

Article

Revealing the Impact of Understory Fires on Stem Survival in Palms (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, the literature on palm resilience to fire is scant. This study investigates post-fire mortality in four understory palms, namely *Bactris maraja* Mart., *Chamaedorea pauciflora* Mart., *Geonoma deversa* (Poit.) Kunth, *Hyospathe elegans* Mart., and juvenile individuals of *Euterpe precatoria* Mart. (açai palm). The 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 palm stem, with temperature sampling using K thermocouples. The results showed varying mortality rates among species, with a larger palm stem diameter correlating to reduced mortality. Crown burning patterns significantly influenced mortality, especially for *Euterpe precatoria*. The species exhibited diverse regrowth capacities, with *B. maraja* showing the highest number and tallest basal resprouts. The variation in morphology among species appeared 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. This study underscores post-fire plant mortality as a critical indicator of fire severity, essential for understanding its ecological impacts.



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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 [6,7]. Surface fires typically exhibit low-to-moderate heat flux intensity and can exert selective evolutionary pressures [8–11]. While wildfires in tropical forests generally do not visibly damage canopy vegetation, the understory layer often experiences greater severity [12–17].

Anthropogenic ignition is widely recognized as the primary source of fires in modern times [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 the edges heighten susceptibility to subsequent fires, potentially of increased intensity and severity [21–24].

In fire ecology, severity and intensity are independent concepts [9,25,26]. 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].

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 bases of trunks, lower crown leaves, seedlings, and young individuals [32–35]. The first event of a surface fire in the understory can arise following edge formation caused by deforestation. This initial fire tends to have low intensity, as it encounters microclimatic conditions, such as temperature and humidity, that are partially preserved. 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^{-2} in such cases [36–39].

Fire severity determines mortality, with studies primarily focused on tree species; little research has been conducted on the survival of herbaceous, shrub, or other 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 the Cerrado and Amazon regions [14,15,35,38,49–55].

The fate of plants after forest fire impact depends on heat-induced injuries, with the 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 crown burning, stem burning, and root heating [60]. Lethal burning occurs when the heat flux raises temperatures above 60°C for one minute [56,61]. It is plausible that there is a direct relationship between bark consumption, flame height, fire intensity, crown and stem burn ratio/height, and plant mortality [37,62].

Crown 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 and is observed shortly after the fire event, being 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].

Due to their unique vascular system anatomy and the presence of adapted underground organs, 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, the 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 five palm species: *Bactris maraja* Mart., *Chamaedorea pauciflora* Mart., *Geonoma deversa* (Poit.) Kunth, *Hyospathe elegans* (Mart.), and the juvenile phase of *Euterpe precatoria* Mart. These are common caulescent understory palm species,

with stem dimensions considered to be sufficiently relevant for the fire impact experiments pursued in this study.

Therefore, the study aimed to (a) compare the post-fire responses of each species individually; (b) develop models to predict mortality based on factors related to fire severity; and (c) evaluate the relative importance of morphological parameters, such as stem height and diameter, in protecting buds from heat exposure. Hypotheses were formulated as follows: (i) severity significantly influences stem mortality, with higher severity positively correlating with increased mortality, and correlates with one morphological variable (height or diameter); (ii) a higher stem height mitigates mortality by reducing high temperatures in the apical buds; (iii) a larger stem diameter reduces mortality rates, as palms with broader stems maintain vascular flow even in the inner regions, which are more protected from conductive heat exposure; and (iv) higher relative humidity 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). The selection of the area was based on the ease of obtaining burn authorizations and the existence of well-preserved forest areas with a traceable edge age. Acre is situated in the extreme southwest of the Brazilian Amazon, between latitudes $07^{\circ}07'$ and $11^{\circ}08'$ S and longitudes $66^{\circ}30'$ and 74° W. 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 2160 mm (ranging from 1600 to 2900 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).

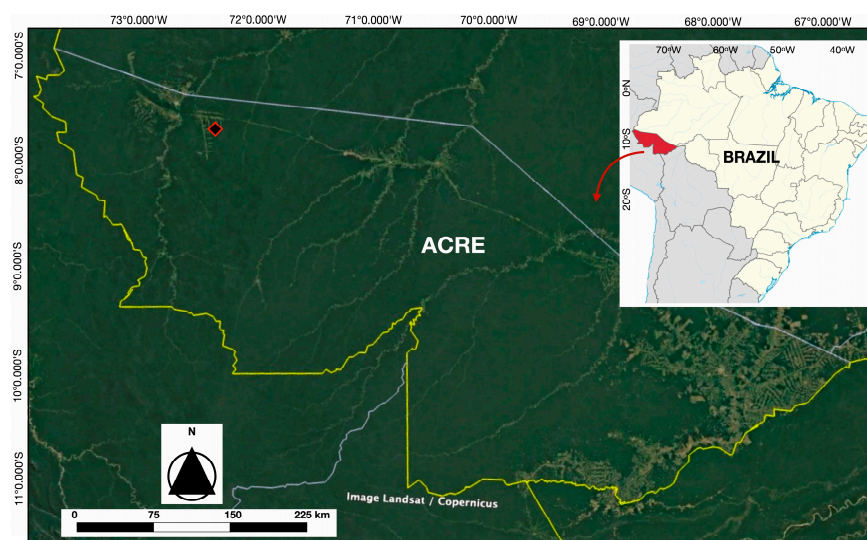


Figure 1. Location map showing the state of Acre in Brazil (right map), and the approximate location of the study area in the western part of the state (black lozenge with a red border)—($7^{\circ}45'$ S and $72^{\circ}22'$ W).

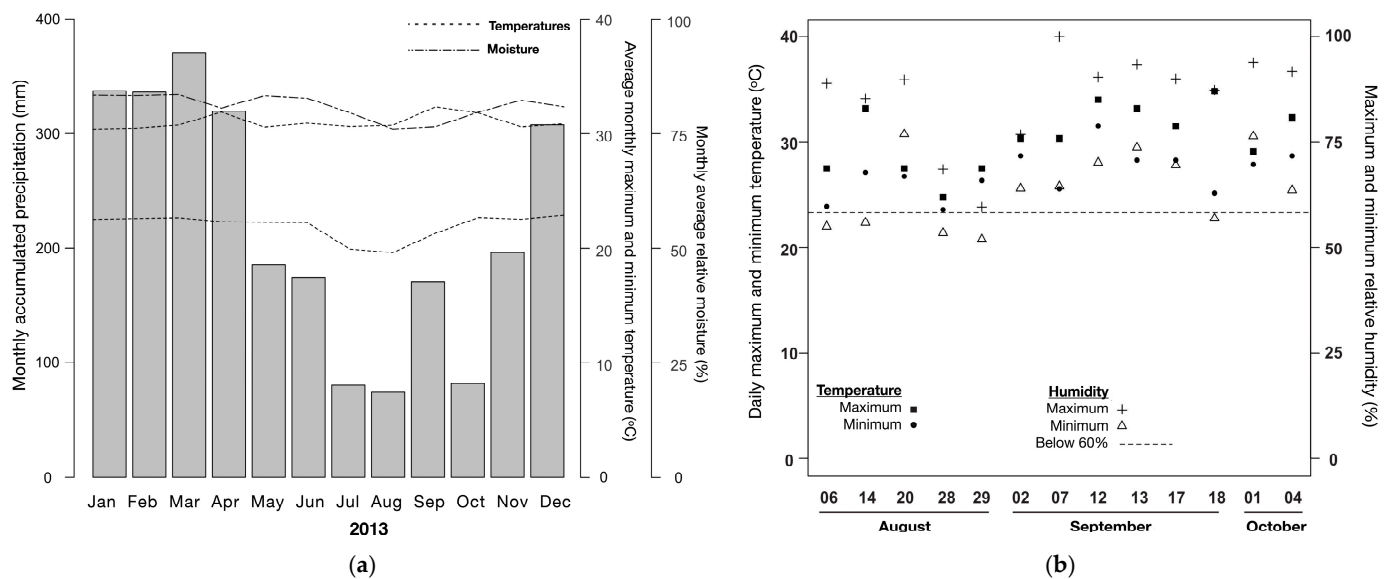


Figure 2. (a) Climatological profile for Acre state, for the period between January and December 2013, with the averages of temperature, humidity, and accumulated monthly precipitation. Source: National Institute of Meteorology database (OMM: 82704). (b) Microclimatic data measured near the sampling 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 a.m. and 5:00 p.m.

The open Ombrophylous forest with palm trees in the area is characterized by a discontinuous canopy and a significant presence of Arecaceae family representatives in greater abundance of individuals than richness [71]. This physiognomy, predominant in Acre, can be found both in upland 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 and Pav., *Oenocarpus bataua* Mart., and *Euterpe precatoria* Mart.

Arecaceae, one of the oldest plant groups on the planet, has a thermocosmopolitan distribution (between 44° N and 44° S) and comprises approximately 2500 species across 184 genera [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 m and forming part of the canopy. The juvenile phase of *E. precatoria* was included in the simulation experiment due to the similarity in stem diameters with those of the other caulescent palms in the study, which inhabit exclusively the understory of the humid forest: *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans*. Generally, these last species do not exceed 10 m 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.

2.1. Phases of the Surface Fire Experiment Simulation

- Phase I (selection of individuals) includes a total of $N = 85$ individuals from the five species of *Bactris maraja* ($n = 14$), *Chamaedorea pauciflora* ($n = 9$), *Geonoma deversa* ($n = 12$), *Hyospathe elegans* ($n = 25$), and *Euterpe precatoria* ($n = 25$) and were subjected to the surface fire simulation experiment (see Table 1 for a 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 (due to the limitations of sensor wire lengths). Each individual was assigned an identification plate and designated as a sampling unit. To maintain similarity between the stem diameters sampled from the five species, 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) included the simulation experimentally reproducing the heat flux generated by an understory fire on a reduced and individualized scale (Table 1 for variables description; Figure S1 for images). 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 1300 °C) were used to record the time–temperature history (Table 2) and connected to a datalogger (TD-890, ICEL, Manaus, Brazil), see Figure 3a.

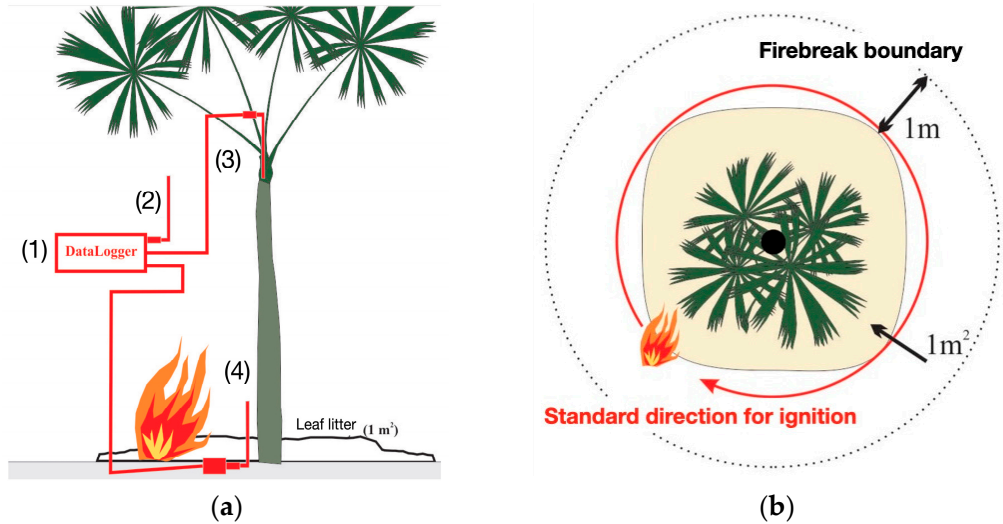


Figure 3. Schematic of the surface fire simulation experiment in the understory of an Amazonian forest in Western Acre, Brazil. **(a)** Temperature recording method: (1) four-channel datalogger; (2) sensor TK1 ambient temperature; (3) sensor TK2 of the plant apex (inside the bud); (4) sensor TK3 of the plant base: 10 cm above ground and 1 cm from the palm stem surface; **(b)** top view with the 1 m² burning area with floor litter; the 1 m circular limit of the safety firebreak boundary (without litter) and the pattern for ignition of the fire.

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
	Stem diameter at ground level	cm	DS	At the base of the palm stem
	Stem 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

Table 1. Cont.

Phases	Parameters	Unit	Acronym	Description
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 Σ of temperatures	°C	SUMT	Sum of values in 360 s interval
	Simulation Average 150 s	°C	MED150	150 s interval average (flare phase)
	Simulation Σ 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 Σ 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
Phase III	Burned leaves on that day ^a	%	PCF	Complete burned leaves/NL $\times$ 100
	Scorched leaves ^b	%	PQF	Number of remaining leaves showing any signs of heat-induced damage/NL $\times$ 100
	Complete crown scorched	%	CNSCAR	PCF + PQF
	Stem scorched height	cm	STSCARH	Base to the uppermost carbonized portion
	Stem scorched proportion ^c	%	STSCAR	STSCARH/SH $\times$ 100
	Resprout ^d	Number	REB	Number of basal resprouts
	Regrowth	cm	RECR	Height of apical regrowth
	Resprout height	cm	HREB	Height of highest basal resprout
	Final fate ^e	-	FATE	Individual: (1) dead; (0) alive

^a Proportion measured immediately after fire extinction, counting leaves that are severely charred or completely burned. ^b Proportion measured in the 1st survey: 2 ± 4 days after fire. ^c Always checked at 1st survey: 2 ± 4 days after fire. ^d 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. ^e The final fate is individual death (mortality total) when no basal resprout or apical regrowth is observed at the experiment end. It also includes individuals with failed resprout, resulting in death.

Table 2. Description and location of the K thermocouple sensors (chromel–alumel; maximum sensitivity 1300 °C, 1 cm maximum cable width) used in 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. The needle-like shape of the sensor tip facilitated its insertion into buds with minimal damage. The variables measured by the sensor in this position during the fire simulation were average temperature, maximum temperature, and cumulative heat flux temperature over 360 s.
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 palm stem.

These parameters, which characterize the behavior of surface fires, can cause damage to understory shrubs, even in small, localized areas. Therefore, the proposed approach was to limit the extent of the fire experimental area to ensure that the damage inflicted mirrors, at least in part, the impact observed in other understory plants [38,43]. Prior to ignition, partial thinning of the understory shrubs surrounding the plants was conducted for safety

reasons. A 1×1 m area of litter was placed around the base of each plant and bordered by a 1 m wide circular firebreak for added protection. Combustion was then initiated using a standardized ignition method, applying 20 mL of kerosene per individual (Figure 3b).

The interval between temperature recordings was set at 1 s, with a maximum recording period of 360 s to cover the 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 [79]). The experiment adhered to safety protocols for controlled burning, including the use of personal protective equipment (PPE), water, and manual fire beaters. The fire simulation experiments were conducted during the Amazon dry season, between August and September 2013, from 11:00 am to 5:00 pm. Post-fire impact assessments began in September and continued through the second week of October.

The environmental parameters of the microclimate in the study area were obtained during Phase II using 36 HOBO[®] sensors (Onset, Bourne, MA, USA) distributed randomly across the area. Each sensor recorded data on air temperature, maximum air temperature, relative humidity, maximum relative humidity, and soil temperature (the 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.

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
Air temperature	27.1 ± 2.1 °C
Maximum air temperature	29.2 ± 3.2 °C
Relative humidity	$73 \pm 11\%$
Maximum humidity	$81 \pm 13\%$
Wind speed	0.0 to 0.3 m s ^{−1}
Soil temperature	24.1 ± 9.2 °C
Leaf litter depth	6 ± 2 cm

- For Phase III (collection of post-fire impact and severity data), the impacts and morphological alterations on palm individuals were assessed on at least three occasions following the fire (Table 1 for parameters description), with the first survey conducted in the first week after the individual fire simulation. On these occasions, the parameters for counting leaves, counting resprouts, regrowth, and other assessments, were carried out. With each new survey, new individuals were added since the burns did not occur simultaneously for all individuals. The intervals between subsequent surveys were as follows: 1st survey: 2 ± 4 days ($n = 28$ individuals assessed); 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 ($n = 85$); and 5th survey: 145 ± 17 days ($n = 85$).

2.2. 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 an analysis of variance (one-way ANOVA). Possible relationships between (a) the independent time–temperature history variables (TMED, TMAX, SUMT, MED150, and SUM150); (b) the fire severity variables (PCF, STSCARH, STSCAR, PQF, and CNSCAR); and (c) the dependent temperature variables measured at the center of the apical bud

(TMEDG, TMAXG, SUMTG, INCMAX, and INCMED) were explored using multiple 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 and 0 for survival or regrowth) [80]. The logistic function was used to convert the linear combination of dependent variables into probabilities. All fire severity variables (CNSCAR and STSCAR) and morphological variables (DS and SH) were included as independent variables. Initially, the models were generated with the independent variables modeled individually, followed by the 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 humidity values obtained on the day of each experiment (Figure 2b).

The different significant models were compared using the Bayesian theoretical approximation technique: Akaike's information criterion (AIC). The Δ AIC, similar to the -2 log likelihood, was also adopted for comparison. The lowest AIC value was used to select the most parsimonious best model among the generated models [81]. 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: the operator sensitivity curve [80,82]. 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 and 0.9 were considered good, with values greater than 0.9 indicating high accuracy for probability prediction. A 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

First, the results of the time–temperature history will be presented. These will be followed by the sampled temperature data for the buds, the post-fire mortality and re-sprout distribution results, and, finally, the mortality modeling outcomes. The variation in morphology among species (Table 4) is presented previously as parameters to be included in the mortality models.

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: palm stem diameter at ground level; NL: number of leaves; LENG: leaf length. Averages $\pm$ standard deviation.

Species	n	DS (cm)	Total Height (cm)	Stem Height (cm)	NL	LENG (cm)
<i>Bactris maraja</i> Mart.	14	1.8 ± 0.3	221 ± 76.4	122 ± 44.2^b	6 ± 2	144 ± 46.2
<i>Chamaedorea pauciflora</i> Mart.	9	1.9 ± 0.7	145 ± 50.0	84 ± 75.7^b	7 ± 2	79 ± 17.7
<i>Geonoma deversa</i> (Poit.) Kunth	12	2.4 ± 1.3	205 ± 131.8	106 ± 81.0^c	11 ± 4	85 ± 30.1
<i>Hyospathe elegans</i> Mart.	25	1.9 ± 0.4	201 ± 81.2	124 ± 43^b	8 ± 2	85 ± 13.3
<i>Euterpe precatoria</i> Mart. ^a	25	3.6 ± 1.4	268 ± 64.7	115 ± 58.2^c	4 ± 1	182 ± 40.5

^a Only individuals in the juvenile stage were sampled, up to 2.5 m in palm stem height. ^b Multi-stemmed species.

^c Single-stemmed species.

3.1. The Heat Flux Distribution of the Time–Temperature History

The heat flux distribution of the time–temperature history measured by the thermocouples ($n = 85$) did not differ among individuals (Figure 4a, Table 5). The maximum temperature applied to the base of the plants was 727 °C. The maximum value of the cumulative sum of temperatures in 360 s was 70,776 °C, and the minimum value of this summation was 12,991 °C. The stem scorched height (STSCARH) was obtained as early as the first week post-fire and considered the maximum height of stem carbonization by fire. STSCARH was 122 cm for *Euterpe precatoria* and 100 cm for the other species (Figure 4b). In some individuals, the stem was entirely charred after fire, and in these cases, the stem scorched proportion (STSCAR) was 100%.

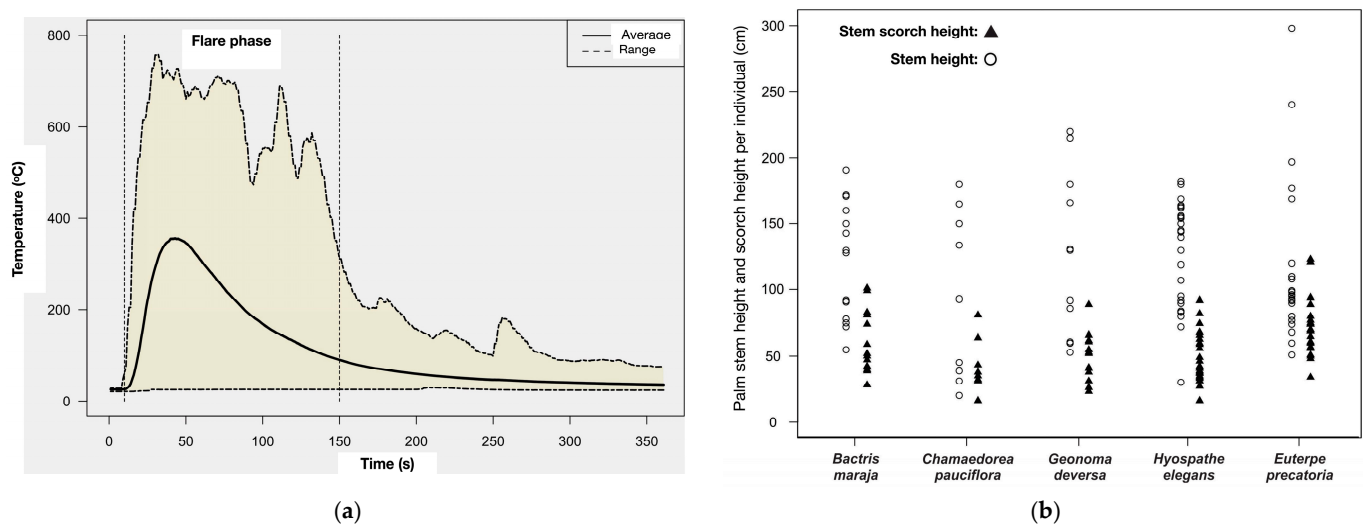


Figure 4. (a) Time–temperature history measured at 10 cm height 1 cm from palm stem for all sampled individuals, showing average and temperature range and 150 s interval (flame extinction stage); (b) distribution of stems heights and maximum stem scorched heights, per sampled individual of the five species ($n = 85$) from the surface fire simulation experiment in the understory of an Amazonian forest in Western Acre, Brazil.

Table 5. Analysis of variance of the time–temperature history obtained at 10 cm height 1 cm from palm stem 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 m² area. $p < 0.05$.

Time–Temperature History	Average ($\pm$ Std. Dev)	D.f.	<i>F</i>	<i>p</i>
Maximum (°C)	437 $\pm$ 175	4.80	0.370	0.829
Average (°C)	112 $\pm$ 35	4.80	0.110	0.979
Sum (°C)	40,655 $\pm$ 12,822	4.80	0.110	0.979
Average 150 s (°C)	180 $\pm$ 65	4.80	0.192	0.942
Sum 150 s (°C)	32,370 $\pm$ 11,590	4.89	0.192	0.942

The estimated total leaf loss, complete crown scorched (CNSCAR) was 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 limbs and partially burned limbs. In some cases, when the leaves fell horizontally to the ground, they were quickly consumed by the fire upon contact, resulting in complete combustion. The crown was completely scorched for 81% of the individuals after ~144 days of the experiment. Those with a total leaf loss of less than 70% that did not resprout were classified as fire survivors.

3.2. Mortality and Temperature Variation in Apical Buds

Temperatures measured at the apical bud varied but did not explain mortality. Increasing the percentage of the stem scorched proportion (STSCAR) positively influenced the external (conduction of heat through the plume), and internal (conduction of heat through the palm stem) heat flow in the bud temperature variation. The maximum temperature increased in the center of the apical bud (INCMAX) for all four species except *Euterpe precatoria* ($n = 60$), which had a linear relationship with an increasing proportion of stem char plus an increasing sum of temperatures at the base of the palm stem (SUMT) ($R^2 = 0.53$; $\text{g.l.} = 2.50$; $F = 30.55$; $p < 0.001$), see Figure 5.

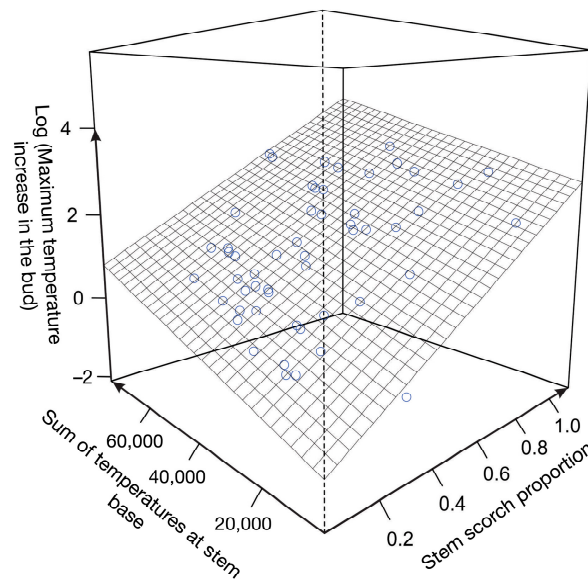


Figure 5. Regression surface of the maximum bud center temperature increment (bud center temperature minus ambient temperature: INCMAX) as a function of palm stem scorch proportion and the sum of temperatures at the base of the palm stem (SUMT), for *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans* ($n = 60$). $R^2 = 0.53$; $\text{g.l.} = 2.50$; $F = 30.55$; $p < 0.001$; during the surface fire experiment in the understory of an Amazonian forest in Western Acre, Brazil.

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

3.3. All Species Post-Fire Mortality and Resprout Distribution

The distribution of post-fire mortality varied among understory species (Kruskal–Wallis, $H = 8.11$; $\text{g.l.} = 3$; $p = 0.044$; $n = 60$), with diameter having a greater influence on mortality than height. *Hyospathe elegans* (65%) and *Chamaedorea pauciflora* (55%) were the species with the highest numbers of stems lost post-fire. Although *Bactris maraja* had a higher number of regrowing individuals (71.5%) compared to the other species, the difference between the amount of regrowing individuals was not significant (Kruskal–Wallis, $H = 6.79$; $\text{g.l.} = 3$; $p = 0.079$; $n = 60$). The same was true for survival (Kruskal–Wallis, $H = 2.81$; $\text{g.l.} = 3$; $p = 0.421$; $n = 60$), see Figure 6a.

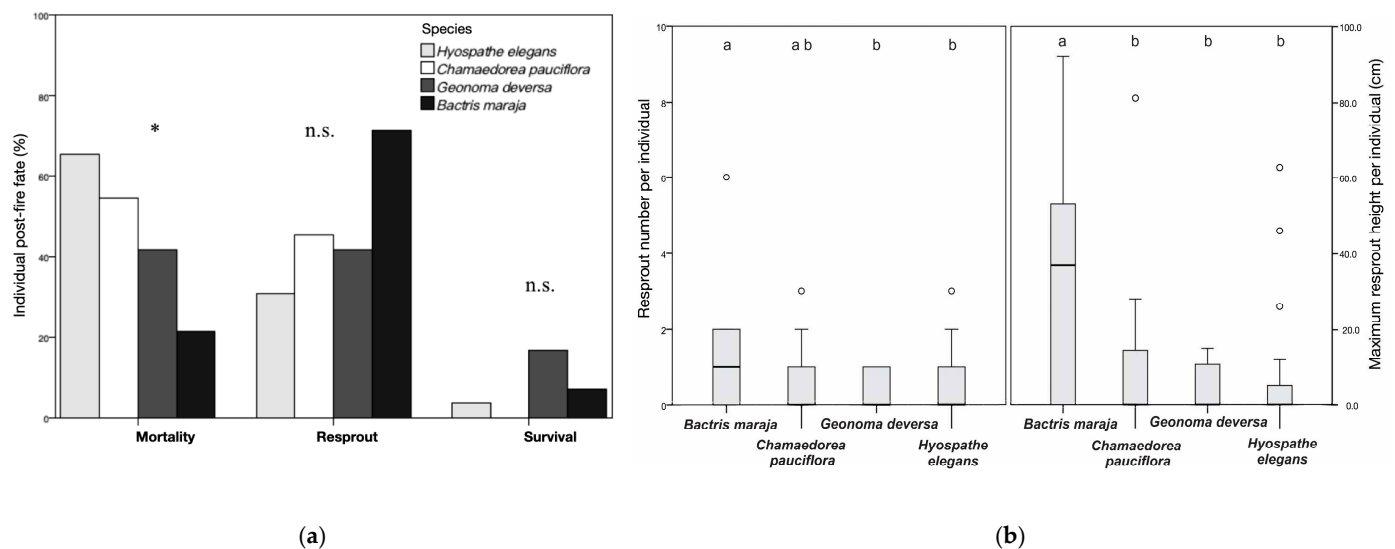


Figure 6. (a) Distribution of individuals of *Bactris maraja*, *Chamaedorea pauciflora*, *Geonoma deversa*, and *Hyospathe elegans* ($n = 60$) by total post-fire fate. Mortality (total): mortality without resprout + failed resprout mortality. Resprout (total): basal resprout + apical regrowth. Survival (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.

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 the 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 6b.

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

The variables stem scorched proportion (STSCAR), crown scorched proportion (CNSCAR), in addition to the orthogonal distance from the sampled individual to the forest edge (DIST), and the minimum relative humidity, representing the microclimate at the time of the experiment (RHMIN), were significant. In the logistic regression using the significant variables from the GLM analysis, for the group of four species minus *E. precatoria*, five models appeared to be significant in explaining the mortality of the palm stems (Table 6). The best model was number 2 and had the lowest AIC (Akaike's criterion), 32.08, and

contained the variables crown scorched proportion (CNSCAR) and diameter at ground height (DS).

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	Δ AIC ^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 palm stem; ^e total proportion of scorched crown; ^f proportion of the stem scorched height; ^g orthogonal distance of the individual from the forest edge; ^h minimum relative humidity 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 all variables in the model was 1; Sig: p values for each model's probability coefficient.

Variables	B	Standard Error	Wald	Sig
Intercept	0.161	2.023	0.006	0.937
Stem diameter at the ground level (DS)	−1.076	0.497	4.699	0.030
Crown scorched proportion (CNSCAR)	4.919	1.978	6.183	0.013

An increase in the probability of mortality was conditioned by an increase in the proportion of leaf burn in smaller-diameter plants (Figure 7a). The best model was 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 was 88%. An analysis of the area under the ROC curve (area of 0.92; Table 6; Figure 7b) reinforced the determination of model 2 as the best fit to the data, with a greater power to predict and explain the mortality of individuals of the four species.

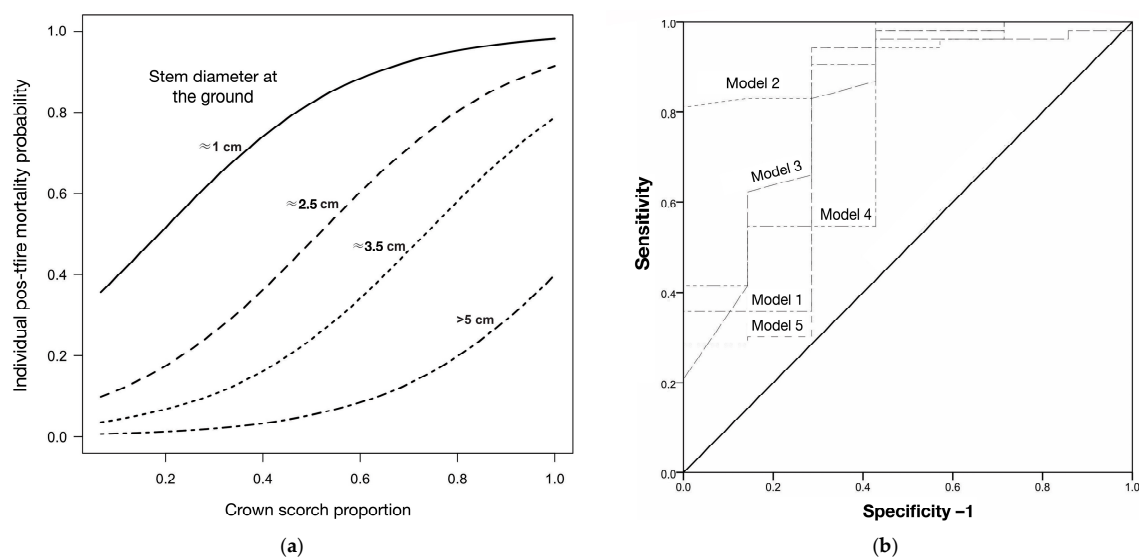


Figure 7. (a) Adjusted curves of the individual probability of mortality as a function of the crown scorched proportion (CNSCAR) and of four levels of diameter at ground height (DS) of the species

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 ($p < 0.05$). (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. A ROC curve plots the true positive rate (sensitivity) against the false positive rate ($1 - \text{specificity}$) and helps interpret the trade-off between true positives and false positives for different threshold values, with a higher area under the curve (AUC) indicating better model performance.

The regression equation, considering the significant variables in the best model, is:

$$\ln\left(\frac{\hat{p}(x)}{1 - \hat{p}(x)}\right) = -1.076x_{DS} + 4.919 x_{CNSCAR} \quad (1)$$

3.4. *Euterpe precatoria* Mortality

Also, for *E. precatoria*, the crown scorched proportion plus the diameter of the base of the palm stem were determinants of mortality of individuals. Other variables did not appear significant in the model construction, and the best model was significant against the null (only the intercept) when χ^2 (2, $n = 25$) = 16.75, $p < 0.001$. This best model had 88% of the power to predict mortality and an AIC (Akaike's criterion) of 21.9 (Table 8). For the mortality estimation of *E. precatoria*, the logistic regression equation (Table 9) is:

$$\ln\left(\frac{\hat{p}(x)}{1 - \hat{p}(x)}\right) = -1.241x_{DS} + 5.712 x_{CNSCAR} \quad (2)$$

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 R^2	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 palm stem at ground; ^e proportion of scorched crown; ^f palm stem 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 all variables in the model was 1; Sig: p values for each model's probability coefficient.

Variables	B	Standard Error	Wald	Sig
Stem diameter at the ground level (DS)	−1.241	0.511	5.889	0.015
Crown scorched proportion (CNSCAR)	5.712	2.215	6.649	0.010

This means that, for an increase from 2 to 6 cm in diameter at the base of the stem, considering an individual with 100% burned leaves, the chance of mortality falls from 97% to only 15% respective to the diameter. On the other hand, with the crown with only half of the leaves burned, this same ratio of 2 to 6 cm in diameter of the stem increases from 83% to 1%, respectively, of the probability of death (Figure 8a).

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

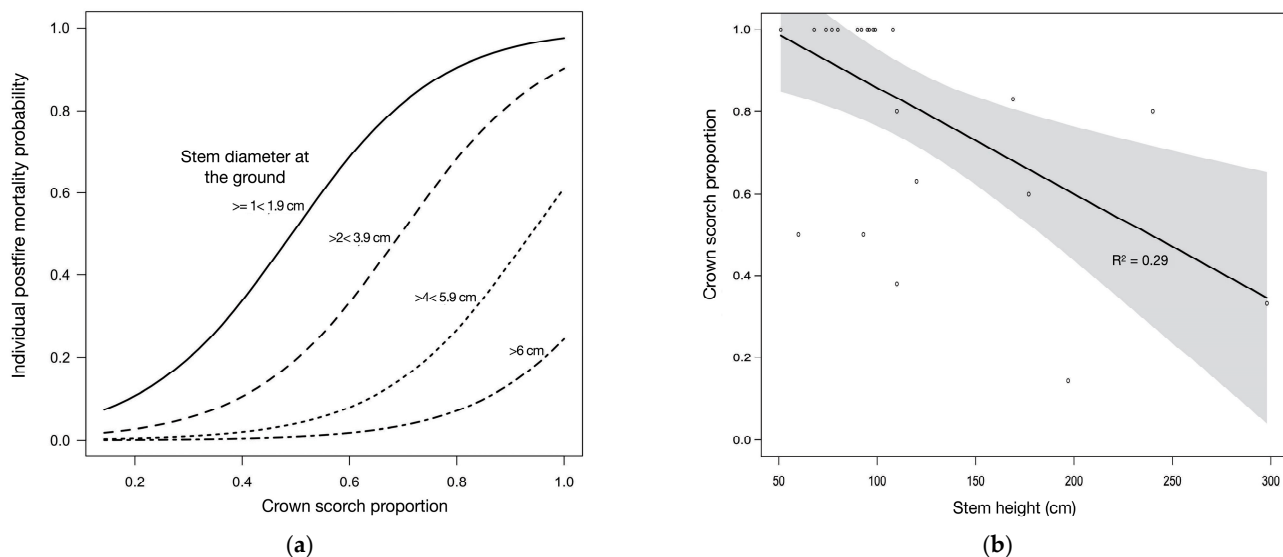


Figure 8. (a) Adjusted curves of individual mortality probability as a function of the proportion of crown scorched (CNSCAR) and of five intervals of diameter at ground level (DS): $\geq 1 < 1.9$ cm, $> 2 < 3.9$ cm, $> 4 < 5.9$ cm and > 6 cm, for *Euterpe precatoria* species ($n = 25$) ($p < 0.05$). (b) Linear regression and Confidence band between the total proportion of crown scorched (CNSCAR), and the height of the *Euterpe precatoria* stem ($n = 25$), four months after the surface fire simulation experiment in the understory of an Amazonian forest in Western Acre, Brazil ($p < 0.05$).

A graphical analysis showed that, at smaller diameters, diameter contributed minimally to the probability of mortality (Figure 8a). As the total proportion of scorched crown was low, these same smaller diameters will have the highest probability of mortality, which will increase conditioned by the proportion of the crown scorched until a cut point near 4 cm diameter. At this point, even with high rates of leaf burning, the probability of death could be reduced by half. Those individuals that have the largest diameter at ground level (above 4 cm) and that still have part of the crown unburned will survive.

Palm stem height has some influence on the proportion of leaf burn. The higher the lower part of the leaf crown (as measured by the height of the stem or height of the base of the leaf lamina), the lower the proportion of burned leaves ($R^2 = 0.29$; $F_{1,23} = 11.24$; $n = 25$; $p = 0.002$), see Figure 8b. Although significant in protecting leaves from heat flux, neither stem height nor total plant height are significant variables in the overall model and the 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 the green leaves in the crown. In any case, the apical regrowth for this species started even when there were more than 30% of leaves in the crown. 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*.

4. Discussion

4.1. Fire and Palm Stem Survival

Post-fire plant survival is a recognized indicator of fire intensity, as demonstrated by the 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 [37,58,83]. Predictive models based on logistic regression serve as powerful tools for modeling post-fire mortality events [84]. These models are also employed in predicting mortality from other disturbances, such as wind [85] and natural mortality [86].

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 palm stem burning, the findings suggest that height plays a more significant role in mortality [49,87,88], contrary to expectations. Diameter emerged as the most critical morphological trait influencing post-fire plant mortality [37,83,89,90], 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 (first-order processes). One hypothesis emphasizes that heat flux, the duration of heat exposure, and critical temperatures [91] cause 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 the heat flux from surface fires, affecting solute viscosity and functional tissue area [92].

The 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 (Figure S2). None of the bud temperature variables were significant in explaining mortality.

The relative importance of severity variables, such as stem burn or crown burn, varies widely in the literature [37,93], with much research focused on temperate forest species. While crown burning is often associated with bud death in studies, assuming individuals are populations of meristems [37,94], this study did not confirm this. Even with over 70% of the crown burned, the sampled palms showed a regrowth of meristematic apices, indicating minimal damage from heat flux at the base. Modeling crown 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 the 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, namely the phellem, phellogen, phelloderm, parenchyma, and 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 [94].

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 [95,96]. This anatomical arrangement provides palms with an advantage in protecting internal tissues compared to dicotyledons [94,95].

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 [15,35,97]. To understand the advantage of palm stem 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 a reduced movement of water and nutrients from the soil [58,92,98,99]. Vascular system obstructions reduce water and nutrient movement [34], a phenomenon observed in palms as well [99]. Plant hydraulic failure occurs when transpiration water loss exceeds water uptake by the roots [34]. In systems where soil humidity remains at field capacity, vascular system embolism can cause aerial part mortality due to leaf dehydration [34,36,98]. 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 [92,98,100].

The results indicate that the mortality of small-diameter palm stems results from two main processes: (1) leaf heating in the crown contributing to dehydration and (2) vascular system disruption due to temperature-induced cell coalescence [34,100]. 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 [101]. 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 palm stem 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 [26,89].

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] and is 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 [102]. Rapid regrowth of individuals can obscure assessments of post-fire mortality, as observed in the present study. Although there was a 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 palm stem regrowth. Understanding species resilience post-disturbance is crucial given the current and projected global climate changes and increased pressure from forest logging [103–105]. 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 [106]. The 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 humidity or proximity to edges, microclimatic changes resulting from recurrent fires at the edges or global climate change [107] 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, with distance from the edge and microclimatic factors playing significant roles in post-fire outcomes, although these parameters were not included in the best explanatory model. High palm stem mortality was found to be expected, alongside observed regrowth rates, though the survival outcomes varied. The proportion of scorched crown emerged as a critical indicator for predicting stem mortality across the species sampled in our study. Palm stem mortality is primarily influenced by heat at the stem base, where a larger diameter plays a more crucial role in preventing mortality than palm stem 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, including the influence of microclimatic variables and distance from the forest edge, to inform conservation strategies aimed at preserving the biodiversity and resilience of these ecosystems.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fire8010002/s1>, 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 Environmental Clearance Certificate no. 22/2012 from IMAC (Instituto de Meio Ambiente do Acre), ACRE.

Informed Consent Statement: Not applicable.

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

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