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Revealing the Impact of Understory Fires on Stem Survival in Five Palm Species (Arecaceae): An Experimental Approach Using Predictive Models

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Abstract: Amid increasing deforestation, surface fires reaching the forest understory are one of the primary threats to Amazonian ecosystems. Despite extensive research on post-fire mortality in woody species, literature on palm resilience to fire is scant. This study investigates post-fire mortality in four understory palms—*Bactris maraja* Mart., *Chamaedorea pauciflora* Mart., *Geonoma deversa* (Poit.) Kunth, *Hyospathe elegans* Mart., and juvenile individuals of *Euterpe precatoria* Mart. Objectives included: a) comparing post-fire responses; b) developing mortality models based on severity variables; and c) evaluating if diameter protects bud stems from heat flux. Conducted at the edge of an Ombrophylous Forest in Alto Juruá Acre, Brazil (7°45'S, 72°22'W), the experiment subjected 85 individuals to controlled burning in a 1 m² area near the stipe, with temperature sampling using K thermocouples. Results showed varying mortality rates among species, with larger stipe diameter correlating to reduced mortality. Canopy burning patterns significantly influenced mortality, especially for *Euterpe precatoria*. Species exhibited diverse regrowth capacities, with *B. maraja* showing the highest number and tallest basal resprouts. This study underscores post-fire plant mortality as a critical indicator of fire severity, essential for understanding its ecological impacts.

Keywords: Amazon Rainforest; surface fires; Acre; Brazil; post-fire fate

1. Introduction

Surface fires are the most common type of fire in natural ecosystems globally [1]. In the Amazon, surface fires affected more than 85,500 km² of forest between 1999 and 2010, comprising 2.8% of the entire forest area, a rate higher than deforestation during the same period [2–4]. During the 2015 drought, the frequency and extent of forest fires in the Amazon increased by 36% compared to the previous 12 years [5]. These high rates of surface fire occurrence are linked to changes in land use and anthropogenic ignition sources [6, 17]. Surface fires typically exhibit low to moderate heat flux intensity and can exert selective evolutionary pressures [7–10]. While wildfires in tropical forests generally do not visibly damage canopy vegetation, the understory layer often experiences greater severity [11–16].

Anthropogenic ignition is recognized as the primary contemporary source of ignition [6]. Forest edges and their understory are most threatened by surface fires, which can spread tens of kilometers into the forest interior [18, 19]. Altered physical and environmental conditions at forest edges, such as reduced relative humidity and increased temperatures, amplify fire severity [20, 21]. Recurrent fires at edges heighten susceptibility to subsequent fires, potentially of increased intensity and severity [21–24].

In fire ecology, severity and intensity are independent concepts [8, 25, 26]. Fire intensity measures fire behavior in terms of thermal energy production rate, heat release, and temperature, depending on complex interactions among fuel structure, weather conditions, and the physical environment [27–30]. Severity encompasses the physical impacts of fire related to combustion and heat transfer, interacting with species morphology, physiology, and system characteristics [31].

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Surface fire severity is driven by the fire's insidious nature, allowing it to slowly advance into the understory, where it can persist near plants, releasing high heat rates and burning the base of trunks, lower canopy leaves, seedlings, and young individuals [32–35]. The first surface fire in the understory tends to have low intensity due to preserved temperature and moisture conditions. Flames typically range from 10 to 30 cm in height, with a propagation speed of around 0.25 m min^{-1} [18, 23]. Temperatures at the base of intercepted plants along the fire's path can reach up to 760°C, with intensities reaching 50 kW m^{-1} in such cases [36–39].

Post-fire severity determines mortality, with studies primarily focused on tree species; little research has been conducted on the survival of herbaceous, shrub, or understory species [40–45]. Controlled experimental studies on plant mortality related to fire are rare in Brazil and globally. Typically, studies assess mortality retrospectively, collecting information some time after a fire event [46]. Conversely, in North America and Europe, abundant research exists, especially on prescribed fires for large forest fire control [47, 48]. In Brazil, post-fire studies are mainly conducted in Cerrado and Amazon regions [13, 14, 35, 38, 49–55].

The fate of plants after forest fire impact depends on heat-induced injuries, with outcomes being either survival or death [56]. Fate correlates directly with morphology (plant architecture), physiology, and fire behavior [55, 57]. Predicting post-fire mortality is challenging due to the complex interactions involved [37, 58, 59]. Key factors include canopy burning, stem burning, and root heating [60]. Lethal burning occurs when heat flux raises temperatures above 60°C for one minute [56, 61]. There is a direct relationship between bark consumption, flame height, fire intensity, crown and stem burn ratio/height, and plant mortality [37, 62].

Canopy burning results from convective smoke heat energy and radiation heat energy, causing necrosis of branches, leaves, and buds, measurable in height and proportion [37, 63]. Stem burning, caused by radiation and heat conduction, leads to charring or scorching, observed shortly after the fire event and also measured in proportion and height [64]. Severity is typically assessed through variables such as crown burn and stem burn, reflecting the amount of heat energy released by the fire (intensity or fire behavior), which are essential for mortality models [59].

Palms are recognized for their fire resistance in various ecosystems worldwide [65–68]. It is suggested that at least 30% of the species in this family exhibit fire resistance [65]. However, literature addressing this topic is sparse [66, 68]. Based on these concepts and assumptions about palm fire resistance, this study aimed to experimentally investigate the post-fire fate of four understory palm species: *Bactris maraja* Mart., *Chamaedorea pauciflora* Mart., *Geonoma deversa* (Poit.) Kunth, *Hyospathe elegans* (Mart.), and the juvenile phase of *Euterpe precatoria* Mart.

Therefore, the study aimed to: a) compare post-fire responses among each species; b) develop mortality models based on severity variables, distance from the forest edge, and microclimatic factors; and c) assess whether height or stem diameter primarily protects buds from heat flux. Hypotheses were formulated as follows: i) severity significantly influences stem mortality and correlates with one morphological variable (height or diameter); ii) higher stem height mitigates mortality by reducing high temperatures in apical buds; iii) larger stem diameter reduces mortality rates; and iv) higher relative moisture and/or greater distance from the edge positively enhance individual survival.

A noteworthy advancement was made in this study by thoroughly investigating post-fire mortality processes in selected native palm species in the Amazon, employing an innovative methodology that simulates fire on individual plants, targeting specific plants rather than large forest areas.

2. Materials and Methods

The surface fire simulation experiment was conducted on an agro-extractive settlement property in the municipality of Cruzeiro do Sul, in the Alto Juruá Region of Acre State, Brazil (Figure 1). Acre is situated in the extreme southwest of the Brazilian Amazon, between latitudes 07º07' and 11º08' S and longitudes 66º30' and 74ºW. The region experiences a hot and humid equatorial climate (Am type in the Köppen classification), with a dry season lasting approximately four months. The mean annual rainfall is 2,160 mm (ranging from 1,600 to 2,900 mm per year), the mean annual temperature is 26°C, and the relative humidity is 84%. The soil in the area is a typical dystrophic yellow Argissolo, with primary vegetation cover comprising a combination of open forest with palm trees and dense forest [69, 70]. The climatological profile for 2013 indicates typical dry months in July and August, with an atypically rainy September (Figure 2).

The Open Ombrophylous Forest with Palm Trees in the area is characterized by a discontinuous canopy and a significant presence of Arecaceae family representatives, more in species abundance than richness [71]. This physiognomy, predominant in Acre, can be found both in terra firme areas and alluvial terrains, often forming associations with patches of dense forest or sharing territory with open forest with bamboo. In the study area, the canopy is predominantly composed of *Iriartea deltoidea* Ruiz & Pav. and *Oenocarpus bataua* Mart., and *Euterpe precatoria* Mart.

The Arecaceae family has a thermocosmopolitan distribution (between 44ºN and 44ºS) and comprises approximately 2,500 species in 184 genera, making it one of the oldest plant groups on the planet [72, 73]. In the Amazonian flora, there are between 200 and 250 species, with numerous endemics [74-76]. In Acre, 24 genera and 82 species have been recorded, highlighting the region as a hotspot of diversity for this family [71, 77]. *Euterpe precatoria* is distinguished by its presence in open forests, reaching up to 30 meters and forming part of the canopy. The juvenile phase of *E. precatoria* was included in the simulation experiment due to its morphological resemblance to other stiped palms in the study, which inhabit exclusively the understory of the humid forest: *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa* and *Hyospathe elegans*. Generally, these species do not exceed 10 meters in height, exhibit a palm-like growth during their juvenile and adult stages, and often show clonal *ramet* behavior, forming clusters. In the present study, only *E. precatoria* and *Geonoma deversa* do not exhibit this characteristic.

2.2. Phases of the Surface Fire Experiment Simulation

- Phase I (Selection of Individuals): A total of N = 85 individuals from the five species were subjected to the surface fire simulation experiment (Table 1 for description of morphological parameters sampled at this Phase). These individuals were randomly selected along three 600 m parallel transects perpendicular to the forest edge, each separated by 100 m. The following criteria were applied for selection: a) a minimum distance of ten meters between individuals; b) location on flat topography; and c) a maximum height of 2.5 m. Each individual was assigned an identification plate and designated as a sampling unit. Of the five species included in the experiment, for *Euterpe precatoria* only the juvenile phase was considered, thus it was analyzed separately from the set of four understory species.

- Phase II (Surface Fire Simulation Experiment): The simulation experimentally reproduces the heat flux generated by an understory fire on a reduced and individualized scale (Table 1 for variables description). The parameters used for the simulation outline a surface fire with a maximum height of 30 cm, an intensity of 50 kW m-1, and a maximum temperature of 760°C, with a propagation speed ranging from 0.1 to 0.35 m min-1 [23, 36–39, 78]. Three type K thermocouple sensors (chromel-alumel; maximum sensitivity 1,300 °C) were used to record the time-temperature history (Table 2), connected to a datalogger (Omega® HH140, four channels) - Figure 3a.

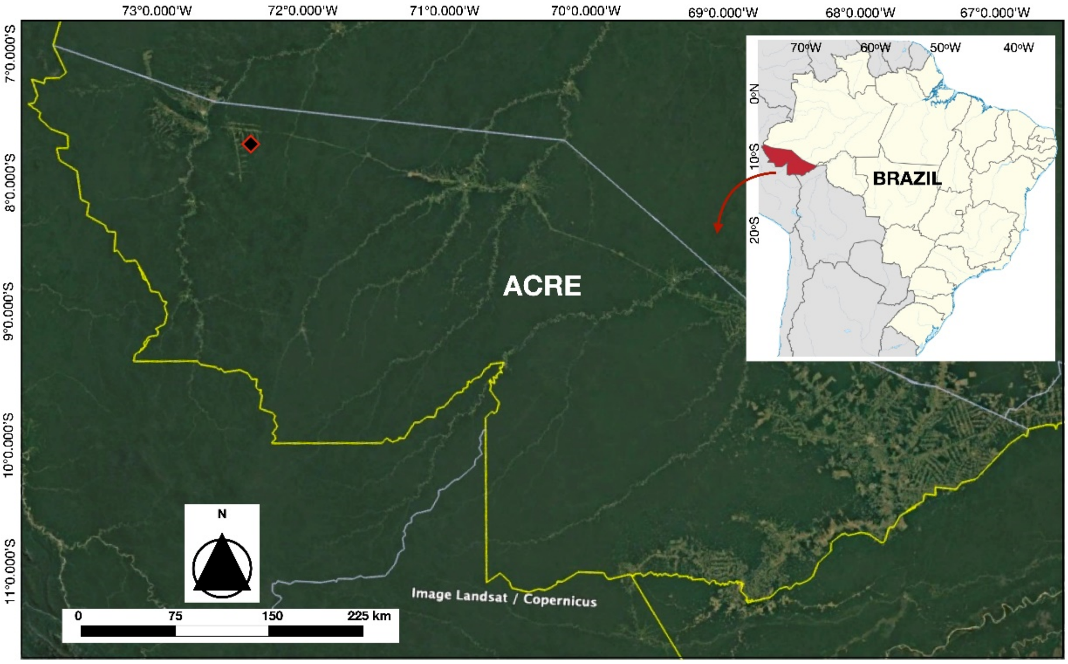


Figure 1. Location map showing the state of Acre in Brazil (right map), and the approximate location of the study area in the western part of the state (black lozenge with a red border) - (7º45′ S e 72º22′ W).

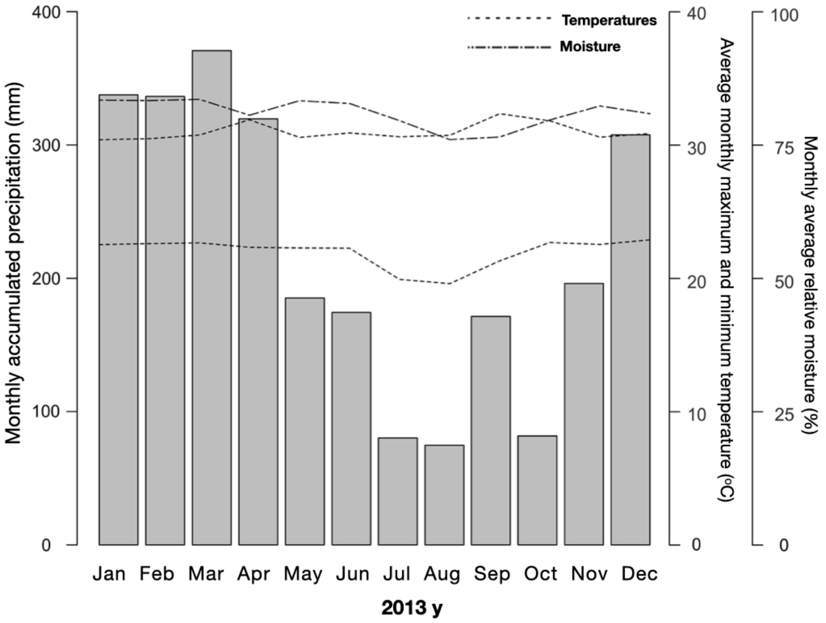


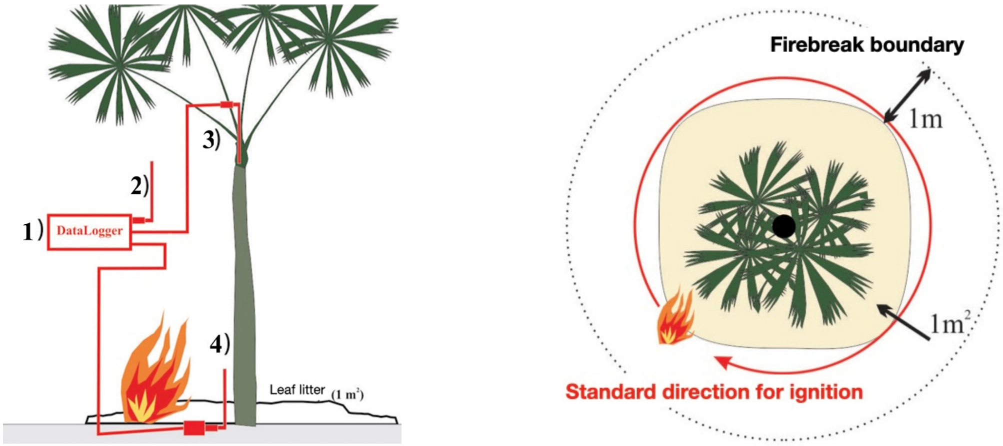
Figure 2. Climatological profile for Acre state, for the period between January and December 2013, with the averages of temperature, moisture, and accumulated monthly precipitation. Source: National Institute of Meteorology database (OMM: 82704).

Table 1. Description of the variables sampled in the three phases of the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. Phase I: pre-fire morphological variables. Phase II: time-temperature history variables and immediate impact. Phase III: post-fire variables measured at each post-fire survey (see text).

Phases	Parameters	Unit	Acronym	Description
Phase I	Total height	m	HT	From the ground to uppermost leaf
	Leaf length	cm	LENG	From the petiole base to the apex
	Stipe diameter at ground level	cm	DS	At the base of the palm stipe
	Stipe height	cm	SH	Soil to base of leaf sheaths
	Number of leaves	Number	NL	Count of healthy leaves
	Distance from the edge	m	DIST	Orthogonal to the forest edge
Phase II	Ambient temperature	°C	TAMB	Continuous record
	Simulation Average temperature	°C	TMED	360 s interval
	Simulation Minimum temperature	°C	TMIN	360 s interval
	Simulation Maximum temperature	°C	TMAX	360 s interval
	Simulation ∑ of temperatures	°C	SUMT	Sum of values in 360 s interval
	Simulation Average 150 s	°C	MED150	150 s interval average (flare phase)
	Simulation ∑ of temperatures 150 s	°C	SUM150	Sum of values in 150 s (flare phase)
	Bud Average temperature	°C	TMEDG	Average inside the bud in 360 s
	Bud Maximum temperature	°C	TMAXG	Maximum temperature inside the bud/360 s
	Bud ∑ of temperatures	°C	SUMTG	Inside bud temperatures at 360 s
	Bud Maximum increment	°C	INCMAX	TMAXG - TAMB
	Bud Average increment	°C	INCMED	TMEDG - TAMB
	Bud time of maximum temperature	s	IGMAX	Between ignition and maximum temperature inside the bud
	Burned leaves on that day	%	PCF	Burned leaves/ NL x 100
Phase III	Complete burned leaves	Number	FC	Leaf coloration other than green
	Partial scorched leaves	Number	FP	Leaf lamina with partial discoloration
	Scorched leaves	%	PQF	FC + ½ FP/ NL x 100
	Complete canopy scorched	%	CNSCAR	PCF + PQF
	Stipe scorched height	cm	STSCARH	Base to the uppermost carbonized portion
	Stipe scorched proportion[a]	%	STSCAR	STSCARH / SH x 100
	Resprout[b]	Number	REB	Number of basal resprouts
	Regrowth	cm	RECR	Height of apical regrowth
	Resprout height	cm	HREB	Height of highest basal resprout
	Failed resprout	-	RFAL	Failed basal resprout or regrowth

Final fate^{c}	-	FATE	Stipe: (1) dead; (0) alive

(a) Always checked at the first inspection, i.e., up to one week post-fire. b)Basal resprout starts at the base of the plant - new ramet, while regrowth is apical. However, there may be both cases in the same individual, so we consider basal + apical regrowth as separate variable. c)Mortality is understood in this work as "topkill", in other words, mortality of the stipe (palm stems).



(**a**) (**b**)

Figure 3. Schematic of the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. (**a**) Temperatures recording method: 1) four-channel datalogger; 2) sensor TK1 ambient temperature; 3) sensor TK2 of the plant apex (inside the bud); 4) sensor TK3 of the plant base: 10 cm above ground and 5 cm from the stipe surface; (**b**) Top view with the 1m^{2} burning area; the 1m circular limit of the safety firebreak boundary and the pattern for ignition of the fire.

Table 2. Description and location of the K thermocouple sensors (chromel-alumel; maximum sensitivity 1,300^{o}C) used in the Phase II of the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.

Thermocouple number	Description
TK1	For continuous sampling of the ambient temperature, positioned 3 m away from the experiment.
TK2	For temperature sampling in the central meristematic apex of the plants, inside the bud, with the sensor tip positioned at a depth not exceeding 5 cm.
TK3	For recording the temperature at the base of the plant, partially buried, with its tip 10 cm above the ground and one centimeter from the surface of the plant stipe.

Before the burning, partial thinning of the vicinity was conducted for safety reasons. A 1 x 1 meter area of burlap was placed near the base of the plant, bordered by a 1-meter wide circular safety firebreak boundary, and combustion was initiated using standardized kerosene ignition (20 ml per individual) (Figure 3b).

The interval between temperature recordings was set at 1 second, with a maximum recording period of 360 seconds to cover ignition, flame, smolder, and extinction phases. If the fire was not fully extinguished within this period, it was manually extinguished. All sensors featured mineral insulation and a three-meter long K extension cable (ANSI MC 96.1 standard). The experiment adhered to safety protocols for controlled burning, included the use of Personal Protective Equipment (PPE), water, and manual fire beaters. The burns were conducted during the Amazon dry season, between August and September 2013, from 11:00 am to 5:00 pm.

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The environmental parameters of the microclimate in the study area were obtained during Phase II using 36 HOBO® sensors distributed randomly across the area. Each sensor recorded data on air temperature, maximum air temperature, relative humidity, maximum relative humidity, and soil temperature (sensor buried in the soil at a depth of 3 cm). Wind speed was measured three times a day, and the leaf litter depth was measured once for each individual prior to burning (Table 3). These variables serve as parameters for comparison with drier year conditions.

- Phase III (Collection of post-fire impact and severity data): The condition of palm individuals was assessed on at least three occasions following the fire, with the first survey conducted within two weeks of the experiment (Table 1 for parameters description). The interval between subsequent surveys varied (1st survey: 2 ± 4 days, n = 28; 2nd survey: 8 ± 9 days, n = 28 + 20 new individuals; 3rd survey: 36 ± 17 days, n = 48 + 37 new individuals; 4th survey: 85 ± 17 days, n = 85; 5th survey: 145 ± 17 days, n = 85).

Table 3. Mean values of environmental parameters obtained for the period (Midday 12:00 am to 5:00 pm) of the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.

Parameters	Average	Unit
Air temperature	27,1 ± 2,1	°C
Maximum air temperature	29,2 ± 3,2	°C
Moisture	73 ± 11	%
Maximum moisture	81 ± 13	%
Wind speed	0,0 to 0,3	m s^{-1}
Soil temperature	24,1 ± 9,2	°C
Leaf litter depth	6 ± 2	cm

2.3. Statistical Analysis

The time-temperature history was assessed for variance in relation to the sample units using normality tests (Kolmogorov-Smirnov) and homoscedasticity tests (Bartlett), followed by analysis of variance (one-way ANOVA). Possible relationships between: (a) the independent time-temperature history variables (TMED, TMAX, SUMT, MED150, SUM150); (b) the fire severity variables (PCF, STSCARH, STSCAR, PQF, CNSCAR); and (c) the dependent temperature variables measured at the center of the apical bud (TMEDG, TMAXG, SUMTG, INCMAX, INCMED), were explored using simple linear regressions.

The individual probability of post-fire mortality for the four understory species and *Euterpe precatoria* was modeled using binary logistic regression (1 for death or regrowth; 0 for survival) [79]. The logistic function was used to convert the linear combination of dependent variables into probabilities. All fire severity variables (CNSCAR, STSCAR) and morphological variables (DS, SH) were included as independent variables. Initially, the models were generated with the independent variables modeled individually, followed by interactions relevant to biological explanations. Through generalized linear model analysis (binomial GLM), independent variables were included in each regression model when statistically significant ($p < 0.05$), using the 'stepwise selection' method. Correlations between variables were examined *a priori*, and when Spearman's test values for the correlated pair exceeded 0.5, only one of the variables was chosen for the model. To explore the influence of the edge microclimate on mortality, models were also generated consisting of the orthogonal distance from the edge to the individual and the minimum relative moisture values obtained on the day of each experiment (Figure 4).

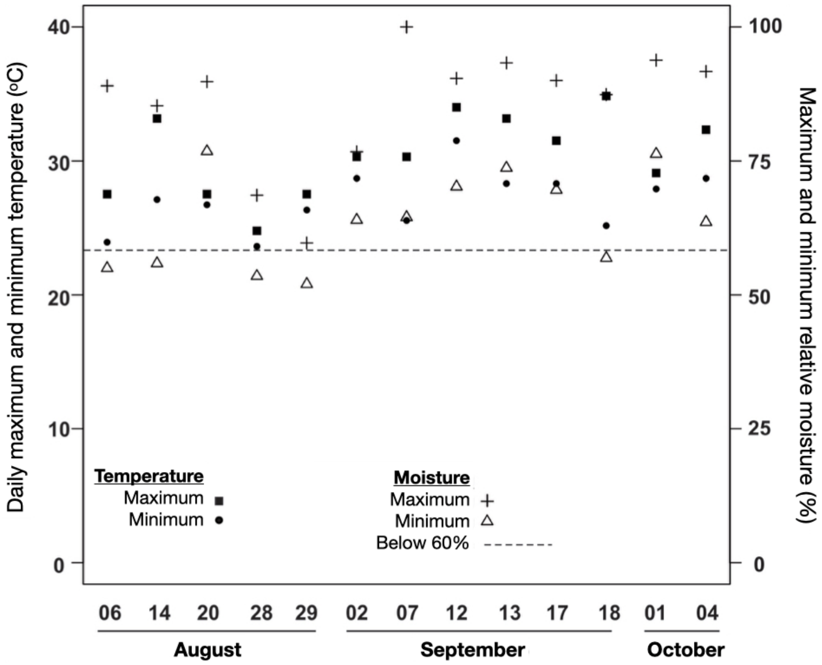

Figure 4. Microclimatic data measured near the sampling units on the days of the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil, in August, September and October 2013. Values refer to the midday period: between 11:00 am and 5:00 pm.

The different significant models were compared using the Bayesian theoretical approximation technique: Akaike's Information Criterion (AIC). The ΔAIC, similar to the -2 log likelihood, is also adopted for comparison. The lowest AIC value was used to select the most parsimonious final model among the generated models [80]. To test the fit of the data and the performance of the model as a predictor of individual mortality, three test criteria were adopted: (a) likelihood ratio statistics, comparing the generated model to the null (with only the intercept) using the χ^2 test; (b) Nagelkerke's pseudo R^2 value, considered equivalent to the R^2 coefficient of determination for linear models; and (c) the area under the ROC (Receiver Operating Characteristic) curve: Operator Sensitivity Curve [79, 81]. The ROC curve is a non-parametric technique that tests the performance of a binary model independently of the isolated effects of the variables. The area under the curve ranges from 0.5 (no predictive ability) to 1 (perfect predictive ability). Models with values between 0.7-0.9 are considered good, with values greater than 0.9 indicating high accuracy for probability prediction. Statistical analysis was conducted in R 3.0.3 (R Development Core Team) using the packages stats 3.0.3 and rockchalk 1.8.0.

3. Results

Post-fire mortality varies among species, and for all species, the larger the diameter of the base of the stipe, the lower the mortality. Additionally, the mortality of *Euterpe precatoria* and the other four species in the experiment is strongly influenced by the pattern of canopy burning. The probability of mortality increases in proportion to the extent of leaf burning. Temperature at the apical bud is variable; however, it does not explain the mortality of the stipes. Stipe height and total height of the individual do not influence mortality. In explaining post-fire mortality, the variation in morphology among species (Table 4) appears to be more important than the amount of heat flux applied to each individual involved in the experiment, as no significant difference was observed in the time-temperature history measured.

Table 4. Palm species characterization (ARECACEAE, subfamily ARECOIDEAE) sampled in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil (total individuals: N = 85). n: number of individuals per species. Morphological characteristics listed in Table 1. DS: stipe diameter at ground level; NL: number of leaves; LENG: leaf length. Averages ± standard deviation.

Species	**n**	**DS (cm^{-1})**	**Total height (cm^{-1})**	**Stipe height (cm^{-1})**	**NL**	**LENG (cm^{-1})**
Bactris maraja Mart.	14	1,8 ±0,3	221 ±76,4	122 ±44,2	6 ±2	144 ±46,2
Chamaedorea pauciflora Mart.	9	1,9 ±0,7	145 ±50,0	84 ±75,7	7 ±2	79 ±17,7
Geonoma deversa (Poit.) Kunth	12	2,4 ±1,3	205 ±131,8	106 ±81,0	11 ±4	85 ±30,1
Hyospathe elegans Mart.	25	1,9 ±0,4	201 ±81,2	124 ±43	8 ±2	85 ±13,3
Euterpe precatoria Mart.[a]	25	3,6 ±1,4	268 ±64,7	115 ±58,2	4 ±1	182 ±40,5

(a) Only individuals in the juvenile stage were sampled, up to 2,5 m in stipe height.

3.1. The heat flux at each individual base was applied equally

The heat flux distribution of the time-temperature history measured by the thermocouples (n = 85) did not differ among individuals (Figure 5a, Table 5). The maximum temperature applied to the base of the plants was 727°C, and the maximum value of summation of temperatures in 360s was 70,776°C, and the minimum value of this summation was 12,991°C. The stipe scorched height (STSCARH) was obtained as early as the first week post-fire, and considered the maximum height of stipe carbonization by fire. STSCARH was 122 cm for *Euterpe precatoria* and 100 cm for the other species (Figure 5b). In some individuals the stipe was entirely charred after fire, and in these cases, the stipe scorched proportion (STSCAR) was 100%.

The estimator total leaf loss, complete canopy scorched (CNSCAR) is the final result of the sum of leaf consumption on the day of the experiment with the proportion of burned leaves in the five subsequent visits, adding leaves with totally burned limb and partially burned limb. In some cases, when leaves fell horizontally to the ground, they were quickly consumed by the fire upon contact, resulting in complete combustion. Canopy was complete scorched for 81% of the individuals after ~144 days of the experiment. Those with total leaf loss of less than 70% that did not resprout were classified as fire survivors.

Table 5. Analysis of variance of the time-temperature history obtained with TK3 sensor, during the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil, for n = 85 individuals. Recording interval is 360 s, immediately after ignition; leaf litter fuel in 1 m^2 area. $p < 0.05$.

Time -Temperature History	**Average (±Std. Dev)**	**D.f.**	***F***	***p***
Maximum (°C)	437 ±175	4,80	0,370	0,829
Average (°C)	112 ±35	4,80	0,110	0,979
Sum (°C)	40.655 ±12.822	4,80	0,110	0,979
Average 150 s (°C)	180 ±65	4,80	0,192	0,942
Sum 150 s (°C)	32.370 ±11.590	4,89	0,192	0,942

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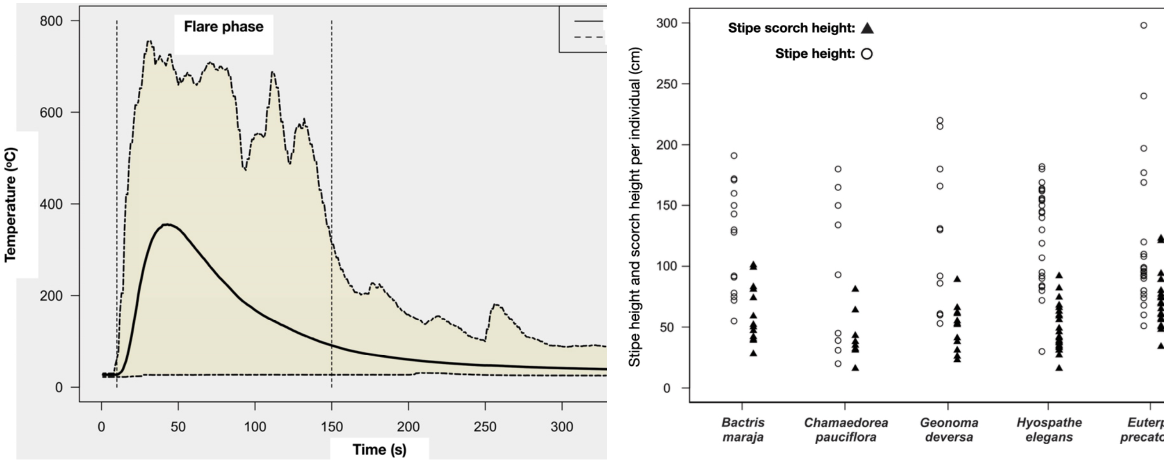


(**a**) (**b**)

Figure 5. (**a**) Time-temperature history measured with the TK3 sensor for all sampled individuals, showing average (TMED) and temperature range, and 150 s interval (flame extinction stage); (**b**) Distribution of stipe heights (SH) and maximum stipe scorched heights (STSCARH), per sampled individual of the five species (n = 85) from the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.

3.2. Temperatures measured at the apical bud vary, but does not explain mortality

As the proportion of burnt stipe increases, more heat energy reaches the bud, by both internal and external conductive influence. Increasing the percentage of the stipe scorched proportion (STSCAR) positively influences the external (conduction of heat through the plume), and internal (conduction of heat through the stipe) heat flow in the bud temperature variation. Maximum temperature increase in the center of the apical bud (INCMAX), for all four species except *Euterpe precatoria* (n = 60), has a linear relationship with increasing proportion of stipe flaring plus increasing sum of temperatures at the base of the stipe (SUMT) ($R^2 = 0.53$; l.g. = 2.50; F = 30.55; $p < 0.001$.) - Figure 6.

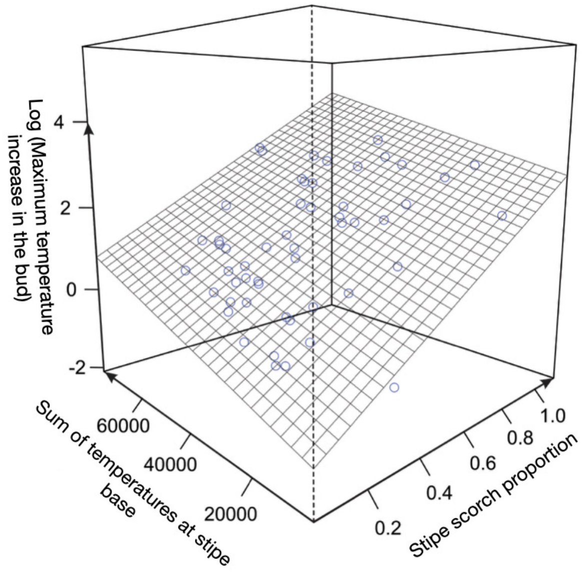


Figure 6. Regression surface of the maximum bud center temperature increment (bud center temperature minus ambient temperature: INCMAX) as a function of stipe scorch proportion and the sum of temperatures at the base of the stipe (SUMT), for *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans* (n = 60). $R^2 = 0.53$; g.l. = 2.50; F = 30.55; $p < 0.001$; during the surface fire experiment in the understory of an Amazonian forest in western Acre, Brazil.

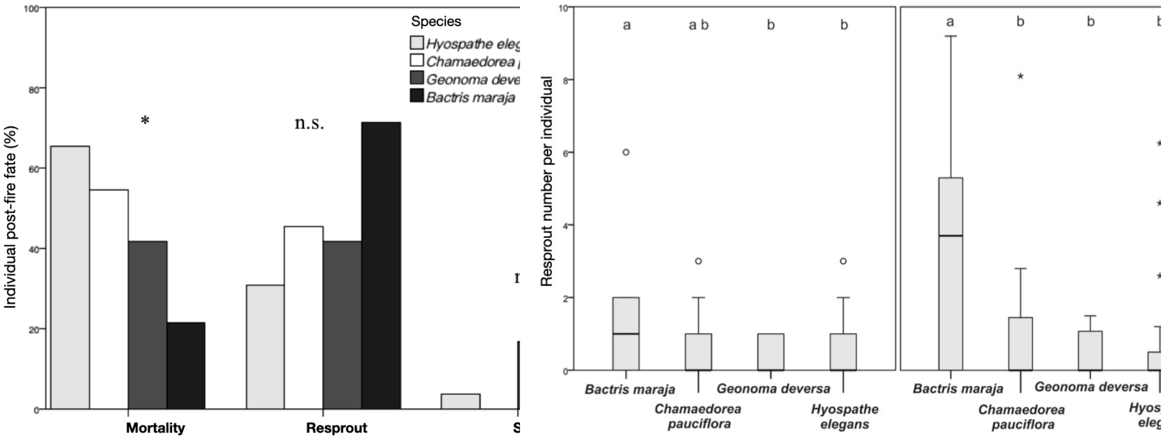
Also the sum of inside bud temperatures (SUMTG) as well as the mean bud temperature (TMEDG) has positive linear relationship with STSCAR + SUMT ($R^2 = 0.48$ for both variables). Among the inside bud temperature variables, the maximum temperature increment is the best fit with respect to the increase in the proportion of stipe firing. However, neither INCMAX, nor the measurements of maximum temperature at the bud (TMAXG), mean temperature at the bud in 360 s (TMEDG), and summation of temperatures at the bud (SUMTG) has a relationship with total leaf burn (CNSCAR) or mortality of individuals, as will be described further.

3.3. Mortality and resprout vary among species, with diameter having a greater influence on mortality than height

The distribution of post-fire mortality varies among understory species (Kruskal-Wallis, H = 8.11; g.l.: 3; *p* = 0.044; n = 60). *Hyospathe elegans* (65%) and *Chamaedorea pauciflora* (55%) are the species with the highest number of stipes lost post-fire. Although *Bactris maraja* has a higher number of regrowing individuals (71.5%) compared to the other species, the difference between the amount of regrowing individuals is not significant (Kruskal-Wallis, H = 6.79; g.l.: 3; *p* = 0.079; n = 60). The same is true for survival (Kruskal-Wallis, H = 2.81; g.l.: 3; p = 0.421; n = 60) - Figure 7a.

With the death of the aerial part, the underground part of all sampled species, except *E. precatoria*, responded positively. After four months of the fire experiment, *B. maraja* had the highest number of basal shoots per individual (total shoots = 20; 1.43 ±1.5 shoots ind^{-1}) and highest height of shoots (34.6 ±27.5 cm ind^{-1}). Both the number of shoots per individual and the average height of shoots varied among species (Kruskal-Wallis, number of shoots: H = 8.1; l.g.: 3; *p* = 0.043; n = 60; height of shoots: H = 12.1; l.g.: 3; *p* = 0.007; n = 60) - Figure 7b.

For all species including *E. precatoria*, the characteristic exerting the greatest influence on stipe mortality is diameter at ground level (DS), not stipe height (Table 6). The total proportion of scorched canopy (CNSCAR) participates together with DS in explaining the mortality of the stipes of *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa* and *Hyospathe elegans* (n = 60). Also for *Euterpe precatoria* (n = 25), CNSCAR plus DS explain the mortality of the stipes (Table 7). For all species, higher DS correlated with lower mortality, whereas stipe height and total height of individuals did not appear as significant variables in any of the tested models. And even though there is a positive influence of the stipe scorched proportion (STSCAR) on the increase in temperature in the apical bud, this temperature in the bud has no relationship with the mortality of the stipes. The non-significant models containing the variables of height and bud temperatures were excluded based on Generalized Linear Model (GLM) analysis.



(**a**) (**b**)

Figure 7. (**a**) Distribution of individuals of *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa* and *Hyospathe elegans* (n = 60) by total post-fire fate. Mortality (total): mortality without resprout + failed resprout mortality. Resprout (total): basal resprout + apical regrowth. Survival (total): remained alive

without resprout. * significant difference in distribution $p < 0.05$, by Kruskal-Wallis test; n.s.: not significant; (**b**) Distribution of the number of resprouts and maximum height of post-fire resprouts per individual for the same species (n = 60) (Letters above the bars indicate significant difference $p < 0.05$), from the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.

Table 6. Logistic regression models for post-fire mortality of *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans* individuals (n = 60) from the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. Models ordered by the lowest value of Δ of AIC. Only significant models are shown, $p < 0.05$.

Model	Variables	-2 Log Likelihood	AIC[a]	ΔAIC[b]	Nagelkerke R^2	ROC area[c]
2	Intercept+DS[d]+CNSCAR[e]	26,082	32,08	0	0,45	0,92
4	Intercept+DS+STSCAR[f]:DIST[g]	28,618	34,61	2,53	0,42	0,78
3	Intercept+DS	33,863	35,86	3,78	0,22	0,81
1	Intercept+DS+STSCAR	31,309	37,30	5,22	0,35	0,79
5	Intercept+DS+STSCAR:RHMIN[h]	31,801	37,80	5,72	0,33	0,78

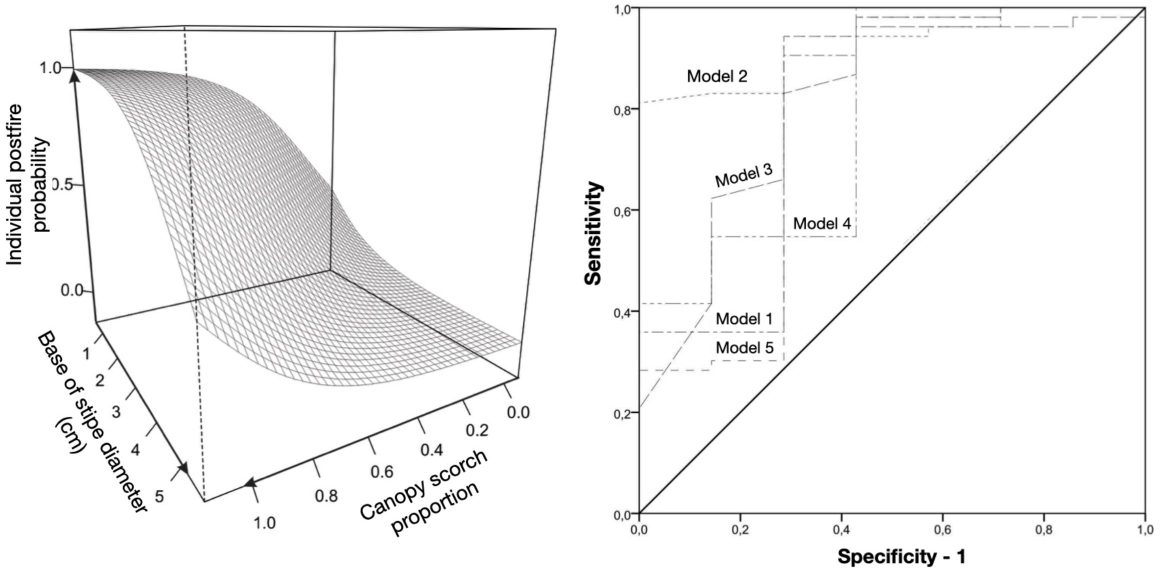
a) Akaike's information criterion; b) Difference between the AIC of the model and the smallest AIC value among the models; c) Area under the Operator Sensitivity Curve (ROC); d) Diameter of the base of the stipe; e) Total proportion of scorched canopy; f) Proportion of the stipe scorched height; g) Orthogonal distance of the individual from the forest edge; h)Minimum relative moisture at the time of individual burning.

Table 7. Coefficients of model 2 of the logistic regression of post-fire mortality of individuals of the species *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans* (n = 60), in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. B: regression coefficient of the model; Wald: Wald statistic values; D.f.: degrees of freedom of each variable in the model; Sig: p values for each model's probability coefficient.

Variables	B	Standard Error	Wald	D.f.	Sig	Confidence Interval 95% Exp(B)	
						lower	higher
Intercept	0,161	2,023	0,006	1	0,937		
Stipe diameter at the ground level (DS)	-1,076	0,497	4,699	1	0,030	0,129	0,902
Canopy scorched proportion (CNSCAR)	4,919	1,978	6,183	1	0,013	2,83	6610

The variables stipe scorched proportion (STSCAR), canopy scorched proportion (CNSCAR), in addition to the orthogonal distance from the sampled individual to the forest edge (DIST), and the minimum relative moisture, representing the microclimate at the time of the experiment (RHMIN), are significant. In the logistic regression using the significant variables from the GLM analysis, for the group of four species minus *E. precatoria*, five models appear as significant in explaining the mortality of the stipes (Table 6). The final model was number 2 and has the lowest AIC (Akaike's criterion): 32.08 and contains the variables canopy scorched proportion (CNSCAR), and diameter at ground height (DS).

An increase in the probability of mortality is conditioned by an increase in the proportion of leaf burn in smaller diameter plants (Figure 8a). The final model is significant when compared to the null model (intercept only) χ^2 (2, n = 60) = 15.75; $p < 0.001$, and the predictive power of this regression is 88%. Analysis of the area under the ROC curve (area of 0.92; Table 6; Figure 8b) reinforces the determination of model 2 as the best fit to the data, with greater power to predict and explain the mortality of individuals of the four species.



(**a**) (**b**)

Figure 8. (a) Post-fire mortality as a function of base of stipe diameter (DS) and canopy scorch proportion (CNSCAR), for the species *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa* and *Hyospathe elegans* (n = 60)($p < 0.05$). (b) ROC curves (Operator Sensitivity Curves) generated for the five models of highest significance in modeling post-fire mortality of individuals of the same species in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil.

The regression equation considering the significant variables in the final model is:

$$\ln\left(\frac{\hat{p}(x)}{1-\hat{p}(x)}\right) = -1{,}076x_{\mathrm{DS}}+4{,}919x_{\mathrm{CNSCAR}} \qquad (1)$$

In calculating the probabilities derived from the equation, it is possible to estimate that for an individual of stipe with 5 cm diameter at the base, the probability of mortality is low (approximately 38%) even with 100% of the leaves affected by fire. For individuals with stipes ≈3 cm in diameter the probability of mortality is already 76% with 100% of the crown burned. For this same diameter but with half of the crown burned, the probability of death drops to 21%. In stipes close to 1 cm in diameter, the probability of mortality is always greater than 50%, regardless of the canopy burning conditions - Figure 9.

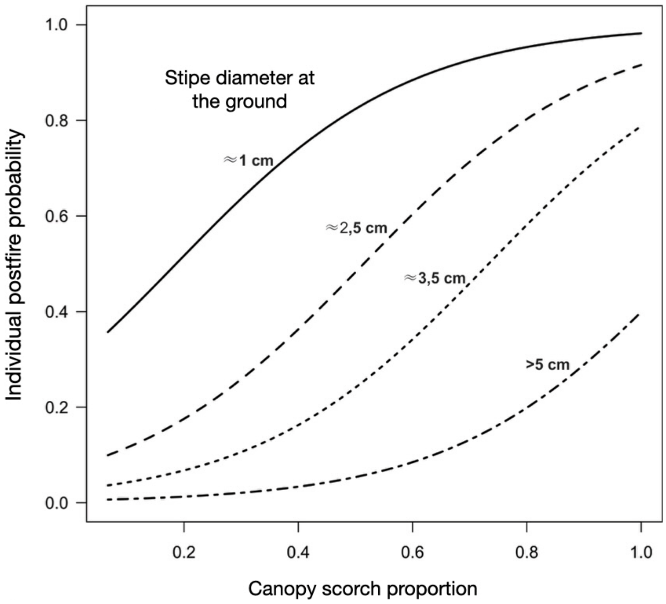


Figure 9. Adjusted curves of the individual probability of mortality as a function of the canopy scorch proportion (CNSCAR) and of four levels of diameter at ground height (DS), of the species *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa* and *Hyospathe elegans* (n = 60), in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil ($p < 0.05$).

3.4. Euterpe precatoria mortality is defined by canopy scorch impact

Also for *E. precatoria*, canopy scorched proportion plus diameter of the base of the stipe are determinants of mortality of individuals. Other variables do not appear significant in the model construction and the final model is significant against the null (only the intercept) when $\chi^2(2, n = 25) = 16.75$, $p < 0.001$. This final model has 88% of the power to predict mortality and an AIC (Akaike's criterion) of 21.9 (Table 8). For mortality estimation of *E. precatoria* the logistic regression equation (Table 9) is:

$$\ln\left(\frac{\hat{p}(x)}{1-\hat{p}(x)}\right) = -1{,}241x_{DS} + 5{,}712x_{CNSCAR} \tag{2}$$

This means that for an increase from 2 to 6 cm in diameter at the base of the stipe, considering an individual with 100% of burned leaves, the chance of mortality falls from 97% to only 15% respective to the diameter. On the other hand, with the canopy with only half of the leaves burned, this same ratio of 2 to 6 cm in diameter of the stipe, increases from 83% to 1%, respectively, of probability of death (Figure 10).

The final model that considers the proportion of scorched canopy (CNSCAR) is superior in quality of fit than the one that considers the proportion of stipe scorched height (STSCAR) as predictor. Although both are significant, model 2, with the CNSCAR variable has higher area under the ROC curve (Table 9): 0.90, higher than the 0.70 that means a good model fit for predicting *Euterpe precatoria* mortality.

Table 8. Logistic regression models for mortality of *Euterpe precatoria* individuals (n = 25), in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. Models ordered by the smallest value of Δ of AIC. Only significant models are shown, $p < 0.05$.

Model	**Variables**	**-2 Log Likelihood**	**AIC**[a]	**Δ AIC**[b]	**Nagelkerke R²**	**ROC area**[c]
2	Intercept +DS[d]+CNSCAR	17,90	21,9	0	0,65	0,90
1	Intercept+CNSCAR[e]	22,84	24,9	3	0,69	0,81
3	Intercept +DS+STSCAR[f]	25,61	29,6	7.7	0,40	0,88

a)Akaike's information criterion; b)Difference between the AIC of the model and the smallest AIC value among the models; c)Area under the Operator Sensitivity Curve (ROC); d) Diameter of the base of the stipe at ground; e)Proportion of scorched canopy; f) Stipe scorched proportion.

Table 9. Coefficients of model 2 of the logistic regression of post-fire mortality of *Euterpe precatoria* individuals (n = 25), in the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil. B: regression coefficient of the model; Wald: Wald statistic values; D.f.: degrees of freedom of each variable in the model; Sig: p values for each model's probability coefficient.

Variables	**B**	**Standard Error**	**Wald**	**D.f.**	**Sig**	**Confidence interval 95% Exp(B)**	
						Lower	**Higher**
Stipe diameter at the ground level (DS)	-1,241	0,511	5,889	1	0,015	0,106	0,788
Canopy scorched proportion (CNSCAR)	5,712	2,215	6,649	1	0,010	3,936	23257

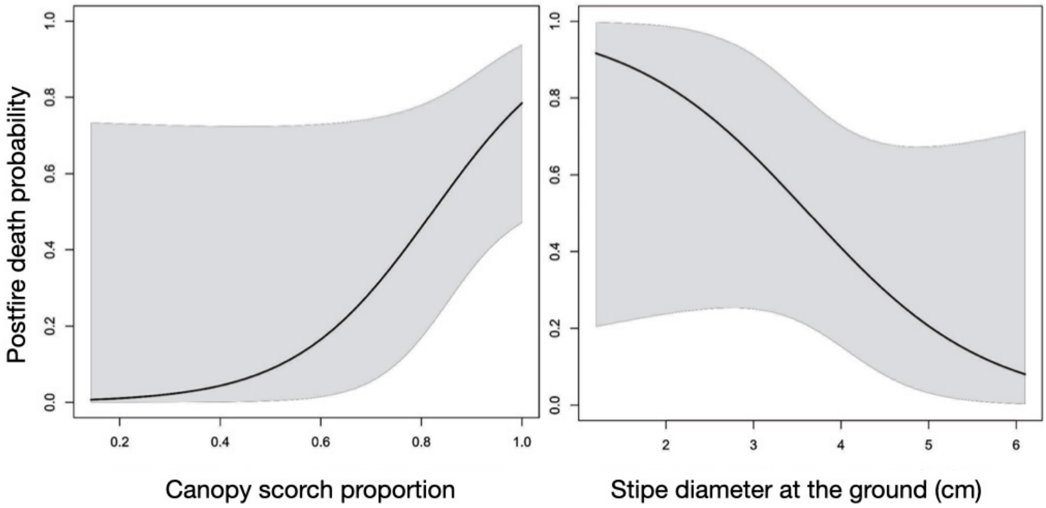
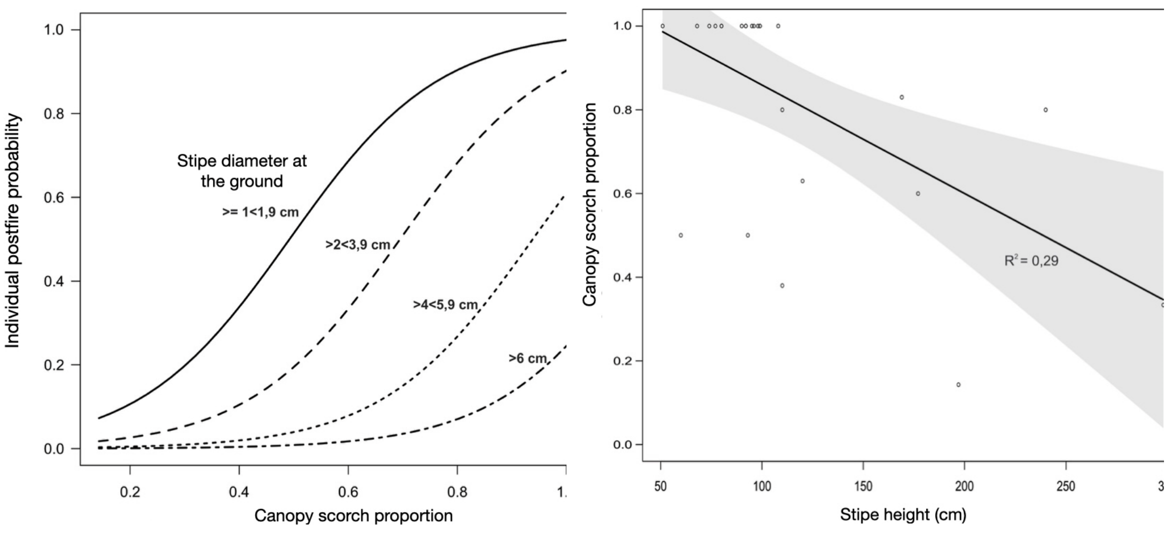


Figure 10. Partial probabilities of mortality as a function of canopy scorch proportion (CNSCAR), and diameter at the ground level (DS), for the species *Euterpe precatoria* (n = 25), four months after the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil ($p < 0.05$). Dark area refers to confidence intervals. .

Graphical analysis shows that at smaller diameters, diameter contributes minimally to the probability of mortality (Figure 11a). As the total proportion of scorched canopy is low, these same smaller diameters will have the highest probability of mortality, which will increase conditioned by the proportion of the canopy scorched, until a cut point near 4 cm diameter. At this point, even with high rates of leaf burning, the probability of death can be reduced by half. Those individuals that have the largest diameter at ground level (above 4 cm) and that still have part of the canopy unburned will survive.

Stipe height has some influence on the proportion of leaf burn. The higher the lower part of the leaf canopy (as measured by the height of the stipe or height of the base of the leaf lamina), the lower the proportion of burned leaves ($R^2 = 0.29$; F1,23 = 11.24; n =25; $p = 0.002$) - Figure 11b. Although significant in protecting leaves from heat flux, neither stipe height nor total plant height are significant variables in the overall model and regression models that explain the mortality of the species.

E. precatoria does not regrow from the base like the other understory species sampled in this work. However, apical regrowth was verified, that is, the regrowth of the apical apex, which was accounted for when there were no more than 30% of green leaves in the canopy. In any case, the apical regrowth for this species started even when there were more than 30% of leaves in the canopy. Seven individuals responded to fire and leaf loss with apical regrowth (28%, n = 25), but only four of the 25 individuals sampled maintained apical regrowth up to four months post-fire (16% of individuals). No variable was found to significantly explain apical bud regrowth in *E. precatoria*.



(**a**) (**b**)

Figure 11. (**a**) Adjusted curves of individual mortality probability as a function of the proportion of canopy scorched (CNSCAR), and of five intervals of diameter at ground level (DS): ≥ 1 < 1.9 cm, > 2 < 3.9 cm, > 4 < 5.9 cm and > 6 cm, for *Euterpe precatoria* species (n = 25) ($p < 0.05$); (**b**) Linear regression between the total proportion of canopy scorched (CNSCAR), and the height of the *Euterpe precatoria* stipe (n = 25), four months after the surface fire simulation experiment in the understory of an Amazonian forest in western Acre, Brazil ($p < 0.05$).

4. Discussion

4.1. Fire and stipe survival

Post-fire plant survival is a recognized indicator of fire intensity, demonstrated by direct correlations between fire severity and mortality [26, 36, 45, 58]. The present study addressed the limitations of this descriptor [26] by conducting an immediate post-fire assessment within one week of the event. Understanding survival as a measure of severity in a broader context, modeling survival and mortality is crucial for predicting future ecosystem changes [37, 58, 82]. Predictive models based on logistic regression serve as powerful tools for modeling post-fire mortality events [83]. These models are also employed in predicting mortality from other disturbances, such as wind [84] and natural mortality [85].

In this study, the models developed—both the general model for understory palms and the specific model for *Euterpe precatoria*—effectively predicted the mortality of these small-diameter palms when tested interchangeably and independently for each species. While it was anticipated that mortality would correlate with the extent of stipe burning, findings suggest that height plays a more significant role in mortality [49, 86, 87], contrary to expectations. Diameter emerged as the most critical morphological trait influencing post-fire plant mortality [37, 82, 88, 89], with its relationship to crown burn helping to explain how understory palms succumb to fire.

Two primary hypotheses explain post-fire plant mortality, focusing on the immediate effects of burning (1st order processes). One hypothesis emphasizes heat flux, the duration of heat exposure, and critical temperatures [90], causing necrosis of cambium cells [34 for a review]. The other hypothesis highlights the impact on conductive tissues, rather than cambium, disrupting phloem conductivity due to heat flux from surface fires, affecting solute viscosity and functional tissue area [91].

Results indicate vertical heat transfer from the base to the apex of the plant, with some individuals experiencing a maximum temperature increase (maximum bud center temperature minus ambient temperature) of up to 30°C. In certain cases, bud center temperatures approached 50°C, potentially lethal for buds; however, some individuals showed bud regrowth despite temperature fluctuations (up to 30°C), indicating continued metabolic activity and survival. None of the bud temperature variables were significant in explaining mortality.

The relative importance of severity variables such as stem burn or canopy burn varies widely in the literature [37, 92], with much research focused on temperate forest species. While canopy burning is often associated with bud death in studies assuming individuals are populations of meristems [37, 93], this study did not confirm this. Even with over 70% of the canopy burned, sampled palms showed regrowth of meristematic apices, indicating minimal damage from heat flux at the base. Modeling canopy burn as indicative of bud death may not apply uniformly to monocotyledonous trees compared to dicotyledons.

The concept that greater diameter offers greater protection against fire holds true for small-diameter palms as well. Until now, no research has addressed experimental mortality of individuals < 10 cm in diameter in the Amazon. While it is understood that diameter is crucial for protection in dicotyledons, no studies have focused on palms. However, drawing a physiological parallel between palms and dicotyledons regarding diameter-influenced mortality requires addressing the anatomical structures of these two large groups. In woody dicotyledons, heat transfer is impeded or reduced by various histological barriers from the outside to the inside of the plant: phellem, phellogen, phelloderm, parenchyma, phloem, until reaching the cambium—these tissues collectively form the simplified concept of 'bark', which acts as an efficient anti-thermal shield of variable thickness [93].

In palms, the anatomical organization of tissues differs significantly. Bark, as found in dicotyledons, is absent, and the vascular system is organized into vascular bundles without ring tissues. These bundles are surrounded by tissue cells with thickened walls, often associated with abundant sclerenchymatous fibers of high specific hardness [94, 95]. This anatomical arrangement provides palms with an advantage in protecting internal tissues compared to dicotyledons [93, 94].

When palms and dicotyledons are exposed to the same heat flux, the anatomical structure of palms may provide them with a morphological advantage. In this study, individuals with a base diameter near 10 cm survived fire impacts, whereas other studies indicate nearly total mortality for dicotyledons with diameters ~20 cm subjected to fire [14, 35, 96]. To understand the advantage of palm stipe response compared to stems of similar diameter, the physiological processes leading to post-disturbance mortality must be considered.

The death of aerial plant parts under physiological stress is linked to reduced movement of water and nutrients from the soil [58, 91, 97, 98]. Vascular system obstructions reduce water and nutrient movement [34], a phenomenon observed in palms as well [98]. Plant hydraulic failure occurs when transpiration water loss exceeds water uptake by roots [34]. In systems where soil moisture remains at field capacity, vascular system embolism can cause aerial part mortality due to leaf dehydration [34, 36, 97]. As carbohydrate utilization is closely tied to water transport, plant death results from combined carbohydrate support failure and physiological drought, with the time to death dependent on the balance between these processes [91, 97, 99].

The results indicate that mortality of small-diameter palm stipes results from two main processes: 1) leaf heating in the canopy contributing to dehydration; and 2) vascular system disruption due to temperature-induced cell coalescence [34, 99]. Dehydration-induced leaf loss may exacerbate vascular system malfunction, or vice versa, resulting in water stress that impedes leaf recovery and normal physiological function.

Many understory palm species seem capable of regenerating leaves at adequate rates [100]. This suggests that post-fire mortality of the aerial parts in understory palms is primarily due to hydraulic system failure caused by the heat flux from surface fires reaching the stipe bases. To deepen understanding, physiological studies in palms should explore tissue water potential, utilization rates, access to carbohydrate reserves, and their potential links to osmoregulatory failure. Anatomical studies should consider tissue wall adaptations and deformations caused by temperature flux.

By employing a non-avoidance technique in fire ecology, this study advances the controlled use of fire for scientific purposes. By targeting fire specifically to research subjects—here, understory palms—the impact on neighboring plants is minimized, and better control over fire conditions is achieved. Metrics such as flame residence time, temperature peaks, and cumulative temperatures provide more suitable information for studying post-fire mortality than fire intensity alone. Translating fire intensity into fire severity is crucial for understanding fire impacts on ecosystems [26, 88].

4.2. Fire and species resilience

This study demonstrated that understory palms can regrow after fire, though the rate and extent of regrowth vary among species. It was initially anticipated that *Euterpe precatoria* would not regrow due to its lack of clonability, unlike another species within the same genus, *E. oleraceae*. Nonetheless, unexpected regrowth at the apex occurred, suggesting that the sampled bud temperature was insufficient to suppress its activity and indicating a diameter threshold (more than 4 cm for this species) beyond which continued bud growth is possible.

Regrowth is considered a response to fire rather than an indicator of severity [26], analyzed as a species-specific characteristic linked to resilience within the ecosystem. In another study conducted in the Amazon, no significant differences were found between burned and unburned areas sampled three years post-fire for palms with a DBH between 10 and 20 cm [101]. Rapid regrowth of individuals can obscure assessments of post-fire mortality, as observed in the present study. Although there was substantial loss of aerial parts, regrowth was robust for *Bactris maraja* and *Chamaedorea pauciflora*, while *Hyospathe elegans* showed low regrowth and high mortality, with practically no survival.

Despite focusing on a diameter range smaller than most studies (< 10 cm) and assessing only four months post-fire, this study provides insights into the regeneration process through stipe regrowth. Understanding species resilience post-disturbance is crucial given current and projected global climate changes and increased pressure from forest logging [102-104]. Knowledge of species' abilities to recover post-disturbance provides an advantage in predicting their resilience under altered fire frequencies and regimes in the Amazon.

Understory palm species, particularly *Bactris maraja* and *Chamaedorea pauciflora*, may lose their aerial parts due to fire impact, but as indicated by the data, they exhibit significant individual recovery, highlighting species resilience in their environment. Changes in species distribution coupled with post-fire effects have been documented across various ecosystems [62], potentially facilitating the invasion of non-native species [105]. Low resilience observed in *Hyospathe elegans* and particularly in *Euterpe precatoria* suggests an increased risk of population decline for these species in forest edges susceptible to surface fires. The absence of basal regrowth in *E. precatoria* individuals after fire indicates that if the stem dies, the entire plant dies.

The findings are applicable for predicting species mortality under specific topographical and microclimatic conditions. While the study did not establish a direct relationship between mortality and low moisture or proximity to edges, microclimatic changes resulting from recurrent fires at edges or from global climate change [106] may heighten mortality risks and predictions for these species. The study serves as a comparative baseline for potential environmental changes and increased disturbances in ecosystems where these species reside. Further research is needed on tropical forest plant species to better understand species-specific risks and resilience to fire.

5. Conclusions

In conclusion, variable responses to low-intensity surface fires were observed in understory palm species. High stipe mortality was found to be expected, alongside observed regrowth rates, though survival outcomes varied. The proportion of scorched canopy emerged as a critical indicator for predicting stipe mortality across the species sampled in our study. Stipe mortality is primarily influenced by heat at the stipe base, where a larger diameter plays a more crucial role in preventing mortality than stipe height.

The findings underscore the resilience of certain understory palm species, such as *Bactris maraja* and *Chamaedorea pauciflora*, which exhibit robust regrowth following fire events. In contrast, species like *Hyospathe elegans* and particularly *Euterpe precatoria* are faced with significant challenges, with low regrowth rates and higher mortality post-fire. These insights are crucial for understanding the dynamics of fire impacts on tropical forest ecosystems, especially under changing environmental conditions. Further research is needed to refine our understanding of species-specific responses to fire and to inform conservation strategies aimed at preserving the biodiversity and resilience of these ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: Preprints.org, Figure S1. Surface fire simulation images; Figure S2. Basal and apical resprouts (red arrows) of various palm species, four months after being subjected to the impact of experimental surface fire.

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Institutional Review Board Statement: The experiment followed the safety protocol for controlled burning and authorization was obtained through the Environmental Clearance Certificate no. 22/ 2012 from IMAC (Instituto de Meio Ambiente do Acre), ACRE.

Data Availability Statement: The original contributions presented in the study are included in the article, further inquiries can be directed to the corresponding author.

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Conflicts of Interest: The author declare no conflicts of interest.

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