p = 0.001$). The overall probability of retrogression was significantly higher for *S. platiphylum* than for *A. canaliculatus*, *A.*

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schirensis, *H. diplandra* and *L. simplex* (Tukey HSD test, $p < 0.01$). *H. smithiana* presented a higher probability of retrogression than *A. canaliculatus* and *H. diplandra* (Tukey HSD test, $p = 0.02$, Figure 4b).

The "Fire treatment x Species" interaction had a significant effect on the retrogression probability (Table 2). The impact of circumference differed between fire treatments (Table 2, significant interaction between fire treatment and circumference, Figure 4c) and species (Table 2, significant interaction between species and circumference, Figure 4d). Tussock probability of retrogression increased slower with circumference for the mid-season fire than for all other fire treatments (Tukey HSD test, $p < 0.01$). It increased quicker for *S. platiphylum* and *A. canaliculatus* than for *L. simplex* (Tukey HSD test, $p = 0.013$ and $p = 0.042$ respectively).

Fecundity

The interaction between fire treatment, species and circumference significantly affected the number of seeds produced by grass tussocks (Table 2). Overall, whatever the fire treatment (Figure 5c) and the species (Figure 5d) the number of seeds significantly increased with tussock circumference (Figure 5d). More seeds were produced by tussock on the no fire plots than on the early and mid-season fire plots (significant fire treatment effect, Table 2 and Tukey HSD test, $p = 0.002$ and $p < 0.001$ respectively, Figure 5a). *Hyparrhenia smithiana* and *S. bipennatum* produced more seeds than the other species (significant effect of species, Table 2 and Tukey HSD test, $p < 0.001$, Figure 5b). The "species x fire treatment" interaction was significant (Table 2): *S. bipennatum* had more seeds in the no fire treatment than in the other fire treatments (Tukey HSD test, $p < 0.001$). *Brachiaria brachylopha* did not produce any seed on the early and late fire plots. *Loudetia simplex* produced more seeds on the mid-season fire plots but none on the no fire plots. *Schizachyrium platiphylum* did not produce any seed on the early and mid-season fire plots. The number of seeds increased quicker with

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circumference for the no fire treatment than for the other fire treatments (significant interaction between circumference and fire treatment, Table 2, Tukey HSD test, $p < 0.01$. Figure 5c). The number of seeds increased quicker with circumference for *H. smithiana* and *S. bipennatum* than for the other species (significant interaction between circumference and species, Table 2, Tukey HSD test, $p < 0.01$. Figure 5d).

The production of new tussocks per adult tussock varied with the species (Table 2, $F_{8.51} = 4.38$; $p = 0.0004$). *Brachiaria brachylopha* produced more new tussocks than all the other species (Tukey HSD test, $p < 0.05$. Figure 6) except *S. bipennatum* (Tukey HSD test, $p = 0.25$). The fire treatment and the interaction between fire and species had no effect on grass new tussock production (Table 2, $F_{24.51} = 1.66$; $p = 0.06$).

DISCUSSION

Tussock mortality

Although tussock mortality was low (11%) in our study compared to values obtained in Namibia (57%) by Zimmermann et al. (2010) or in Argentina (55 – 85%) by Pelaez, Boo, Mayor, & Elia (2001), it remained very high compared to that obtained by Gignoux et al. (2006) in the Lamto savanna. Grass mortality decreased with tussock circumference irrespective of the fire treatment and the species showing that small individuals are more likely to die than larger ones, as reported by other studies that considered basal diameter as a measure of size for grass tussocks (Garnier & Dajoz, 2001; O'Connor, 1994; Silva, Raventos, & Caswell, 1990). Overall, this confirms that the size of plant individuals allows predicting their fate (Silva & Castro, 1989). The causes of the death of tussocks are not precisely identified but, most probably, small tussocks are more vulnerable to accidents (e.g. trampling by buffalos in Lamto savanna) and to the exhaustion of resources due to repeated fires burning aboveground biomass and to the competition with larger tussocks. Indeed, small

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tussocks have fewer tillers, lower root biomass, and can therefore store less photosynthates in their roots during the dry season (Gignoux et al., 2006).

The late fire and the no fire treatments caused higher mortality than the mid-season and early fire treatments. This can be explained by the fact that late fire occurs at the beginning of the wet season, when grasses are vulnerable because they have already resumed their annual development cycle. The underground living buds ensuring their survival have already started their development, making them more vulnerable to fire. In turn, this probably makes small tussocks more vulnerable to late fire because they have fewer meristems: these tussocks cannot regrow if all their meristems have been killed and thus die. Silva et al. (1990) obtained similar results with two perennial grass species on a plot burned at the end of the dry season. The effect of the no fire treatment could be explained by the accumulation of dead aboveground biomass (Zimmermann et al., 2010) that could be detrimental to the resumption of tussock growth at the beginning of the rainy season. Moreover, the absence of fire could exacerbate competition between tussocks and increase the success of larger tussocks (Milton & Dean, 2000). Fire allows the access to light to all tussocks, regardless of their size, at least at the beginning of the dry season, when there is a low aboveground biomass. Conversely, the absence of fire could directly kill small tussocks that have not stored enough photosynthates to grow through the accumulating aboveground dead biomass.

The difference of mortality observed between species confirms that species differ by the effect of tussock size on demographic parameters. The studied grass species can be sorted in three distinct groups according to their tussock circumference i.e. large, medium and small size species (Koffi et al., 2019). In this context, the high mortality of *S. platiphylum* can be explained by the fact that the species is mostly represented by small tussocks.

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Tussock fragmentation

As found by César (1992) and Gignoux et al. (2006), we demonstrated the existence of tussock fragmentation in Lamto grasses. Such fragmentation has already been observed for tussock grass species (*Festuca gracillima*) in South America (Oliva, Collantes, & Humano, 2005), in North American prairies (*Schizachyrium scoparium*, Butler & Briske (1988)), in Australia (*Astrebla* spp. - Orr, 1980) and for several other perennial grass species in South Africa (Hartnett & Bazzaz, 1985; O'Connor, 1994).

Fragmentation probability increased with tussock circumference. This is consistent with César (1992) and Oliva et al. (2005) who found that larger grass tussocks produced new individuals by fragmentation. The process of tussock fragmentation has never been thoroughly analyzed. Nevertheless, it is clearly due to the death of the tillers in some parts of the tussock. The probability of fragmentation could increase with tussock circumference for at least three reasons. (1) Large tussocks produce more biomass and thus more fuel for fires, which could locally increase fire intensity (Lata, 1999). However, the probability of fragmentation also increased with tussock size in the no fire treatment. (2) This suggests that the death of tillers could also be due to a higher competition for water, mineral nutrients and light between tillers in larger tussocks. Tillers from the center of the tussocks would lose this competition because they have less access to light and, maybe, water and mineral nutrients than external tillers. (3) Finally, since tussocks are growing by the production of new tillers at their periphery (Lata, 1999), tillers from the tussock centers are likely to be older and could be senescent, which would increase their mortality.

The probability of tussock fragmentation was higher for the late fire, probably due to the same mechanism that increases mortality in this fire treatment: late fire is more likely to kill tillers that are resuming their growth at the beginning of the rainy season, when only a fraction of tillers dies, fragmentation may occur.

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Andropogon canaliculatus and *A. ascinodis* had higher probabilities of fragmentation than *A. schirensis*, *H. diplandra* and *L. simplex*, but there was no interaction with fire treatment or tussock circumference. *Andropogon canaliculatus* was the species that formed the largest tussocks while *A. ascinodis* possessed medium size tussocks. These two species were opposed to *A. schirensis* and *L. simplex* that had small tussocks and *H. diplandra* that formed large tussocks (Koffi et al., 2019) but with fewer large tillers (personal observation). This supports the assumption that tussock fragmentation is influenced by the size and the number of tillers by tussock.

Tussock growth and retrogression

The tussock probability to grow was significantly lower for the late fire regime. This could be explained by the severity of this fire regime (Louppe, Oattara, & Coulibaly, 1995). Such fire regime could prevent tussock growth by killing some tillers. Some authors showed, on the contrary, that the growth of perennial grass tussocks was higher in the case of intensive disturbance (O'Connor, 1994; Yuan et al., 2016). According to them, the late fire should rather stimulate tussock growth by reducing aboveground biomass, subsequently reducing competition and increasing light availability (Zimmermann et al., 2010). The stronger negative impact of the late fire, that does not have a higher intensity than the other fire regimes in Lamto savanna (N'Dri et al., 2018), is likely explained by the fact that grass tussocks have resumed their growth at the moment of late fire, so that late fire as a stronger negative impact on growth (and other demographic parameters, see above).

Tussock probability to grow decreased with circumference whatever the fire treatment and the species. Indeed, the larger a tussock is, the less resource (water, mineral nutrients, light) becomes available because the local tiller density increases, which likely increases competition between tillers and decreases the capacity to grow new tillers. In comparison to the mid-season fire, the absence of fire can also be detrimental to tussock growth as shown by

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Garnier and Dajoz (2001) or Loydi, Eckstein, Otte & Donath (2013). For these authors, the accumulation of unburned litter could reduce the growth of seedlings that have lower access to light.

There were small differences between species in their probability to grow. For example, *S. platiphylum* had overall a lower probability to grow that is only weakly sensitive to tussock size. On the contrary, *A. ascinodis* had a higher overall probability to grow than other species and this probability was high whatever the tussock size. This is consistent with the observed differences in tussock size between species (Koffi et al., 2019). *Schizachyrium platiphylum* generally formed small tussocks with few thin and short tillers (personal observation). Due to competition with taller tussocks, this could prevent *S. platiphylum* tussocks from absorbing enough light and from producing new tillers to enlarge their tussocks. On the contrary, *A. ascinodis* had many tall tillers (personal observation), which could facilitate the accumulation of resources that can be used to grow more tillers and enlarge its tussocks (Fetcher & Shaver, 1982).

The probability of tussocks retrogression increased with tussock circumference. Retrogression is due to the death of tillers, especially at the periphery of tussocks (Canales et al., 1994). Our result would again be due to a decrease in resource availability with tussock size, or maybe to a local increase in fire intensity with tussock biomass, as for fragmentation. The retrogression of tussocks was significantly more likely for the late fire than for the other fire regimes, certainly due to the same mechanism explaining the lower growth and higher mortality of tussocks for this fire regime.

The probability of retrogression was significantly higher for *S. platiphylum* than for *A. canaliculatus*, *A. schirensis*, *H. diplandra* and *L. simplex*, and *H. smithiana* presented a higher probability of retrogression than *A. canaliculatus* and *H. diplandra*. This is consistent with the fact that *S. platiphylum* and *H. smithiana* had on the average small tussocks (Koffi et

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al., 2019): higher rates of retrogression tend to lead to small tussocks. As for the effect of tussock size on growth, this could be explained by the lower capacity of resource accumulation of the smaller tussocks.

Fecundity

The number of seeds per tussock significantly increased with tussock circumference. Garnier & Dajoz (2001) obtained similar results with *H. diplandra* in both burned and unburned plots of the Lamto savanna. This confirms that for plants, size strongly influences fecundity (Watkinson & White, 1986; Weaver & Cavers, 1980) and suggests that this relation between plant size and plant fecundity is linear (Rees & Crawley, 1989). This is due to the fact that larger tussocks have more tillers, can produce more biomass and, everything else being equal, more seeds.

More seeds per tussock were produced in the no fire than in the early and mid-season fire treatments. This could be due to the return of more dead biomass and mineral nutrients to the soil in the absence of fire, because fires lead to the loss of the aboveground biomass and an important fraction of the mineral nutrients it contains (N'Dri, Kone, Loukou, Barot, & Gignoux, 2018). This is in agreement with Crowley & Garnett (1999). However, Brys et al. (2005) found that seed production was two times higher and seedling density six time higher in burned than in unburned savanna plots. Several other grass species have also been shown to produce more seeds in burned plots (Canales et al., 1994; Garnier & Dajoz, 2001). The reason for these contrasting results remains unclear. The absence of difference between the no fire and late fire treatments could be explained by the fact that, tussocks have the same time to produce and mature seeds in these treatments. While tillers stop growing during the dry season, some leaves remain green during at least a part of this season, which likely favors seed feeling and maturation till the death of aboveground biomass at the end of the dry season or due to fire, i.e. in March in the late and no fire treatments. Moreover, the number of seeds

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increased quicker with circumference for the no fire treatment than for the other fire treatments. This is likely due to the increased competition for light in the no fire treatment and the fact that this treatment favors large tussocks.

Hyparrhenia smithiana and *S. bipennatum* produced more seeds per tussock than the other species and their number of seeds increased quicker with circumference. As seen above, these two species are among the ones with the lowest probability of fragmentation and the smallest tussocks (Koffi et al., 2019). This suggests that small size species reproduce less by fragmentation but more by seeds likely explaining why these two species invest more in seed production relatively to their size. In particular, seed production might decrease in a fire treatment because it requires a particular timing from flower development to seed filling and because this timing is disturbed by fire (Brys et al., 2005; Silva & Ataroff, 1985). This could be for example the case for *B. brachylopha* in the early and late fire treatments, and *S. platyphyllum* in the early and mid-season fire.

The production of new tussocks by seed germination varied with the species but not with the fire treatment. Such effects should depend on differences in seed production, seed germination or seedling survival and growth (Brys et al., 2005). In our case, *B. brachylopha* produced more tussocks and fewer seeds than *H. smithiana* and *S. bipennatum*. This suggests that *B. brachylopha* has a higher germination rate or higher seedling survival rate than *H. smithiana* and *S. bipennatum*. In turn, this suggests that the seeds and seedling of *B. brachylopha* are more adapted to fire than *H. smithiana* and *S. bipennatum.* Testing further these hypotheses would require monitoring seed germination and the dynamics of young seedlings in the different fire treatments.

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Conclusion

In the humid savanna of Lamto, the grass species differ by their demographic parameters and the sensitivity of their demographic parameters to both fire regimes and tussock circumference. Overall our results confirm that the most benign fire treatment for grasses is the mid-season fire treatment. This treatment, which has been applied for more than 50 years in Lamto savanna, is likely to maintain the highest diversity of perennial grasses because it is not particularly detrimental to any of their dominant species. Outside the Lamto reserve, due to farmer activities, the fire often burns savannas before the period of the mid-season fire (i.e. mid-January). Because of an absence of fire-break around the Lamto reserve, these fires often also burn the reserve savanna, disturbing the prescribed mid-season fire regime. However, our results show that such perturbations and the early-fire regime are not too detrimental to the demography of perennial grasses. On the contrary, the late fire regime would likely decrease the abundances of all perennial grass species and should be avoided to maintain the integrity of the grass community. Nevertheless, the late fire is likely the fire regime that has also the stronger negative impact on tree demography because, as for grasses, tree saplings and seedlings resume their growth at the beginning of the rainy season and are likely more vulnerable to fire (Laris, Koné, Dadashi, & Dembele, 2017). This would suggest that maintaining at the same time savanna structure (the tree grass equilibrium) and the grass community would require alternating mid-season and late fires.

New results are required to test the long term impact of fire regimes on grass biomass and the abundance and diversity of forbs (Abella & Fornwalt, 2015). To predict the long term consequences of the fire regimes on the relative abundance of the different grass species, it is necessary to integrate all demographic parameters within the same framework. This will be achieved using our data to parameterize matrix population models (Caswell, 1989). Such models could predict the effect of the date and frequency of fires on the grass community.

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Finally, the mechanisms explaining the differences between species are so far largely unknown. They could be determined by further analyzing the grass species traits: the use of mineral nutrient, water and photosynthesis efficiency, phenology, classical root and leaf traits (Violle et al., 2007).

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Data Availability Statement: Our raw data are now available to the scientific community on the Mendeley repository website at: http://dx.doi.org/10.17632/jvx4f5gt6t.1

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Table 1: Abundance and proportion of perennial grasses on all plots the first and second years of study (overall tussocks).

Species	Abundance the first year	Proportion the first year (%)	Abundance the second year	Proportion the second year (%)
Andropogon ascinodis	105	2	116	2
Andropogon canaliculatus	1588	31	1842	34
Andropogon schirensis	494	10	494	9
Brachiaria brachylopha	81	2	127	2
Hyparrhenia diplandra	1351	26	1326	25
Hyparrhenia smithiana	188	4	176	3
Loudetia simplex	777	15	823	15
Sorghastrum bipennatum	294	6	282	5
Schizachyrium platyphyllum	238	5	169	3

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Table 2: Table showing (1) the χ^2 values of binary logistic regressions analyzing the effect of fire treatment, grass species, tussock circumference and two and three way interactions the interactions on tussock probability to die, to become fragmented, to grow and to retrogress using the glmer procedure, (2) the F values for linear regression analyzing the effect of fire treatment, grass species, tussock circumference and two and three way interactions on the number of seed produced by grasses and the production of new tussocks using the lm procedure. Only significant effects are displayed: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. df: degrees of freedom.

Explained variables	Explanatory variables	Procedure used	Value of the statistic	*df*	*p*-value
Tussock mortality	Circumference	glmer	$\chi^2 = 212.43$	1	***
	Fire treatment		$\chi^2 = 435.67$	3	***
	Species		$\chi^2 = 128.55$	8	***
	Circumference × Fire treatment		$\chi^2 = 11.13$	3	**
	Circumference × Species		$\chi^2 = 33.63$	8	***
	Fire treatment × Species		$\chi^2 = 104.1$	23	***
Tussock fragmentation	Circumference	glmer	$\chi^2 = 149.95$	1	***
	Fire treatment		$\chi^2 = 31.79$	3	***
	Species		$\chi^2 = 33.92$	8	***
Tussock growth	Circumference	glmer	$\chi^2 = 98.81$	1	***
	Fire treatment		$\chi^2 = 167.52$	3	***
	Species		$\chi^2 = 88.74$	8	***
	Circumference × Fire treatment		$\chi^2 = 59.1$	3	***
	Circumference × Species		$\chi^2 = 18.85$	8	*
	Fire treatment × Species		$\chi^2 = 62.13$	23	***
Tussock retrogression	Circumference	glmer	$\chi^2 = 529.96$	1	***
	Fire treatment		$\chi^2 = 168.92$	3	***
	Species		$\chi^2 = 28.91$	8	***
	Circumference × Fire treatment		$\chi^2 = 36.05$	3	***
	Circumference × Species		$\chi^2 = 28.69$	8	***
	Fire treatment × Species		$\chi^2 = 54.09$	23	***
Seed production	Circumference	lm	F = 40.24	1	***
	Fire treatment		F = 10.34	3	***
	Species		F = 14.65	8	***

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	Fire treatment × Species		F = 6.36	24	***
	Fire treatment × Circumference		F = 3.1	3	*
	Species × Circumference		F = 7.1	8	***
	Fire treatment × Species × Circumference		F = 2,97	23	***
Production of new tussocks	Species	lm	F = 4.38	8	***

Figure 1: Tussock mortality as a function of fire treatment, grass species and tussock circumference. Boxplots (a and b): horizontal bold lines of boxes indicate the median, the lower and upper bounds of boxes represent the 25th and 75th percentiles, respectively. The vertical doted bars include all values except outliers (circles). Significant differences between fire treatments and grass species are indicated by different letters (Tukey HSD test). EF, Early fire; LF, Late fire; MF, Mid-season fire; NF, No fire; AA, *Andropogon ascinodis*; AC, *Andropogon canaliculatus*; AS, *Andropogon schirensis*; BB, *Brachiaria brachylopha*; HD, *Hyparrhenia diplandra*; HS, *Hyparrhenia smithiana*; LS, *Loudetia simplex*; SB, *Sorghastrum bipennatum*; SP, *Schizachyrium platiphylum*. Logistic regressions (c and d): the colored lines indicate the probability of mortality as a function of tussock circumference as predicted by logistic regression. Each color represents a fire treatment (c) or a species (d).

Figure 2: Fragmentation of tussocks as a function of fire treatment, grass species and tussock circumference. Boxplots (a and b). Logistic regressions (c and d): the colored lines indicate the probability of tussock fragmentation as a function of their circumference. Each color line represents a fire treatment (c) or a species (d). Otherwise same legend as for Fig. 1.

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Figure 3: Tussocks growth as a function of fire treatment, grass species and tussock circumference. Boxplots (a and b). Logistic regressions (c and d): the colored lines indicate the probability of tussock growth as a function of circumference. Each color line represents a fire treatment (c) or a species (d). Otherwise same legend as for Fig. 1.

Figure 4: Tussock retrogression as a function of fire treatment, grass species and tussock circumference. Boxplots (a and b). Each color line represents a fire treatment (c) or a species (d). Otherwise same legend as for Fig. 1.

Figure 5: Seed production by tussock as a function of fire treatment (a), grass species (b) and tussock circumference (c and d). (c) and (d) represent the regression of the number of seed on the tussock circumference. Each colored line represents a fire treatment (c) or a species (d). Otherwise same legend as for Fig. 1.

Figure 6: Fecundity measured as the number of new tussocks per tussock of the same species as a function of species. Otherwise same legend as for Fig. 1.

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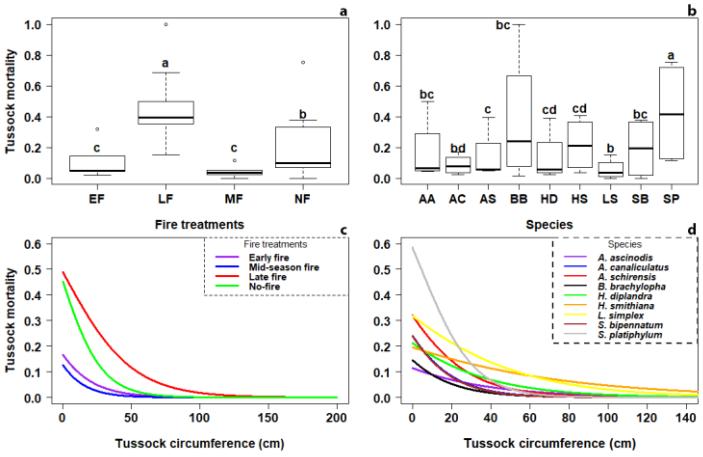

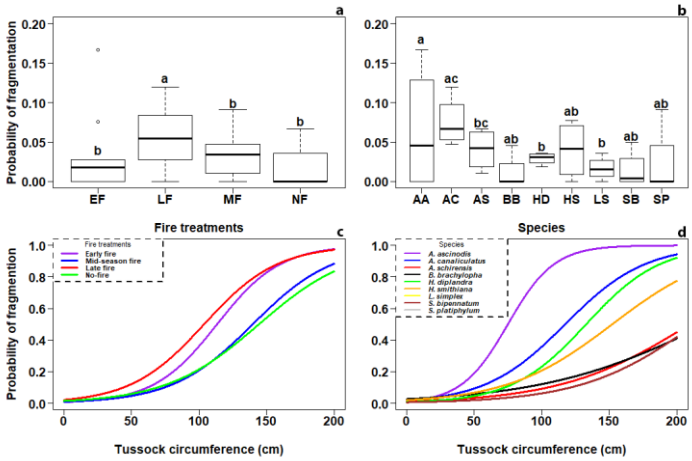

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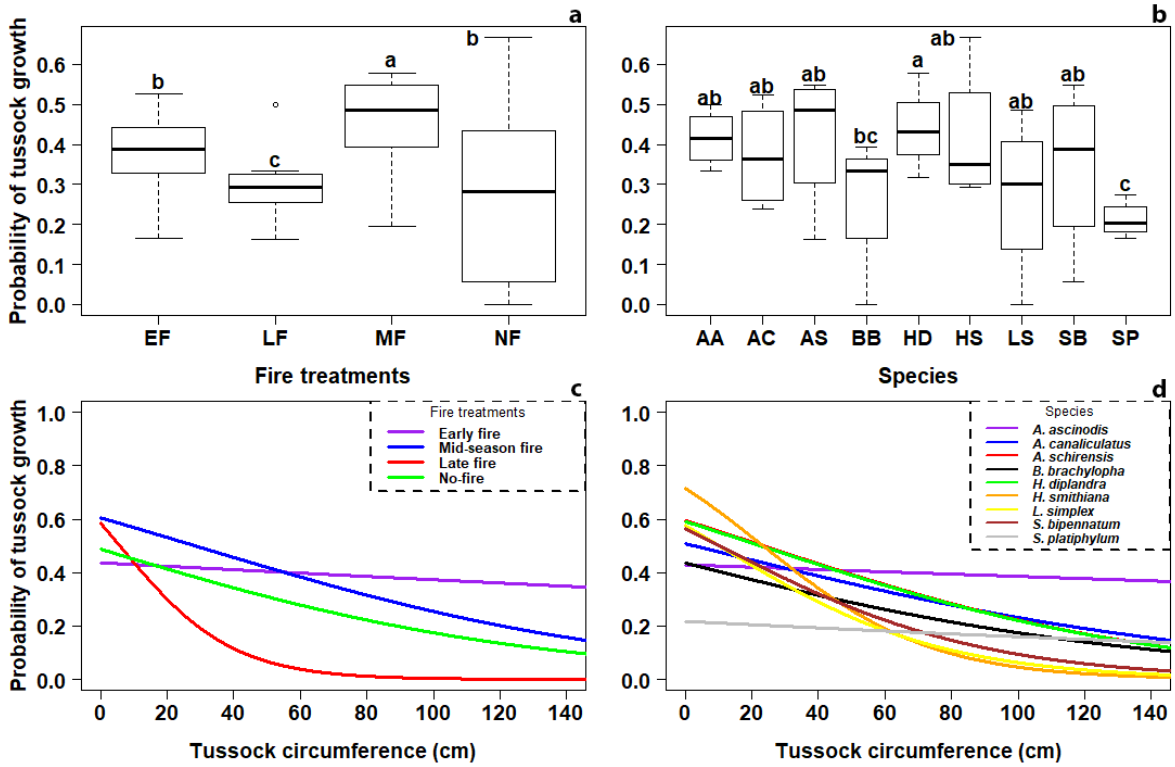

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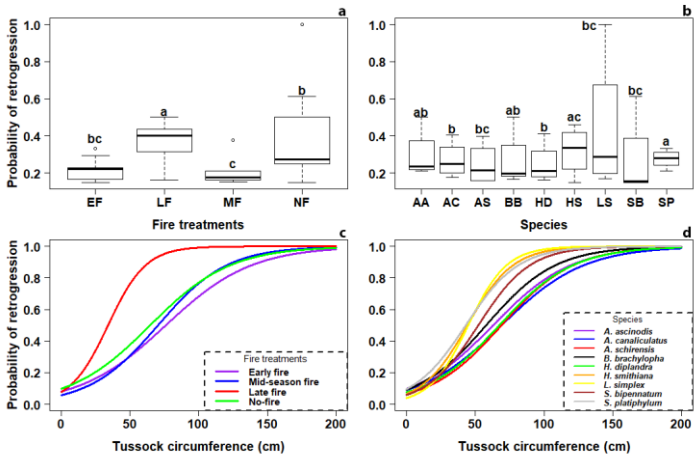

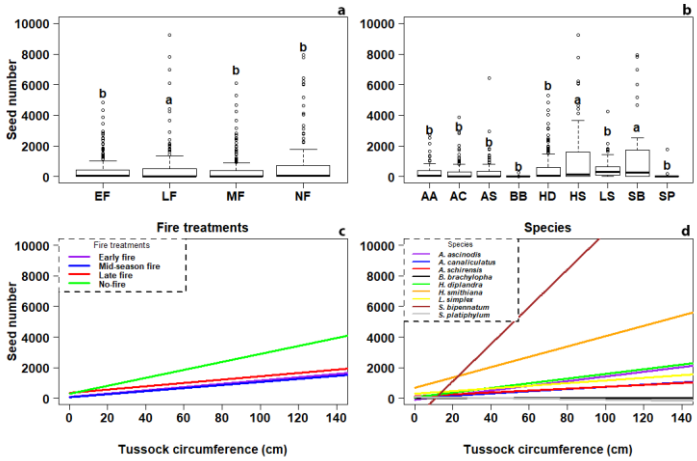

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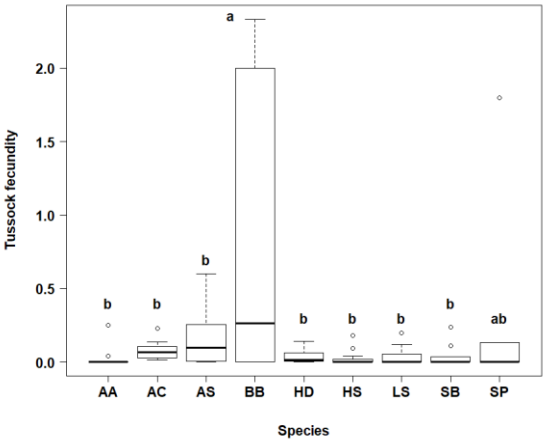

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