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The Demographic Response of Grass Species to Fire Treatments in a Guinean Savanna

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Abstract: Fighting tree encroachment using fire promotes C4 perennial grasses but likely affects their demography according to the fire date during the dry season. We analyzed the impact of four fire treatments (early, middle, late and no fire) on the demography of the four dominant perennial grasses (*Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Loudetia simplex*) in a Guinean savanna of West Africa (Lamto, Côte d'Ivoire). We carried out a yearly demographic monitoring of each grass individual during five years (2015–2019) on three plots by treatment and parametrized a size-classified matrix model with five circumference classes. The results showed that *A. schirensis*, *H. diplandra* and *L. simplex* declined ($\lambda < 1.0$) under late fire and will disappear after 10 years, as did *L. simplex* under the middle fire. Stasis influenced the most λ values and stable class distribution was nearly achieved in all species under all treatments. The size of *L. simplex* should increase under early and late fires. Our results suggest that late fire is the most detrimental fire regime for grasses in this Guinean area, contrary to early and middle fires, which could be recommended to savanna managers.

Keywords: fire treatment; Guinean savanna; perennial grass; demography; population growth rate; size-classified matrix model

1. Introduction

Savannas are defined by the coexistence of trees and grasses maintained by disturbances such as fires, when the annual rainfall is above 650 mm [1]. In fact, fire permits the fighting of tree encroachment which threaten savannas and their biodiversity, by preventing an increase in tree cover and colonization by forest plants. To assess the effectiveness of fire in fighting tree encroachment, many studies have addressed its impact on tree demography [2–4], while studies on grass demography are rare (but see Garnier and Dajoz [5]). However, in humid savannas, perennial grasses dominate the grass stratum because they represent 70–98% of the total above-ground biomass [6], which make them the main source of fuel for fire [7,8]. The biomass of grass and its dryness change throughout the dry season; fire characteristics also change depending on its timing. Therefore, there are currently debates on the impact of this timing on savanna functioning and the best fire period to manage vegetation and biodiversity [9–11].

It is well known that savanna trees and grasses are adapted to fire [12,13] with fairly well-known underlying mechanisms. For example, trees have developed several mechanisms allowing them to persist as avoiders (species that grow quickly in the absence of fire), resisters (species that develop thick bark) or resprouters (species that regenerate from their

underground parts protected from fire) [14–16]. Grasses persist by allocating reserves to their belowground system and producing aerial buds that insure their regrowth [17]. Thus, the mechanism of grass adaptation to fire is similar to the strategy employed by resprouting trees, as they both lose their aerial part during fire while keeping their underground parts, which allows growth to resume after fire [18].

Because fire intensity depends on the period of burning [19,20], this period should have contrasting effects on the demography of savanna trees [21,22] and perennial grasses [5,23,24]. Indeed, despite their adaptation to fire, fire regularly kills them, especially if it occurs at the beginning of their development cycle at the beginning of the wet season [24,25]. Moreover, fires occurring at the beginning of the wet season burn a very dry biomass and are more intense [26,27]. Thus, fighting tree encroachment may involve fire management, which implies choosing the best fire period to maintain the abundances and diversity of grasses and the desired tree density. Because tree encroachment is a worldwide issue in savannas [28], people could advise fire regimes such as late fires that are detrimental to trees [22,25]. However, are these regimes favorable to grasses? For these reasons and to determine the best timing for fires to conserve savanna biodiversity, a team of savanna managers started test four fire treatments (the absence of fire and three fire timings) in the Lamto savanna in 2013. These treatments are the early fire set at the beginning of the dry season in November, the middle fire in January (in the middle of the dry season), the late fire in March (at the end of the dry season) and the no-fire treatment. Using matrix models, we studied here the impact of these four fire treatments on the demography of the four dominant perennial grass species.

Koffi et al. [29] have already compared the demography of the four species for the middle fire. This study showed a difference in demography between species and years, depending on variations in stasis in different size-classes and on the species. One species declined with $\lambda < 1.0$ over three one-year transitions while the others were apparently stable. Our goal here was to determine the impact of the four fire treatments on the demography of the savanna perennial grasses. We parameterized the matrix demographic models for the four dominant grass species for which enough data was available to estimate transition rates [30] in the four fire treatments to compare the response of the grass species to these fire treatments. These models allowed us to compare various integrative demographic features (such as the asymptotic growth rate or the mean age within a stage) between the fire treatments. We tested the following hypotheses: (1) The late fire has a negative effect on the demography of all species because it occurs when grasses have restarted their annual development so that their leaves and buds are vulnerable to fire. (2) The no-fire treatment negatively affects the demography of the species by killing the seedlings and some adults through shading by the dry biomass (that has not been removed by any fire). (3) The early fire has a low negative effect on grass species because it has a low intensity and occurs when biomass is still wet and burns poorly. (4) As each species is effectively the same life-form but with different characteristics (e.g., tussocks of the different species have different sizes [24]), they have contrasting responses to each fire treatment.

2. Material and Methods

2.1. Study Site

Field data were collected at the Lamto Reserve in Ivory Coast (West Africa: 6°9′–6°18′ N; 5°15′–4°57′ W) between semi-deciduous forests and humid savannas [31] in the wettest end of the Guinean savanna domain. The weather is composed of a long rainy season from March to July, a short dry season in August, a short rainy season from September to November, and a long dry season from December to February. The average annual precipitation reaches 1200 mm and the mean annual temperature is about 27 °C. During the study (from 2015 to 2019), the mean annual rainfall was 1167 mm and the main temperature was 29 °C. This shows that the study years were overall slightly hotter and drier than the average values, which could influence fire characteristics and grass demography.

The vegetation of Lamto Reserve is composed of forests and savannas, with variable shrub and tree densities and a herbaceous stratum dominated by perennial grasses [6]. About 10 perennial grass species of the Andropogoneae tribe coexist in this savanna [32]. All these species are C4 and the dominant ones are: *Andropogon ascinodis* C.B.Cl., *Andropogon canaliculatus* Schumach., *Andropogon schirensis* Hochst. ex A. Rich., *Hyparrhenia diplandra* (Hack.) Stapf, *Hyparrhenia smithiana* (Hook.f.) Stapf and *Loudetia simplex* (Nees) C.E. Hubbard [6].

2.2. Study Plots

The four studied fire treatments (early, middle, late and no fire) were implemented on three replicated 3.72 ha blocks, each divided into four 50 × 100 m plots, one per fire treatment since September 2013 [20]. We monitored grass demography on a 5 × 5 m subplot delimited on each early, late and no-fire plots, and a 5 × 10 m subplot delimited on each middle fire plot (the usually used fire regime). We used 5 years of census (from 2015 to 2019) encompassing four one-year transitions (2015–2016; 2016–2017; 2017–2018 and 2018–2019).

2.3. Data Collection

The four dominant perennial grass species (*Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Loudetia simplex*) were considered in this study because they had enough individuals on all plots to carry out demographic studies except *L. simplex*, which does not maintain in the absence of fire. However, this species was overall the third most abundant species before *A. schirensis* [30]. We conducted a systematic sampling of all the individuals of each species with more than five tillers (to facilitate species identification) on all plots. We permanently marked all individuals from 2015 onwards between April and May using metal labels tied to metal pegs. We measured the circumference of each tussock using a measuring tape at the ground level. All labeled tussocks were censused every year until 2019, to determine their status (dead or alive, fragmented or not, retrogressed or recruited) as in Koffi et al. [24], and the circumference (cm) at the ground level of all living tussocks was measured. The new seedlings with at least 5 tillers were also labeled from 2016 onwards during each field campaign and integrated into the data. These seedlings were distinguished from small fragments of tussocks by the absence of remaining burnt stems at the base.

2.4. Matrix Models

For these perennial grasses, size-classified matrix model is appropriate for several reasons: (1) their survival, growth and reproduction depend more on their size than their age [33,34]; (2) they exhibit clonal reproduction; and (3) their age is difficult to determine [35,36].

Thus, a size-classified matrix model was designed for each combination of the four grass species and the four fire treatments. This model was parameterised separately for the 60 combinations of four grass species, four fire treatments and four one-year transitions, minus the 4 matrices of *L. simplex* missing in the no-fire treatment. Average matrices of the four one-year transitions were used to derive an average matrix for each species in each fire treatment and to compare species and fire treatments (overall 15 matrices, 4 species × 4 fire treatments—1 matrix for *L. simplex* under the no-fire treatment). Individuals were classified into five circumference classes: 3–10 cm (the smallest tussocks measuring 3 cm), 10–20 cm, 20–35 cm, 35–50 cm and 50 cm and more. These 5 size-classes were chosen to have a good enough description of the life history and robust parameter estimation, which requires having enough individuals in each size-class. Thus, the two first size-classes, where more individuals were found, are smaller than the following three size-classes [30].

Koffi et al. [29] have already established the life-cycle diagram of the perennial grasses (Figure S1). It shows that all transitions are possible between all size-classes in these species. The transitions lead to matrices of stasis, growth, retrogression, fragmentation and birth. These matrices contain, respectively, the probabilities of staying in the same class,

growing from a small class to a larger one, retrogressing from a large class to a smaller class, producing clones in a small class by individuals in a larger class and the number of seedlings produced by each class. These matrices are summed to three types of matrices: the survival matrix (stasis, growth and retrogression), the fragmentation matrix and the birth matrix, because the calculation of the age-based parameters required these three types of matrix. All these matrix types were then summed to the transition matrix, describing the contribution of each size-class to the others. Then, the survival, fragmentation and birth matrices were used for the calculation of age parameters and the transition matrix was used for all other demographic analyses. The number of individuals in each class during each field campaign was described by a five-entry vector.

2.5. Demographic Analyses

Demography is generally summarized by the equation $N_{(t+1)} = AN_{(t)}$ [37], where $N_{(t)}$ and $N_{(t+1)}$ are vectors of abundances in each size-class at time t and t + 1, respectively. This enables us to predict the asymptotic behavior of the population, i.e., asymptotic growth rate of the population (λ, the dominant eigenvalue of the transition matrix) and the stable or predicted size structure (the left eigenvector of the matrix; [37]). The standard error and the 95% confidence intervals of λ were calculated according to Caswell [34] to test whether λ was significantly different from 1.0 or not.

The elasticity of λ in relation to the matrix parameters [37,38] was also computed as an index of the relative influence of each matrix entry on λ. In other words, this measures the contribution of each matrix entry to changes in λ [37,39].

We conducted a loglinear analysis [40] to determine whether the transition matrices depended on the species, the transition year, the fire treatment or the previous state of the individuals. The response variable was the fate (death or living in a new size-class), while the explanatory variables were the species, the fire treatments, the transition years (2015–2016; 2016–2017; 2017–2018 and 2018–2019), and the state (the initial size-classes).

We used life-table response experiment (LTRE) analyses to quantify the contribution of each transition matrix entry to differences of λ between fire treatments. Contributions were calculated using Caswell's method [37]. To better highlight the contribution of each demographic parameter, the entries of the contribution matrix were summed in: stasis, i.e., all entries on the diagonal; fecundity, i.e., all the matrix entries on the first line minus the first; retrogression, i.e., the entries under the fecundities and above the stasis; and growth, i.e., under the first diagonal.

We used the mean matrices of the four one-year transitions for all demographic analysis and to calculate the age-based parameters for each fire treatment and species. We used the method of Cochran and Ellner [41] to calculate the age-based parameters and their standard deviation because perennial grasses exhibited clonal reproduction. We calculated (1) the mean age of individuals in each size-class, (2) the mean age of residence in each size-class, (3) the mean time to first reach a given class from the class 1, (4) the conditional remaining life-span of individuals in the given class and (5) the total conditional life-span if a class was reached [41,42].

In addition, we used Keyfitz's metric [43] to assess the difference between the observed size-class distribution and the predicted size-class distribution, i.e., the stable size-class distribution. This metric is a measure of the distance between any two probability vectors, i.e., it provides a measure of how far a population is from the predicted distribution at the time the distribution was observed. Keyfitz's formula allowing such analysis is:

$$\Delta = \frac{1}{2}\sum_i |n_{0,i} - w_i|$$

where $n_{0,i}$ is the observed proportion of individuals in size-class *i* and w_i is the proportion expected at stable size-class distribution. This formula provides values ranging from 0.0 (no difference) to 1.0 (high difference). The 'popbio' package [44] was used in R software version 4.0.5 [45] for all these parameter calculations and analyses.

3. Results

### 3.1. Average Matrix of Species in the Fire Treatments

The total number of grass tussocks recorded for the different fire treatments were 952, 1784, 873 and 531 in 2015 (after 2 years of fire experimentation), and 1020, 1842, 500 and 456 in 2019 (after 6 years of fire experimentation), respectively, for the early, middle, late and no-fire treatments. *L. simplex* had a single individual in the no-fire plots during the whole period, so the demography of this species was not studied in this treatment.

3.2. Asymptotic Growth Rate (Λ) of Grass Species under the Fire Treatments

The growth rates of all species were not significantly different from 1.0 under the early fire, as well as for *A. canaliculatus* regardless of the three other fire treatments (Table 1). The λs of *A. schirensis* and *H. diplandra* were not significantly different from 1.0 under the early and no-fire treatments. The following three species, *A. schirensis*, *H. diplandra* and *L. simplex*, exhibited low growth rates ($\lambda < 1.0$) under the late fire, as well as *L. simplex* under the middle fire (Table 1). Overall, the late fire caused the decline of three species (*A. schirensis*, *H. diplandra* and *L. simplex*). Projecting the population size over time (Figure 1) showed a reduction in the total population of 13%, 32% and 67%, respectively, in 10 years, and a trend towards extinction after 10 years. *L. simplex* also declined under the middle fire by 67% of the total population in 10 years. The population of this species grew exponentially over time under the early fire (Figure 1).

Table 1. Asymptotic grow rates (λs), the associated standard errors (SE) and 95% confidence intervals calculated for the mean transition matrix of the four species in each fire treatment. The ($-$) denote that there was no value for *L. simplex* in the no-fire treatment because there was almost no individual of this species in this treatment.

Species	Fire Treatments	λs	SE	95% Confidence Interval
Andropogon canaliculatus	early fire	0.978	0.040	[0.899, 1.057]
	middle fire	0.969	0.031	[0.907, 1.030]
	late fire	0.945	0.047	[0.853, 1.037]
	no fire	0.915	0.055	[0.807, 1.024]
Andropogon schirensis	early fire	0.989	0.099	[0.794, 1.185]
	middle fire	0.985	0.047	[0.893, 1.078]
	late fire	0.670	0.103	[0.467, 0.872]
	no fire	0.920	0.123	[0.677, 1.162]
Hyparrhenia diplandra	early fire	0.951	0.043	[0.865, 1.036]
	middle fire	0.953	0.036	[0.881, 1.025]
	late fire	0.783	0.065	[0.655, 0.912]
	no fire	0.933	0.054	[0.826, 1.040]
Loudetia simplex	early fire	1.061	0.060	[0.943, 1.179]
	middle fire	0.872	0.042	[0.788, 0.955]
	late fire	0.758	0.064	[0.632, 0.885]
	no fire	-	-	-
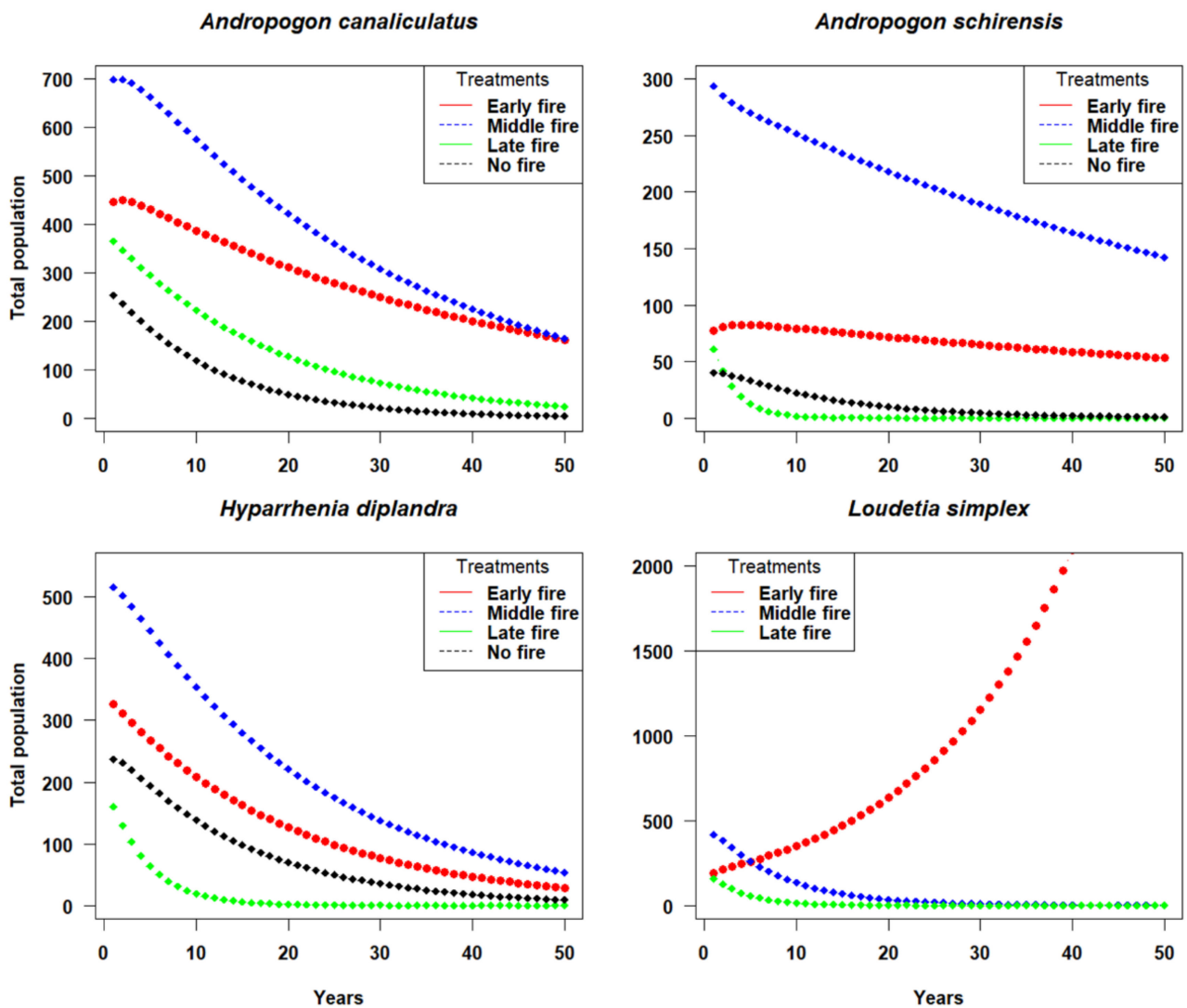
Figure 1. Total population size projected over 50 years by species and fire treatment using the average transition matrices.

3.3. Loglinear Analysis

There was a significant effect of the treatment × species interaction and main effects of both treatment and species on the fate of the grass individuals (log-linear test $p < 0.001$, Table 2). This effect of the interaction was a clear increase in the death rate and decrease in the probability of transition in the two largest size-classes for *A. schirensis, H. diplandra* and *L. simplex* under the late fire treatment (Table 3). The effect of the middle fire was a reduction in the mortality of *A. canaliculatus, A. schirensis* and *H. diplandra*. The effect of the middle fire on *L. simplex* was an increase in mortality and a decrease of the probability of transition in class 5. The early fire exhibited a noticeable low mortality for *H. diplandra* and *L. simplex* and low growth of *L. simplex* toward the largest size-classes. The main effect of the no-fire treatment was a reduction of the transition probability in the smallest size-class for *A. canaliculatus* and *H. diplandra* (Table 3).

Table 2. Loglinear analysis of the transition frequency table showing the effects of the treatments (T), the species (E) and the interaction on the demographic fate (D) of the four perennial grass species, conditional on the initial state (S). The DS,SET is the null model. This model contains the main effects of species and treatment and the interaction. It also excludes all interaction between fate and any combination of species and treatment. Comparing the null model to the model obtained after adding the species or treatment or the interaction in the null model give the corresponding effect. The log-likelihood ratio (G2) calculated after adding 0.5 to each table cell, as suggested by Fingleton [40], measures the goodness-of-fit of the loglinear model. The variation of G^2 (ΔG^2) assesses the significance of the observed effects. The degree of freedom (df) is the difference between the number of cells in the table and the number of parameters in the model.

Model	Effects	G^2	ΔG^2	df	Δdf	*p*-Value
DS,SET		1573.7		375		<0.001
DSE,SET		1176.1		300		<0.001
DE,DSE	Species		397.6		75	<0.001
DST,SET		900.9		300		<0.001
DT,DST	Treatment		672.8		75	<0.001
DSE,DST,SET		515.0		225		<0.001
DT,DST	Treatment		661.1		75	<0.001
DE,DSE	Species		385.9		75	<0.001
DSET		0.0		0.0		1.000
DET,DSET	Species $\times$ Treatment		515.0		225	<0.001

Table 3. Effect of the treatment $\times$ species interaction on the fate of grass individuals shown by the loglinear analysis. Table entries give the proportions (%) of transitions from individual initial states to six possible fates (dead, classes 1–5). The total number of individual in each fate by species and treatment was used in the calculations.

Species	Treatments	Fate					
		Dead	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**
Andropogon canaliculatus	early fire	11.2	11.4	24.7	23.6	14.6	14.6
	middle fire	7.0	15.2	29.5	25.1	11.0	12.2
	late fire	14.7	16.4	30.8	21.9	10.1	6.1
	no fire	16.3	9.1	20.8	25.8	16.9	11.2
Andropogon schirensis	early fire	11.9	9.9	33.8	24.8	14.6	5.0
	middle fire	5.3	7.2	23.3	31.4	19.3	13.5
	late fire	36.8	10.1	32.0	14.5	4.8	1.8
	no fire	17.3	12.8	19.6	20.7	12.3	17.3
Hyparrhenia diplandra	early fire	8.6	7.2	25.1	28.3	16.3	14.6
	middle fire	7.2	9.7	25.6	29.9	17.1	10.5
	late fire	33.7	12.8	29.0	18.7	4.7	1.1
	no fire	13.2	8.4	24.0	27.4	16.3	10.7
Loudetia simplex	early fire	5.1	14.0	40.9	33.4	5.4	1.3
	middle fire	10.3	24.3	30.2	22.5	8.1	4.6
	late fire	27.3	14.7	30.0	23.1	4.0	1.0
	no fire	-	-	-	-	-	-

3.4. Elasticity Analysis

The proportional sensitivity of λ to the variations in the different categories of demographic parameters followed the same pattern for all species and fire treatments (fecundity < retrogression < growth < stasis) except for *A. schirensis* and *H. diplandra* that exhibited higher elasticity to growth than to stasis under the late fire (Table 4): the λs of *A. schirensis* and *H. diplandra* showed the highest elasticity to variations in growth under the late fire, whereas in other combinations of treatment and species, this highest elasticity of λs was seen in variations in stasis. Considering the size-classes, the proportional sensitivity of λs to variations in demographic parameters was highest for stasis whatever the species

and the fire treatments (Figure 2). The highest elasticity of λ of *H. diplandra* to variations in stasis was observed in class 3 under all treatments, unlike the other species which exhibited highest elasticity of λ in different classes according to the fire treatments. This highest elasticity of λ to variations of stasis were found in the class 3 for *A. canaliculatus* (0.166) and *A. schirensis* (0.131) under the no-fire treatment and for *A. canaliculatus* in the classes 5, 2 and 3, respectively, in the early fire (0.134), the middle fire (0.260) and the late fire (0.127). *A. schirensis* showed highest elasticity of λ to variations of stasis in the classes 2 and 3, respectively, in the early fire (0.155) and the middle fire (0.259), while the highest elasticity of λ to variations of stasis was obtained in class 2 for *L. simplex* in the early and late fires (0.21 and 0.193, respectively) and in class 1 under the middle fire (0.231).

Table 4. Elasticity as the contribution (%) of fecundity, stasis, retrogression and growth to the λs of all species under each fire treatment. The (-) denote that there was no value for L. simplex in the no-fire treatment.

Species	Treatments	Matrix Entry Categories			
		Fecundity	Stasis	Retrogression	Growth
Andropogon canaliculatus	early fire	7.5	46.4	19.0	26.8
	middle fire	9.4	55.9	12.0	22.5
	late fire	8.2	49.3	13.4	28.9
	no fire	4.4	51.3	17.4	26.7
Andropogon schirensis	early fire	6.9	50.2	15.6	27.1
	middle fire	3.1	59.3	16.4	21.0
	late fire	10.5	33.0	20.7	35.6
	no fire	12.1	42.5	12.6	32.5
Hyparrheniadiplandra	early fire	4.9	55.1	16.2	23.5
	middle fire	5.5	52.2	16.5	25.7
	late fire	15.0	34.9	13.0	36.9
	no fire	8.1	41.0	17.6	33.0
Loudetiasimplex	early fire	13.3	44.7	13.0	28.8
	middle fire	16.8	48.9	9.0	25.0
	late fire	16.2	39.9	11.3	32.3
	no fire	-	-	-	-

3.5. Stable Size Distribution Analysis

The distance between the observed and predicted size-class distributions given by the Keyfitz metric ranged from 0.025 (for *A. canaliculatus* under the late fire) to 0.23 (for *L. simplex* under the middle fire) showed that the two size-class distributions were not much different for all species under each fire treatment (Table S1). The predicted size-class distribution changed with the fire treatment (Figure 3). The predicted distribution exhibited the same shape for all species under the late fire treatment, with the highest proportions of individuals in class 2. The highest proportions of individuals in the predicted distribution were found for *H. diplandra* in class 3 under the other treatments. In the other cases, there were no clear patterns describing the predicted size-class distribution: the highest proportions were obtained in class 2 for *A. canaliculatus*, *A. schirensis* and *L. simplex* for the early fire. These proportions were found in classes 2, 3 and 1 for the middle fire for the same species, respectively. For the no-fire treatment, *A. canaliculatus*, and *A. schirensis* exhibited the highest proportions of individuals in classes 3 and 2, respectively. The lowest proportions (sometimes zero) were found in class 5 in all cases (Figure 3).
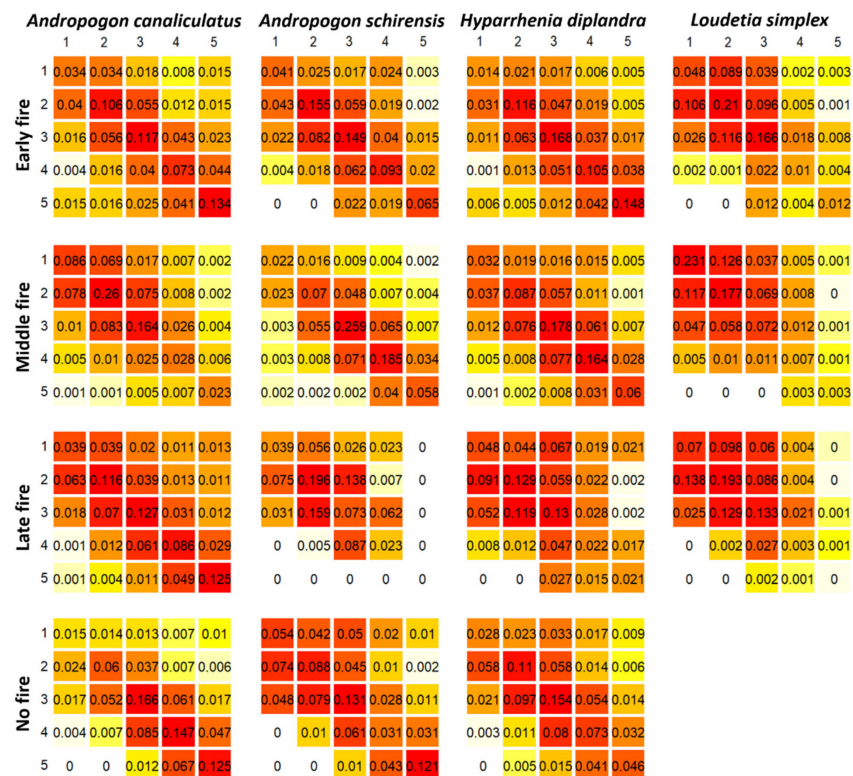
Figure 2. Elasticity matrices of all species in the four fire treatments. The redder the color, the higher the value.
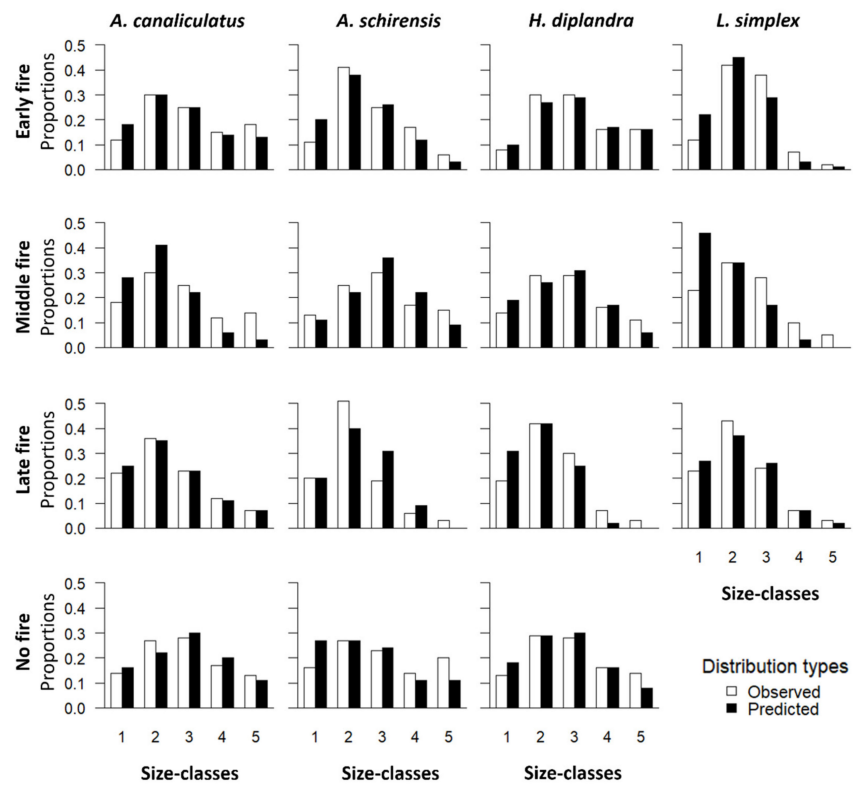
Figure 3. Comparison of observed and predicted distributions of individuals in size-classes for each combination of species (*Andropogon canaliculatus*, *Andropogon schirensis*, *Hyparrhenia diplandra* and *Loudetia simplex*) and fire treatments. The predicted size distributions were calculated using the mean matrices over the four one-year transitions.

3.6. LTRE Analysis

Table 5 shows the difference of λ between the fire treatments, the overall contribution of each treatment to this difference and the influence of each demographic parameter on this difference. The population of *A. canaliculatus* grew faster under the early fire compared to the other treatments. In this species, growth was the parameter that contributed the most to the difference between this treatment and the middle and late fires, with the highest growth for the early fire. The difference between the early fire and no fire was marked by a higher retrogression for the early fire than the no-fire treatment. The λ of *A. canaliculatus* was higher for the middle fire than for the late fire due to higher stasis for the middle fire. Higher growth and lower fecundity for the no-fire treatment than for the middle and late fires, respectively, explained the difference of demography between no fire and these treatments.

Table 5. Contribution of the grouped demographic parameters (Fec.: fecundity, Sta.: stasis, Ret.: retrogression and Gro.: growth) to the demographic difference between treatments in each species, analysed by the life-table response experiment. When the demographic parameters are higher in treatment 2 than in treatment 1, contribution values are positive and vice versa. Treatment 1: the first of the two compared fire treatments; treatment 2: the second treatment; $\Delta\lambda = \lambda_{(treatment\ 2)} - \lambda_{(treatment\ 1)}$: the difference between the asymptotic growth rates (λ) of treatment 1 and treatment 2; C-value: the global contribution value calculated by summing all the entries of the contribution matrix from the comparison between the corresponding treatment. The (-) denote that there was no possible comparison between the other treatments and no fire in *Loudetia simplex*.

Species	Treatment 1 × Treatment 2	$\Delta\lambda$	C-Value	Demographic Parameters			
				Fec.	Sta.	Ret.	Gro.
Andropogon canaliculatus	middle fire × early fire	0.0091	0.0108	−0.016	−0.095	0.008	0.114
	middle fire × late fire	−0.0238	−0.0249	0.006	−0.086	−0.013	0.069
	middle fire × no fire	−0.0531	−0.0545	−0.019	−0.085	−0.037	0.088
	early fire × late fire	−0.0329	−0.0312	0.028	0.020	−0.015	−0.064
	early fire × no fire	−0.0623	−0.0631	−0.003	0.008	−0.038	−0.029
	late fire × no fire	−0.0293	−0.0290	−0.026	−0.012	−0.014	0.024
Andropogonschirensis	middle fire × early fire	0.0041	0.0036	0.035	−0.069	0.072	−0.034
	middle fire × late fire	−0.3157	−0.3150	0.020	−0.361	0.059	−0.033
	middle fire × no fire	−0.0656	−0.0630	0.076	−0.180	−0.017	0.058
	early fire × late fire	−0.3198	−0.3172	−0.013	−0.281	−0.006	−0.015
	early fire × no fire	−0.0697	−0.0681	0.035	−0.113	−0.084	0.094
	late fire × no fire	0.2500	0.2484	0.066	0.155	−0.055	0.082
Hyparrhenia diplandra	middle fire × early fire	−0.0026	−0.0028	−0.026	0.011	−0.036	0.048
	middle × late fire	−0.1698	−0.1681	0.047	−0.208	0.014	−0.022
	middle fire × no fire	−0.0199	−0.0198	0.003	−0.108	0.001	0.084
	early fire × late fire	−0.1672	−0.1744	0.092	−0.223	0.047	−0.091
	early fire × no fire	−0.0173	−0.0171	0.033	−0.122	0.041	0.029
	late fire × no fire	0.1499	0.1519	−0.053	0.108	−0.017	0.113
Loudetia simplex	middle fire × early fire	0.1890	0.1862	−0.051	0.043	0.020	0.173
	middle fire × late fire	−0.1138	−0.1142	−0.037	−0.120	−0.010	0.054
	middle fire × no fire	-	-	-	-	-	-
	early fire × late fire	−0.3028	−0.3012	0.010	−0.166	−0.034	−0.110
	early fire × no fire	-	-	-	-	-	-
	late fire × no fire	-	-	-	-	-	-

In *A. schirensis*, *H. diplandra* and *L. simplex*, λ values were ordered as follows for the fire treatments: early fire > middle fire > no fire > late fire. The difference of demography between the early fire and the middle fire was mostly due to a higher retrogression for the early fire than the middle fire for *A. schirensis* and a higher growth for the early fire than the middle fire for *H. diplandra* and *L. simplex*. The demographic differences between the

middle fire and the late fire, the middle fire and no fire, and no fire and the late fire were mostly due to stasis. This stasis was higher under the middle fire than no fire, then the middle fire than for the late fire, and no fire than the late fire.

3.7. Age-Based Life-History Parameters

The average age of individuals was between 12.2 y and 72.2 y; they resided from 3 y to 34 y in each size-class and their total conditional life-span was between 6 y and 46 y. Overall, these species can live between 24 y and 120 y. The mean age of *A. canaliculatus* in the different size-classes was high under all fire treatments (Table S2) with values ordered as follows: early fire (57.3 y) > late fire and no-fire treatments (45.7 y for both) > middle fire (38.9 y). In the class 1, this species was older under the late fire (36.1 y) than the middle fire (30.7 y) and the no-fire treatment (28.3 y). *A. canaliculatus* resided longer in the size-classes for the early fire (25.4 y) than for the middle fire (18.6 y), the late fire (13.7 y) and the no-fire treatments (9.6 y). All other age-based life-history parameters of this species followed the same trend except for mean time to first reach the other classes from class 1, which did not change much between the early fire (10.2 y) and the middle fire (10.4 y). This parameter showed lower values in classes 1, 2 and 3 and higher values in classes 4 and 5 under the middle fire than the early fire.

Andropogon schirensi had older individuals for the middle fire in all size-classes (72.2 y) than for the other treatments except the late fire, under which the age in the first class was the highest (Table S2). This species can live more than 100 y under the middle fire condition, since its mean remaining life-span was about 34.5 y and it resided longer in each size-class (33.9 y). The other age-based life-history parameters exhibited the following trend: middle fire > early fire > no fire > late fire. The mean age in each size-class of *A. schirensis* under the late fire (59.9 y) did not reflect the values of the other parameters, as the species spent less time in each size-class (3.7 y), quickly reached the other size-classes from class 1 ($\approx$3.2 y) and had a low remaining life-span ($\approx$2.9 y and 6.1 y).

All age-based life-history parameters of *H. diplandra* exhibited higher values for the early fire than for the middle fire, followed by no fire and the late fire (Table S2). This species was about two or three times older in the early fire (61.7 y) than in the other treatments, which did not show clear differences in the mean age (29.3 y, 21.9 y and 17.9 y), respectively, for the middle fire, the no fire and the late fire treatment. However, individuals of this species in the class 1 were older for the late fire (13.4 y) than for the no-fire treatment (12.8 y).

The mean age of *L. simplex* was higher in all size-classes for the middle fire (37.6 y) than for the early fire (19.2 y) and the late fire (16.6 y). The other parameters did not match the mean age values in the size-classes since they exhibited too-low values compared to the mean age (Table S2). The calculations gave unrealistic values for the mean age of residence in the size-classes, the mean time to first reach the classes from the class 1, the conditional remaining life-span in the classes, and the total conditional life-span under the early fire treatment for this species.

Moreover, there was no common pattern between the species regarding the variation of age-based life-history parameters according to the fire treatments. Similarly, the values of age-based life-history parameters of these species did not always follow the same order according to the fire treatments. For example, *A. schirensis* exhibited a higher value of mean age for the late fire treatment compared to the other species, whereas for the other parameters and this same fire treatment, it presented the lowest values. Finally, no general effect of a specific fire treatment was noticed on the age-based life-history parameters of these grass species.

4. Discussion

4.1. General Effect of the Fire Treatments on the Demography of the Grass Species

The late fire: The late fire caused a strong decline in the populations of three of the four species (*A. schirensis*, *H. diplandra* and *L. simplex*). This also leads to a decrease in the

proportion of individuals in the two largest size-classes (stable size distribution). These results confirm the studies by Koffi et al. [24], who suggested that the late fire had high negative impacts on the demography of the dominant grasses. These negative effects can be explained by the fact that the late fire, with its high intensity [27], increases mortality, fragmentation and retrogression [24]. In turn, fragmentation and retrogression decrease the size of individuals, which likely make them more vulnerable to fire [24]. This general pattern is likely due to the late fire occurring at the beginning of the rainy season, when grasses have started to grow, so that their terminal buds become vulnerable to fire. This may lead to the death of parts of the tussocks (therefore increasing fragmentation and retrogression) or the death of whole tussocks (therefore increasing mortality). Indeed, dry-season fires have been shown to lead to lower risk of population decline than rainy-season fires [46], considering that early and middle fires are dry-season fires and the late fire is a rainy season fire. During the period of the late fire, grass phenological state could be crucial because fire could kill parts of the tillering of larger tussocks that have already been resprouted, as explained by Koffi et al. [24], which would also promote fragmentation and retrogression and increase death rate. The tussocks of *L. simplex* have a naturally small size and are therefore easily killed by the late fire. Moreover, on our late fire plots, *Imperata cylindrica*, one of the 100 most harmful invasive species in the world according to Lowe et al. [47], has become largely dominant over the years. Perhaps competition of this species for nutrients is partly responsible of the decline of *A. schirensis*, *H. diplandra* and *L. simplex* under this fire treatment.

The middle fire: The middle fire induced a decline of *L. simplex* by increasing death rate and reducing the probability of transition to class 5. These effects could be explained by the low capacity of this species to compete with other species for light [48]. Indeed, this species is characterized by frail and rather short tillers that are dominated by the other species at the end of their vegetation cycle, which could increase the death of individuals. This is confirmed by Raventos and Silva [49], who showed that competition with neighbours decreases the tillering capacity of perennial grasses. Thus, the synergy between the small size of *L. simplex* tussocks and the fairly high intensity of the middle fire could increase the death of *L. simplex* individuals [27]. The other species were not significantly declining under the middle fire, confirming their adaptation to this fire regime that has always been applied since at least 50 years in the area. The low mortality rate of these species under the middle fire revealed by the loglinear analysis confirmed this result. This agrees with Hiers et al. [50], who consider that the middle fire is the best management strategy for savanna species because it coincides with the historical fire regimes under which species have always evolved.

The no-fire treatment: This fire treatment did not induce the growth or decline of *A. schirensis*, *H. diplandra* and *A. canaliculatus* (the λ values were not significantly different from 1.0). However, we had no demographic data for *L. simplex* under the no-fire treatment because only one individual was recorded. In fact, this treatment leads to the accumulation of dead leaves and tillers [51], including from species that have higher tillers than *L. simplex*. This likely strongly reduces the species' capacity to have access to light and would increase strongly its mortality. This agrees with studies by Kaye et al. [52] and Silva et al. [53], who reported a similar decline in populations of perennial grasses from other areas protected from fire. Contrary to *L. simplex*, the other species did not decline under the no-fire treatment, certainly because of their generally large tussock size that allows them to better resist shading by the accumulation of dead aerial biomass. Conversely, the absence of fire would have favorable effects (in comparison to all fire treatments) by suppressing the increase in mortality, retrogression and fragmentation due to fire. This would contribute, as shown by the observed size-class distribution, to a low proportion of individuals in the small size-classes.

The early fire: The early fire did not induce the growth or decline of any species. This treatment induces a low fire intensity due to the abundant but very humid fuel [27], which decreases fire capacity to increase mortality, fragmentation and retrogression [24].

Particularly in *L. simplex*, seed dispersal takes place early (a few weeks before the early fire), so the seeds are disseminated before this fire treatment at the base of the tussocks [54] and are more likely to settle deeper in the litter or soil before the fire is set [46]. Since early fire often has a weak impact on vegetation, these seeds can be spared. After fire, nutrient availability, microbial activity and nitrogen fixation are increased [55,56]. This can induce abundant seed germination and rapid seedling growth [57] and increase population growth rate [58]. Thus, seeds of *L. simplex*, spared from the early fire, can germinate, especially when soil is fairly wet (as it was the case at the time of this fire treatment), and then take advantage of resource availability after fire to grow and form new tussocks. Higher growth, resulting in higher fecundity and recruitment in annually burnt populations [53], could explain the high growth rate of 1.061 observed in this species under the early fire.

4.2. Responses of the Grass Species to Fire Treatments

4.2.1. Similarities in the Response of Species to the Fire Treatments

Elasticity, stable size distribution, LTRE and age-based life-history parameter analyzes showed that perennial grass species had similarities in their responses to fire treatments. Indeed, all species were more sensitive to variations in stasis under all fire treatments. This high proportional sensitivity of λ to variations in stasis agrees with the fact that, for most long-lived plants in arid and semi-arid environments, stasis is the single most important demographic process [59,60]. In our case, all species we studied were long-lived plants (up to 120 y) but in a humid savanna [29]. Thus, the high elasticity of λ to stasis can also be a characteristic of long-lived plants in humid environments. Though the four species are adapted to their fire-dominated environment [61], increasing the survival of individuals would be the best way to increase the growth of their populations.. Another common point between the four species is that they were all close to the stable size-class distribution predicted by the matrix models under all fire treatments. Similar results were obtained on a perennial grass species: *Andropogon semiberbis* in Venezuela [53], and on a range of herb, shrub, and tree species [62]. One could predict, as Clutton-Brock and Coulson [63] and Ujvari et al. [64] did, that environmental disturbances such as fire lead to a difference between the predicted and the observed size-class distributions. This suggests that the four studied species adjust quickly their size distributions to disturbances. In any case, this proximity between the two distributions suggests, according to Williams et al. [62], that relying on the equilibrium assumption to make demographic analyzes of populations was valid.

4.2.2. Contrasting Responses of the Grass Species to the Fire Treatments

The demographic parameters of each species were impacted differently by the fire treatments, showing dissimilarity between the demography of the species. The fact that population growth was higher for the early and the middle fires than for the late fire for *A. canaliculatus* agrees with Liu and Menges [65], who found that recruitment was stronger with dry season fires for *Chamaecrista keyensis*, our late fire sometimes coinciding with the rainy season. Changes in the shape of the predicted size-class distribution of each species according to the fire treatment confirmed that the fire treatments acted slightly differently on the size distribution of each species [24]. The highest proportion of *A. canaliculatus* individuals was predicted in class 2 for all fire regimes, but in class 3 for the no-fire treatment, indicating that the demography of this species is maintained when submitted to fire but changes in absence of fire. The competitive ability of this species for resources would certainly increase for the no-fire treatment compared to the other treatments because individual size (the highest proportion of individuals in class 3 under the no-fire treatment) and competitive ability increases with plant size [66,67]. This could explain the difference of demography of *A. canaliculatus* between fire and no-fire treatments and confirms the fact that *A. canaliculatus* is a very fire-adapted species. The response of *H. diplandra* to the fire treatments was a strong reduction of the size of individuals predicted for the late fire. The same result was obtained for *A. schirensis* for the early fire, the late fire and the

no-fire treatments compared to the middle fire. Indeed, the middle fire is the fire regime that is usually applied in the Lamto savanna and to which all species are already adapted. According to Miller et al. [68], changes from the fire treatment to which species are adapted tend to generate a mismatch between different fire-adaptation traits, which negatively affect population dynamics. For example, the highest proportion of individuals of *A. schirensis* was predicted in class 2 for early and late fire régimes and in class 1 for the absence of fire, whereas for the middle fire, the highest proportion of individuals was predicted in class 3. For the same type of reason, *L. simplex*, contrary to *A. schirensis*, exhibited an increase of individual size when submitted to other fire regimes than the middle fire: the predicted proportion of individuals was the highest in size-class 2 instead of size-class 1 for the middle fire.

The life-history parameters of all species differed by fire treatment. Some species had older individuals in the early fire and others in the middle fire treatment, while some species lived longer in the late fire and others in the no-fire treatment. The other age-based parameters also were characteristic. This difference in species response to fire treatments was more marked between size classes as shown by Schemske et al. [69] and Kesler et al. [70]. This probably reflects both the discussed differences in their demographic responses and the complexity in plants of the links between size and age. This complexity is probably increased here by the regression and fragmentation of tussocks.

5. Conclusions

Our results demonstrated that only the *A. canaliculatus* population declined, but not significantly (λ not significantly lower than 1.0), under all fire treatments, while the late fire caused decline in all other species. This suggests that applying the late fires alone should be avoided to maintain grass diversity. The early and middle fire treatments could be recommended to savanna managers, as they are less detrimental to almost all grass species and have less effect on the stasis, which is the most sensitive parameter in the demography of grasses. However, this implies that these fire treatments must also be efficient in reducing or maintaining tree density. If not, it would be appropriate to test other methods such as the combination of these fire treatments.

In fact, applying a mixture of middle, early, late and no-fire treatments in space or time could favor grass diversity and differences in grass size structure of their tussocks, as suggested by differences in their responses to these fire regimes. For example, in the case of the Lamto savanna, the late fire could be applied, for instance, every 5 years, instead of the usual annual middle fire, to regulate the populations of woody species as suggested by N'Dri et al. [22], probably without being detrimental to perennial grass biodiversity. The no-fire treatment alone cannot normally be considered as a treatment that helps to preserve savanna biodiversity because it leads to a rapid declining of some grass species and the transformation of savanna into forest [71]. However, a fire regime based on the number of years between two fires could be applied as studied in other savanna types [72]. This should not be detrimental to perennial grass diversity, even to *L. simplex*, which tends to disappear without fire.

We have so far studied the demography of the four dominant grass species as independent phenomena, while facilitation (which could occur through the local enhancement of soil fertility [73]) and competition (e.g., for light) could likely lead to interactions between these species. It would be thus interesting to study the competition/facilitation relationships between the perennial grass species using an experimental approach, by artificially reducing the density of individuals of one or more species and monitoring the demographic effect of this reduction on their demography. This could allow parameterising a matrix population model in which demographic rates would depend on tussock densities [34].

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fire5060193/s1.

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