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FIRE IMPACTS ON THE PLANT INDIVIDUAL LEVEL AND FUTURE DIRECTIONS OF FIRE ECOLOGY IN THE AMAZON RAINFOREST

IMPACTOS DO FOGO AO NÍVEL INDIVIDUAL DAS PLANTAS E FUTURAS PESQUISAS DE ECOLOGIA DO FOGO NA FLORESTA AMAZÔNICA

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ABSTRACT

In the present days Amazon rainforest reveal no more natural protections against fire. Although fire always acted in vegetation structuring, even though independent of human existence, nowadays fire regimes are changing worldwide, as in the Amazon, motivated by global climate change and climate anomalies. Forest fires impact vegetation differently, depending on the ecosystem, soil type, and plants' features. Many species can respond positively, with survival mechanisms. Here will be presented data examples on palm species (Arecaceae) in individual level, considering fire can act positively and negatively over the species family. By including questions and presenting knowledge gaps, we intend to suggest news research asks. A better understanding of how Amazon plants respond to fire impact is necessary, to recognize if Amazon is actually still moist forest fire-immune, and how this contributes to species resilience on altered environments.

Keywords: forest fires, hydraulic-death, cambial-death, surface-fires, natural regeneration, Arecaceae

RESUMO

Nos dias atuais, a floresta amazônica não garante mais proteções naturais contra o fogo. Embora o fogo sempre tenha atuado na estruturação da vegetação, apesar de independente da existência humana, atualmente os regimes de fogo estão mudando em todo o mundo, como na Amazônia, motivados pelas mudanças climáticas globais e pelas anomalias climáticas. Os incêndios florestais impactam a vegetação de maneira diferente, dependendo do ecossistema, tipo de solo e características das plantas. Muitas espécies podem responder positivamente, com mecanismos de sobrevivência. Aqui serão apresentados exemplos de dados sobre espécies de palmeiras (Arecaceae) em nível individual, considerando que o fogo pode atuar positiva e negativamente sobre as espécies da família. Ao incluir perguntas e apresentar lacunas de conhecimento, pretendemos sugerir novas pesquisas. É necessário um melhor entendimento de como as plantas da Amazônia respondem ao impacto do fogo, para reconhecer se a Amazônia ainda está imune a incêndios florestais úmidos e como isso contribui para a resiliência das espécies em ambientes alterados.

Palavras-chave: incêndios florestais, morte hidráulica, morte cambial, incêndios de superfície, regeneração natural, Arecaceae.

1. INTRODUCTION

The forest fires expansion in the Amazon accompanies the rate of forest deforestation. Notably, fire in the moist forest seemed to be a contradiction until the last century. Actually, moist forests are no more protected against fire. Devastating forest fires observed in the northern region of Brazil (Acre, Roraima, Pará), Asia and Central America show this [1, 2]. The fire in the Amazon forest is a reality and the research interest has been intensified in the last years.

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Fire ecology research provides the conditions for understanding the fire effects on ecosystems. Traditionally these studies have been more frequent in those fire-dependent ecosystems, like savannas, chaparral vegetation and temperate forests [3]. Therefore, the fire ecology is a science in expansion in the Amazon and grows at the same pace in which the interest by the fire also grows among ecology researches and environmentalists.

The Amazon basin is the place of more than half of the remaining tropical forests in the world [4], covering approximately 5.4 million km^2 and playing a key role as carbon and biodiversity reservoirs. Amazon biological diversity count approximately 40,000 plant species, more than 430 mammals species and 1,300 birds species, now all threatened by deforestation, large-scale agriculture, big development projects, and logging effects [5–12]. The effects of these degradations are widening the forests edges, exposing the forest understory to the fire advance.

Climate change and global warming have already increased the fires occurrence in several world ecosystems, even in those with natural fire regimes. In tropical rain forests such as the Amazon basin, normally the climate and the weather conditions would prevent this threat (see [13] for a revision). The synergism between human activities, like forest fragmentation, and climate alterations has provide better condition to fire occurrence in the moist forest. Historical series of the last 16 years indicate that the fire frequency and impacted area has increased dramatically (State of Acre data [14]), and, considering the inability of the new government of Brazil (2019–2020) to contain the deforestation advance, associated with climate projections indicating temperature increase, Amazon forest fires and consequences will probably be more intense and frequent.

Currently is operating in Brazil a set of geospatial tools that inform, almost in real time, deforestation rates, hot points and fire risk for all country [15]. Studies are advancing in the search for information on fire scars and recurrence in Amazon [14]. The challenge now is to correlate spatial fire data with *in situ* data – individual level – of plants subjected to the fire heat. Several sites in the Amazon, especially drier regions, are facing a deviation in the secondary succession, where invasive species become dominant preventing the natural regeneration of native species [16]. Very important to know the species' abilities and the individual responses to the impacts, in order to understand what paths of resilience the forest will take in the future.

Among the various types of fires that occur in the world's vegetation, surface fire is the most common. The surface fire heat reaching a plant individual in the forest is variable in

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intensity (energy released per area), therefore the plants' fate after the fire will depend only on species morphology and ecology and micro-environmental features, sometimes altered too. Thus functional attributes such capacity and vigor on resprouting, heat tolerance, as well the morphological characteristics such as bark thickness or a leaf sheath shield presence, are interesting to be revisited in this overview.

In this perspective, the understanding of fire ecology in the plant individual level will be illustrate here by papers and work in progress data and natural history about the post-fire fate of arboreal monocotyledons, specifically palm trees and understory species of Arecaceae Family [17]. Furthermore, Arecaceae Family will be emphasized because is a well-studied botanical family with regard to ecology and also impacts [18]. Arecaceae species distributed throughout the world present fire adaptations evidence [19-21], Table 1.

The content of the present article continues in section 2 with an assessment about fire regimes in Amazon rainforest and the global fire ecology. Subsections will address a brief review about types of forest fires and environmental characteristics, as well the fire general consequences on the Amazon moist vegetation. In section 3 will be discussed the hypotheses and mechanisms that control the post-fire plants' fate, based on considerations about plants' morphology, physiology, and anatomy. Section 4 contains the summary and conclusions.

Table 1. Non-exhaustive list of Arecaceae species that are cited to have some kind of post-fire resilience in the different eco-regions of the planet.

Ecological Region and country		**Species**	**Ref**
Subtropical Humid Forest	Madagascar/ South Africa	*Hyphaene coriacea* Welw.	[25]
Temperate Forest	North America	*Sabal etonia* Swingle	[26]
		Sabal palmetto Lodd. ex Schult.f.	[27]
		Serenoa repens (W.Bartram)Small	[26]
Tropical Moist Deciduous Forest/ Savanna	Brazil (Cerrado)	*Acanthococos emensis* Toledo	[28]
		Allagoptera campestris Kuntze	[29]
		Allagoptera leucocalyx Kuntze	[30]
		Butia paraguayensis L.H.Bailey	[28]
		Syagrus flexuosa Becc.	[29]
		Syagrus glauscescens Becc.	[31]
		Astrocaryum gynacanthum Wallace	[32]
	Ivory Coast	*Borassus aethiopum* Mart.	[33]
	Madagascar	*Bismarckia nobilis* Hild.& H.Wendl.	[25]
		Borassus sambiranensis Jum.&H.Perrier	[25]
		Borassus madagascariensis Bojer&Becc.	[25]

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Tropical Dry Forest	Argentina	*Trithrinax campestres* Drude&Griseb.	[28]
		Copernicia alba Morong	[34]
Tropical Rainforest	Brazil (Amazon)	*Attalea maripa* Mart.	[17,35]
		Attalea phalerata Mart.	[35]
		Bactris maraja Mart.	[17]
		Euterpe precatoria Mart.	[17]
		Oenocarpus bataua Mart.	[17]
	Brazil (Atlantic forest)	*Allagoptera arenaria* (Gomes) Kuntze	[36]
		Attalea humilis Mart. ex Spreng.	[37]
		Attalea geraensis Barb.Rodr.	[38]
	French Guiana	*Astrocaryum sciophilum* Pulle	[39]
	Trinidad	*Mauritia flexuosa* Linn	[40]
Tropical Shrubland	Australia	*Corypha utan* Lam.	[41]
		Hydriastele ramsayi W.J.Baker&Loo	[41]
		Livistona benthamii F.M.Bailey	[42]
		Livistona eastonii C.A.Gardner	[42]
		Livistona humilis R.Br.	[42]
		Livistona inermis R.Br.	[42]
		Livistona loriphylla Becc.	[42]
		Livistona muelleri F.M.Bailey	[42]
	Mediterranean	*Chamaerops humilis* L.	[43]

2. FOREST FIRES REGIMES IN THE PERSPECTIVE OF GLOBAL CLIMATE CHANGES

Fire is an important process present in most of the world's ecosystems, influencing the hydrological, geomorphological, geochemical and ecological processes [44–48]. Between 2001 and 2006 fires occurred in 40% of the terrestrial vegetation [49], appearing in regions of dense or wet vegetation (tropical moist forests), or very sparse vegetation (deserts) [47, 50].

The distribution of the largest biomes of the world - deserts, tundra, grasslands, savannas and forests (tropical, temperate and boreal) – is traditionally explained by temperature and precipitation [51]. In Brazil, the vegetation maximum development is understood as *climatic climax* [52]. However, the world vegetation distribution in biomes owes much to the action of fire regimes [46, 50]. This perspective extends what we knew traditionally, thus, the world vegetation cannot be understood without considering the action of fire [53].

The fire regimes vary between ecosystems result of the synergy between physical factors (climate, time), vegetation properties and stochastic factors [46, 50]. In humid and productive

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regions, such as the tropical forest, the quantity of fuel is not a limiting factor (see [54] for fine fuels moisture importance in the Amazon Region), and the fire activity will be determined by the climatic conditions. The flammability increase when more dry and warmer is the climate [47, 56, 57].

The global climate changes are modifying the fires regimes [58–60], not only in regions usually influenced by fire but also in very humid regions such the tropical forests [60]. As the socioeconomic patterns and climate change, ecosystems with little flammability before, become in highly fire susceptible environments, or even increase the intensity and frequency of fires in these environments [62–66].

'Fire regime' is the general pattern which fires occur in an ecosystem and can be *sensu stricto* and *sensu latu* regime [67]. Fire regime *sensu stricto* definition is characterized by: (a) <u>when</u> (frequency, seasonality, synchrony), (b) <u>where</u> (size, shape, etc.), c) <u>source</u> (type of fire - canopy, surface, underground, latent) and (d) <u>physical aspects</u> (intensity, spread rate, residence time, flame height, fuel consumption, etc.). The fire regime *sensu latu* expands the description of the regime and the fire impacts, using additional parameters: (a) conditions for the fire occurrence (climate, temperature, winds); b) the primary effects (mortality, severity, etc.); and (c) the combined effects of previous parameters.

The combination of fires recurrence time, fires frequency and distribution in a given space (burned location) produces a landscape mosaic of fire stories, which will include areas that have burned with different sizes and frequencies [68]. Changes in the structure of the vegetation can occur when the frequency of fires differs significantly from the normal cycle or natural history [53, 68].

2.1. Environmental characteristics and forest fires types

From the perspective of fire as an ecosystem process, there should be a minimum primary productivity to fire spread, at the same time that a specific climatic seasonality is needed to convert the vegetation in available fuel [57]. Thus, the regimes and types of fire will depend on the *ignition frequency*, and *ignition susceptibility* (dry season; no rain total period; canopy openness and understory moisture reduction, for example), and the available fuel structure [44, 55].

Fuel structure and consumption by fire is an indicator of the total amount of energy released. The fuel structure includes: (i) moisture; ii) structure *per se* (biomass density, biomass volume m^3 ratio, biomass and necromass ratio, thin litter *vs* thick litter, decomposition times and understory - low branches - canopy continuity); and (iii) the fuel chemical composition, very important in vegetation with high levels of volatile organic compounds [69–72].

Fire severity and fire intensity are distinct concepts [73]. Fire intensity is a measure of the fire behavior, related to the production of thermal energy rate (fuel characteristics), and is measured in terms of heat release and temperature [74, 75]. Severity understands the physical impacts of fire directly associated with the combustion and heat transfer, interacting with the species morphology and physiology and system physical characteristics. Fire severity is a concept, and cannot be defined in a single measurement [76].

The intensity depends on the complex interaction between fuel structure, climate and physical environment (elevation, topography and soil type, wind characteristics). Intensity varies between the different types of fire. In forest fires, the temperature can vary between 50 ºC to > 1,500 °C, and the heat release rate can vary from 2,110 $J.Kg^{-1}$ until > 2 million $J.Kg^{-1}$, while the propagation rate varies from 0.5 m $week^{-1}$ in the underground fire until more than 7 $km.h^{-1}$ in large crown fires [77, 78].

The underground fire is characterized by burning underground layers of organic matter, through the combustion without flame or smoldering fire. The spread rate is extremely slow, and these fires remain for months or years. Comparatively, the temperature is lower than the surface fire (between 500 – 700 °C for temperature peaks; 200 ºC in average). Underground fires can lead surface fires ignition along their area of propagation [79]. The underground fire occurs in forests with old and thick organic matter layers and carbon emissions from this type of fire are very intense and possibly exceed 300 Mg C ha^{-1} [80].

The crown fire, or replacement fire, it is the type of fire that presents greater intensity. In the conifers forests or in the Californian chaparral, crown fire can reach more than 50,000 kW m^{-1}, and propagate by areas of up to more than 100,000 ha [62]. These fires cause total annihilation of the aboveground biomass of the forest, even the trees with more than 30 m height. The combustible accumulation turns less flammable prone environments in to more large intensity fires [47, 53, 81].

The ground fire or surface fire is perhaps the most common and constant type of fire at world level [82]. Surface fires have low or moderate intensity, and are extremely selective, which often does not imply total damage to plants, and may exert greater evolutionary pressure than the other types of fire [22, 63, 83–85].

The surface fire moves slowly along the forest understory, or even fast when in the open field areas. Due to this spread peculiarity keeps long rates of retention next to plants, burning

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the base of the trunks, the crown leaves, seedlings and young individuals [1, 17, 82, 87, 88]. Part of surface fire temperature can be transferred to the subsoil, influencing the seed bank and plant roots [78, 89].

The temperature profiles along different soil depths will vary according to the fire intensity on the surface, the fire duration, soil type and moisture [78]. In the crown fires with thick organic mineral soils, the temperature can reach up to 250 ºC to 10 cm depth [90, 91]. In the tropical forests moist soil the temperature variation happens in the first cm from the ground, but the temperature increase is negligible at depths below 15 cm. The latent heat of evaporation prevents the temperature exceeds 95 °C [90, 92].

There are many papers that focus fire impact experimentally or fire management in the temperate forests [93–95]. In the tropical forest, however, there are few studies that promoted an experimental approach to surface fire problem and the associated tree mortality [17, 88, 96, 97]. With regard to the slash and burn physical aspects and postfire regeneration in the Amazon, we can highlight the large-scale experiments of the National Institute of Spacial Research (INPE) [97–99].

In the Amazon rainforest, distinct geographic regions influence differently the post-fire plant responses [100]. Each plant individual will respond to the fire according to the soil conditions, but also according to their morphology, physiology and life phase. Therefore, there is intraspecific variation, when individuals of the same species may react differently to fire, and interspecific variation when species have different characteristics of protection in response to fire. The fire impact result achieved on a forest ecosystem will depend on the balance between resistant species, fire survivors species (resprouters or seeders) and species that have succumbed after repeated fires.

2.2. Fire consequences on the moist tropical forest

The occurrence of fire is independent of the human existence and has always acted structuring the vegetation [53, 101]. The coal records of fire-prone ecosystems showed that the evolution of vegetation was also conditioned changes to fire occurrence. For example, in the Cretaceous period started the "fire-grassy” cycle with C4 grasses with high biomass productivity, associated with high levels of oxygen and intense lightning occurrence [46]. Tropical ecosystems with grasses and herbaceous incidence, among them the savannas, are the environments that more burn in the modern world [102].

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Forest fires and climate are closely related processes [60]. The weather conditions can be classified in *time for fire*: fire conditions in a specific season of fires, and *climate for fire*: daily climate situation in a season of occurrence of fires (average temperature, humidity, wind, etc.). With the atmospheric CO_2 increase it is expected changes in all the atmospheric conditions, such as temperature, humidity, wind, precipitation and clouds formation [60, 103].

Climate change and global warming already increase the occurrence of fires in regions such as the Amazon basin, where normally the climate and the weather conditions would prevent this threat [50, 56, 60, 104, 105]. The Amazon paradigm of 'forest immune to the fires' was changed, resulting in successive cycles of microclimate and vegetation impoverishment, thus increasing the fire risk and susceptibility [106, 107].

A greater fire severity, climate-related, has been verified in the el Niño Southern Oscillation (ENSO) 1997-1998 years in which the Amazon experienced severe drought. Approximately 40,000 km^2 of understory forest was affected by surface fires in these years [108–110]. New satellite detection techniques registered between 1999 and 2010 that the ground fire affected more than 85,500 km^2 of forest understory, or 2.8% of the whole Amazon forest [111].

The fire has been influencing the structure and composition of the Amazonian forest for thousands of years. Soils with charcoal indicate fire occurrence during at least the past 6,000 years when the climate was drier, and there was a predominance of escleromorphic vegetation [96]. The calculated frequency of fire in these ancient periods was 400-700 years interval [112], i.e., fires in the Amazon forest have always existed, although with very low frequency (major recurrence intervals). Long term responses of vegetation to climate – changes in the forest flammability – can lead changes in fire regimes [62], what would reflect changes in the time of recurrence, an important factor considering a forest with low resilience to fire [113].

The primary land use conversion in Amazonia is the *slash and burn* practice. In fact, it is becoming increasingly common for the fire to escape from these points of burning to the forest understory. However, it is extremely difficult to follow the surface fire inside the intact forest, forcing the researcher to seek the fire-scars long times after fires occurrence. The surface fire is regarded as the most detrimental impact on forests and difficult to detect by satellite [114, 115]. Ground fires have the capacity to spread over 10 kilometers inside forest understory [24, 111],

When the understory of a forest experience the first fire, the intensity tends to be low, with flame height 10 to 30 cm, in low speed (0.25 $M.min^{-1}$) [105, 115]. The temperature in the

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base of plants intercepted on the fire propagation can reach the limit of 760 ºC, and intensity may reach 50 kW.m-^{1} [96, 78, 97]. Depending on the environmental conditions and also fuel structure, mainly the litter continuity with low branches, the surface fire can achieve higher forest strata [24].

Moist forests, with higher canopy openness, are experiencing extreme weather stress with little precipitation. These cases the understory microclimate changes radically, increasing the ambient temperature and soil temperature and decreasing the air relative humidity and litter humidity [9, 10, 109]. These factors combination increases the probability of new understory fires occurrence, increasing the severity, the recurrence and the distances of fire penetrability inside the intact forest [6, 11, 56, 65, 111, 117–119].

Is still incipient the understanding of surface fire consequences on reducing seed availability, species fruiting and flowering [120]. Little is known about the ability of burned areas remain free from invasive grasses and lianas, which delay natural regeneration and increase the susceptibility to fire recurrence [116, 121, 122]. The fire impacts in the food plant decrease availability, such as palm trees (assai, buriti, patawa) and timber species are also scarcely estimated.

The transitions between different biomes, conditioned by the interaction of fire and climatic variables are being called *tipping points* [64, 65, 123]. More extensive periods of frequent and severe droughts are expected for the Amazon region [124]. Cumulative records already indicate a 0.32% year^{-1} annual precipitation decrease [60]. The tendency for regions with impacted forests and altered precipitation patterns are changing the vegetation structure [125]. These changes in structure also mean changes in its capacity to resist fire (*fireproof*).

On a global scale would provide a redistribution of fire-prone ecosystems [126]. In the physiognomic aspect, savannas would prevail over those of forests, creating derived savannas with different floristic composition from old-growth-savannas [125]. In these new environments, low-intensity fires would act to exclude species from the rainforest [66] as well facilitate taxonomic homogenization [127].

The forests deterioration, the altered precipitation patterns, and greater fires intensity and extent guide the occurrence of a savanna *vs*. moist forest 'breaking point'. The Amazon savannization concept summarizes this process [83, 128, 129]. The natural regeneration of the forest is also affected when empty spaces left by the fire, are colonized by ferns (*Pteridium* spp.), lianas [130], grasses [131] and bamboo [132–134].

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3. HYPOTHESES AND MECHANISMS OF POST-FIRE PLANTS' FATE

The plants' post-fire individual fate depends on the injuries caused by heat to the plant organs (leaves, stem, and roots), affecting the plant physiology among other characteristics. The result is binary: survival or death. However, the processes that determine the post-fire plant fate are still not well clarified. Therefore, plant mortality caused by the fire is difficult to predict [87, 91, 135–138].

In fire ecology, the events and mechanisms that determine the imbalance between the ambient and cellular temperatures, such as the heating of the stem and leaves by the surface fire, or heating the roots by underground fire, motivate historical studies and intense debates [87, 91, 135, 139, 140], and involve physical processes of combustion, sometimes neglected by fire ecologists [141].

The physical process of combustion is characterized by the energy heat flow over a given material. The physical processes in heat-plant interaction are: i) convection, which includes the direct contact of flame with leaves or stems, but is mainly related to the fire plume movement; ii) radiation, main heat source when there is no direct contact by convection; and (iii) conduction, least important of all three, because potential of heat conduction of wood is low [136]. The studies to predict plants' mortality induced by fire uses empirical models with visual indicators, such as the stem burning degree (*stem height scorch*), and the degree of leaf burning (*canopy scorch*), related to diameter and/or thickness of the cortex [141–143]. The term *fire scar* is used for stems of larger diameter [144–146].

For most plants, fire can kill the aerial portion (*top kill*) through the crown fire (replacement fire), or the selective death through the surface fire impact. Especially on savanna ecosystems that have interspersed trees with shrubs and sparse vegetation, the surface and replacement fires can occur together [77]. The aboveground plant biomass suppression does not imply the individual death, because many species have the ability to post-fire resprouting, with mechanisms that allow the environment recolonization (72, 84, 147–149). Thus, the fire can kill totally the individual (stems and roots), will lead a population decline; or fire will only top-kill, causing a "partial" death with obligatory resprout, which does not directly affect the population size, but can lead to increase biomass.

The fire affects the plant through three different ways: i) canopy scorch; (ii) roots heating, and (iii) stem heating [136]. These processes, acting independently or synergistically, can result in resprout, tolerancy or plant death. The canopy scorch is caused by the convective smoke heat

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and radiation energy, above the surface fire, and provides necrosis to branches, leaves, and buds [78, 136]. Vegetal leaves of the moist forests are generally thin, very moisturized, so the leaves invariably dry and often fall in high temperatures [78, 150].

The root burning occurs through the underground fire activity or sub-soil heating by heat-conductive surface fire [136]. Little is known about this process [79, 147], but for some understory palm species the underground buds have higher resprout ability than apical buds [17]. The stem heating occurs by radiation and conduction, and the consequent heat conduction inside the stem, through the bark to live tissues, can cause phloem necrosis and/ or vascular cambium embolism [87, 135, 143, 151].

The interactions of the above processes are classified as 1st or 2nd order. The 1st order is the direct effects of heat transfer on the organism, for example, the production of necrotic tissues. The 2nd order processes are consequences of 1st order effects and can determine the plant mortality by indirect effects such as the secondary alterations of physiological processes and increased susceptibility to infection by pathogens or insect attack [72, 138, 139]. The 2nd order processes may take many years to definitely kill the individual [120].

The fire can also modify soil properties, nutrient cycles, light availability, and the seed bank composition [88–90]. The combination of these factors when in a negative way can accelerate the individuals death, especially in fire-sensitive ecosystems (ecosystems with species without past adaptations to fire), or even act in a positive manner, on fire-prone ecosystems (ecosystems where abound fire adapted species), selecting positively species that have morphology and physiology better adapted to the severity of the fire [46].

The resilience to fire may be determined by evolutionary characteristics linked to fire (ex. bark thickness, lignotubers, woody fruits), resulting in different fire susceptibilities. There is also intraspecific variability because distinct development stages also respond differently to the fire impact. This can be observed in particular mortality rates according to stems diameters and heights. The height can be negatively related with the stem death vulnerability. Thus, plant height can provide an 'escape' function, being an important dimension to prevent stem death by fire [154–156].

3.1. Arecaceae post-fire resilience: study cases

Resprouts are common in palm trees (Arecaceae) submitted to environmental impacts [156, 157] Table 1. Some palm species resprout and resist after the fire impact [17, 20, 158–161]. Populations of determined palm species can become dominants in altered environments.

In the east Amazonia, the babassu (*Attalea speciosa* Mart. ex Spreng) is one of the main species regenerating in the intensive cattle-raising or in the abandoned areas [162].

Similar to the babassu is *Attalea maripa* Aubl. Mart. (maripa palm) in the cattle fields of west Amazonia. Although this species presents regular distribution in the tropical forest [163] populations can increase in number in fire-impacted forest edges, or in adjacent open areas. It is possible that *A. maripa* reach greater inter-specific competitive advantage under an increased fire influence. This competition could exclude food economic palm species from the forest edges, such as: assai (*Euterpe precatoria* Mart.) and patawa (*Oenocarpus bataua* Mart.). These are current issues for research going forward.

Most palm trees have apical meristems secured on the forest underground, below the litter and the ground level, at least in the juvenile phase [164]. Leaves, petioles, and sheaths attached to the base of the palm stems can be form a layer protecting the inside tissues against fire heat. In addition, another morphological feature can promote the apical regrowth: the "saxophone stem" [158], Figure 1.a. The underground apical meristem appears curved and associated to the base of the leaves sheaths, forming a quite compact set of tissues, like a shield, which could reduce the heat flux at the apical meristem protecting against fire heat [165].

Usually, studies focus mainly on the bark thickness - and in a general way the thickness of inner bark (live tissues) plus outer bark (cork, dead cells with suber). Bark acts as a thermal insulator with the capacity to resist the surface fire [139, 143, 166, 167]. The temperature on the vascular cambium increases and decays soon after the flame front pass the tree. Tissue cell mortality will occur from a combination of exposure time and temperature effects [135, 168].

In dicotyledons angiosperms the meristematic tissue is ring-shaped, and if fire encircles the tree, may cause girdling and tree death or vascular cambium partial necrosis [87, 143]. This concept provides the limit temperature of 60 ºC to cambium necrosis. However, temperatures below this value with greater times of exposure can also cause cambium necrosis [169]. Stems exposure times to the flames are variable, but generally are shorter in surface fire (from 30 sec to 5 min). However, the time of exposure is not proportional to the heat that the vascular cambium receives, because the variation in the bark thickness, diameters, etc. will influence this time and temperature.

The heat from the surface fire is more important in the induction of cambium necrosis than in the leaves burning, mainly in smaller stem diameters plants [88, 167–171]. The post-fire girdling block the photosynthates translocation, which eventually will cause the death of the stem by starvation and roots desiccation. To understand the girdling is necessary to quantify

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the exchange rate of temperatures between the tissues, by thermal diffusivity: κ (m^2s^{-1}) [thermal conductivity *k* (kJ s^{-1} $^oC^{-1}$), divided by specific heat product *c* (kJ $kg^{-1}C^{-1}$) multiplied by tissue-specific density ρ (kg m^{-3})]. The plant superficial tissues heat relatively slowly by having low κ, and even the *k* is variable among the plants, κ is considered as constant for a wide variety of tissues moisture and density [78, 139].

It is interesting that for the monocots trees - palm trees (Figure 1.b), the processes that cause stem death by fire act differently than in the dicotyledons trees, (Figure 1.c). This is due to anatomical differences between the two groups of arboreal plants, especially the particular secondary growth process of each one [172]. In secondary growth dicots, heat flow is prevented or diminished as its crosses several histological barriers: cork, cork cambium, phelloderm, parenchyma, secondary phloem, until the vascular cambium. All tissues together are the bark, an efficient and variable anti-thermal shield [150].

The tissue structural organization in palm trees is distinct from other arboreal dicotyledons. Palm trees have no bark, no ring tissues, and the entire vascular system is organized into fasciculate vascular bundles, surrounded by more or less thick wall parenchyma and sclerenchyma fibers [173]. Clusters of highly thickened cells play the periderm role (Figure 1.d). An abundant associated sclerenchyma fiber appears with high specific hardness [173, 174]. This structural organization allows an advantage of internal tissues protection in comparison to dicotyledons [150, 175].

If the same heat flux reaches arboreal palms and dicotyledons indistinctly, is the internal structure of palm trees a morphological advantage? Plants survival undergoing physiological stress is related to the reduction of the soil-plant-water movement [176]. Palm trees have a decreased water movement follow vascular cells obstructions and plant failure occurs when the water amount lost by transpiration exceeds the water amount captured by roots [87, 176]. Hence considering only the diameter as thermal protection, arboreal monocots will tolerate more the stem heating than same diameter dicotyledons. Such tests are yet to be made in science.

There is a certain consensus that the mortality of trees after the surface-fire is understood as death by vascular cambium necrosis, or *Vascular cambium death hypothesis* [87]. Besides the xylem conductivity interruption or discontinuity is another important mechanism that can explain the post-fire mortality, this being recognized as the *Hydraulic death hypothesis* [151, 177, 178].

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Figure 1. Some features that improve monocot against fire heat, and can ensure the post-fire resilience: a) longitudinal seccion of the "saxophone stem" where the underground apical meristem appears curved and associated to the base of the leaves sheaths; b) buriti (*Mauritia flexuosa*) stem showing an post-fire "waist": stem thinning by recurrent fires, which does not prevent the individual's survival; c) assai (*Euterpe precatoria*) stem showing the roots forming a collar and it is possible that this system protects the stem against fire heat; d) transversal secccion of a *Astrocaryum* stem showing the extreme lignification of the tissues just below the periderm.

The heat causes the xylem cavitation because it reduces the water surface tension as the temperature increases (decreases 22% between 0 - 100°C). Cavitation is when the air embolism affects conductivity, stopping the flow of sap (cohesion-tension solute), reducing the hydraulic functionality of the xylem and causing malfunction. At the same time, vessel functional area decreases because heat deforms the vessels walls (thermal energy softening the cell wall polymers) [87, 138, 146, 177, 178].

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The obstruction of the vascular system by air embolism, when soil moisture remains in field capacity, may be the major causes of canopy scorch and stem mortality [78, 87]. Since carbohydrates use by the plant is closely associated with water use and transport, plant will die as a consequence of carbohydrate support failure and physiological drought: the time until death will depend on balance between these processes [176].

It seems quite plausible that for stemmed palms, even for understory forest species, a larger stem diameter is very important for post-fire surviving. More than having a thick bark. Plants with less than 10 cm diameter suffer from disruption of vascular system continuity by cell coalescence and xylem cavitation [87]. Leaves losses from dryness contribute to the malfunction of the vascular system and vice-versa. The water stress will delay the leaves recovery and the normalization of the physiological activities.

The ability to return leaves at appropriate rates is not a problem for many understory palm species, therefore post-fire top-kill in understory palms depends almost exclusively from the hydraulic system failure, caused by the surface fire heat flux. For a better understanding, it is necessary to develop physiological studies in palm trees that consider the tissues hydric potential, rates of utilization of carbohydrate reserves, as well anatomical studies addressing the tissues and cell walls deformation by the fire heat.

4. CONCLUSIONS

The deteriorated capacity of the Amazon forests in retaining moisture is the major cause in increase fire susceptibility. Furthermore the global climate changes are affecting the precipitation patterns, longer dry periods diminish further the capacity of forests to retain moisture. The combination of dry climate with dry vegetable fuel and human ignition, turn the moist tropical forest before immune to fire, now in sensitive and threatened.

The fire has always existed in the world natural history, but fire regimes alterations (>frequency) are recent in the majority of the world's ecosystems, including in the Amazon. From the forests altered edges the *surface fire* progresses slowly in the understory burning litter with low temperatures, dangerous enough to kill individuals selectively that do not have any kind of defense and/or strategy to resprout or survive.

As emphasized, ground fire can modify soil properties, nutrient cycles, light availability, seed bank composition, seed availability, and species phenology. More research needs to understand about the ability of burned areas remain free from invasive grasses and lianas and

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that feedback to the fire recurrence. Species without post-fire features to persistence, such as resprouting ability, bark thickness or a fasciculated vascular system may disappear if fire is consolidating as the crucial factor of disturbance in Amazon.

It is quite acceptable the fire impact is benefiting some palm species in Amazon. How exactly this happens, needs to be better investigated. At the same time, Arecaceae understory species are at risk with surface fires invasions. It is necessary to know more about the fire impacted species physiology, and also the histology consequences. Monocotyledonous vs. dicotyledonous comparative anatomy may provide more answers about the tropical species post-fire survival behaviors. According to the examples presented here, resprouts are common in palm trees submitted to environmental impacts. Probably also the palm trees are more fire-tolerant than dicotyledons.

It is essential to anticipate the extent of future impacts caused by more severe fires. The investigation should consider the fire effect on the selective vegetation mortality, assessing the individual strategies of each species, using *in situ* experiments whenever possible. Thus, it will be necessary an interdisciplinary approach considering species morphology, physiology, and anatomy, as well the ecological attributes.

Efforts should be development to achieve results of research aimed at the level of the plant individual subject to fire, an attempt to compute these results to the global models of vegetation fire impact, adding further information of global climate changes at the level of the landscape. Models addressing fire-altered ecosystems should consider the perspective of post-fire impact at the species – individual - level. The same goes for changes predictions of the Amazon physiognomies, as well to understand the altered savanna pathways.

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