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RONALD NOUTCHEU

IMPACT OF CHRONIC ANTHROPOGENIC DISTURBANCE AND ENVIRONMENTAL FACTORS ON NATURAL REGENERATION IN CAATINGA DRY FOREST

RECIFE, FEVEREIRO DE 2022

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Tese apresentada ao
Programa de Pós-Graduação em
Biologia Vegetal da Universidade Federal de
Pernambuco, como requisito parcial para
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DEDICATION

"In loving memory of my dad Jean Ndopgang who did not see the end of this adventure and for his endless love, support and encouragement"

"To my dear daughter Andrea Kayliah for your patience during the absence of your father and the light you bring in our lives"

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ABSTRACT

Natural regeneration is a complex and very important ecological process involving various factors that contribute to the recovery of tropical forest ecosystems. Understanding how these natural and human factors affect this highly disturbed biome will be a great step for its conservation and restoration. Thus, the aim of this study was to investigate the effects of chronic anthropogenic disturbances and environmental factors (aridity, soil fertility and light availability via leaf area index) on regeneration mechanisms (seed rain, soil seed bank, woody plant regenerating assemblages, and resprouts) (Chapter 1) and to assess how seedling-sized resprouts respond to experimental coppicing along disturbance and environmental gradients (Chapter 2) in a human modified landscape of Caatinga dry forest. The structure, richness, diversity and composition of regeneration mechanisms data were collected from 18 plots (20m×50m) and, while experimental coppicing from 15 plots (20m×50m) in the Catimbau National Park, Buíque, Pernambuco, Northeast Brazil. We found very low dense and impoverished regenerating assemblage, with the seed rain density ranging from 0.2 to 432.3 seeds per m2, density of viable soil seed bank varing from 5 to 2555 seeds per m2, density of true seedling ranging from 0 to 5.91 ind/ m2, true sapling density from 0 to 0.66 ind/ m2 and sprout density from 0 to 1.28 ind/ m2. Resprouting was the most important mechanism of regeneration in terms of species richness and abundance, mostly from the stem with 63% of regenerating assemblages. Abundance and species richness of regeneration mechanisms were contrasting related to CAD and environmental factors. Species composition of soil seed bank, all regenerating assemblages and resprouts were explained only by aridity. In relation to coppicing response, we observed a high resprouting capacity as all 19 species tested and around 74% of all individuals presented new shots after experimental coppicing. We found that only the number of new shoots was negatively influenced by rainfall and soil fertility. Moreover, considering the five species distributed in at least five plots across the focused gradients, negative effect of chronic disturbance, leaf area index and rainfall were observed in new shoot length, new shoot diameter and resprouting capacity indices (shoot diameter and stem diameter ratio) of *Annona leptopetala* and *Trischidium molle*, and positive effect of rainfall was observed in new shoot length, new shoot diameter and resprouting capacity indices of *Cnidoscolus bahianus*. These results demonstrate the negative effect of chronic anthropogenic disturbances on regenerating assemblages and show the capacity of seedling-size resprouts to persist in disturbed area. Thus, the predicted increased aridity associated to increased human disturbance in the Caatinga region can lead to unknow effects on long-term forest dynamic, biodiversity persistence and forest resilience.

Key words: Aridity; Climate change; Human disturbance; Plant assemblages; Regeneration mechanisms; Seasonally dry tropical forests.

RESUMO

A regeneração natural é um processo ecológico complexo e muito importante que envolve diversos fatores que contribuem para a recuperação dos ecossistemas florestais tropicais. Entender como esses fatores naturais e antrópicos afetam esse bioma altamente perturbado será um grande passo para sua conservação e restauração. Assim, o objetivo deste estudo foi investigar os efeitos de perturbações antrópicas crônicas e fatores ambientais (aridez, fertilidade do solo e disponibilidade de luz via índice de área foliar) nos mecanismos de regeneração (chuva de sementes, banco de sementes do solo, assembleias de regenerantes de plantas lenhosas e rebrotas) (Capítulo 1) e avaliar como rebrotas do tamanho de plântulas respondem a poda experimental ao longo de gradientes de perturbações antrópicas e ambientais (Capítulo 2) em uma paisagem humana modificada de floresta seca da Caatinga. Os dados de estrutura, riqueza, diversidade e composição dos mecanismos de regeneração foram coletados em 18 parcelas (20m×50m) e os de poda experimental, em 15 parcelas (20m×50m) no Parque Nacional do Catimbau, Buíque, Pernambuco, Nordeste do Brasil. Encontramos assembleia de regenerantes muito pouco densa e empobrecida, com densidade de chuva de sementes variando de 0,2 a 432,3 sementes por m2, densidade de banco de sementes de solo viável variando de 5 a 2555 sementes por m2, densidade de plântulas verdadeiras variando de 0 a 5,91 ind/ m2, densidade de jovens verdadeiras de 0 a 0,66 ind/m2 e densidade de rebrota de 0 a 1,28 ind/m2. A rebrota foi o mecanismo de regeneração mais importante em termos de riqueza e abundância de espécies, principalmente a partir do caule com 63% das assembleias regenerantes. A abundância e a riqueza de espécies do mecanismo de regeneração foram conflitantes relacionadas à CAD e fatores ambientais. A composição de espécies do banco de sementes do solo, de todas as assembleias de regenerantes e de rebrotas foram explicadas apenas pela aridez. Em relação à resposta da poda experimental, observamos uma alta capacidade de rebrota, pois todas as 19 espécies testadas e cerca de 74% de todos os indivíduos apresentaram novas rebrotas após a poda experimental. Descobrimos que apenas o número de novas rebrotas foi influenciado negativamente pela aridez e pela fertilidade do solo. Além disso, considerando as cinco espécies distribuídas em pelo menos cinco parcelas dos gradientes enfocados, foi observado efeito negativo da perturbação crônica, índice de área foliar e aridez nos índices de comprimento de novos brotos, diâmetro de novos brotos e índices de capacidade de rebrota (razão entre o diâmetro dos novos brotos e diâmetro do caule) de *Annona leptopetala* e *Trischidium molle*, e efeito positivo da aridez foi observado nos índices de comprimento de novos brotos, diâmetro de novos brotos e capacidade de rebrota de *Cnidoscolus bahianus*. Esses resultados demonstram o efeito negativo de perturbações antropogênicas crônicas nas assembleias de regenerantes e mostram a capacidade de rebrotas do tamanho de plântulas persistirem em áreas perturbadas. Assim, o aumento da aridez previsto, associado ao aumento da perturbação humana na região da Caatinga, pode levar a efeitos desconhecidos na dinâmica florestal de longo prazo, persistência da biodiversidade e resiliência florestal.

Palavras-chave: Aridez; Mudanças climáticas; Perturbação humana; Assembleias de plantas; Mecanismos de regeneração; Florestas tropicais sazonalmente secas.

CONTENTS

1 INTRODUCTION

Tropical forests are experiencing natural and human disturbances that cause definitive, temporary and localized shifts in ecosystem (Mouillot et al., 2013). As species and communities have evolved in the presence of natural disturbance, they present adaptations to deal with it (Denslow, 1987). For instance, recovery of forest is closely linked to gap dynamic in tropical forest undergoing natural disturbance (Denslow, 1987). In contrast, tropical forest under anthropogenic disturbances does not allow species and communities to evolve adaptations that enable them to tolerate the abiotic conditions resulting from disturbances (Singh, 1998). The possibilities of recovery of forest under anthropogenic disturbance can be very limited (Singh 1998). Moreover, the combination of anthropogenic disturbance and climate change can lead to changes and important perturbations of ecological processes as natural regeneration (Sala et al., 2000).

Natural regeneration has played an important role in reducing deforestation rates over these last year's worldwide. In certain tropical countries, including El Salvador, Puerto Rico, and Costa Rica, there is a net gain of forest cover over the past 20 years (Chazdon, 2017). In addition, several countries show hopeful signs of declining deforestation rates due to afforestation and natural forest regeneration (Chazdon et al., 2007). Although, these secondary forests cannot fully replace old-growth forests in term of structure, composition, and function they represent a significant component for securing sustainability of forest and forest dynamic due to their potential for the development of future generations, to maintain carbon stock and to recover some ecosystem functions (Chazdon, 2017). In order to sustain recovery of tropical forest it is important to understand the underlying environmental factors and mechanism that influence this ecological process following anthropogenic disturbances.

In this thesis, the objective was to investigate the effects of chronic anthropogenic disturbances and environmental factors (aridity, soil fertility and light availability via leaf area index) on regeneration mechanisms (seed rain, soil seed bank, and regenerating woody plant assemblages, and resprouts) (Chapter 1) and to assess how seedling-sized resprouts respond to experimental coppicing along disturbance and environmental gradients (Chapter 2) in a human modified landscape of Caatinga dry forest. Our general hypothesis is that disturbance and environmental factors will reduce Caatinga regeneration via seeds and true seedling and saplings while promote resprouting because they create adverse environmental conditions (Silva et al., 2019), which favorite vegetative reproduction (McDonald et al., 2010, Vanderlei et al., 2021). Thus, our predictions are: (1) Increasing chronic disturbance, aridity, soil infertility and lower leaf area index negatively affect abundance and species richness of the seed rain, soil seed bank, true seedlings and true saplings and positively affect resprouts (2) Increasing chronic disturbance, aridity, soil infertility and lower leaf area index stimulate coppicing response of seedling-sized resprouts; (3) Increasing chronic disturbance, aridity, soil infertility and lower leaf area index lead to a significant rearrangement of regenerating plant assemblages (seed rain, soil seed bank, true seedlings and true saplings and positively affect resprouts) via the replacement of disturbance-sensitive-species by disturbance-adapted species.

2 THEORETICAL BACKGROUND

2.1 IMPORTANCE OF OLD-GROWTH FORESTS

Contrary to tropical secondary forests that refer to forest reestablished following a disturbance which removes existing vegetation (Chazdon et al., 2014), old-growth forests are those in late successional stage. Tropical old growth forests are featured by a relative stability of taxonomic, phylogenetic, and functional diversity, structural and compositional features (Chazdon, 2013) and they are among the most diverse ecosystems on Earth. On the base of the global forest resources assessment, old-growth forests roughly count 21% of the world total area (Fao, 2010).

Due to their importance in maintaining biodiversity, it is relevant to understand the ecology of old-growth forests and how they react to human disturbances and environmental factors. Old-growth forests have an important role to play for the provision of regulating and supporting ecosystem services and the ecological functions (Millennium Ecosystem Assessment, 2003). They store a significant amount of carbon per unit area that mitigate carbon emissions from deforestation and land degradation (Martin & Thomas, 2011; Chazdon et al., 2016; Poorter et al., 2016). Moreover, studies have shown that old-growth forests can hold 30% to 70% of aboveground and belowground biomass more than in secondary or disturbed forests (Kormos et al., 2018). Additionally, the fact that carbon stock of old growth forests is more stable, will allow them to be more resilient to human disturbances and climate change (Kormos et al., 2016). For biodiversity, although recent study shows that disturbances in plant attributes and forest functioning in secondary forests after 20 years is similar to those of old-growth forests (Poorter et al., 2021), disturbances can lead to the loss of disturbances sensitive species while promoting generalist species (Ribeiro et al., 2015; Derroire, 2016; Filgeiras et al., 2021). Although secondary forests cannot fully replace old-growth forests in term of structure, function and composition, they can represent a significant component for securing sustainability of forest and forest dynamic due to their potential for the development of future generations, to maintain carbon stock and to recover some ecosystem functions (Chazdon, 2017). In order to sustain recovery of old growth tropical forest it is important to understand the underlying environmental factors and mechanism that influence the regeneration of this ecosystem following anthropogenic disturbances.

2.2 TROPICAL FOREST REGENERATION

Forest regeneration is the forest regrowth process on land that was formerly or not forested (Chazdon, 2016). It is a natural way of restoring forests ecosystems following natural disturbances (Chazdon, 2017; Uriarte & Chazdon, 2016). Moreover, it is a result of a long-term arrival of diaspores, seedling recruitment, adult individual establishment, and species replacement in a successional process during which composition of species become gradually enriched and increase in structural and functional complexity (Chazdon, 2017). The pool of species available, dispersal events and the nature, environmental conditions, in addition to intensity, frequency and history of disturbance represent a base of the regeneration process (Larson and Funk, 2016; Chazdon, 2017). Understand the underlying mechanism of this process will be an important step toward the sustainability and dynamics of forests, given that it has a significant potential for the development of next generations, carbon stock, and recovery of ecosystem functions (Khaine et al., 2018).

Understanding how forest regenerate has been a major preoccupation of ecology of plant community for more than a century (McIntosh, 1999), yet some information related to the processes underlying recovery of forests following natural and human disturbances are still actively researched (Norden et al., 2015). Although, deterministic and stochastic processes have a significant role in abundance, spatial distribution and composition of species, the contribution of each process in forest recovery dynamic represents a major challenge nowadays (Chazdon, 2008). Deterministic processes can be defined as predictable changes in species abundance determined by climate, soils, and species life history, while stochastic processes are influenced by random events that are not predictable in nature (Derroire, 2016; Norden et al., 2015). Furthermore, niche-based processes such as the competition–colonization trade-off and successional niche theory will permit characterizing species as early-successional versus late-successional (Chazdon, 2008, 2017). But these processes can vary widely across forests within the same region and climate (Chazdon, 2017).

The forest regeneration structure after natural and or human-made disturbances over time follows multiple successional pathways (Mesquita et al., 2015; Martin et al., 2013). The type of initial disturbances, ability of development of forest structural and capacity of tree to colonize are features that allow forest regeneration, where the sequence and duration of each successional phase can vary considerably among tropical forests (Chazdon, 2008). According to Mesquita et al., (2015), biomass, age, or size structure of tree populations and species composition are criteria used to define forest regeneration. Moreover, these criteria with the studies of past stand history represent a good way to distinguish changes across the forest regeneration (Martin et al., 2013) Otherwise, previous disturbance land-use can be an origin of multiples successional pathways observing within a particular tropical region (Mesquita et al., 2001).

Forest regeneration in tropical forests is influenced by multiple interacting factors that act from local to regional scales. The scale, intensity and frequency of these factors vary among the stages of forest regeneration (Chazdon et al., 2017). The early stage of forest regeneration is the first affected by these factors where stochastic processes of dispersal and colonization are likely to influence community composition most strongly, whereas later in regeneration, deterministic processes, such as species fidelity to environment, may become more powerful factors (Chazdon et al., 2008).

2.2.1 Factors influencing tropical forest regeneration

2.2.1.1 Abiotic environmental factors

Biotic environmental factors strongly influence ecosystem processes, but they are not the only actor on the stage. Several environmental filters can potentially influence tropical forest regeneration at scales ranging from the region to the site (Derroire, 2016). Climatic wetness (annual rainfall), soils conditions (nutrients concentrations and water availability) and light availability are significant for the plant growth and can have different importance across forest regeneration (Lebrija-Trejos et al., 2008).

Forest regeneration process rates increase with climatic wetness (most often measured by annual rainfall), although both at very high and very low rainfall may reduce ecosystem processes (Becknell *et al.*, 2012). Furthermore, the recovery of aboveground biomass is affected the precipitation regimes (Poorter et al., 2016) and the relative relevance of vegetative versus seed reproduction (McDonald et al., 2010).

The structure, dynamics, and species richness and composition of forest regeneration can be affected by soil properties of the site (Ceccon et al., 2003; Powers et al., 2009). In a general way, high soil water availability and high soil nutrients generally increase ecosystem processes (Telles et al., 2003, Malhi et al., 2004). Heterogeneity of soil can play an important role at local spatial scales in these processes (Roy & Singh, 1994).

Light availability may vary locally due to natural or anthropogenic disturbances (Unger et al., 2013). It can also vary at larger spatial scales due to differences in vegetation structure, such as high light availability in dry forest with low total biomass (Brokaw, 1987; Denslow, 1980).

2.2.1.2 Surrounding landscape

Given that dispersal of seeds is an important regeneration mechanism, composition of surrounding landscape that acts as a source of seeds, will determine the number and nature of species present in the seed rain and seed bank (Chazdon et al., 2014). According to Lopes et al., (2012) the proximity to the nearest forest and size of remnant forest in the landscape influences the composition and species diversity. In forest regeneration, the dominant wings may also affect the relative proportion of seeds with different dispersal mode (Janzen, 2002; Castillo-Nunez et al., 2011). Additionally, scattered trees and live-fences improve seed dispersal in the landscape because they act as stepping stones and corridors for animal dispersers (Estrada et al., 1993; Chazdon et al., 2011).

2.2.1.3 Previous and current land use

Past and current land uses type and intensity influence natural regeneration (Larkin et al., 2012; Chazdon, 2017), such as species richness and composition of the seed rain, seed bank, and structure and rate of biomass accumulation on regenerating assemblages (Ferguson et al., 2003; Larkin et al., 2012; Martin et al., 2013). Moreover, the soil texture and clay content as well as the fate of carbon and nutrients in the soil depend to the type and intensity of past land-use. Overall, the intensity, severity, extent and duration of land use have significant effect on regeneration processes from seeds dispersal to seedlings establishments (Chazdon et al., 2017).

Human disturbances are important drivers for the forest ecosystem dynamic (Hooper et al., 2004). Disturbances can enhance local biodiversity with the decreases of species richness and changes the species composition by favoring disturbance-tolerant species and species able of resprouting (Rico-Gray & Garcia-Franco, 1992; Marod et al., 2002;) and can promote β diversity of species (Willig & Presley, 2018). Moreover, it can have a negative effect on natural regeneration mechanisms by destroying the soil seed bank and killing roots when its intensity is high (Kennard et al., 2002).

2.2.1.4 In situ vegetation

Forest regeneration is a long-term ecological process where in situ vegetation following disturbances have a significant role (Martins and Engel, 2007). Although forest regeneration pathways can vary among forests types (Poorter et al., 2019), in general way, the early phase of forest regeneration is dominated by grasses and exotic species which can have a negative effect on regenerating plant species. According to Maza-Villalobos et al., (2011) presence of herbaceous soil seed banks during regeneration including the early stages can be related to their dormancy capacity. Studies have demonstrated the negative effect of herbs in the establishment of plant species (Thaxton et al., 2010; Wolfe & Van Bloem, 2012) though Esquivel et al., (2008) found that the presence of some grasses species can contribute to the establishment of plant species. Forest regeneration is featured by the increase of the structure and the complexity of vegetation a long-term ecological process where early vegetation resulting from past disturbances can initiate the process (Guevara et al., 1992; Carrière et al., 2002 a; Schlawin & Zahawi, 2008) through resprouting (Kammesheidt, 1999; Sampaio, 2007), seed rain and soil seeds bank (Guevara et al., 1986; Slocum & Horvitz, 2000; Carrière et al., 2002b; Chazdon, 2014).

2.2.2 Mechanisms of regeneration

Besides environmental and biotic factors, tropical forest regeneration closely depends of sources where new vegetation recruits arise from (Du et al., 2007). The newly dispersed seed, soil seed bank, seedlings and saplings, and resprouting that survived from disturbance are the major sources of this process (Chazdon et al., 2017).

2.2.2.1 Seed Rain

The seed rain is an important regeneration mechanism characterized by the dispersion of viable seeds in a particular area, where this mechanism represents one of the initial phases of forest regeneration process (Holl, 1999). Seed rain is a reflection of standing vegetation because it can allow to have more information to the species dispersal potential, and the persistence or potential for change of the standing vegetation (Page et al., 2002). Moreover, seed rain it has an important role in restoration ecology by providing information about how some species can attain a restored area (Turnbull et al., 2000) and how it allows the arrival of seed into the suitable uncolonized area (Baker, 1974). Additionally, the estimation of seed arrival can give information on direction of successional process by predicting the probabilities of propagule arrival (D’Angela et al., 1988).

Seed traits (size and water content) have a great importance in seed dispersal process and they will contribute to the difference among the types of forests and among the mode of dispersion (Scariot et al., 2008). For example, tropical rain forest has a low (0–16%) proportion of species dispersed by wing because is dominated by vertebrate-dispersed species, (Morellato et al., 2000); tropical dry forest is dominated by wind dispersal species due to fruits that are dried with small, low–water content seeds (Griz & Machado, 2001; Figueiredo, 2002).

Given that seed rain plays a crucial role in plant community, understanding the direct relation between seed rain and established vegetation will be a good step to the restoration of the area.

2.2.2.2 Soil seed bank

Soil seed bank represents a reserve of viable and non-germinated seeds in a soil which are potentially capable to replace an adult plant following natural or artificial death (Roberts, 1981; Baker, 1989). They can be classified as: allochthonous (originating from other places) and/or autochthonous (seeds from local species) (Santos et al., 2018). According to Thompson & Grime (1979) there are two types of soil seed bank: transient and persistent. They defined transient soil seed bank as seeds which could not remain viable for one year after year of their production and persistent seed bank are one and more year old. However, some authors have described soil seed bank on base of germination season (Walck et al., 2005). Thus, the difference between a persistent and transient seed bank is based on the presence of the alive or not alive seed bank in the next germination season respectively. A persistent soil seed bank represents a good asset for understanding regeneration mechanism.

The soil seed bank has a crucial role for population renewal and structuring of plant communities (Santos et al., 2013). They can allow the coexistence of plant species by supplying spatial and temporal heterogeneity over time and by ensuring regeneration of degraded ecosystems (Leck et al., 1989; Grime and Hillier 1992; Garwood 1989; Thompson, 1992). And at the same time, soil seed bank can allow to have information on past environmental conditions and vegetation established previously (Bakker et al., 1996; Thompson, 2000). Moreover, knowledge about the composition and density of soil seed bank provide significant information about natural dynamics, regeneration and restoration of degraded forest ecosystem following disturbance (Gerhardt & Hytteborn 1992).

Viable soil seed bank is influenced by various factors as environmental including precipitation (Hu et al., 2019), temperature (Hoyle et al., 2013), light (Liu et al., 2020), the presence of seed predators and pathogens (Santos et al. 2013, 2016) and physiological factors such as germination (Garcia-Fayos & Verdu, 1998), dormancy (Degreef et al., 2002) and viability (Shiferaw et al., 2018) strongly influence soil seed bank dynamic. Next to environmental and physiological factors, soils seed bank is highly characterized by anthropogenic disturbances (Santos et al., 2018). In order to sustain recovery of tropical forest it is important to understand the underlying environmental, physiological factors and mechanism that influence this ecological process following anthropogenic disturbances.

The relation between soil seed bank and standing vegetation have been studied in some ecosystems (Yang D. and Li W., 2013; Luo et al., 2017). These studies have shown that soil seed bank can reveal the potential of recovery of forest following disturbance, successional pathways after land use and susceptibility to biological invasions (Loydi et al., 2012). However, detailed information between established vegetation and seed bank is a major challenge nowadays.

2.2.2.3 Resprouting

Vegetative regeneration (resprouting) is the common regeneration strategy in plant species that occurs in disturbed environments (Scariot et al., 2008). On functional aspect, it is a tolerance trait which confers persistence at the plant level, allowing it to survive diverse disturbance regimes (Clarke et al., 2013). Bud bank represent a source of resprouting ability of species, its development, protection and resourcing will increase a capacity of species to resprout, which can be based on aerial, basal and below-ground part of the plant (Meier et al., 2012). Moreover, at the community level resprouting ability will allow the vegetation to be resilient to severe disturbances (Ackerly, 2003). It is a regeneration mechanism widely spread across ecosystems that face all kinds of disturbances, from rainforest (Poorter et al., 2010) and conifer forests (Dietze & Clarke, 2008) to desert shrublands (Nano & Clarke, 2011), savanna (Higgins et al., 2000; Lawes et al., 2011), Mediterranean-type ecosystems (Keeley et al., 2012) and tropical dry forest (McLaren & McDonald, 2003; Kennard et al., 2002).

Studies have shown a high frequency of vegetation sprouting after disturbance (Chazdon 2017; Poorter et al., 2010; Dietze & Clarke, 2008; Nano and Clarke, 2011). For example, resprouts represent 81-86% of individuals and 68-81% of tree species in abandoned shifting cultivation fallows in Eastern Amazonia (Viera & Proctor, 2007). Moreover, density of resprouts in shifting cultivation fallow varies with fallow age (Kammesheit, 1999). According to some authors (McLaren & McDonald, 2003; Kennard et al., 2002), there is a perception that sprouting ability is more common and more important mechanism of regeneration in tropical dry forests than in rainforests. The comparison of these ecosystems following heavy disturbance found a higher percentage of resprouts in tropical dry forest than in rainforests (Vest & Westoby, 2004). Resprouting ability varies as well among tree species (Sampaio et al., 1993; Kammasheidt 1999; McLaren & McDonald, 2003), and it is currently impossible to generate models to predict the number of species and individuals able to resprout (Bond & Midgley, 2001; Vesk & Westoby, 2004). Most clades and families have both strong sprouter and non sprouter species and individuals, and this trait is not preserved along phylogenetic lineages (Vesk & Westoby, 2004). The reasons why the sprouting is a particularly relevant regeneration mechanism are not certain, but the ability of sprouting will depend on the precipitation regime, frequency, intensity and duration of disturbance (Mc Donald et al., 2010).

Despite of fact that resprouting is an important mechanism of species persistence in ecosystems, it has received a little attention in models and theories of forest succession or forest diversity (Scariot et al., 2008). Instead, the emphasis has been on recruitment limitations (Clarck et al., 1999) or specialization of saplings for different microsite requirements such as those created by tree-fall gaps (Brokaw & Busing, 2000). Sprouting will alter forest dynamics by favoring self-replacement after stem death, even if the tree is not shade tolerant. It is most important where stem death is caused by disturbance rather than crowding or disease (Scariot et al., 2008).

Resprouting ability is really important for the conservation and management of plant species Non sprouters will be more vulnerable to recruitment failure after severe disturbance. They are more vulnerable to the problems associated with small population size, including inbreeding effects or loss of pollinators and dispersers (Bond, 1999).

2.3 SEASONALLY TROPICAL DRY FORESTS

2.3.1 Definition, distribution and conservation state

Seasonally tropical dry forests (STDFs) occur in tropical regions where there are several months of severe or absolute drought (Mooney et al., 1995). They occur in frost-free areas where the annual biological temperature is above 17 °C, annual mean precipitation ranges from 250 to 2,000 mm, and potential evaporation is greater than precipitation for a significant part of the year (Becknell et al., 2012;). The number of dry months from three to six is considered in definition of STDFs by some authors (Sanchez-Azofeifa et al., 2005; Gerhardt & Hytteborn, 1992). The seasonality of precipitation is an important environmental factor affecting the ecological processes of both STDFs and savannas, but they have distinct vegetation types differing in their structure and ecology (Dexter et al., 2015; Veenendaal et al., 2015). STDFs are dominated by trees, and have a relatively closed canopy and a higher aboveground biomass, savannas on the other hands, have a sparse tree cover and frequent fire which allow grass to dominate (Pennington et al., 2006; Pennington et al., 2009).

STDFs encompass everything from tall, semi deciduous forests to scrubland vegetation dominated by cactus (Menaut et al., 1995; Murphy & Lugo, 1995; Sampaio, 1995) and due to their variability in climate and appearance, they have been referred to by many different names in the literature (Murphy & Lugo, 1995). As following: deciduous forest, semi-deciduous forest, semi-evergreen forest, woodland, and dry seasonal forests. Local names are also used: caatinga in Brazil, miombo in southern Africa, and chaco in parts of South America (Van Bloem, 2004). Hence, generalizations about SDTFs are rare (Murphy & Lugo, 1986).

Tropical dry forests have a relative good density of species (30–90 tree species, based on surveys of 1–3 ha), 10–40 m of canopy height, and 17–40 m^2/ha of basal area (which represents 50% of wet forests), with a great variation among sites (Murphy & Lugo, 1986). Although rain forests have more net primary productivity than dry forests, similarity of growth was observed among both during the rainy season of dry forests. (Ewel, 1980; Murphy & Lugo 1986). However, due to the simple structure of dry forests the process of forest recovery following disturbances is faster than rain forests (Ewel, 1980; Murphy & Lugo 1986; Kennard, 2002).

SDTF cover more than 1 million km^2 across the three tropical regions and the neotropics is the region with the main proportion (66%) (Miles et al., 2006). SDTFs have been extensively deforested due to their attractive climate for human activities and the current extent covers only a fraction of their original one (Aronson et al., 2005), being the tropical terrestrial ecosystem most threatened worldwide (Derroire, 2016). The main sources of human disturbance in SDTF are forest fragmentation, climate change and chronic anthropogenic disturbance (CAD) such as slash and burn agriculture, grazing by livestock, collection of timber and non-timber forest products (Singh, 1998; Ribeiro et al., 2015). Despite these threats and importance of SDTFs, these latter have been neglected compared with tropical rain forests, where there are four to five times more studies on regeneration pathways (Viera & Scariot, 2006). It is important to recognize that a good understanding of how their environmental characteristics and factors (light, soils properties and water availability) affect their dynamic is important for their conservation and restoration.

2.3.2 Seasonality and variability in the dry forest climate

The strong seasonality of precipitation represents the most characteristic feature of tropical dry forests (Mooney et al., 1995). Despite this general pattern, there is considerable inter and intra annual variability in rainfall within and among SDTFs (Murphy and Lugo

1986). Tropical forests, even wet or rain tropical forests, are to some extent seasonal with respect to rainfall (Walter & Lieth, 1967), a limiting factor to ecosystem structure and function. Seasonality in SDTFs is well distinctive among sites, with water and light as factors limiting performance of plants species during the dry and rainy season respectively (Derroire, 2016).

Rainfall seasonality becomes a dominant ecological parameter when temporal patterns of biological activities such as germination, growth or reproduction become synchronized with the water availability or when the geographic distributions of plant or animal taxa are constrained by moisture limitations during certain periods of the year. The coexistence of plant species during a dry season in STDFs is related to their strategies linked to tolerance of water limitation (Giraldo & Holbrook, 2011). For example, tree species have leaf phenological patterns ranging along a gradient of deciduousness (Frankie et al., 1974; Borchert, 1994).

Another temporal aspect of climate that is not between seasons is year-to-year variability. Variability in the annual amount of rainfall and variability in the intensity and timing of wet and dry periods have relevant considerations in tropical areas. Variability is important for ecosystems near threshold levels of water supply, that is, systems that include numerous plants or animal components near the margins of their drought tolerance. The high level of water stress occurring during dry years is a common cause of tree mortality (Pook et al., 1966). According to Doley (1981), the extreme years, rather than the average years, may be of most significance in molding overall structural, compositional, and functional properties of dry forest ecosystems.

2.3.3 Regeneration specificity in STDFs

Forest regeneration in SDTFs is different from that in rainforests (see reviews in Vieira & Scariot, 2006 and McDonald et al., 2010). The type and size of canopy are principals' mechanism of regeneration in rainforests because they provide light and shade that are necessary for seed germination and seedlings establishments (Hardwick et al., 1997; Hoffmann, 2000). Whereas, in STDFs the rainy season (timing and duration of rainfall) is crucial for the regeneration due to the availability of water that soil seed bank needed for germination and for successful establishment of seedlings (McDonald et al., 2010; Anderson-Teixeira et al., 2013). Besides environmental factors, regeneration of SDTFs closely depends of sources where new vegetation recruits arise from. Regeneration in SDTFs is featured by the low density (Derroire, 2016) of soil seed bank and these seeds are facing to predation, water shortage, pathogens and competition with exotic grass (Scariot et al., 2008; Derroire, 2016). Further, vegetative reproduction through sprouting is a relevant source of regeneration in SDTFs (Vieira & Scariot 2006; Barros, 2018). Studies have shown a high frequency of vegetation sprouting after disturbance (Viera & Proctor, 2007; Chazdon, 2017).

The capacity and rate of forest recovery after disturbance in terms of structure, composition and functioning is a major topic nowadays (Arroyo-Rodriguez et al., 2016; Derroire, 2016). In STDFs, sprouting demonstrated a high degree of resilience after pasture implementation (Scariot et al., 2008) and following logging and cyclones (Chazdon, 2017). Otherwise, anthropogenic disturbance and climate may reduce regenerating trees and consequently reduce the resilience of this ecosystem (Tylianakys et al., 2007), as well as, complicated interactions between intrinsic and extrinsic factors can affect resilience of forest (Lebrija-Trejos et al., 2010). This ecological process has no long started to be addressed despite its importance for maintaining biodiversity under anthropogenic pressures (Vieira & Scariot, 2006 and McDonald et al., 2010).

2.4 CAATINGA

Caatinga is a part of the world's largest and most diverse seasonally dry tropical forest with over 800.000 km^2 (Rito et al., 2017; Silva et al., 2017). It is composed of geo environmental units (at least 135) and nine ecoregions (Silva et al., 2017). This particular composition allows it to sustain several species and to be home of endemic species (Silva et al., 2017).

The Caatinga vegetation, including human populations that inhabit in the area, is a diverse and threatened biota. Human population living in the region (28 million of people; Silva et al., 2017) are highly dependent of natural resources extracted from Caatinga. These populations impose acute and chronic disturbances by means of wood extraction, subsistence agriculture, cattle ranching, which may lead to the complete desertification (Rito et al., 2017). The region is undergoing a climate change characterized by an impressive increase of temperature and a reduction in levels of rainfall (Magrin et al., 2014). This climate change can affect the ecosystem services provide by this tropical forest to human population for their wellbeing. In this context, the Caatinga is a good opportunity to investigate the effects of disturbance and climate change, especially the reduction in precipitation, on plants communities of dry forests, as well as to characterize the patterns of community organization that emerge from the transformations caused by human activities in these habitats.

Besides to describe the classical mechanisms of forest regeneration (seed rain, seed bank, seedling bank and vegetation sprout), studies of this forest will allow understanding the contribution of different mechanisms in the Caatinga vegetation with different levels of human disturbance and environmental factors. As previous studies indicate that deterministic replacement of plant species along forest succession is not observed (Barros, 2018) and disturbances negatively affect the seed dispersion by ants (Leal et al., 2014; Oliveira et al., 2019; 2020; Silva et al., 2019), this study can bring some light on how plant communities re-organize after disturbance and which is the most important mechanism of forest regeneration. Additionally, studies that analyze the effects of environmental factors (light, soils properties and water availability) on natural regeneration at the same time are scarce, although they are crucial for a better understanding of factor underlying the patterns of plant recruitment. These knowledge gaps are particularly intense in the seasonally dry tropical forests as Caatinga, compared to temperate ecosystems or tropical rainforests (Tabarelli et al., 2008; Lebrija-Trejos et al., 2010).

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3 EFFECTS OF CHRONIC ANTHROPOGENIC DISTURBANCES AND ENVIRONMENTAL FACTORS ON REGENERATION MECHANISMS IN CAATINGA DRY FOREST

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Effects of chronic anthropogenic disturbances and environmental factors on regeneration mechanisms in Caatinga dry forest

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Abstract

Natural regeneration is an important ecological process for the understanding of forest recovery following natural and human disturbances. But while regeneration mechanisms received substantial attention in tropical rain forests, they have received little attention in tropical dry forests. To address this knowledge gap, we assessed the effects of chronic anthropogenic disturbances and environmental factors on regeneration mechanisms (seed rain, soil seed bank, true seedlings, true saplings and resprouts) in the Caatinga dry forest.

We used a multi model approach to evaluate the isolated and combined effects of chronic disturbance, soil fertility, light (via leaf area index) and aridity on abundance, species richness, and species composition of seed rain, soil seed bank, true seedlings, true saplings and resprouts in 18 0.1-ha plots in the Catimbau National Park, NE Brazil.

We found very sparse and impoverished regenerating assemblages with high variability across the different regeneration mechanisms with the seed rain density ranging from 0.2 to 432.3 seeds/m^2, density of viable soil seed bank varying from 5 to 2555 seeds/m^2, density of true seedlings ranging from 0 to 5.91 ind/m^2, true sapling density from 0 to 0.66 ind/m^2 and resprout density from 0 to 1.28 ind/m^2. Resprouting was the most important mechanism of regeneration in term of abundance and species richness, mostly from the stem with 63% of regenerating assemblages. The influence of chronic disturbance and environmental factors on abundance and species richness of regenerating mechanisms varied depending on the size class and source of plant regeneration (seeds, true seedling and saplings or sprout). Abundance of the seed rain, soil seed bank, true seedling and saplings and resprouts and species richness of true seedlings were negatively explained by chronic disturbance. Seed rain richness and true sapling abundance were positively and negatively affected by leaf area index, respectively, though interaction between leaf area index and rainfall was positively related to soil seed bank richness. Differences in structure and species composition of the soil seed bank, true seedlings, true saplings and resprouts were explained only by aridity.

Our results demonstrate the negative effect of increasing chronic disturbance and aridity on regenerating woody plant assemblages. Thus, given the predicted increased aridity associated to increased human disturbance, the Caatinga dry forest may experience shifts in its regeneration patterns with unknow effects on long-term forest dynamic, biodiversity persistence and forest resilience.

Key-words: community assembly, human disturbance, aridity, regenerating plant assemblages, resprouting, seasonally dry tropical forests, seed rain, seed soil bank, seedlings, saplings.

Introduction

Environmental factors, natural and human-made disturbances and forest degradation in general are important drivers of forest ecosystems dynamics and regeneration (Sheil, 2016; Grime, 1977; Pickett *et al*.,1999; Walker and Willig, 1999). They have a significant role in shaping biodiversity (Kannan *et al*., 2009; Huston, 1979; Franklin *et al*., 2002; Kuuluvainen and Aakala, 2011; Thom and Seidl, 2016; Drakare *et al*., 2006) and can enhance local biodiversity through their positive and or negative effects on individual recruitment and species distributions (Garcıa-Valdes *et al*., 2015). Moreover, they can promote biodiversity (mainly the β level) which depend on the intensity, extent and frequency of disturbances and species present in the community (Willig and Presley, 2018; Mantyka-Pringle *et al*., 2015). Studies have shown that disturbance regimes, forest degradation and climate change are key drivers of ecological assemblages and processes (Sala *et al*., 2000). Thus, attention to their combined and interactive effects are necessary to understand functioning of the ecosystems in the changing world.

Chronic anthropogenic disturbance (hereafter chronic disturbance) refers to forest biomass removal through the extraction of firewood collection, non-timber forest products exploitation, livestock raising, introduction of exotic plant as forage, hunting among other natural resource use, widespread in developing countries (Singh, 1998). This continuous use of forest resources and its combination with slash-and-burn agriculture (i.e., forest degradation sensu Gazhoul *et al*., 2015) leads natural ecosystem to a state of anthropogenically induced arrested succession, where ecological processes that underlie forest dynamics are diminished or severely constrained (Gazhoul *et al*., 2015). In fact, past studies on such chronic disturbance have demonstrated negative effects on stem density and taxonomic diversity of plant assemblages, (Hernandez-Oria *et al*., 2006; Ribeiro *et al*., 2015; Rito *et al*., 2017), phylogenetic diversity (Ribeiro *et al*., 2016), functional diversity (Rito *et* *al*., 2018; Ribeiro *et al*., 2019), the distribution of plant reproductive traits (Silva *et al*., 2019) and the homogenization of biotic communities (Ribeiro-Neto *et al*., 2016; Singh *et al*.,1997; Ribeiro *et al*., 2015). In addition, chronic disturbance can also reduce seed dispersal, seedling recruitment and seeding bank (Leal et *al*., 2014, Knochelman *et al*., 2020, Trindade *et al*., 2020, Vanderlei *et al*., 2022) and then may negatively affect natural regeneration. Yet, studies that investigate how chronic disturbance affects regeneration of plant communities are still limited.

Environmental factors are also determinants of the morphology, phenology and physiology of organisms (Yu *et al*., 2016), the ecology of seed dispersal (Travis *et al*., 2013), the distribution and abundance of species (Mair *et al*., 2014), the composition of, and interaction within communities (Rubenstein, 1992), the functioning of ecosystems (Walther *et al*., 2002) and natural regeneration (Hishe *et al*., 2021; Ceccon *et al*., 2006). Light intensity is linked to phenological, morphological and physiological changes of plant species (Zervoudakis *et al*., 2012; Muraoka *et al*., 2002; De Carvalho Gonçalves *et al*., 2005) and structuring and organization of plant communities (Valladares and Niinemets, 2008). In addition to light, water and soil nutrient availability are key environmental factors that are linked with the development of seedlings and saplings, the growth of adult trees and the seed dispersal event (Niinemets and Valladares, 2008; Niinemets, 2010; Travis *et al*., 2013). Although, chronic disturbances interact with environmental factors such as precipitation regime, light, water availability and soil fertility to affect species organization and distribution in the community (Morana *et al*., 1999; Rito *et al*., 2018), more information is needed for understanding their isolated and combined effect on regeneration processes.

Forest regeneration can be defined as a process through which a forest regrows following natural or anthropogenic disturbances (Chazdon, 2017; Vieira and Scariot, 2006; McDonald *et al*., 2010). The seed rain, seed bank, assemblages of seedlings, saplings, and resprouts following disturbances represent a critical stage of forest regeneration (Maza-Villalobos *et al*., 2010). They have a significant potential for the development of the next generation, carbon stock and ecosystems functions (Khaine *et al*., 2018). Moreover, a joint consideration of seed and seedling banks and standing vegetation can improve knowledge on dynamic, structure and composition of adult plant assemblages (Gomes *et al*., 2019; Dalling *et al*., 2002), response of disturbances (Auffret and Cousins 2011), ecosystem resilience (Hopfensperger, 2007) and even restoration (Savadogo *et al*., 2016). Nevertheless, seed predation, grass competition, exotic or invasive plant competition, drastic environmental conditions and soil compaction threaten the recruitment of regenerants (Zimmerman *et al*., 2000; Aide and Cavelier, 1994, Nepstad *et al*.,1996; Loik and Holl, 1999, Alvarez-Aquino *et al*., 2004; Derroire, 2016). In dry forests, due to their seasonality and short rainy season, these threats are more pronounced (Murphy and Lugo, 1986). Considering that regeneration depends on rapid increase in the vegetation (Khurana and Singh, 2000; Chazdon, 2017), resprouting is a common regeneration strategy for plant species following disturbances (Scariot *et al*., 2008; Poorter *et al*., 2010; Dietze and Clarke, 2008; Nano and Clarke, 2011). Thus, understanding how biotic and abiotic factors influence this regeneration mechanism and regenerating assemblages will be important for the management of these ecosystems.

The Brazilian Caatinga is the world’s most extensive and most diverse seasonally dry tropical forest (Silva *et al*., 2017). The Caatinga is an ecosystem with the most extreme climate, high temperature, low rainfall and a relative fertile soil (Silva *et al*., 2017). Human population living in the region are highly dependent on natural resources for their livelihood and impose a common set of disturbance/degradation such as slash-and-burn agriculture, wood extraction, exploitation of non-timer forest products, cattle ranching, which have enormous impact on the remaining forests ecosystems (Rito *et al*., 2017; Silva *et al*., 2017; Ribeiro *et al*., 2015; 2016). Additionally, Caatinga region is undergoing a climate change characterized by an impressive increase of temperature up to 6°C and a reduction in rainfall up to 22% until the end of this century (Magrin *et al*., 2014). This projection of climate change will exacerbate ecological filters imposed to Caatinga biota and can affect the ecosystem services provided by this tropical forest to human population for their wellbeing. In this context, the Caatinga is a good target for investigating the effects of disturbance and environmental factors, especially the rainfall reduction on regeneration mechanisms of dry forests, as well as to characterize the patterns of regenerating plant assemblage organization that emerge from the transformations caused by human activities in these habitats.

In this study, we evaluated the effects of chronic anthropogenic disturbances and environmental factors (rainfall, soil fertility, light availability) on regeneration mechanisms in Caatinga dry forest. Our general hypothesis is that disturbance and harsher environmental conditions will negatively affect reproductive regenerating mechanisms (seed rain, soil seedbank, true seedling and true sapling) while promoting resprouting. Thus, our predictions were: (1) increasing chronic disturbance, aridity, soil infertility and light penetration negatively affect the abundance, richness, of seed rain, soil seed bank, true seedlings and true saplings while positively affect resprouts, (2) resprouts are the main regeneration mechanism and resprouts by roots are more frequently represented; (3) increasing disturbance, aridity, soil infertility and light penetration lead to a significant rearrangement of regenerating plant assemblages via the replacement of seeds and recruits of disturbance-sensitive-species by disturbance-adapted species.

Materials and methods

Study site

The study was carried out in the Catimbau National Park (8°24'00″-8°36'35″ S; 37°00'30″-37°10'40″ W, Fig. 1), a protected area with 607 km² in rural Pernambuco State, northeastern Brazil. The climate type is semi-arid bsh’ with the transition to the tropical rainy As’ according to the Köppen classification system. The annual precipitation ranges between 440 to 1100 mm with a significant interannual variation (Rito *et al*., 2017). Most rain (60-75%) falls between March and July; from August to February a long dry season occurs. The annual average temperature is around 23°C, with the maximum (December) and minimum (July) of 25°C and 21°C, respectively. Seventy-two percent of the Park area is covered by quartzite sandy soils supporting low stature caatinga vegetation (Rito *et al*., 2017). The vegetation is dominated by the families Leguminoseae, Euphorbiaceae, Boraginaceae and Burseraceae (Rito et al. 2017). The Park was created in 2002, and low-income rural populations still live in the park, using it for grazing and browsing by livestock, collection of living and dead wood, harvesting of non-timber forest products, and hunting (Rito et al. 2017).

Experimental design

Field work was carried out between July 2018 and July 2020 in eighteen 0.1-ha permanent plots (20 m x 50 m) from the Catimbau Long-Term Ecological Project (https://www.peldcatimbau.org/), which cover a wide range of rainfall and disturbance intensity (Rito et al. 2017) (please see Fig. 1). All plots were on sandy soil, on flat terrain, and supported old-growth vegetation that had not experienced slash-and-burn agriculture for at least 50 y. Plots were separated by a minimum of 2 km and located within a total area of 21,430 ha (Rito et al. 2017).

Measurement of chronic anthropogenic disturbances index

Data on the level of chronic anthropogenic disturbance of each plot was obtained by global multi-metric chronic anthropogenic disturbances (CAD) index (Arnan *et al*., 2018), considering three main sources of disturbance in the region: livestock pressure, wood extraction and exploitation of non-timber forest products. The livestock pressure was estimated in the field by measuring goat-trail length and counting goat and cattle dung. The wood extraction was measured in the field by direct counting of stem cuts (live-wood extraction) and collection of course woody debris (fire wood exploitation) in the field. The exploitation of non-timber forest products index was calculated based on two indirect measures of accessibility to our plots as surrogates for the intensity of harvesting of non-timber products. First, two distances were measured, proximity to the nearest house and proximity to the nearest road, using satellite imagery and ArcGIS 10.1 software. Since distance is inversely related to level of disturbance, we used the inverse of distance as our metric. Then, we identified the nearest village to each plot using GIS and then conducted informal and semi structured interviews to assess the number of people in each village, which we weighted by distance from the plots. Data from these eight disturbance indicators (goat trail, goat dung, cattle dung, live-wood extraction, fire wood collection, proximity to house, proximity to road, and number of people) were integrated into a single CAD index (for methodological details, see Arnan et al. 2018b). The index ranges from 2 to 58 (from the lowest to the highest disturbance intensity) among the plots.

Environmental variables

Mean annual rainfall data was extracted from the worldclim global climate repository data (Hijmans et al., 2005), with a spatial resolution of 1 km recorded with the maptolls package ofR 3.6.1. This package provided the mean annual rainfall for each plot, ranging from 510 mmto 940 mm. This significant difference among plots in the same area provided   a goodopportunity for assessing the effect of this environmental factor on regeneration processes. Providing such extreme variation in a small geographic area the study area provides a good opportunity for assessing the effect of this environmental factor on regeneration processes.

To determine the soil fertility of each plot, three soil samples of 10×10 cm^2 of superficial soil were selected randomly from 0 to 30 cm depth. The soil samples were sent for laboratory-based analysis of soil physico–chemical properties related to nutrient availability (Al, H, S, P, CTC, Ca, PH, K), water content, organic matter and acidity (Sfair *et al.*, 2018). These analyses followed the procedures recommended by the Brazilian Ministry of Agriculture for soil analyses (Embrapa, 1997; Barros et al., 2021). The formula SF = [Ca + Mg + K − log(1 + A1)] × OM + 5 was used to determine soil fertility of each plot, where SF = soil fertility, Ca = exchangeable calcium (cmolc dm^{-3}), Mg = exchangeable magnesium (cmolc dm^{-3}), K = exchangeable potassium (cmolc dm^{-3}), Al = exchangeable aluminium (cmolc dm^{-3}), and OM = organic matter (g kg^{-1}).

To assess light conditions (leaf area index and canopy openness) of each plot, 10 hemispherical photographs were taken 1.50 m from the ground level, at 5-m intervals and at dawn before sunrise or at dusk after sunset to avoid direct solar radiation in any part of the canopy (Whitmore *et al.* 1993; Siqueira et al. 2018). Photographs were taken again across the same plots and during the same time in the morning three times during the year 2016 within the seasons. We analyzed the hemispherical photographs with the Gap Light Analyser software (GLA, version 2.0) in order to obtain the leaf area index and canopy openness index of each plot (Frazer *et al.*, 1999, Siqueira et al. 2018).

Seed rain sampling

Seed traps were used to collect the seed rain. The seed trap was composed of a deep squared plastic tray with an effective trapping area. Holes were drilled through the tray to drain out rainwater. The tray was covered with a piece of brown cloth for easy collection of seeds and it was then covered by wire mesh in order to exclude vertebrate seed predators. We randomly placed 5 seed traps of 1 m^2 at 1 m of the soil level in each plot. Seed rain was collected monthly between July 2018 and July 2020. The materials in the cloths were carefully screened and identified in the laboratory. All visible and healthy seeds were counted and extracted

Soil seed bank sampling

Ten soils samples were collected in 20 cm × 20 cm × 5 cm square at random in each plot at the end of both dry and rainy season for two consecutive years. A viability assessment of tetranozol test was used to know viability of seeds and, only soil seed tested positive of tetratnozol was considered (Souza *et al*., 2016).

Measurements of adult and regenerating assemblages

At each plot, adults, saplings and seedlings of woody species were sampled using standard forestry methods (Köhl and Magnussen, 2016). Adults were defined as individuals with diameter at soil level (DSA) > 3 cm and height > 1.5, saplings were defined as individuals with DSA <3 cm and height between 1 and 1.5 m; and seedlings were defined as individuals with height <1 m (Ribeiro et al. 2015). We sampled adult trees in each 50 m × 20 m plot, saplings were recorded in three 5 m × 5 m subplots located in the centre of each 50 m × 20 m plot and separated by 10 m. Seedling communities were sampled in two 2 m × 1 m subplots located in the centre of each 5 × 5 m subplot. All plants were identified at species level according to the botanical nomenclature followed by the Angiosperms Phylogeny Group (APG IV 2016) and Brazilian flora list. The community of saplings and seedlings in each plot was examined for sprouting by digging a 30 cm hole around each stem when was necessary. Individuals were classified as true seedling/saplings if they were not connected to an adult tree or as resprouts if they were connected to an adult individual that was not a sprout or a ramet. The presence of sprout scars on the stems were also observed and considered. Resprouts were classified according to their organ of origin: (i) stems (resprouts from stumps or thin stems); (ii) root collars; or (iii) roots (lateral or taproot). We used the adult-to-offspring ratio for the most abundant adult species according to Pausas and Keley (2014) to determine the natural regeneration capacity of species.

The sample completeness of each plot and each ontogenetic stage was calculated with the sample coverage estimator recommended by Chao and Jost (2012) as the following equation:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right].$$

Where f_1 and f_2 represent the number of species with one and two individuals respectively, and n is the number of individuals. Due to the low species richness in plots, sample coverage was variable among the plots and ontogenetic stages and sample completeness differences could bias sample coverage (Chao and Jost 2012). Thereby, coverage-based extrapolations of the INEXT software (Hsieh, Ma and Chao 2013) were used to estimate the species richness of adult, sapling and seedling.

Statistical analyses

To assess the collinearity among the predictor variables, we conducted Spearman correlations among them and only the correlation matrix value lower than 0.4 were considered, canopy openness, Al, H, S, P, CTC, Ca, PH, K variables were excluded and chronic anthropogenic disturbance index, rainfall, soil fertility and leaf area index (LAI) were considered for further analyses (Table S1). To determine the spatial independence of plots, the species composition similarity among plots (Bray-Curtis index) and inter-plots distance matrix (one per ontogenetic stages) were assessed with the Mantel test. Mantel results indicated a spatial independence of our plots for all ontogenetic stages (adult r=0.07 p=0.37; sapling r=0.01 p=0.5 and seedling r=-0.03 p= 0.65).

To determine the structure of woody plant regenerating assemblage in each plot, abundance (i.e., the number of seeds in the rain, in the soil bank, seedlings, saplings and adults), species richness (i.e., the number of species of seeds in the rain, in the soil bank, seedlings, saplings, and adults) and diversity (Shannon diversity) of seed rain, soil seed bank, seedlings, saplings and adults were compared. To assess diversity and species richness among regeneration mechanism and adult trees, we used the interpolation and extrapolation method in iNEXT (Chao *et al.*, 2014; Hsieh *et al.*, 2016). Rarefaction and extrapolation curves were performed in iNEXT (Chao *et al*., 2014) and compared among the regeneration mechanism and adult trees. Kruskal-Wallis test followed by pairwise Wilcoxon test was used when the response variable did not meet the assumption of a one-way ANOVA.

To test the influence of isolated and combined explanatory variables (chronic disturbance index, annual rainfall, soil fertility, and leaf area index on response variables (abundance and species richness) of seed rain, soil seed bank, true seedlings, true saplings, resprouts and total regenerating assemblage, we used a model selection approach. Firstly, general linear models (GLM) and General Linear Mixed Models (GLMM) were constructed and, a Poisson distribution error was fixed for all models, and, in case of overdispersion, a quasi-Poisson distribution error was fixed. Candidate models for each response variables (species richness and abundance) were chosen based on our explanatory variables and empirical support. Then, the Akaike's information criterion with a correction for small samples (AICc) were used to select the best models. In case of overdispersion, qAICc was used instead of AICc for models ranking (Calcagno and Mazancourt 2010). To select the best models, set models with AICc (or qAICc) differences lower than 2 were selected (Burnham and Anderson 2002). The most important predictors were contained in the best-supported models where intercept was not the only component (Burnham and Anderson 2002). The model selection was conducted using the dredge function in the MuMin package in R (R core team, 2019). The selected model among the best models (D ((Q)AICc) < 2) was the model with the highest R^2 (Burnham and Anderson 2002).

The effects of abiotic factors on species composition of regenerating assemblages were assessed using the non-metric multidimensional scaling (NMDS) and the envif method from vegan package (Oksanen *et al*., 2016) was used to obtained the effect of each variable on the composition of the community. Correlations between species richness of total regenerative community and adult tree species richness, and, between abundance of all regenerative community and abundance of adult tree were realized using regression linear.

Results

Seed rain and soil seed bank, regenerating assemblages and adult trees

We collected a total of 5239 seeds in the seed rain traps and 932 in the soil bank from 40 and 33 species and 15 and 12 families respectively (Table 1). Considering only seed rain, Fabaceae and Euphorbiaceae were also most diverse with 15 and 14 species respectively; at species level, *Pityrocapa moniliformis, Cnidoscolus bahianus* and *Senegalia piauhiensis* were most frequent occurring in 12, 10 and 10 plots respectively (Table S1). In the soil seed bank, Fabaceae (15 species) and Euphorbiaceae (10 species) were also the most diverse families, and *Pityrocapa moliliformis, Byrsonima gardneriana and Commiphora leptophloeos* were species most frequent species occurring in 10, 9 and 9 plots respectively (Table S1). In relation to regenerating assemblages, 663 individuals (seedlings, saplings and sprouts) were collected across all studied plots from 103 species and 32 families (Table S1). Again Fabaceae (12 species) Euphorbiaceae (10 species) were also the most diverse family; Jatropha mutabilis and Pityrocapa moliliformis were most widely distributed species and occurred in 11 and 9 plots, respectively (Table S1). In adult trees, we surveyed 3896 individuals belonging to 97 species and 27 families (Table S1). The most species rich family were Fabaceae (27 species), followed by Euphorbiaceae (15 species) and Myrtaceae and Boraginaceae (with 6 species both). Among surveyed genera, *Croton*, *Jatropha*, *Pityrocarpa* and *Poincianela* were the most speciose and widely distributed, while *Oxandra*, *Solanum* and *Myroxylon* were rarest (Table S1). *Poincianela mycrophyla* occurred in 15 plots, while *Xylosma ciliatifolia, Stillingia trapezoidea, Solanum rhytidoandrum, Sideroxylon obtusifolium, Senna splendida, Senna spectabilis, Oxandra reticulata* etc. were registered for one plot only (Table S1).

Relationship between adult trees, seed rain and seed bank and regenerating assemblage

Regarding relationships between adult assemblages and regeneration mechanisms across studied plots, the abundance of adult trees did not correlate to the abundance of seed rain (R^2=0.04, F=1.664, P=0.219) and soil seed bank (R^2=0.03, F=0.422, P=0.525) abundance. Although there was no relationship between the abundance of adult tree and the abundance of true seedling (P=0.584, F=0.559, R^2=0.02), true saplings (P=0.04, F=-2.02, R^2=0.23) and resprouts (P=0.05, F=2.08, R^2=0.21) abundance were negatively and positively related to abundance of adult tree respectively (Fig 2a and Fig. 2b).Adult tree richness was not correlated with the richness in the seed rain (P=0.188, F=1.922, R^2=0.06), soil seed bank (P=0.265, F=1.338 R^2=0.01), true seedling (P=0.9, F=0.02, R^2=0.01), true saplings (P=0.25, F=1.16, R^2=0.08) but was positively correlated with (P=0.006, F=3.14, R^2=0.38) (Fig. 2c). Regenerating assemblages were highly variable in relation to true seedling, true sapling and resprouts with very low plant abundance and species richness (Table 2). Overall, the density of all regenerants type varied from 0.01 to 1.62 individual per m^2 (ind/m^2). True seedling density varied from 0 to 5.91 ind/m^2, true sapling density varied from 0 to 0.66 ind/m^2 and sprout density varied from 0 to 1.28 ind/m^2.

Despite the low density of regenerating assemblages, abundance and species richness were significantly different among regenerating assemblages (ANOVA, F= 13.87, P= 1.55e-05; Kruskal-Wallis, F= 17.473, P= 0.0001 respectively), with resprouts showing the highest values followed by seedlings (Fig. 3). Resprouting from stems was the most abundant type of regenerating assemblages (ANOVA, F= 8.346, P=0.0007 Fig.4). In regenerating assemblages, resprouts represent 63% and among the more abundant species, the genera *Jatropha* was the only that we did not find any resprouts. Regeneration capacity of species of the most abundant adult species indicated a highest adult-to-offspring ratio in true seedlings for *Jatropha mutabilis* (0.279) followed by *Trichidium molle* (0.208) (Table 2). *Jatropha* *mutabilis* was also the species with the highest adult-to-offspring ratio (0.201) followed by *Croton nepetifolius* (0.005). Contrary to true seedlings and true saplings among the most abundant species, the high adult-to-offspring ratio for resprouts was observed in *Cnidoscolus bahianus* (1.33) followed by *Senegalia piauhiensis* (1.28) (Table 2). Some of these species are exotics and they are autochorous as dispersal mode (Table 3).

Effects of environmental factor and chronic disturbance on regeneration mechanisms

GLMM and GLM showed that the influence of chronic disturbance and environmental factors on abundance and species richness of seed rain, soil seed bank and regenerating assemblages varied depending on the regenerant type. More precisely, the abundance of seed rain and soil seed bank was negatively related to chronic disturbance (GLMM, t=-2.38; df=13; p=0.01 and GLMM, t=-1.93; df = 16; p=0.05 respectively). Richness of seed rain was positively related to leaf area index (GLMM, t=1.19; df=13; p= 0.05,), as well as to the interaction between leaf area index and rainfall (GLMM, t=0.11; df=13; p=0.01). In regenerating assemblages, abundance of all regenerating assemblages combined was negatively influenced only by chronic disturbance (GLM, P=0.01, F=-2.62; Table 4). Given that true seedling abundance was not affected by any explicative variables, , true sapling abundance was also negatively affected by leaf area index (GLM, P=0.004, F=-3.34; Table 4) and resprout abundance was also negatively affected by chronic disturbance (GLM, P=0.05, F=-2.08; Table 4). Species richness of all regenerating assemblages combined was not related nor to chronic disturbance and to environmental factors (Table 4). And, only species richness of true seedlings was negatively related to chronic disturbance (GLM P=0.05, F=-1.893; Table 4). Contrary to our expectations none of combined interactions among explicative variables was selected and related to response variable regarding regenerating assemblages (Table 5). The results of NMDS indicated that species composition of soil seed bank, all regenerating assemblages and sprouts were explained by annual rainfall (R2=0.36, P=0.03, Fig. 5a; R2=0.35, P=0.03, Fig. 5b; R2=0.35, P=0.05, Fig.5c).

Discussion

Our study investigated the influence of chronic anthropogenic disturbance and environmental factors on woody plant regenerating assemblages. Our results suggest that the Caatinga dry forest on sandy soils supports low-density and taxonomically impoverished seed rain and soil bank, as well as all regenerating assemblages (seedling, saplings and resprouts). Additionally, chronic disturbance shapes the structure of seed rain, soil seed bank and all regenerating assemblages, while aridity alter species composition of soil seed bank, all regenerating assemblages and sprout, separately,. There is a difference between the adult and regenerating assemblages in terms of abundance and richness, showing that most species have a limited regeneration. Finally, resprouts are the most important regeneration mechanism across studied plots and resprouting from stems is the most widespread type of vegetative recovery**.**

These findings are in accordance to previous studies in tropical dry forests around the worldwide (Scariot *et al*., 2007; Murphy and Lugo, 1986; Swaine, 1992;), as well as in Caatinga dry forest (Ribeiro *et al*., 2015; Barros et al. 2021, Vanderlei et al. 2021, 2022). For instance, in the same study area Vanderlei et al. (2022) observed very low dense and impoverished seedling assemblages, and Trindade et al. (2020) reported a functionally structured seedling assemblage mediated mostly by water availability more than time since abandonment (4-70 years) in chronosequence of forest regeneration. Moreover, Barros et al. (2021) and Vanderlei et al. (2021) suggested that regeneration of areas that previously supported slash-and-burn agriculture rely mostly on resprouting. However, disturbance may have a negative effect even on resprouts as demonstrated in dry forests (Kennard *et al*., 2002), deciduous forest (Ferreira *et al*., 2017) and savanna (Franklin *et al*., 2010). Finally, resprouting from roots has been found as the most frequent mechanism of regeneration in dry forests of Central Brazil (Scariot *et al*., 2008).

The very sparse and impoverished seed rain, seed soil bank and regenerating assemblages may be a result of dispersal limitations and low capacity to establish new seedling and saplings in consequence of severe environmental conditions of Caatinga dry forest in addition to chronic disturbance. Dispersal limitation is a major constraint in dry forest regeneration (Janzen, 1998), as is seed predation (Jones *et al*., 2003; Scariot *et al*., 2008). The environmental conditions of Caatinga are very severe (open and disclaimed, with high temperature and low availability of water) which impede regeneration. There are severe environmental filters in Caatinga. In addition, the ecological filtering, dense and species rich regenerating assemblages may be explained by negative interaction with native weeds and exotic invasive species (Holl *et al*., 2000). Nascimento *et al*., (2014) reported for example, that the presence of *Prosopis juliflora* individuals in the community negatively affects regeneration by reducing seedling growth and increase of seedling mortality of native plant species in the Caatinga dry forest. Additionally, *Lantana camara* found in our regeneration community is known as invasive species in dry forest worldwide and study realized in the seasonally dry forest of Mudumalai, southern India revealed that it has affected the establishment of native seedlings (Ramaswami and Sukumar 2011). Moreover, very aggressive herbaceous species (for instance, some Malvaceae species in the Catimbau area, Vieira et al., 2022) can also affect seed germination and seedling establishment due to competition for the available resources (Holl, 1999; Holz *et al*., 2009). Given that herbaceous species are more abundant in the Caatinga vegetation than juveniles of woody species (Knoechelmann *et al*., 2020; Menezes *et al*., 2020), their role as barriers of recruitment by trees can explain some of our results. Additionally, seed dispersed and established seedlings can be also attacked by pathogens (Myster, 2004) which affected regeneration. According to

Gerhardt and Hytteborn (1992); Swaine, (1992) and Ceccon *et al*., 2006), regeneration is indeed commonly very low in dry tropical forest.

Given that natural regeneration represents the mechanism by which species colonize a previously disturbed area (Chazdon, 2017), a high adult-to-offspring ratio is related to a good potential for recovering assemblages, whereas species with a low ratio were considered to have limited regeneration. In this study, the adult-to-offspring ratio of true seedling, true sapling and resprouts were low, revealing a limited capacity of these species to recolonize the area. Although, eighty per cent of the species were primarily dispersed by autochory (Table 3), with a great capacity for resprouting. These characteristics allow them to resist and overcome the environmental and anthropogenic barriers to seedling survival and establishment (Chazdon, 2003; Quesada *et al*., 2009). These results were contrary to some previous studies which showed that the first stage of regeneration in dry tropical forest was by wind dispersed species (Chazdon *et al*., 2007; Viera and Scariot, 2006; Sabogal, 1992). Resprouts in relation to regenerating assemblages were the most important regeneration mechanism across the studied plots. Moreover, the highest abundance and species richness of resprouts were found in the least disturbed plots. These results were contrary to our expectations, and can be explained by the fact that some species can lose resprouting ability with repeated disturbance (Bellingham and Sparrow, 2000). The higher frequency of resprouting from stems can be explained by coppicing by local residents who use certain parts of the plant for their needs (Table 3). Additionally, bud banks in stems, responsible for resprouting, are highly sensitive (Ferreira *et al*., 2017) in dry tropical forest. Although tropical forests regenerate primarily through resprouting following disturbances (Viera and Proctor 2007; Chazdon 2017), the reasons why sprouting is a particularly relevant regeneration mechanism are not certain because there are many viewpoints. The first one is that the ability to sprout will depend on the rainfall regime, frequency, intensity and duration of disturbance

(Mc Donald *et al*., 2010). Secondly, according to Schwilk and Ackerly (2005) resprouting ability of plant species results from ancestral conditions and the failure of resprouting is an evolutionary derived trait. Moreover, according to Pausas and Keley (2014) resprouts receive resources from adult individuals that true seedlings do not. Thus, they have advantages in low resource environments such as disturbed areas with desiccating climatic regime, where soils are exhausted. However, one of the species more abundant in adults, true seedlings and true saplings was *Jatropha mutabilis* apparently does not regenerate via reprouting, which can be related to the lack of carbohydrates stock (Vanderlei et al., 2021). Given these contrasting trends, there is obviously still much to learn about resprouting in the Caatinga.

Abundance (seed rain and soil seed bank, all regenerating assemblages and resprouts,) and species richness (true seedlings) of woody plant regenerating assemblages were negatively affected by chronic disturbance, which indicate low resilience of Caatinga dry forest to human disturbance. In tropical dry forests, disturbances leave the environments more open, hot, dry and desiccated which negatively influences the germination of seeds, the survival and the recruitment of seedlings (Chazdon *et al*., 2007, Bhadouria *et al*., 2016).

Rainfall seems to be an important driver of regenerating assemblage organization species composition of seeds, juveniles and resprouts. Our results also indicate an interaction between rainfall and disturbances as the effect of reduced rainfall was more pronounced in disturbed areas (Figure S). It is known that rainfall represents a strong environmental factor in dry forest for the germination, establishment and survival of plant species (Chazdon *et al*., 2007; Rito *et al*., 2018; Seiler *et al*., 2015; Ceccon *et al*., 2006). In fact, we found that among environmental factors, only aridity was related to species composition of regeneration (all regeneration community, resprouts and soil seed bank), but not to abundance and richness. This indicates that communities may change with compensatory dynamics, where some species increase while others decrease due to reduced rainfall, allowing species with tolerance to these conditions due to traits such as sprouting or waiting for a rainy period to germinate, to increase their dominance (Ceccon *et al*., 2006; Lieberman and Li, 1992).

Studies in dry tropical forests have shown that disturbances affect the availability of some nutrients to growing species (Griscom and Ashton 2011) and survival of species is highly correlated with soil fertility (Ceccon *et al*., 2003; Huante *et al*., 1995). Studies have shown that soil fertility has a key role in shaping biodiversity in tropical forests (Potts *et al*., 2002; Poulsen *et al*., 2006) and it positively influences species abundance in the Caatinga (Pinho *et al*., 2019); in contrast, other studies report that soil fertility has no effect on species diversity (Clinebell *et al*., 1995; Pena-Claros *et al*., 2011). Our results did not show an effect of soil fertility on abundance and species richness, suggesting that the increase in dominance is related to an increase in soil fertility.

We found that light had contrasting effect on regeneration. This is probably related to the frequent and constant disturbances in the plots. The canopy structure and sparse tree cover of the Caatinga allows light penetrating through the canopy to the ground, yet regeneration in their first stage of growth requires shade (McLaren and McDonald, 2003; Santiago-Garcia *et al*., 2008) and moisture (Ceccon *et al*., 2006). Negative and positive effect of leaf area index on richness of seed rain and abundance of true sapling, respectively were found in our study. Studies have shown a contrary to our results, i.e., that light had no effect on plant species in dry tropical forests (Quesada *et al*., 2009; Lebrija-Trejos *et al*., 2010; Lévesque *et al*., 2011).

In summary, we found negative effects of chronic disturbance on true seedlings, true saplings and resprouts, seed rain and soil seed bank in the Caatinga vegetation. These drivers affected true seedling and sapling abundance, resprouts persistence and aridity altered species composition. Given that larger individuals are more resistant and small size individuals are more susceptible of these perturbations and harsh environmental factors, and, chronic disturbances will continue and increase due to the population who is still living in the park

(Albuquerque and Melo, 2018) and rainfall is predicted to decrease in the region (Magrin *et al*., 2014). Thus, measures should be taken in order to limited the ongoing drivers in the area which can lead to the desertification whether nothing is done to safeguard Caatinga vegetation.

In addition, our results showed that some species in the community are exotic species, which represent a potential threat for the native species and forest regeneration. Therefore, sustainable management is required to regulate a population of exotic species in order to avoid them to turn in invasive species and to contribute in the maintenance of this ecosystem.

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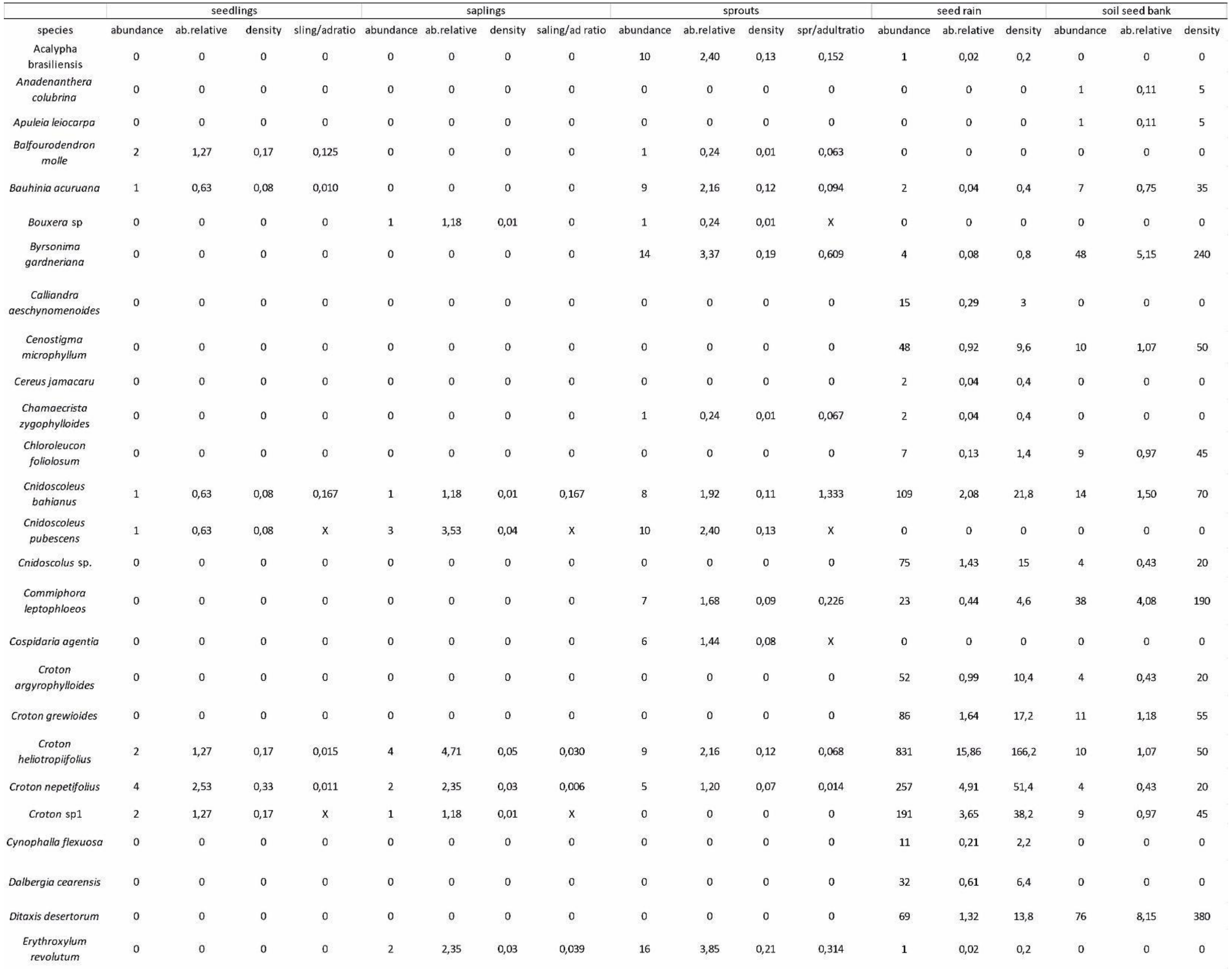
Table1. Community characteristics of trees adults and regenerants in 18 0.1-ha plots surveyed in the Caatinga dry forest of NE Brazil.

Characteristics of sample and community	**Seed rain**	**Seed soil**	**seedlings**	**Saplings**	**Adults**
Plots	15	18	108	54	18
Abundance (total no of individual)	5239	932	482	181	3896
Observed species (no)	40	33	34	24	97
Estimated richness (mean+SE)	43.59±3.85	50.9±23.5	38.16 ± 4.87	34.61 ± 10.21	100 ± 2.80
Shannon diversity	9.02	8.05	16.56	11.75	27.91
Estimated Shannon diversity (mean+SE)	9.05±0.18	8.26±0.41	17.26 ± 0.89	12.99 ± 1.15	28.29 ± 0.57
Species with one or two individual (%)	21	21	26	41	23

Table 2. Abundance, relative abundance, density and the adult-to-offspring ratio of seedlings, saplings and resprouts, seed rain and soil seed bank of tree species in regeneration community in 18 plots



	seedlings				saplings				sprouts				seed rain			soil seed bank		
species	abundance	ab.relative	density	sling/adratio	abundance	ab.relative	density	saling/ad ratio	abundance	ab.relative	density	spr/adultratio	abundance	ab.relative	density	abundance	ab.relative	density
Acalypha brasiliensis	0	0	0	0	0	0	0	0	10	2,40	0,13	0,152	1	0,02	0,2	0	0	0
Anadenanthera colubrina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,11	5
Apuleia leiocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,11	5
Balfourodendron molle	2	1,27	0,17	0,125	0	0	0	0	1	0,24	0,01	0,063	0	0	0	0	0	0
Bauhinia acuruana	1	0,63	0,08	0,010	0	0	0	0	9	2,16	0,12	0,094	2	0,04	0,4	7	0,75	35
Bouxera sp	0	0	0	0	1	1,18	0,01	0	1	0,24	0,01	X	0	0	0	0	0	0
Byrsonima gardneriana	0	0	0	0	0	0	0	0	14	3,37	0,19	0,609	4	0,08	0,8	48	5,15	240
Calliandra aeschynomenoides	0	0	0	0	0	0	0	0	0	0	0	0	15	0,29	3	0	0	0
Cenostigma microphyllum	0	0	0	0	0	0	0	0	0	0	0	0	48	0,92	9,6	10	1,07	50
Cereus jamacaru	0	0	0	0	0	0	0	0	0	0	0	0	2	0,04	0,4	0	0	0
Chamaecrista zygophylloides	0	0	0	0	0	0	0	0	1	0,24	0,01	0,067	2	0,04	0,4	0	0	0
Chloroleucon foliolosum	0	0	0	0	0	0	0	0	0	0	0	0	7	0,13	1,4	9	0,97	45
Cnidoscoleus bahianus	1	0,63	0,08	0,167	1	1,18	0,01	0,167	8	1,92	0,11	1,333	109	2,08	21,8	14	1,50	70
Cnidoscoleus pubescens	1	0,63	0,08	X	3	3,53	0,04	X	10	2,40	0,13	X	0	0	0	0	0	0
Cnidoscolus sp.	0	0	0	0	0	0	0	0	0	0	0	0	75	1,43	15	4	0,43	20
Commiphora leptophloeos	0	0	0	0	0	0	0	0	7	1,68	0,09	0,226	23	0,44	4,6	38	4,08	190
Cospidaria agentia	0	0	0	0	0	0	0	0	6	1,44	0,08	X	0	0	0	0	0	0
Croton argyrophylloides	0	0	0	0	0	0	0	0	0	0	0	0	52	0,99	10,4	4	0,43	20
Croton grewioides	0	0	0	0	0	0	0	0	0	0	0	0	86	1,64	17,2	11	1,18	55
Croton heliotropiifolius	2	1,27	0,17	0,015	4	4,71	0,05	0,030	9	2,16	0,12	0,068	831	15,86	166,2	10	1,07	50
Croton nepetifolius	4	2,53	0,33	0,011	2	2,35	0,03	0,006	5	1,20	0,07	0,014	257	4,91	51,4	4	0,43	20
Croton sp1	2	1,27	0,17	X	1	1,18	0,01	X	0	0	0	0	191	3,65	38,2	9	0,97	45
Cynophalla flexuosa	0	0	0	0	0	0	0	0	0	0	0	0	11	0,21	2,2	0	0	0
Dalbergia cearensis	0	0	0	0	0	0	0	0	0	0	0	0	32	0,61	6,4	0	0	0
Ditaxis desertorum	0	0	0	0	0	0	0	0	0	0	0	0	69	1,32	13,8	76	8,15	380
Erythroxylum revolutum	0	0	0	0	2	2,35	0,03	0,039	16	3,85	0,21	0,314	1	0,02	0,2	0	0	0

Guapira graciliflora	0	0	0	0	0	0	0	0	0	0	0	0	521	9,94	104,2	8	0,86	40
Handroanthus impetiginosus	0	0	0	0	0	0	0	0	0	0	0	0	11	0,21	2,2	4	0,43	20
Jatropha mollissima	4	2,53	0,33	2	10	11,76	0,13	5	0	0	0	0	0	0	0	0	0	0
Jatropha mutabilis	72	45,57	6,00	0,279	52	61,18	0,69	0,008	0	0	0	0	22	0,42	4,4	8	0,86	40
Jatropha ribifolia	0	0	0	0	1	1,18	0,01	0,333	0	0	0	0	1	0,02	0,2	0	0	0
Lantana camara	0	0	0	0	1	1,18	0,01	0,125	0	0	0	0	2	0,04	0,4	0	0	0
Manihot carthagenensis	0	0	0	0	0	0	0	0	0	0	0	0	3	0,06	0,6	10	1,07	50
Melochia tomentosa	0	0	0	0	0	0	0	0	18	4,33	0,24	0,254	0	0	0	0	0	0
Myracrodruon urundeuva	0	0	0	0	0	0	0	0	0	0	0	0	106	2,02	21,2	0	0	0
Neocalyptrocalyx longifolium	0	0	0	0	0	0	0	0	9	2,16	0,12	X	0	0	0	0	0	0
Oxalis sp	11	6,96	0,92	X	1	1,18	0,01	X	5	1,20	0,07	X	0	0	0	0	0	0
Peltogyne pauciflora	1	0,63	0,08	0,006	0	0	0	0	11	2,64	0,15	0,069	8	0,15	1,6	0	0	0
Piptadenia stipulacea	0	0	0	0	0	0	0	0	7	1,68	0,09	0,109	77	1,47	15,4	9	0,97	45
Pityrocapa moliliformis	24	15,19	2	0,039	0	0	0	0	96	23,08	1,28	0,155	2116	40,39	423,2	511	54,83	2555
Poincianela microphylla	8	5,06	0,67	0,020	0	0	0	0	33	7,93	0,44	0,084	0	0	0	1	0,11	5
Poincianela pyramidalis	0	0	0	0	0	0	0	0	2	0,48	0,03	0,065	0	0	0	1	0,11	5
Sapium glandulosum	0	0	0	0	0	0	0	0	0	0	0	0	10	0,19	2	0	0	0
Sebastiania macrocarpa	0	0	0	0	0	0	0	0	0	0	0	0	1	0,02	0,2	0	0	0
Senegalia bahiensis	1	0,63	0,08	0,014	0	0	0	0	14	3,37	0,19	0,192	158	3,02	31,6	37	3,97	185
Senegalia piauhiensis	2	1,27	0,17	0,051	0	0	0	0	50	12,02	0,67	1,282	267	5,10	53,4	43	4,61	215
Senna acuruensis	0	0	0	0	0	0	0	0	3	0,72	0,04	X	1	0,02	0,2	17	1,82	85
Senna rizzini	0	0	0	0	0	0	0	0	0	0	0	0	40	0,76	8	10	1,07	50
Spondias tuberosa	0	0	0	0	0	0	0	0	0	0	0	0	1	0,02	0,2	1	0,11	5
Stigmaphyllon paralias	0	0	0	0	0	0	0	0	9	2,16	0,12	X	0	0	0	0	0	0
Strychnos rubiginesa	0	0	0	0	0	0	0	0	2	0,48	0,03	0,105	0	0	0	0	0	0
Syagrus coronata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	1,29	60
Trischidium molle	21	13,29	1,75	0,208	6	7,06	0,08	0,059	54	12,98	0,72	0,535	15	0,29	3	11	1,18	55
Varonia leucoxyflora	0	0	0	0	0	0	0	0	4	0,96	0,05	0,069	61	1,16	12,2	2	0,21	10
Zanthoxylum stelligerum	1	0,63	0,08	0,07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ziziphus joazeiro	0	0	0	0	0	0	0	0	1	0,24	0,01	0,063	0	0	0	0	0	0
sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0,11	5

Table 3. Tree species with the adult-to-offspring ratio surveyed in 18 0.1-ha plots surveyed in the Caatinga dry forest of NE Brazil. Uses are Me: medicinal, Ct: construction, Or: ornamental, Fd: food, Fl: fuel, Ot: others

Species	**Status**	**Seed dispersal**	**Uses**	**Seedling/adult**	**Sapling/adult**	**Sprout/adult**
Jatropha mutabilis	native	autochory	Me	0.27	0.07	-
Pityrocarpa moniliformis	native	autochory	Me, Ct, Ot	0.03	-	0.15
Trischidium molle	exotic	zoochory	Or	0.20	0.05	0.53
Senegalia piauhiensis	native	autochory	Ct, Fl	0.05	-	1.28
Poincianela microphylla	native	autochory	Me, Ct, Ot	0.02	-	0.08
Melochia tomentosa	exotic	autochory	Me,Or	-	-	0.25
Erythroxylum revolutum	exotic	zoochory	Me	-	0.03	0.31
Senegalia bahiensis	native	autochory	Ct, Fl	0.01	-	0.19
Bauhinia acuruana	native	autochory	Me,Fd,Fl	0.01	-	0.09
Peltogyne pauciflora	exotic	zoochory	Ct	0.006	-	0.06
Croton nepetifolius	native	autochory	Me,Fl	0.01	0.005	0.01
Cnidoscoleus pubescens	native	autochory	Me	-	-	-
Oxalis sp	exotic	autochory	Fd	-	-	-
Croton heliotropiifolius	native	autochory	Me,Fl	0.01	0.03	0.06

Byrsonima gardneriana	native	autochory	Fd	-	-	0.6
Cnidoscoleus bahianus	native	autochory	Me	0.16	0.16	1.33
Piptadenia stipulacea	native	autochory	Ct, Fl, Fr	-	-	0.11
Acalypha brasiliensis	native	autochory	Or	-	-	0.15
Neocalyptrocalyx longifolium	native	zoochory	Fd	-	-	-
Stigmaphyllon paralias	native	zoochory	Ct	-	-	-
Senna acuruensis	native	autochory	Me	-	-	-
Jatropha mollissima	native	autochory	Me	2	5	-

Table 4. Best-supported models (D(q)AICc < 2) analyzing the isolated and combined effects of chronic anthropogenic disturbances and environmental factors (AP: annual precipitation, LAI: leaf area index, SF: soil fertility) on the abundance and species richness of true seedling, true sapling, sprout, all regenerants combined, seed rain and soil seed bank surveyed in 18 0.1-ha plots surveyed in the Caatinga dry forest of NE Brazil.

	variable response	selected model	df	logLik	QAICc	delta	weight	R^2
abundance	true seedlings	mod2	2	-76	46.07	0	0.21	0.31
		mod3	2	-75.99	46.11	0.04	0.21	0.3
		mod4	2	-77.78	47.02	0.95	0.13	0.15
		mod21	3	-72.10	47.51	1.44	0.10	0.55
		mod1	2	-79.20	47.73	1.66	0.09	0.01
	true saplings	mod3	2	-24.91	55.60	0	0.17	0.63
		mod4	2	-24.92	55.61	0.01	0.17	0.001
		mod1	2	-25	55.62	0.02	0.17	0.03
		mod2	2	-25	56.16	0.55	0.13	0.04
		mod20	3	-24	57.60	1.99	0.06	0.66
	resprouts	mod15	4	-111	156.52	0	0.31	0.994
		mod21	3	-116	158.44	1.92	0.12	0.991
	regecom	mod2	2	-112	37.60	0	0.58	0.96
	seed rain	glmer1	3	-99	205.21	0	0.34	0.9
	soil seed bank	glmer1	3	-86	180.82	0	0.40	0.88
		glmer12	3	-87	182.52	1.71	0.17	0.78
richness	true seedlings	mod2	2	-26	58.36	0	0.33	0.18
		mod1	2	-27	60.18	1.82	0.13	0.09
	true saplings	mod3	2	-24.91	55.60	0	0.17	0.03
		mod4	2	-24.92	55.61	0.01	0.17	0.02

	mod1	2	-24.92	55.62	0.02	0.17	0.02
	mod2	2	-25.19	56.16	0.55	0.13	0.001
	mod20	3	-24.47	57.60	1.99	0.06	0.07
resprouts	mod3	2	-44.22	70.75	0	0.29	0.24
	mod21	3	-42.53	71.71	0.96	0.18	0.37
	mod2	2	-45.06	71.96	1.20	0.16	0.17
regecom	mod15	4	-26.03	63.61	0	0.99	0.44
seed rain	glmer13	3	-34.81	77.74	0	0.42	0.22
soil seed bank	glmer13	3	-41.88	92.43	0	0.26	0.09
	glmer7	5	-39.21	92.87	0.44	0.21	0.32
	glmer1	3	-42.43	93.53	1.10	0.15	0.04
	glmer12	3	-42.52	93.70	1.28	0.14	0.03
	glmer11	3	-42.79	94.25	1.82	0.11	0.001

Table 5. Results from general linear model and general linear mixed model (GLM and GLMM) to compare regenerating community in terms of abundance and richness of all regeneration community, true seedling, true sapling, sprout, seed rain and soil seed bank between environmental factors of 18 plots at Catimbau National Park, northeastern Brazil

	Variable response	Model selected	Variable explicative	df	F(t)	P
abundance	true seedlings	mod21	CAD	16	-1.23	0.238
			LAI	15	-1.25	0.229
	true sapling	mod20	SF	16	0.911	0.37
			LAI	15	-3.31	**0.004**
	resprouts	mod15	AP	16	0.96	0.35
			CAD	15	-2.08	**0.05**
			LAI	14	1.07	0.3
	regecom	mod2	CAD	16	-2.62	**0.01**
	seed rain	glmer1	CAD	13	-2.38	**0.01**
	soil seed bank	glmer1	CAD	16	-1.93	**0.05**
richness	true seedlings	mod2	CAD	16	-1.836	**0.05**
	true sapling	mod20	SF	16	0.991	0.322
			LAI	15	-0.95	0.341
	resprouts	mod21	CAD	16	-1.431	0.172
			LAI	15	1.767	0.09
	regecom	mod15	AP	16	0.62	0.531
			CAD	15	-1.415	0.157
			LAI	14	0.366	0.714
	seed rain	glmer13	LAI	13	1.919	**0.05**
	soil seed bank	glmer7	LAI	16	0.105	0.67
			AP	16	0.109	0.25

LAI:AP	16	0.11	**0.01**

FIGURE LEGENDS

Figure 1. Location of the study area in (a) south America, (b) north-eastern Brazil and Pernambuco state (in grey) and (c) Catimbau National Park showing the distribution of the 18 0.1-ha plots (circles) over chronic anthropogenic disturbance (CAD) and rainfall gradients.

Figure 2. linear Regression between (a) reprouts and adults abundance, (b) reprouts and adults richness and (c) true seedlings and adults richness

Figure 3. Regression linear between abundance and species richness of regenerating woody plant assemblages surveyed in the 18 0.1-ha m^2 plots in the Caatinga dry forest, NE Brazil.

Figure 4. Frequency of different sources of resprouts surveyed in the 18 0.1-ha m^2 plots in the Caatinga dry forest, NE Brazil.

Figure 5. Non-metric multidimensional scaling (NMDS) showing the association of environmental factors with species composition of (a) all regenerants, (b) resprouts, (c) soil seed bank surveyed in the 18 0.1-ha m^2 plots in the Caatinga dry forest, NE Brazil.

FIGURE 1.

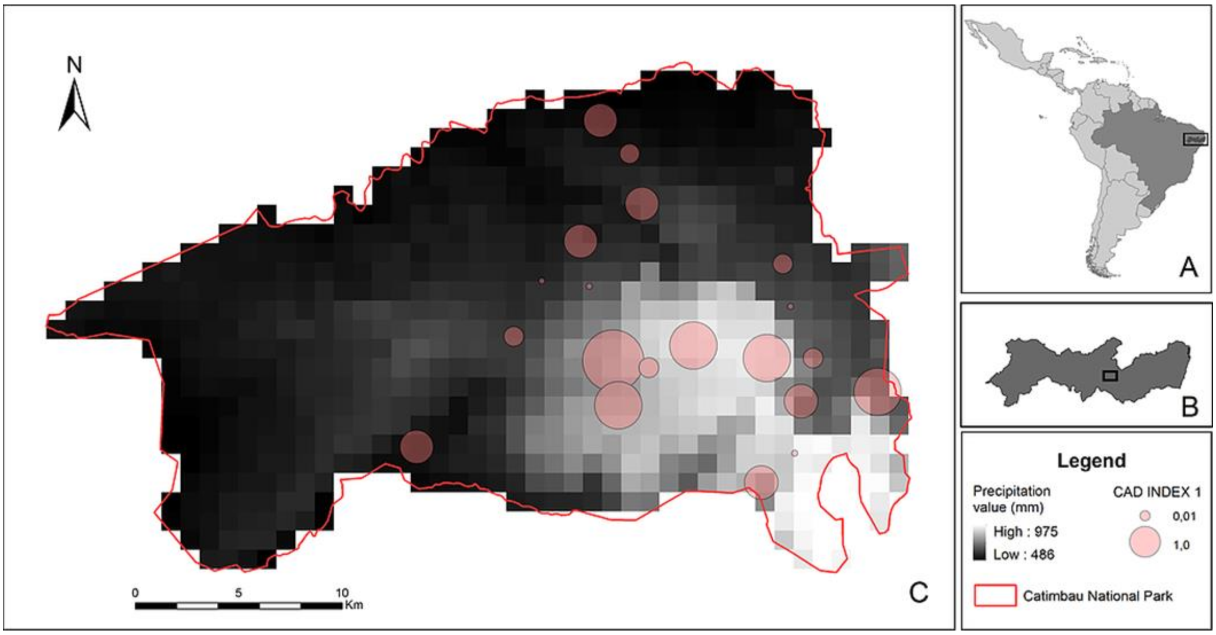

N
0
5
10
Km
C
A
B
Legend
Precipitation value (mm)
High : 975
Low : 486
CAD INDEX 1
0,01
1,0
Catimbau National Park

Figure 2

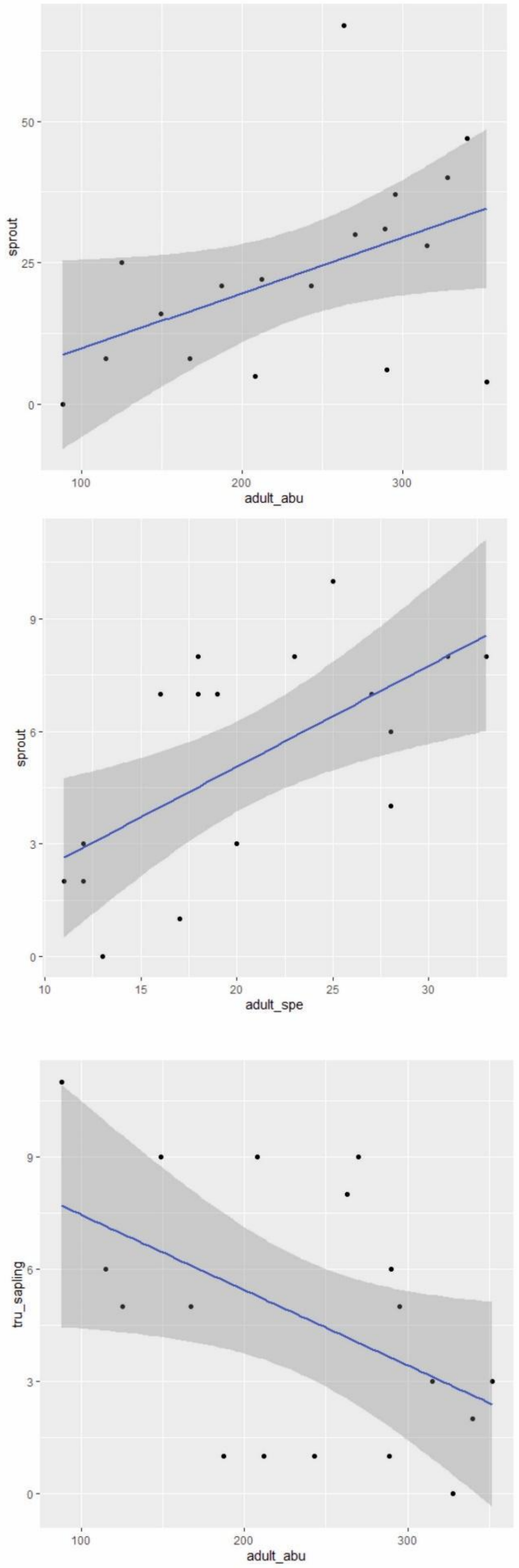

sprout
50
25
0
100
200
300
adult_abu
sprout
9
6
3
0
10
15
20
25
30
adult_spe
tru_sapling
9
6
3
0
100
200
300
adult_abu

Figure 3.

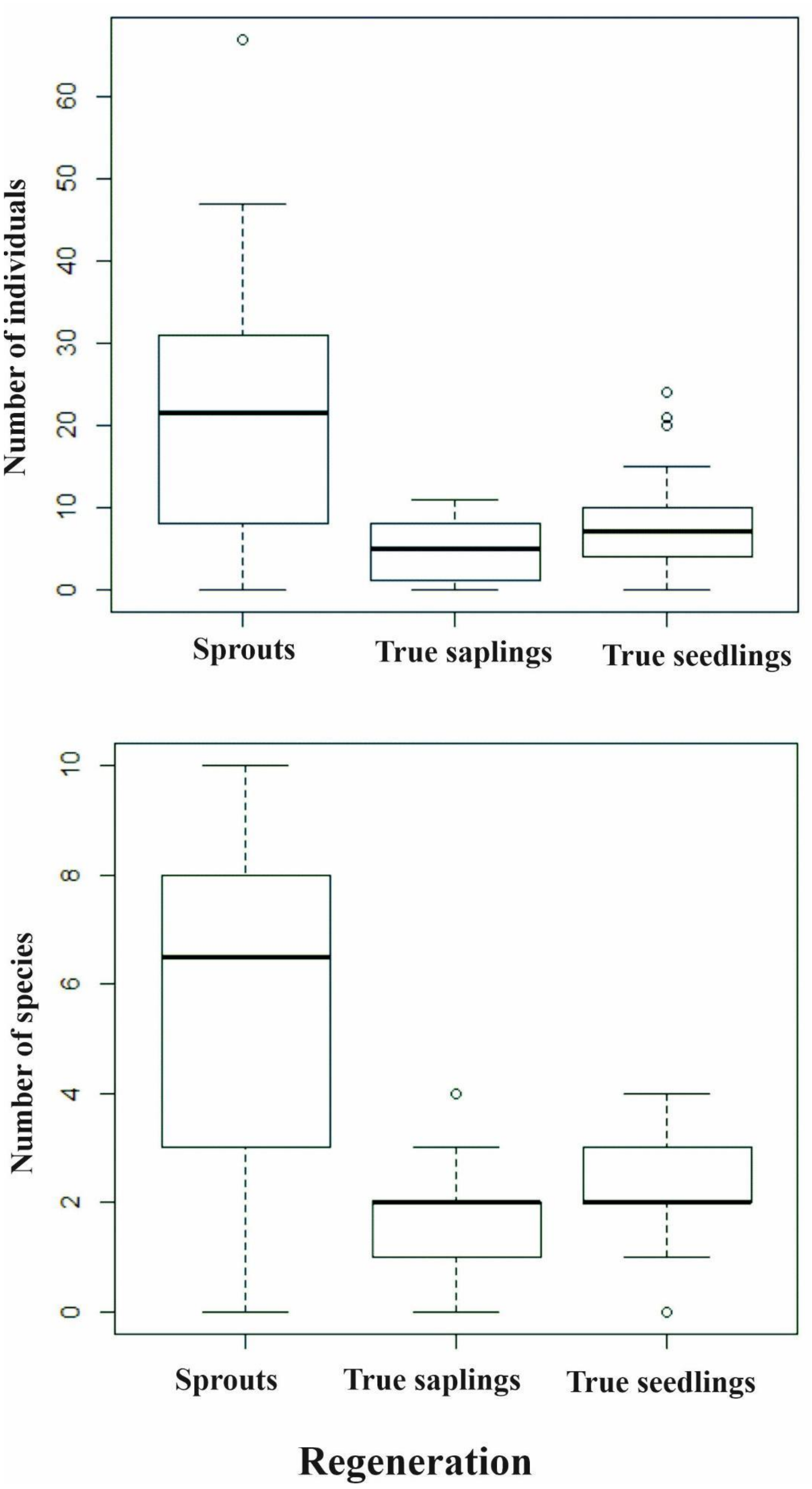

Number of individuals
0
10
20
30
40
50
60
Sprouts
True saplings
True seedlings
Number of species
0
2
4
6
8
10
Sprouts
True saplings
True seedlings
Regeneration

Figure 4

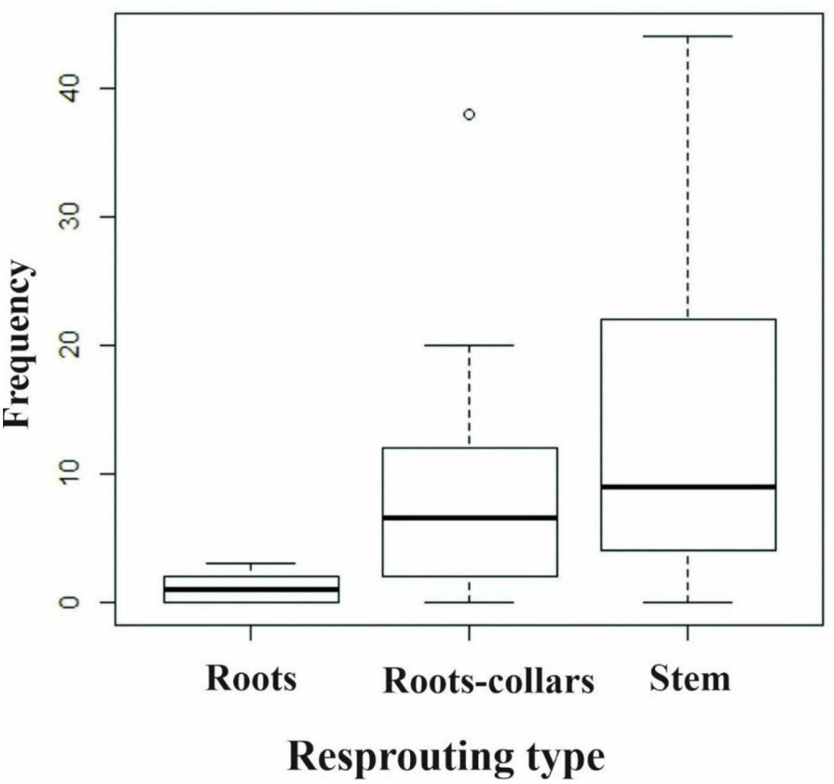
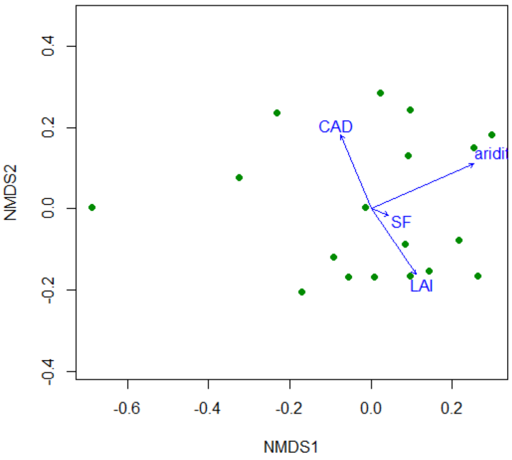
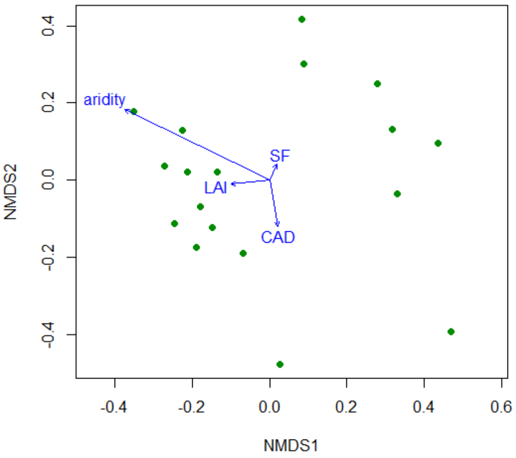
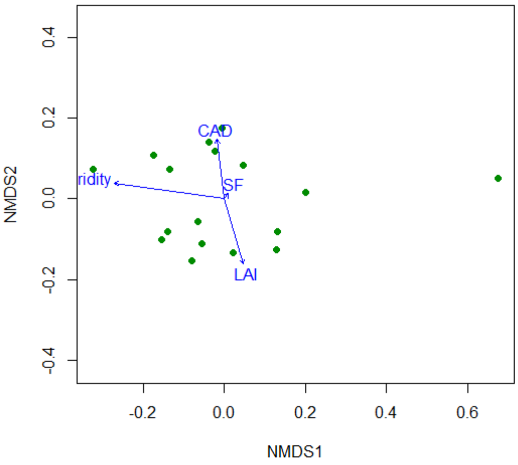

Frequency
0
10
20
30
40
Roots
Roots-collars
Stem
Resprouting type

Figure 5a, 5b and 5c







SUPPLEMENTARY DOCUMENTS

Table S. Abundance. abundance relative and density of adult tree species in in 18 0.1-ha plots surveyed in the Caatinga dry forest of NE Brazil.

Species	Abundance	Ab.relative	Density
Acalypha brasiliensis	66	1.694045175	0.066
Aeschynomene marginata	6	0.154004107	0.006
Allophylus quercifolius	10	0.256673511	0.01
Amburana cearensis	2	0.051334702	0.002
Anacardium occidentale	2	0.051334702	0.002
Anadenanthera colubrina	1	0.025667351	0.001
Anemopaegma laeve	11	0.282340862	0.011
Annona leptopetala	37	0.949691992	0.037
Aspidosperma pyrifolium	1	0.025667351	0.001
Balfourodendron molle	16	0.410677618	0.016
Bauhinia acuruana	96	2.464065708	0.096
Byrsonima gardneriana	23	0.590349076	0.023
Callyandra aschynomenae	12	0.308008214	0.012
Casearia silvestris	7	0.179671458	0.007
Cereus jamacaru	4	0.102669405	0.004
Chamaecrista zygophylloides	15	0.385010267	0.015
Chloroleucon foliolosum	20	0.513347023	0.02
Cnidoscoleus bahianus	6	0.154004107	0.006
Colicodendron yco	96	2.464065708	0.096
Combretum glaucocarpum	1	0.025667351	0.001
Commiphora leptophloeos	31	0.795687885	0.031
Cordia curassavica	4	0.102669405	0.004
Cordia rigida	2	0.051334702	0.002
Cordia trichotoma	12	0.308008214	0.012
Croton argyrophylloides	329	8.444558522	0.329
Croton blanchetianus	26	0.667351129	0.026
Croton heliotropiifolius	132	3.388090349	0.132
Croton nepetifolius	363	9.31724846	0.363
Cynophalla flexuosa	19	0.487679671	0.019
Dahlstedtia araripensis	12	0.308008214	0.012
Dalbergia cearensis	6	0.154004107	0.006
Ditaxis desertorum	3	0.077002053	0.003
Erythroxylum revolutum	51	1.309034908	0.051
Eugenia brejoensis	2	0.051334702	0.002
Eugenia stictopetala	12	0.308008214	0.012
Evolvulus linoides	8	0.205338809	0.008
Gochnatia oligocephala	2	0.051334702	0.002
Guapira sp	8	0.205338809	0.008
Handroanthus impetiginosus	3	0.077002053	0.003
Helicteres velutina	5	0.128336756	0.005
Helicteres velutina	2	0.051334702	0.002

Hyptis suaveolens	6	0.154004107	0.006
Jatropha mollissima	2	0.051334702	0.002
Jatropha mutabilis	258	6.622176591	0.258
Jatropha ribifolia	3	0.077002053	0.003
Jurema	5	0.128336756	0.005
jurema branca	2	0.051334702	0.002
Lantana camara	8	0.205338809	0.008
Lippia gracilis	47	1.206365503	0.047
Lippia grata	35	0.89835729	0.035
Manihot	12	0.308008214	0.012
Manihot esculenta	3	0.077002053	0.003
Manilkara salzmannii	1	0.025667351	0.001
Maytenus rigida	17	0.436344969	0.017
Melochia tomentosa	71	1.82238193	0.071
Mimosa gemmulata	1	0.025667351	0.001
Mimosa lewisii	2	0.051334702	0.002
Mimosa ophthalmocentra	3	0.077002053	0.003
Myroxylon peruiferum	1	0.025667351	0.001
Oxandra reticulata	1	0.025667351	0.001
Peltogyne pauciflora	160	4.106776181	0.16
Pilosocereus gounellei	8	0.205338809	0.008
Pilosocereus pachycladus	13	0.333675565	0.013
Pilosocereus tuberculatus	11	0.282340862	0.011
Piptadenia stipulacea	64	1.642710472	0.064
Pityrocarpa moniliformis	618	15.862423	0.618
Poincianela microphylla	394	10.11293634	0.394
Poincianela pyramidalis	31	0.795687885	0.031
Psidium brownianum	20	0.513347023	0.02
Psidium oligospermum	17	0.436344969	0.017
Psidium schenckianum	1	0.025667351	0.001
Ruprechtia laxiflora	7	0.179671458	0.007
Sapium glandulosum	5	0.128336756	0.005
Senegalia bahiensis	73	1.873716632	0.073
Senegalia polyphylla	10	0.256673511	0.01
Senegalia piauhiensis	39	1.001026694	0.039
Senna rizzinii	20	0.513347023	0.02
Senna spectabilis	1	0.025667351	0.001
Senna splendida	3	0.077002053	0.003
Senna trachypus	13	0.333675565	0.013
Senna velutina	3	0.077002053	0.003
Sideroxylon obtusifolium	2	0.051334702	0.002
Solanum rhytidoandrum	2	0.051334702	0.002
Spondias tuberosa	2	0.051334702	0.002
Stillingia trapezoidea	5	0.128336756	0.005
Strychnos rubiginesa	19	0.487679671	0.019
Sucupira	3	0.077002053	0.003

Syagrus coronata	15	0.385010267	0.015
Tacinga palmadora	168	4.31211499	0.168
Trischidium molle	101	2.592402464	0.101
Tamarindus indica	4	0.102669405	0.004
Turnera cearensis	13	0.333675565	0.013
Varronia globosa	19	0.487679671	0.019
Varonia leucoxyflora	58	1.488706366	0.058
Xylosma ciliatifolia	2	0.051334702	0.002
Zanthoxylum stelligerum	14	0.359342916	0.014
Ziziphus joazeiro	16	0.410677618	0.016

Table S1. Occurrence of seed rain, soil seed bank, regeneration assemblages and adult tree species in in 18 0.1-ha plots surveyed in the Caatinga dry forest of NE Brazil.

		Occurrence			
Species	**Family**	**Seed rain**	**Soil seed bank**	**Regecom**	**Adult**
Acalypha brasiliensis	Euphorbiaceae	1		1	5
Aeschynomene marginata	Fabaceae				4
Allophylus quercifolius	Sapindaceae				4
Amburana cearensis	Fabaceae				2
Anacardium occidentale	Anacardiaceae				1
Anadenanthera colubrina	Fabaceae		1		1
Anemopaegma laeve	Bignoniaceae				4
Annona leptopetala	Annonaceae				9
Apuleia leiocarpa	Fabaceae		1		
Aspidosperma pyrifolium	Apocynaceae				1
Balfourodendron molle	Rutaceae			1	3
Bauhinia acuruana	Fabaceae	2	3	5	6
Bouxera sp				1	
Byrsonima gardneriana	Malpighiaceae	1	9	2	5
Callyandra aschynomenae	Fabaceae	1			4
Casearia silvestris	Salicaceae				1
Cereus jamacaru	Cactaceae	1			2
Chamaecrista zygophylloides	Fabaceae	1		1	3
Chloroleucon foliolosum	Fabaceae	1	1		5
Cnidoscolus bahianus	Euphorbiaceae	10	4	4	1
Cnidoscoleus pubescens	Euphorbiaceae			6	
Cnidoscolus sp	Euphorbiaceae	7	2		
Colicodendron yco	Capparaceae				9
Combretum glaucocarpum	Combretaceae				1
Commiphora leptophloeos	Burseraceae	8	9	2	9
Cordia curassavica	Boraginaceae				2
Cordia rigida	Boraginaceae				2
Cordia trichotoma	Boraginaceae				1
Cospidaria agentia	Bignoniaceae			1	
Croton argyrophylloides	Euphorbiaceae	1	2		6
Croton blanchetianus	Euphorbiaceae				1
Croton grewioides	Euphorbiaceae	4	3		
Croton heliotropiifolius	Euphorbiaceae	6	2	2	6
Croton nepetifolius	Euphorbiaceae	7	2	6	9
Croton sp	Euphorbiaceae	3	4		
Cynophalla flexuosa	Capparaceae	1			4
Dahlstedtia araripensis	Fabaceae				3
Dalbergia cearensis	Fabaceae	4			3
Ditaxis desertorum	Euphorbiaceae	1	6		3
Erythroxylum revolutum	Erythroxylaceae	1		4	8

Eugenia brejoensis	Myrtaceae				2
Eugenia stictopetala	Myrtaceae				3
Eugenia sp2	Myrtaceae			1	
Evolvulus linoides	Convolvulaceae				2
Gochnatia oligocephala	Asteraceae				1
Guapira graciliflora	Nyctaginaceae	6	6		
Guapira sp.	Nyctaginaceae				5
Handroanthus impetiginosus	Bignoniaceae	5	3		1
Helicteres velutina	Sterculiaceae				3
Helicteres velutina	Sterculiaceae				1
Hyptis suaveolens	Lamiaceae				2
Jatropha mollissima	Euphorbiaceae			4	1
Jatropha mutabilis	Euphorbiaceae	5	6	11	13
Jatropha ribifolia	Euphorbiaceae			1	2
Jatropha sp	Euphorbiaceae	1			
Jurema	Fabaceae				2
jurema branca	Fabaceae				1
Lantana camara	Verbenaceae	2		1	4
Lippia gracilis	Verbenaceae				7
Lippia grata	Verbenaceae				5
Manihot	Euphorbiaceae				4
Manihot carthagenensis	Euphorbiaceae	3	6		
Manihot esculenta	Euphorbiaceae				1
Manilkara salzmannii	Sapotaceae				1
Maytenus rigida	Celastraceae				2
Melochia tomentosa	Sterculiaceae			5	2
Mimosa cf. gemmulata	Leguminosae				1
Mimosa cf. lewisii	Leguminosae				1
Mimosa ophthalmocentra	Leguminosae				2
Myracrodruon urundeuva	Anacardiaceae	1			
Myroxylon peruiferum	Fabaceae				1
Neocalyptrocalyx longifolium	Capparaceae			4	
Oxandra reticulata	Annonaceae				1
Oxalis sp	Oxalidaceae			3	
Peltogyne pauciflora	Fabaceae	3		5	11
Pilosocereus cf. gounellei	Cactaceae				2
Pilosocereus cf. pachycladus	Cactaceae				6
Pilosocereus tuberculatus	Cactaceae				6
Piptadenia stipulacea	Mimosaceae	5	4	2	4
Pityrocarpa moniliformis	Fabaceae	12	10	9	12
Poincianela microphylla	Fabaceae			8	13
Poincianella pyramidalis	Fabaceae		1	1	2
Psidium cf. brownianum	Myrtaceae				4
Psidium oligospermum	Myrtaceae				6

Psidium schenckianum	Myrtaceae				1
Ruprechtia laxiflora	Polygonaceae				2
Sapium glandulosum	Euphorbiaceae	3			2
Sebastiania macrocarpa	Euphorbiaceae	1			
Senegalia bahiensis	Fabaceae	5	5	5	4
Senegalia cf. polyphylla	Fabaceae				4
Senegalia piauhiensis	Fabaceae	10	7	6	6
Senna acuruensis	Fabaceae	1	2	2	
Senna rizzinii	Fabaceae	1	2		2
Senna spectabilis	Fabaceae				1
Senna splendida	Fabaceae				1
Senna trachypus	Fabaceae				2
Senna velutina	Fabaceae				2
Sideroxylon obtusifolium	Sapotaceae				1
Solanum rhytidoandrum	Solanaceae				1
Spondias tuberosa	Anacardiaceae	1	1		2
sp1			1		
Stillingia trapezoidea	Euphorbiaceae				1
Stigmaphyllon paralias	Malpighiaceae			1	
Strychnos rubiginosa	Loganiaceae			1	3
Sucupira	Fabaceae				2
Syagrus coronata	Arecaceae		2		5
Tacinga palmadora	Cactaceae				10
Trischidium molle	Fabaceae	1	6	12	11
Tamarindus indica	Fabaceae				2
Turnera cearensis	Passifloraceae				5
Varronia globosa	Boraginaceae				6
Varronia leucocephala	Boraginaceae	3	1	1	3
Xylosma ciliatifolia	Salicaceae				1
Zanthoxylum stelligerum	Rutaceae			1	6
Ziziphus joazeiro	Rhamnaceae			1	2

Regecom= regenerating assemblages

4 EFFECTS OF EXPERIMENTAL COPPICING ON SEEDLING-SIZED RESPROUTS ALONG GRADIENTS OF CHRONIC ANTHROPOGENIC DISTURBANCES AND ENVIRONMENTAL FACTORS IN THE CAATINGA DRY FOREST

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Effects of Coppicing on seedling-size of resprouts along a gradient of chronic anthropogenic disturbances and environmental factors decrease in the Caatinga dry forest

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Highlights

- Resprouts are very important regeneration mechanism in dry tropical forest
- Coppicing is a widespread management practice in dry tropical forest
- Coppicing response is high and varied among species
- Chronic anthropogenic disturbances do not affect coppicing response
- Harsher environmental factors induce positive coppicing response

Abstract

Resprouts are crucial to natural regeneration and silvicultural management of dry tropical forests where top-killing disturbances are common. Given that coppicing is a common practice in these forests, understanding how resprouts react from coppicing along disturbance and environmental factors could give fundamental information for natural regeneration and assisted restoration of dry forests. In this study we assess coppicing responses of seedling-sized resprouts along a gradient of chronic anthropogenic disturbances and environmental factors (annual rainfall, soil fertility and light availability via leaf area index) in the Caatinga dry forest. A total of 150 resprouts representing 19 species were submitted to experimental coppicing in different resprout types (root collars, roots, stems) and the emergence of new shots was monitored during 15 months across fifteen plots. A total of 144 resprouts from all the 19 species submitted to experimental coppicing showed some degree of resprouting ability. The mean density of new shoots was 1.5 ± 1.2 shoots per stump, while the mean height and mean diameter of new shoots were 11.33 ± 10.1 cm and 0.2 ± 0.1 cm respectively with marked interspecific variations. There was no effect of resprout type in new shoot density, new shoot diameter and height and resprouting capacity indices (shoot diameter and stem diameter ratio). Linear Regression have shown that stem diameter was significantly and positively correlated with new shoot density and new shoot length and diameter for most species. The number of new shoots was negatively influenced by rainfall and soil fertility, while neither chronic anthropogenic disturbances, nor leaf area index had a significant effect on new shoot length, new shoot diameter and in the resprouting capacity indices of species. Moreover, considering those species more widely distributed across the focused gradients, negative effect of chronic disturbance, leaf area index and rainfall were observed in new shoot length, new shoot diameter and resprout capacity indices of *Annona leptopetala* and *Trischidium molle,* and positive effect of rainfall was observed in new shoot length, new shoot diameter and resprout capacity indices of *Cnidoscolus bahianus*. The high resprouting capacity of species may be related to the availability and the translocation of stored reserves from stored organs to shoots which were initiated by coppicing. The opposite species-specific tendency might also explain the lack of pattern in some of our results. Our findings confirm the importance of coppicing management in the regeneration and recovery process in dry tropical forest.

Key words: aridity, climate change, human disturbance, plant assemblages, regeneration mechanisms, seasonally dry tropical forests

Introduction

Resprouting is a relevant and widespread regeneration mechanism by which wood plant species can persist in the community (Bellingham and Sparrow, 2000; Bond et al., 2001). It depends on stored resources below-ground (Bellingham and Sparrow, 2000; Clarke et al., 2013), disturbances intensity and frequency, historical disturbances regime and environmental factors (Bond et al., 2001; Del Tredici, 2001; Pausas and Keeley, 2014; Vesk and Westoby, 2004). It is characterized by the development, protection and resourcing of a viable bud bank, which can be located on the aerial, basal and below-ground part of the plant (Clarke et al., 2013; Meier et al., 2012). In dry tropical forests, due to seasonality, low rainfall and high risk of seed and seedling desiccation, resprouts are crucial for ecosystem recovery (Anderson-teixeira et al., 2021; McDonald et al., 2010; Vieira and Scariot, 2006). In fact, coppicing is a common forest management method in dry forest that involves cutting shoot apex of wood species to induce the production of new shoots (Lévesque et al., 2011; Matula et al., 2012) from which the degree of resilience of the community can be assessed. Although some studies have investigated coppicing response and resprouting ability in different ecosystems worldwide (Brokaw, 1989; Lévesque et al., 2011; Pausas and Keeley, 2014; Vesk and Westoby, 2004) the relationship between resprout ability location, disturbances and environmental conditions remains poorly understood.

Disturbances (natural and anthropic) have a significant role in the structure and maintenance of plant community (Barkham, 1992; Mair et al., 2014; Travis et al., 2013; Yu et al., 2016) and commonly affect the resprouting regeneration mechanism and, consequently, the fate of resprouts (Bellingham and Sparrow, 2000; Pausas and Keeley, 2014). In dry tropical forests of central Brazil, stem resprouts represent 60% of individual woody plants, while 61% of resprouts were from root collars and 70% from roots in clear cutting area, stump removal and topsoil stripping area, respectively (Ferreira et al., 2017). However, resprouting ability after chronic anthropogenic disturbances i.e., a continuous removal of small fractions of forest biomass through the extraction of non-timber forest products and livestock grazing (Singh, 1998) have been less studied (Jaureguiberry et al., 2020; Matula et al., 2020; Pausas and Keeley, 2014; Vesk and Westoby, 2004), despite their considerable impact on biodiversity (Martorell and Peters, 2005; Ribeiro-neto et al., 2016; Santos and Tabarelli, 2015) and as a key ecological processes (Leal et al., 2014; Schulz et al., 2016).

Resprouting ability along environmental gradients is also poorly known (Ceccon et al., 2006; Dexter et al., 2015; Murphy and Lugo, 1986). Likewise after disturbance, resprouts represent a relevant regeneration mechanism in areas under strong rainfall seasonality (McDonald et al., 2010). Cue et al., (2020) reported that natural regeneration in the Tumbesian dry forests is more positively affected by rainy season precipitation than any other abiotic factors. In Australian dry forests, (Zeppel et al., 2013) reported that resprouts are high in regions with regular seasonal droughts and increases with increasing interannual variability in rainfall. Additionally, in dry tropical deciduous forest of Mexico, woody seedlings have demonstrated a dependence of light conditions (Rincón and Huante, 1993) and soil fertility (availability of nutrients) (Huante et al., 1995). Given that the striking seasonality, light conditions and soil fertility affect seed production, germination, seedling development and persistence (Khurana and Singh, 2001), resprouts are likely to have a significant role in the regeneration process. Yet, information about the resprouts for the recovery and the maintenance of dry tropical forests is still limited.

Storage reserves in the roots and stumps from disturbed adults allow resprouts to withdraw in disturbed areas (Bond et al., 2001; Vesk and Westoby, 2004). In dry forests, it represents a crucial step in the initiation stage of the regeneration process of the high mortality of seedling from seeds caused by harsh environmental conditions (McDonald et al., 2010; Noutcheu, 2022). (Kabeya and Sakai, 2005) found that environmental factors are important for the development and growth of resprouts. Additionally, resprouts contribute to the rapid recovery of biomass and life area following disturbances (Khaine et al., 2018) and have a significant potential for the development of the next generation, despite the fact that they favour the self-replacement after stem death or injury (Bond et al., 2001). Coppicing responses of resprouts following disturbances and environmental factors are poorly addressed, although its understanding is extremely important for maintaining biodiversity in dry forests under anthropogenic pressure.

Given that the production and development of new shoots following disturbances represent a good step for species persistence in harsh environments, information on the resprouting ability (e.g., the number, length and dbh of new shoots) of woody species is essential to understand regeneration dynamics (Lévesque et al., 2011; Miller, 1999). Studies have reported that resprouting capacity varies with species (Handavu et al., 2018), stump diameter (Luoga et al., 2004), time since cutting (Britez et al., 2020) and resprout location (Bond et al., 2001). However, most of these studies on resprouting capacity have focused on greenhouse experiments (Chong et al., 2007). Thus, information on resprouting capacity and natural dynamic in the field following a gradient of human disturbances and environmental factors are still missing, although their importance for natural regeneration and assisted restoration of dry forests.

The Brazilian Caatinga dry forest provides a good framework for investigating the coppicing response of resprouts. First, recent studies have demonstrated that resprouting represent a primary regeneration mechanism (Noutcheu, 2022; Vanderlei et al., 2021) and it drives successional pathways and resilience in Caatinga dry forest (Barros et al., 2021). Second, the human population in the region (28 million; da Silva et al., 2017) is highly dependent on natural resources and impose acute and chronic disturbances by means subsistence agriculture, firewood collection, non-timber product exploitation, timber harvesting by coppicing trees and cutting branches from adult trees, and livestock raising (Barros et al., 2021; Rito et al., 2017). Finally, Caatinga region is undergoing climate change with a prediction of 22% rainfall decrease, increase of temperature up to 6°C and an impressive increase in the frequency of drought until the end of the century (Magrin et al., 2014). Thus, understanding how chronic disturbance and environmental factors affects regeneration mechanisms will be fundamental for the management and the restoration of this threatened dry tropical forest.

In this study, we assess coppicing responses of seedling-sized resprouts (i.e. < 100 cm high and diameter at soil level ≤ 1 cm) along independent gradients of chronic anthropogenic disturbances and environmental factors (rainfall, soil fertility and light availability measured by leaf area index) in the Caatinga dry forest. Coppicing responses were based on three measurements: shoot density (i.e, the number of new shoots per cut stump), shoot vigor (i.e, mean height and diameter of new shoots), resprouting capacity indices (the diameter of resprouts in relation to the average diameter of new shoots) and mortality rate. Our general hypothesis is that disturbances and harsher environmental conditions will stimulate coppicing response due to severity of the stress (Bond et al., 2001; Peguero and Espelta, 2011; Shibata et al., 2016). We then expect (1) that the coppicing response will be higher at the resprouts located at the stem, followed by the root collars and roots due to the location and size of storage reserves, (2) a positive relationship between coppicing response and high chronic disturbance, and (3) a negative relationship between coppicing response and low rainfall, soil fertility, and leaf area index.

Materials and methods

Study sites

This study was conducted in the Catimbau National Park (8°24'00″-8°36'35″ S; 37°00'30″-37°10'40″ W), a 607 km^2 protected area located in northeastern Brazil. The climate in the region is semi-arid type Bsh, with transition to the tropical rainy type As', according to the Köppen classification. The annual rainfall ranges from 1110 to 480 mm, but 60 to 75% of this is registered between March and July and there is a long critical dry season from August to February (Rito et al., 2017). The mean annual temperature is 23°C while the minimum (July) and maximum (December) annual temperature are 21°C and 25°C respectively. The vegetation of the area comprises low-stature dry forest, with Leguminosae, Euphorbiaceae, Boraginaceae and Burseraceae as dominant woody vegetation (Rito et al., 2017). The Park was established in 2002, but former residents were not indemnified and still live in its area (Siqueira, 2006). Their historical presence has resulted in an enormous mosaic in terms of land use and human pressure on the biota, which makes the Park an excellent opportunity to examine how human disturbance (for instance, grazing and browsing by livestock, collection of living and dead wood, harvesting of non-timber forest products) affects biota of the Caatinga (Rito et al., 2017).

Experimental design

Field data were collected between November 2019 and March 2021 using fifteen 0.1 ha (50 m × 20 m) permanent plots of Catimbau ILTER project (https://www.peldcatimbau.org) distributed along independent gradients of chronic anthropogenic disturbances and annual rainfall (Rito et al., 2017). Plots were established in sites with similar soil type (sandy soil), relief (level terrain) and vegetation low-stature Caatinga dry forest, (Rito et al., 2017). Plots were separated by ≥ 2 km and located within a total area of 214,3 km^2 (Rito et al., 2017).

Chronic anthropogenic disturbances

Data on the level of chronic anthropogenic disturbance of each plot was obtained by global multi-metric CAD index (Arnan et al., 2018), considering the three main sources of chronic disturbance in the area: (1) livestock pressure index (consumption of vegetation, trampling, and other physical damage caused by goats and cattle); (2) wood extraction index (the extraction of dead and live wood for fuel, fence construction, and artisanal production); and (3) extraction of non-timber forest products index (medicinal plants, food items for humans, hunting and livestock fodder). For livestock pressure index (LPI) and woody extraction index (WEI), we conducted field assessments of goat trail length, goat dung, cattle dung, alive wood extraction (stem cuts) and coarse woody debris extraction (litter) within each plot (see Arnan, Leal et al., 2018 for more details). For extraction of non-timber forest products index (NTFPI), we used two approaches: (1) geographic distances based on remote sensing (i.e. proximity to the nearest house and proximity to the nearest road, using satellite imagery and ArcGIS 10.1 software), since distance is inversely related to level of disturbance, we used the inverse of distance as our metric; and (2) interviews with inhabitants of the nearest village to each plot applying informal and semi structured questionaries to assess the number of people living in each village (see Arnan, Leal et al., 2018 for more details). Index values were calculated using the following formula:

$$I = \frac{\sum_{i=1}^{n} (y_i - y_{\min})/(y_{\max} - y_{\min})}{n} \times 100$$

where I is disturbance intensity; y_i is the observed value for a given disturbance metric in plot i; y_{min} is the minimum observed value for the disturbance metric across all plots; y_{max} is the maximum observed value for the disturbance metric across all plots; and n is the number of individual disturbance metrics incorporated in the index. The values of the three individual indexes were standardized between 0 and 1 to make them comparable and integrated into a single CAD multimetric index (i.e. global chronic disturbance index- GI) (see (Arnan et al., 2018) for methodological details).

Rainfall

Mean annual precipitation was obtained from five HOBO Weather Station established around plots. Each Station included: datalogger U30 (NRC) with a memory of 517 k bytes and a sealed battery that is powered by a solar panel 6W; Humidity and Temperature Sensor mod. S-THB-M002 with a high precision (T°=±0.2°C and H=±2.5%) and resolution (T°=0.02°C and H=0.1%) and Annual Deviation < 0.1°C for T° per year and < 1% per year for Humidity; Soil Moisture Sensor S-SMC-M005; Rain gauge mod. S-RGB-M002 and software – BHW – PRO for the extraction of data with a data collection period from 1s to 18 hours. The value of mean annual rainfall at each plot was obtained by the mean of data from November 2019 to March 2021 and Mean annual precipitation was ranged from 46 to 490 mm among plots.

Soil fertility

In the period February to December 2017, three soil samples of $10 \times 10\ \text{cm}^2$ of topsoil were selected randomly from 0 to 30 cm depth. Soil samples were dried in the laboratory and the physical and chemical indicators related to nutrient availability (Al, H, S, P, CTC, Ca, PH, K), water content, organic matter and acidity (Sfair et al., 2018) were measured in accordance with the Brazilian Ministry of Agriculture for soil analyses (EMBRAPA, 1997). The formula $SF = [Ca + Mg + K - \log(1 + A1)] \times OM + 5$ was used to determine soil fertility of each plot, where SF = soil fertility, Ca = exchangeable calcium (cmolc dm−3), Mg = exchangeable magnesium (cmolc dm−3), K = exchangeable potassium (cmolc dm−3), Al = exchangeable aluminium (cmolc dm−3), and OM = organic matter (g kg−1).

Light availability

Ten hemispherical canopy photographs were taken three time in the same place during the year 2016 in each 20m×50m plot. Photographs were taken 1.5 m above the ground at 5m intervals in uniformly forecast conditions in the early morning or in late afternoon in order to avoid direct solar radiation in canopy (Whitmore et al., 1993). Photographs were taken with a levelled Nikon D3000 10.2MP Digital SLR Camera with 18-55mm f/3.5-5.6G AF-S DX VR Nikkor Zoom Lens. Images were analyzed with the Gap Light Analyser software 2.0 in order to obtain the leaf area index of each plot (Frazer et al., 1999), which ranged from 0.02 to 0.48.

Coppicing experiments

In each plot, ten seedling-sized resprouts (i.e. < 100 cm high and diameter at soil level ≤ 1 cm, Ribeiro et al., 2015) were randomly selected, targeted and identified at the species level. We then measured the DAS of each resprouts and applied the experimental coppicing (i.e. the shoot apex was removed). Coppicing was applied in resprouts with different location according to their organ of origin: (i) root collars; or (ii) roots (lateral or taproot); (iii) stems (resprouts from stems) with a proportion of 34%, 12% and 54% respectively. To protect the target resprouts and new shoots from animals, protective wood boxes with nets were used; the design of boxes allowed the coppiced resprouts access to water and sun. The production of new shoots was monitored along 15 months and the total number of new shoots from each sprout was counted, the height and diameter at soil level of each new shoot were measured.

Statistical analyses

To test the effect of resprout location (i.e. roots, root collars and stem) on coppicing responses variables (1) new shoot number, (2) mean new shoot length (cm), (3) mean new shoot diameter (cm), (4) mean resprouting capacity indices (shoot diameter and stem diameter ratio) and mortality rate, we used Kruskal-Wallis tests because residuals did not meet the normality assumption of a one-way ANOVA. To assess how coppicing response variables varied among plant species we also applied Kruskal-Wallis test because lack of one-way ANOVA assumption. To test the relationship between stem diameter and coppicing response variables linear regression analysis was performed.

We used a model selection approach to test the influence of isolated and combined explanatory variables (disturbance index, rainfall, soil fertility and leaf area index) on response variables (new shoot number, mean new shoot length, mean new shoot diameter and mean shoot diameter: stem diameter ratio and mortality rate) with adequate error distribution.

First, we fit General Linear Mixed Models (GLMM) to test the effects of explanatory variables on the number of shoots using a Poisson distribution error and a quasi-Poisson if overdispersion was detected. Then, we fit Linear Mixed Models (LMM) to test the effects of explanatory variables on the mean shoot length and mean shoot diameter, separately, fitting a REML (restricted (or “residual”) maximum likelihood) equal FALSE. The Akaike’s information criterion with a correction for small samples (AICc) were used to select the best models. In case of overdispersion, qAICc was used instead of AICc for models ranking (Calcagno, 2018). We chose the best models based on AICc (or qAICc) differences lower than 2 (Burnham and Anderson, 2002). The most important predictors were contained in the best-supported models where intercept was not the only component (Burnham and Anderson, 2002). The selected model among the best models (D ((Q)AICc) < 2) was the model with the highest R2 (Burnham and Anderson, 2002). The model selection was conducted using the dredge function in the MuMin package (Barton, 2009). Unless otherwise specified, our unit of analysis was species for analyses of Kruskal wallis and regression, and plots as random factors for analysis of GLMM and LMM. Data that did not meet homoscedastic criteria were log(x) +1 transformed. All analyses were performed in R (R Core Team, 2016) and lme4 version 1.1-7 (Bates et al., 2015) to build the GLMM and LMM models.

Results

Emergence and growth of new shoots

After 15 months, a total of 144 out of the 150 resprouts in which we applied the experimental coppicing presented new shoots, representing all the 19 species. The most frequent species (present in more than 5 plots) were *Pityrocarpa moniliformis* (Leguminosae), *Trischidium molle* (Leguminosae), *Annona leptopetala* (Annonaceae), *Poincianela microphylla* (Leguminosae) and *Cnidoscolus bahianus* (Euphorbiaceae). Considering all species together, the average number of new shoots produced after 15 months was 1.5 ± 1.2 and with difference among species (Kruskal-Wallis test = 2.62, df = 18, P < 0.001; Table 1). The highest average number of shoots recorded per sprout was 3.8 ± 1.3 for *Croton heliotropiifolius* (Euphorbiaceae) followed by *Senegalia piauhiensis* (Leguminosae) with 3.0 ± 0.0. The lowest average number of shoots recorded was for *Colicodendron yco* (Capparaceae) with 0.8±0.83 (Table 1). The average percent of individuals found with new shoots within species was 73.61% and seven species maintained 100% of stems with living new shoots after the 15 months.

The diameter and height of new shoots after 15 months was significantly different among species (Kruskal-Wallis test = 1.78, df = 18, P = 0.04 and F=2.76, df=18, P < 0.001, respectively; Table 1). For all species together, the average diameter of new shoots recorded was 0.2 ± 0.1 cm and the species that had the largest diameter at soil level was *Dioclea grandiflora* followed by *Ziziphus joazeiro* (Rhamnaceae) with 0.37 ± 0.11 cm and 0.34 ± 0.05 respectively. *Melochia tomentosa* (Malvaceae) was the species with the smallest average diameter of new shoots 0.08 ± 0.11 cm. For height, the average of new shoots of all species together was 11.33 ± 10.1 cm, ranging from 3.1 ± 2.91 cm for *Colicodendron yco* to 44.0 ± 11.8 cm for *Dioclea grandiflora* (Leguminosae). The average resprouting capacity (i.e. the diameter of resprouts in relation to the average diameter of new shoots) for all species together was 0.55 ± 0.20. Although there was no significant relationship between resprouting capacity among species, *Dioclea grandiflora* presented the highest value with 0.81 ± 0.05.

Coppicing response to resprout type

Contrary to our first hypotheses, there was no effect of resprout type in coppicing responses. In resprouts by stem, the highest number of new shoots produced after coppicing was 3.33 ± 0.0 for *Croton heliotropiifolius*, and 6.0 ± 0.0 for *Trischidium molle* in resprouts by roots. *Croton argyrophylloides* (Euphorbiaceae) had the highest number (3.0 ± 1.4) of new shoots in resprouts by roots collars. The percent of individuals with new shoots was not significantly different among the resprout type with the percentage of 70.58%, 79.59% and 70.51% for roots, roots collars and stem respectively (Table 2; Fig. 2). The average diameter and length of new shoots considering all species together were not different among the resprout type (Table 3). The average highest length (52.75 ± 0.0 cm) and diameter (0.40 ± 0.14) was observed in roots collars from *Dioclea grandiflora* (Table 3).

The relationship between stem diameter and coppicing response

Considering all species together, the general linear model showed a positive relationship between stem diameter of resprouts and the number of new shoots they produced (GLM, $P < 0.01$). At the species level, seven (*Waltheria brachypetala* (Malvaceae), *T. molle, C. argyrophylloides, C.bahianus, Bauhinia acuruana* (Leguminosae), *M. tomentosa, A. leptopetala*) (Fig. 3; Table 4) out of 19 species sampled were found with significant positive relationship between stem diameter and the density of new shoots. Of these seven species, stem diameter explained the highest variation in the number of new shoots produced for *Cnidoscolus bahianus* (95%), while the lowest significant percent variation in the number of new shoots explained by stem diameter was for *Annona leptopetala* (44%) (Fig. 3; Table 4). Moreover, diameter of the most of new shoots produced (78%) varied between 0.3 and 0.6 cm. Although there was no relationship between stem diameter and shoot length considering all species together, ten species (*W. brachypetala, T. molle, Senegalia bahiensis* (Leguminosae), *P. microphylla, A. leptopetala, C. argyrophylloides, C. bahianus, B. acuruana, P. moniliformis, C. yco*)) had a significant positive relationship between stem diameter and average length of new shoots (Fig. 4, Table 4). These results indicated that the stem diameter of *S. bahiensis and C. bahianus* explained the highest and lowest variation of average shoot length with 89% and 42%, respectively. The length and diameter of new shoots were significantly correlated with the majority (11 out of 19) of species ($R^2=0.36$, $P < 0.0001$) (Fig. 5; Table 4). All of 11 species had presented a strong ($R^2 > 0.68$) and positive significant relationship between new shoot length and new shoot diameter (Table 4). Though it was weak (R^2=0.11, P<0.001), 11 out of 19 of species had a positive relationship between shoot diameter and stem diameter for all species. *Croton heliotropiifolius* (R^2=0.95; P =0.01) and *C. argyrophylloides* (R^2=0.36, P=0.04) explained the highest and lowest variation respectively. (Fig. 6; Table 4).

CAD increase and environmental factors effects on coppice response

The results from GLMM showed that rainfall (t=-0.141; df=12; p=0.04) and soil fertility (t=-0.185; df=12; p=0.05) had negative effect on the number of new shoots produced (Table 5). However, new shoots length, new shoots diameter and mortality rate of resprouts were not related neither to chronic disturbance nor environmental factors (Tables 5 and 6). Among the most widely distributed species, *A. leptopetala* new shoot length was negatively related to chronic disturbance (t=-0.47; df=3;p=0.002) and leaf area index (t=-0.52;df=3;p=0.002) and new shoot diameter of was also negatively related to disturbance (t=-0.11; df=3; p=0.0003) and rainfall (t=-0.12; df=3; p=0.0001). The same trend was observed in *T. molle* with new shoot length negatively related with leaf area index (t=-0.22; df=3; p=0.03) and new shoot diameter related with rainfall (t=-0.05; df=4; p=0.03). Contrary of these species, new shoot length and diameter of *C. bahianus* were positively related with rainfall (t=0.66; df=2; p=0.03) and (t=0.2; df=1; p=0.03) respectively (Table 7 and 8).

Discussion

Our study evaluated the effects of increased chronic disturbance and gradients of environmental factors on experimental coppicing of seedling-sized resprouts in Caatinga dry forest. Our results reveal a high resprouting ability as all species and more than 73% of the individuals where coppicing was applied produced new shoots. However, our hypotheses were only partially corroborated as only decreased rainfall and fertility negatively influenced coppicing response. Chronic disturbance did not affect any variable related to production of new shoots. These results indicate that Caatinga woody species have a high potential to resprout in response to biomass removal, which reinforce previous studies demonstrating the role of resprouts in the persistence and recovery of Caatinga vegetation.

Our findings corroborate previous studies in dry tropical forests around the world showing a high resprouting ability of woody plant species (Bellingham et al., 2009; Lévesque et al., 2011; McLaren and McDonald, 2003; Sampaio et al., 1993; Belligham et al., 1994). For instance, all of 19 sprout species produced shoots after 15 months of coppicing with a high proportion of individuals resprouts (73.61%). These results were similar with disturbances type and different ecosystems including slash and burn in Caatinga (Sampaio et al., 1993), hurricane in montane tropical forest (Belligham et al., 1994), coppicing in coastal wetland (Xie et al., 2020), African savanna (Luoga et al., 2004) and Jamaican dry tropical forest (McLaren and McDonald, 2003). These alive species may be considered as an initial stage of the forest recovery although previous studies have shown that the number of new shoots produced decrease with time (Britez et al., 2020; Syampungani et al., 2017).

While all species resprout after coppicing, the average number of new shoots varied among species, which is an indication of the importance of species-specific responses to coppicing (Ky-dembele et al., 2007). This finding was similar to that study of coppicing ability of dry miombo woodland species in Zambia (Syampungani et al., 2017), in which new shot density ranged from 5 to 8 shoots per stumps. In our study, the highest number of new shoots was produced by *Croton heliotropiifolius*, as observed by Sampaio et al., (1993), who found a high number of new shoots in *Croton* species following fire in Caatinga dry forest. Despite being heavily utilized by population (Albuquerque and Melo, 2018), because it had high woody density (Sfair et al., 2017), *Croton* species have a high individual density in the study area (Rito et al., 2017) and in Caatinga dry forest in general (Fernandes et al., 2020), which may be related to the resprouting ability. Average new shoot length and diameter were different among the focused species and previous studies in other dry tropical forest have shown similar results. For instance, Levesque et al., (2011), working in Jamaican tropical dry forest, investigating dynamics and recovery rate of forest following clearance (2000-2009), reported new shoot length and diameter significantly different among the species though they were composed with seedlings and adults species. McLaren and McDonald (2003) found similar results in dry tropical forest located in south coast of Jamaica.

Although studies reported that resprouting ability of species are closely linked to the starch-storage capacity and resprout type (Knox and Clarke, 2005; Bond and Midgley 2001), this was not the case in our study. Similarly, Britez et al., 2020 working with Quercus spp. (oak) in Florida, were assessed coppice response at 0 m, 1 m, and 1 m and split stems reported that sprout numbers were not different. Moreover, the number of sprouts that survived 9 years differed among the source locations. In our study, we found no difference among sprouts survival though approximately 60% sprouts from stem and 12% from roots.

Several studies have documented the relationship between stem diameter and resprouting ability (Putz and Brokaw (1989); Bellingham et al., 1994; Bellingham and Sparrow 2000; Del Tredici 2001). Similar to an adult tree, seedling-sized sprouts exhibited a good relationship between sprout diameter and number of new shoots, new shoot length and diameter. This may be related to availability and the translocation of stored carbohydrate from stored organs to shoots, which was initiated by coppicing (Moyo et al., 2015). Moreover, in Caatinga dry forest, plant species have a complex roots system (Vanderlei et al., 2021), and the fact that the larger root system would offer more surface area for water and nutrient uptake and allow more resprouting ability confirm these results. Similar trend was found in studies in other dry forests worldwide (McLaren and McDonald 2003; Levesque, McLaren and McDonald 2011).

Like acute disturbances, chronic disturbances have been assumed to affect resprouting ability (Bellingham and Sparrow, 2000; Bond et al., 2001). Chronic disturbances may benefit resprouting and resprouts growth due to the availability of stored resources (Noutcheu, 2022). For example, Hjalten et al., (1993) have reported that herbivory has a positive effect on resprouting and plant growth of *Betula pubescens*. In the same way, Syampungani et al., (2017) working in dry miombo woodland found that the constant removal of vegetation for charcoal production had a positive effect on resprouting ability of species. Most of these studies included sapling-sized and adult-sized resprouts which were not the case in our study composed exclusively of seedling-sized resprouts, which lack an effect of disturbance in our study. Moreover, studies have reported that seedling-sized resprouts have a better sprouting ability following coppicing and/or other disturbances (Ashish et al., 2010; Randall et al., 2005; Vesk, 2006). Similarly, chronic disturbances had no effect on mortality rates, this may be attributed to the storage organs which allow them to resist in the area. Generally, mortality rate of species was relatively low and *Pityrocarpa moniliformis* was found with the highest rate (18%) among all studied species in the community.

Although environmental factors are largely recognized as a determinant factor in resprouting ability among dry forest plant assemblage species (Ceccon et al., 2006; Chazdon et al., 2007; Rito et al., 2017; Seiler et al., 2015), we observed contrasting effects considering the different species. Only the new shoot number was negatively affected by rainfall and soil fertility and, and positive and negative effects were observed among the most widely distributed species. Reasons for this pattern may include the season of coppicing, as it was done in November 2019, characterized by the absence of rainfall in most parts of the Park. According to Pawlick, (1989), the season of the year during which the coppicing is made is also an important determinant of the resprouting ability. Similar results were obtained in caribbean tropical dry forest where seasonality in rainfall had a largely effect on shoots numbers (Lévesque et al.,2011). Moreover, according to Malhi et al., (2006) soil fertility can lead to negative effect on plants due to competition among species

This high resprouting ability of Caatinga dry forest species may implicate in a general decreasing in the forest stature or shrub encroachment. The increase in the density and cover of native shrubs (also known as woody encroachment or thickening), is a global phenomenon that occurs in ecosystems ranging from the drylands of eastern Australia to the tundra (Eldridge et al. 2011). But our results indicate that even tree species may have their stature reduced due to continuous coppicing, and this process can change all the fauna that cares for the plants. And it can be positive by facilitating plant access to mutualistic partners such as pollinators, seed dispersers, ants that protect plants against herbivores, etc. But it can also be negative as it facilitates the use of foliage by domestic animals such as goats.

Conclusions

Evaluate the coppice responses of sprouts represents an important step in the understanding forest regeneration/recovery and the management of many ecosystems, particularly in dry tropical forest where true seedling is threatened in harsh environmental conditions. With the persistence of around 74% of individual and all species sampled presenting resprouting ability, it can be assumed that sprouts will play a significant role in the natural regeneration and vegetation recovery of Caatinga dry forest. Some species with a high new shoot production and new shoot growth constitutes important resources for the local population, such as *Croton heliotropiifolius, Senegalia piauhiensis, Ziziphus joazeiro* and *Pityrocarpa moniliformis*, which could be used for the restoration using this coppicing as silvicultural method. However, little is known about the effects of chronic disturbances on coppice response of the different ontogenetic stages, so further research should address these issues. Finally, it is very likely that the ongoing shrub encroachment process of the Caatinga dry forest is a result of the conversion of the old growth and secondary forest into human-degraded landscape, in which sprouts can play a significant role for this new dry forest structure and cascading up to plant attendants in general, mutualists and antagonists. Our results of high resprouting ability of woody species corroborate this hypothesis. This should attract attention of policy makers and park managers to take a necessary measure to limit the ongoing human disturbances in the entire park for the maintenance of the original forest structure and its attendant fauna of this ecosystem. Additionally, given that water availability is a crucial factor underlying tropical dry biome transition (Dexter et al., 2018), and the undergoing climate change with a prediction of 22% rainfall decrease in the Caatinga region, our results suggest that urgently management action is required for the sustainability of this forest.

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Table 1. Production of new shoots of the 19 resprout seedling-sized species in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

Species	N	shoots±sd	HGT ±sd	DIA ±sd	RCI±sd	% stems
Annona leptopetala	11	1±0.89	6.3±6.86	0.14±0.12	0.63±0.41	63.66
Bauhinia acuruana	6	1.3±0.81	8.6±5.98	0.17±0.09	0.52±0.10	83.33
Chamaecrista zygophylloides	3	1.7±0.57	11.8±8.31	0.25±0.05	0.52±0.04	100
Cnidoscolus bahianus	12	1.3±1.15	9.3±9.07	0.21±0.18	0.56±0.25	66.67
Colicodendron yco	5	0.8±0.83	3.1±2.91	0.17±0.17	0.63±0.26	60
Croton argyrophylloides	11	2.6±1.36	13.03±5.05	0.21±0.07	0.44±0.15	90.99
Croton heliotropiifolius	4	3.8±1.5	15.1±5.52	0.25±0.04	0.6±0.02	100
Cynophalla flexuosa	7	1.4±0.97	11.5±6.96	0.23±0.10	0.67±0.20	85.77
Dioclea grandiflora	3	1±0	44.3±11.87	0.37±0.11	0.81±0.05	100
Melochia tomentosa	10	0.8±1.13	4.1±6.90	0.08±0.11	0.47±0.14	40

Pityrocarpa moniliformis	18	0.9±0.99	14.1±16.87	0.17±0.15	0.58±0.27	61.11
Poincianela microphylla	14	1.07±0.82	10.9±10.74	0.21±0.18	0.59±0.09	71.44
Poincianella pyramidalis	3	1.3±0.57	16.9±11.16	0.25±0.05	0.57±0.21	100
Senegalia bahiensis	4	1.5±1.29	6.8±4.84	0.18±0.13	0.64±0.13	75
Senegalia piauhiensis	3	3±0	12.9±5.67	0.18±0.01	0.42±0.13	100
sp1	4	2.3±0.5	27.7±17.29	0.23±0.05	0.54±0.13	100
Trischidium molle	18	2±1.71	8.1±7.20	0.17±0.12	0.49±0.17	72.22
Waltheria brachypetala	5	1.2±1.09	4.9±5.57	0.11±0.12	0.34±0.09	60
Ziziphus joazeiro	3	2±1	17.2±14.03	0.34±0.05	0.47±0.17	100
F-value		2.62	2.76	1.78	1.25	
P-value		0.001	0.0008	0.04	0.23	
d.f.		18	18	18	18	

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[a] Means for each species are given for the total number of stems sampled for each species (N). the average number of new shoots sampled alive (Shoots) and standard error (sd). average height (HGT) of new shoots and average new shoot diameter (DIA). Percentage of the stems of each species with new shoots (% stems), and (rci) coppicing capacity index.

Table 2. Numbers and percentages of seedling-sized resprouts used in the study by resprout location over the 15 months of monitoring after coppicing experiments in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

	Resprouter number	**Alive**	**Dead**	**% alive**	**% dead**
Roots	17	12	5	70.59	29.41
roots collars	49	39	10	79.59	20.40
Stem	78	55	23	70.51	29.48
Total	144	106	38	73.61	26.38

Table 3. Results of a one-way ANOVA of the effect of resprout type on response variables following coppicing experiments in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

Response variables	**Resprouting type**			**p**
	roots	root collars	stem	
New shoot number	2.05±1.83	1.65±1.18	1.30±1.10	0.43
New shoot length	14.99±12.65	11.21±10.30	10.18±10.12	0.36
New shoot diameter	0.22±0.12	0.21±0.13	0.20±0.13	0.51
New shoot diameter: stem diameter ratio	0.48±0.18	0.54±0.18	0.58±0.22	0.19

Table 4. Summary of the regression analysis of stem diameter against the number of new shoots produced and the diameter and height of the new shoots for each of 19 species following coppicing of a Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

	Shoot×StemD		NSL×StemD		NSL×DIA		DIA×StemD	
Species	P	% R	P	% R	P	% R	P	% R
Annona leptopetala	0.01	50	<0.01	58	<0.001	73	<0.01	54
Bauhinia acuruana	0.05	63	<0.01	-	-	85	0.01	81
Cnidoscolus bahianus	<0.001	95	0.02	42	<0.001	68	<0.001	78
Colicodendron yco	-	-	0.02	85			0.04	78
Croton argyrophylloides	<0.01	55	<0.01	60	<0.01	62	0.04	36
Croton heliotropiifolius	-	-	-	-	-	-	0.01	97
Cynophalla flexuosa	-	-	<0.01	77	<0.01	85	0.01	70
Melochia tomentosa	<0.001	86	<0.001	76	<0.001	36	<0.001	94

Pityrocarpa moniliformis	-	-	<0.001	72	<0.001	84	-	-
Poincianela microphylla	-	-	<0.001	88	<0.001	96	<0.001	93
Senegalia bahiensis	-	-	0.05	89	<0.001	99	0.04	90
Senegalia piauhiensis	-	-	-	-	-	-	-	-
sp1	-	-	0.02	94	<0.01	94	-	-
Trischidium molle	<0.001	71	<0.001	76	<0.001	74	-	-
Waltheria brachypetala	0.03	82	0.02	85	<0.01	94	<0.01	90
all species	<0.001	32	-	-	-	-	<0.001	11

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[a] the number of new shoots sampled alive (Shoots), stem diameter (stemD), new shoot length (NSL), new shoot diameter (DIA). Only species showing a significant relationship are shown.

Table 5. Best-supported models (qAICc < 2) analyzing effects of chronic anthropogenic disturbances and environmental factors on the shoot number, shoot diameter, shoot length and shoot diameter and stem diameter ratio and mortality rate in 15 0.1-ha plots surveyed in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil. Only models with delta AICc < 2 were selected for different models. R^2 gives an estimation of the variance explained by the optimal model. BIC gives the proportion of variance explained by random (Plots) factor.

Response variable	**Models**	**Variable selected**	**df**	**logLik**	**BIC**	**delta**	**weight**	**R^2**
Shoot number	glmer12	SF	3	-223.6	462.1	0	0.557	0.3
	glmer3	AP+SF	4	-225.3	465.8	1.513	0.106	0.4
	glmer6	LAI+SF	4	-225.4	465.8	1.996	0.091	0.37
shoot length	lmer10	SF	4	-115.4	250.6	0	0.272	0.15
	lmer11	LAI	4	-115.5	250.9	0.234	0.242	0.13
	lmer1	CAD	4	-115.8	251.6	0.985	0.166	0.08
	lmer8	AP	4	-115.9	251.7	1.047	0.161	0.08
	lmer7	LAI+SF	5	-114.8	254.6	1.154	0.037	0.51
	lmer3	AP+SF	5	-115.1	255.2	1.739	0.028	0.18
	lmer6	CAD+SF	5	-115.2	255.3	1.864	0.026	0.17
shoot diameter	lmer125	SF	4	83.3	-146.7	0	0.261	0.19
	lmer15	CAD	4	83.1	-146.2	0.476	0.206	0.12
	lmer145	AP	4	83.1	-146.2	0.497	0.203	0.11
	lmer135	LAI	4	83.1	-146.2	0.498	0.203	0.16
RCI	lmer10	SF	4	-115.4	250.6	0	0.272	0.22
	lmer11	LAI	4	-115.5	250.9	0.234	0.242	0.21
	lmer1	CAD	4	-115.8	251.6	0.985	0.166	0.17
	lmer8	AP	4	-115.9	251.7	1.047	0.161	0.2
mortality rate	glmer13	LAI	3	-82.5	180.1	0	0.243	0.17
	glmer11	AP	3	-82.6	180.1	0.023	0.240	0.16
	glmer12	SF	3	-82.8	180.5	0.466	0.192	0.13
	glmer1	CAD	3	-82.9	180.7	0.654	0.175	0.13

Table 6. Results from mixed models (GLMM and LMM) to the shoot number, shoot diameter, shoot length and shoot diameter and stem diameter ratio and mortality rate in response to chronic anthropogenic disturbances and environmental factors in 15 0.1-ha plots surveyed in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

Response variables	**variables selected**	**df**	**t**	**p**
shoot number	LAI	12	-0.01	0.831
	SF	12	-0.175	**0.05**
shoot length	LAI	13	1.028	0.304
	SF	13	-1.14	0.25
shoot dbh	SF	13	-0.719	0.472
RCI	SF	13	-1.08	0.27
mortality rate	LAI	13	-0.19	0.357

Rci=shoot diameter/stem diameter; LAI= leaf area index; SF= soil fertility

Table 7. Best-supported models (qAICc < 2) analyzing the effects of chronic anthropogenic disturbances, rainfall, soil fertility and leaf area index on the new shoot number, new shoot diameter, new shoot length and mortality rate for the most widely distributed species in 15 0.1-ha plots surveyed in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil. Only models with delta AICc < 2 were selected for different models. R2 gives an estimation of the variance explained by the optimal model. BIC gives the proportion of variance explained by random (Plots) factor.

Species	**Variable response**	**Models**	**df**	**LogLik**	**BIC**	**Delta**	**Weight**	**R^2**
Pityrocarpa moniliformis	Shoot number	glmer12	3	-22.2357	53.14261	0	0.282383	0.0075
		glmer13	3	-22.9107	54.49258	1.349966	0.14378	0.00034
		glmer1	3	-22.9193	54.50968	1.367067	0.142556	0.00024
		glmer11	3	-22.9251	54.52136	1.378744	0.141726	0.00018
	Shoot length	lmer8	4	-74.1298	159.8211	0	0.273796	0.17
		lmer11	4	-74.6306	160.8228	1.001706	0.165924	0.13
		lmer5	5	-73.6162	161.6843	1.863216	0.107854	0.22
	Shoot dbh	lmer148	4	9.082259	-6.60303	0	0.21874	0.103
		lmer138	4	8.81781	-6.07413	0.528898	0.167911	0.07

		lmer18	4	8.536348	-5.51121	1.091822	0.126719	0.04
		lmer58	5	9.703786	-4.95571	1.647318	0.095988	0.163
		lmer128	4	8.099181	-4.63687	1.966156	0.081843	0.00028
	Mortality rate	glmer11	3	-11.5285	31.72805	0	0.185904	0.054
		glmer131	3	-11.5499	31.77098	0.042932	0.181956	0.051
		glmer111	3	-11.5504	31.77197	0.043919	0.181866	0.05
		glmer121	3	-11.9811	32.63329	0.905235	0.118228	0.0052
		glmer51	4	-10.9538	33.46903	1.740975	0.077847	0.11
Poincianela microphylla	Shoot number	glmer11	3	-15.7031	39.32328	0	0.29475	0.218
		glmer1	3	-16.6383	41.19379	1.870512	0.115685	0.107
		glmer12	3	-16.731	41.3791	2.055826	0.105448	0.08
	Shoot length	lmer104	4	-52.3674	115.2911	0	0.18042	0.032
		lmer114	4	-52.3805	115.3172	0.026134	0.178078	0.029
		lmer84	4	-52.5304	115.6171	0.326007	0.153283	0.0081
		lmer14	4	-52.5762	115.7087	0.417566	0.146424	0.0043

	Shoot dbh	lmer125	4	4.534804	1.486621	0	0.188047	0.034
		lmer135	4	4.435574	1.685081	0.19846	0.170283	0.021
		lmer15	4	4.34194	1.872349	0.385728	0.155062	0.007
	Mortality rate	lmer145	4	4.288525	1.979179	0.492558	0.146997	0.005
		glmer113	3	-7.0151	21.94737	0	0.274667	0.17
		glmer133	3	-7.75766	23.4325	1.485137	0.130711	0.084
Cnidoscolus bahianus	Shoot number	glmer13	3	-14.4238	36.30231	0	0.21024	0.4
		glmer11	3	-14.6887	36.83211	0.5298	0.161313	0.37
		glmer7	4	-13.9716	37.88281	1.580496	0.095393	0.45
		glmer2	4	-13.978	37.89561	1.593294	0.094784	0.44
		glmer1	3	-15.3628	38.18023	1.877918	0.082211	0.3
	Shoot length	lmer33	5	-40.5974	93.61925	0	0.22275	0.32
		lmer13	4	-42.2975	94.53459	0.915337	0.140947	0.1
		lmer83	4	-42.3523	94.64422	1.024971	0.133428	0.09
	Shoot dbh	lmer16	4	5.747364	-1.5551	0	0.158804	0.28

		lmer146	4	5.627695	-1.31576	0.239337	0.140893	0.26
		lmer36	5	6.850015	-1.2755	0.279605	0.138085	0.4
		lmer136	4	5.342967	-0.74631	0.808793	0.105983	0.23
		lmer26	5	6.151712	0.12111	1.676211	0.068687	0.32
		lmer66	5	6.051537	0.32146	1.876561	0.06214	0.31
		lmer86	6	7.254187	0.401067	1.956168	0.059715	0.44
	Mortality rate	glmer13	3	-4.15888	15.77249	0	0.357897	0.39
Annona leptopetala	Shoot number	glmer11	3	-10.7384	28.06857	0	0.213885	0.35
		glmer12	3	-11.124	28.83968	0.771106	0.145458	0.02
		glmer1	3	-11.3925	29.37664	1.308074	0.111208	0.28
		glmer13	3	-11.5646	29.72091	1.652344	0.093622	0.01
		glmer5	4	-10.5612	29.91126	1.84269	0.085123	0.44
	Shoot length	lmer5	5	-24.1788	59.34377	0	0.345114	0.69
		lmer12	6	-23.3686	59.92058	0.576811	0.258648	0.74
	Shoot dbh	lmer55	5	11.82835	-12.6706	0	0.519179	0.62

	Mortality rate	glmer53	4	-1.38629	11.56149	0	0.237526	0.56
		glmer113	3	-2.64131	11.87428	0.312797	0.203137	0.32
Trischidium molle	Shoot number	glmer1	3	-33.4668	75.60477	0	0.198929	0.08
		glmer11	3	-33.6286	75.92825	0.323484	0.169221	0.03
		glmer13	3	-33.6719	76.01489	0.410123	0.162047	0.02
		glmer12	3	-33.8255	76.32212	0.717349	0.138972	0.01
		glmer2	4	-32.9104	77.38229	1.777522	0.081793	0.1
	Shoot length	lmer11	4	-58.2359	128.0332	0	0.315673	0.23
		lmer8	4	-59.067	129.6955	1.662233	0.137495	0.16
		lmer2	5	-57.757	129.9658	1.932592	0.12011	0.27
	Shoot dbh	lmer145	4	14.9728	-18.3841	0	0.294361	0.19
		lmer135	4	14.62422	-17.6869	0.697162	0.207728	0.16
	Mortality rate	glmer133	3	-9.69338	28.05787	0	0.248606	0.09
		glmer113	3	-9.97957	28.63026	0.572386	0.186732	0.07
		glmer13	3	-10.4733	29.61771	1.559837	0.113972	0.01

	glmer123	3	-10.6302	29.93151	1.873637	0.097422	0.05

Table 8. Results from mixed models (GLMM and LMM) analyzing the effects of chronic anthropogenic disturbances, rainfall, soil fertility and leaf area index on the new shoot number, new shoot diameter, new shoot length and mortality rate for the most widely distributed species in 15 0.1-ha plots surveyed in the Caatinga dry forest, Catimbau National Park, Buíque, PE, Northeast Brazil.

	Variable response	Variable selected	df	t	P
Pityrocarpa moniliformis	shoot number	SF	4	-0.122	0.262
	shoot length	LAI	3	1.881	**0.05**
		AP	3	-1.480	0.13
	shoot dbh	LAI	3	1.410	0.22
		AP	3	-1.287	0.19
	RCI	LAI	3	1.345	0.17
		AP	3	-1.181	0.23
	mortality rate	CAD	3	0.974	0.3
Trischidium molle	shoot number	AP	4	-1.227	0.22
	shoot length	CAD	3	-0.991	0.32
		LAI	3	-2.520	**0.01**
	shoot dbh	LAI	4	-1.944	**0.05**
		AP	4	-0.732	0.46
	RCI	LAI	3	-2.122	**0.02**
	mortality rate	LAI	4	1.251	0.12

Annona leptopetala	shoot number	AP	3	-1.291	0.35
		SF	3	1.580	0.23
	shoot length	CAD	2	-0.375	0.07
		LAI	2	0.282	**0.02**
		SF	2	0.370	0.08
	shoot dbh	CAD	3	-0.021	0.48
		LAI	3	-0.052	0.13
	RCI	AP	3	0.243	0.2
		CAD	3	0.136	**0.001**
		SF	3	0.138	0.5
		LAI	3	0.386	**0.002**
	mortality rate	CAD	3	0.128	0.89
		LAI	3	-0.305	0.76
		SF	3	-0.189	0.85
Poincianela microphylla	shoot number	LAI	4	1.167	0.24
		AP	4	1.797	0.07
	shoot length	SF	4	-0.669	0.50
	shoot dbh	AP	4	0.882	0.37
	RCI	LAI	4	0.170	0.86
		AP	4	1.113	0.26
	mortality rate	LAI	4	-1.190	0.23
		AP	4	-1344	0.17

Cnidoscolus bahianus	shoot number	CAD	2	-0.915	0.36
		LAI	2	-1.709	0.08
	shoot length	CAD	2	-2.368	**0.01**
		AP	2	1.965	**0.05**
	shoot dbh	CAD	1	-2.143	**0.03**
		LAI	1	-1.168	0.242
		AP	1	1.595	0.150
	RCI	LAI	2	-1.119	0.26
		SF	2	0.864	0.38
	mortality rate	LAI	3	0.015	0.98

Legend for figures

Figure 1. Location of the study area in (a) south America, (b) north-eastern Brazil and Pernambuco state (in grey) and (c) Catimbau National Park showing the distribution of the 15 0.1-ha plots (circles) over chronic anthropogenic disturbance (CAD) and environmental factors.

Figure 2. Proportions of seedling-sized resprouts alive in each resprout type after the 15 months of monitoring since the coppicing experiments conducted in the Catimbau National Park, Buíque, PE, Northeast Brazil.

Figure 3. Relationships between new shoot number and stem diameter for species that showed significant relationship (with a minimum of 6 individuals) after 15 months of monitoring since the coppicing experiments were conducted in the Catimbau National Park, Buíque, PE, Northeast Brazil. Models for new shoot density were developed using log transformed data for some species presented

Figure 4. Relationships between new shoot length and stem diameter for species that showed significant relationship (with a minimum of 6 individuals) after 15 months of monitoring since the coppicing experiments were conducted in the Catimbau National Park, Buíque, PE, Northeast Brazil. Models were developed using log transformed data for some species presented

Figure 5. Relationships between new shoot length and new shoot diameter for species that showed significant relationship (with a minimum of 6 individuals) after 15 months of monitoring since the coppicing experiments were conducted in the Catimbau National Park,

Buíque, PE, Northeast Brazil. Models were developed using log transformed data for some species presented

Figure 6. Relationships between stem height and new shoot length for Cnidoscolus bahianus that showed significant relationship (with a minimum of 6 individuals) after 15 months of monitoring since of monitoring since the coppicing experiments were conducted in the Catimbau National Park, Buíque, PE, Northeast Brazil.

Fig. 1.

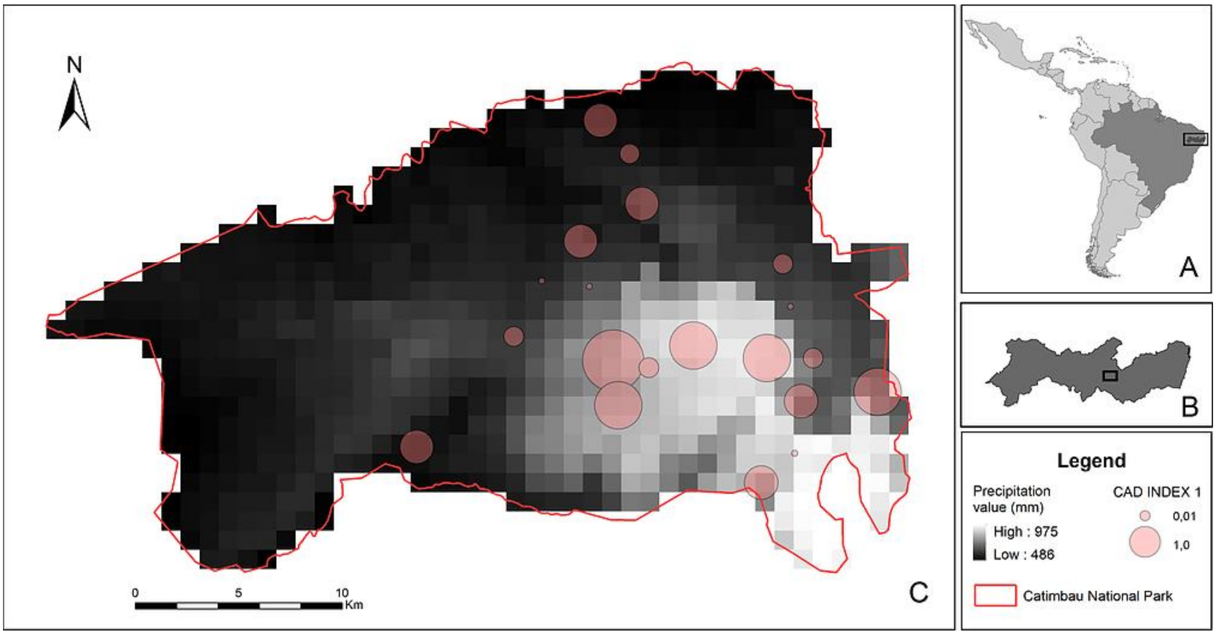

N
0
5
10
Km
C
A
B
Legend
Precipitation value (mm)
High : 975
Low : 486
CAD INDEX 1
0,01
1,0
Catimbau National Park

Fig. 2.

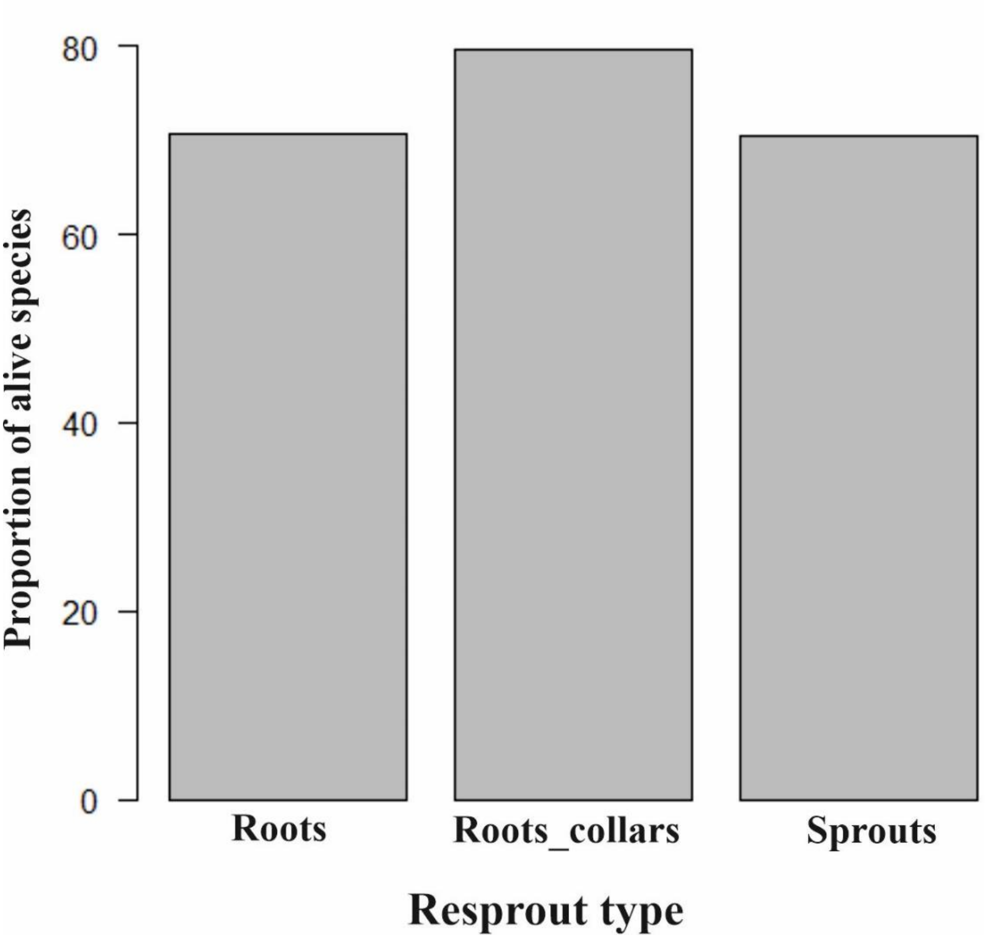

80
60
40
20
0
Proportion of alive species
Roots
Roots_collars
Sprouts
Resprout type

Fig. 3.

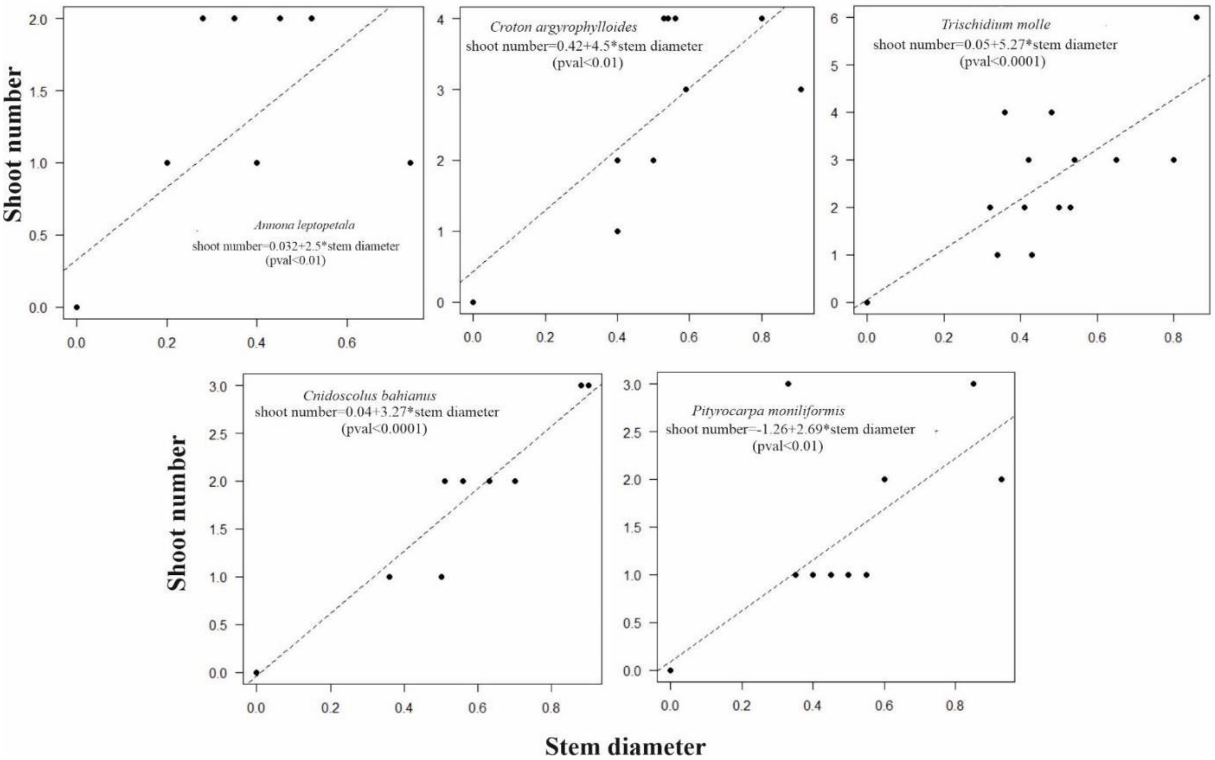

Shoot number
Annona leptopetala
shoot number=0.032+2.5*stem diameter
(pval<0.01)
Croton argyrophylloides
shoot number=0.42+4.5*stem diameter
(pval<0.01)
Trischidium molle
shoot number=0.05+5.27*stem diameter
(pval<0.0001)
Shoot number
Cnidoscolus bahianus
shoot number=0.04+3.27*stem diameter
(pval<0.0001)
Pityrocarpa moniliformis
shoot number=-1.26+2.69*stem diameter
(pval<0.01)
Stem diameter

Fig.4.

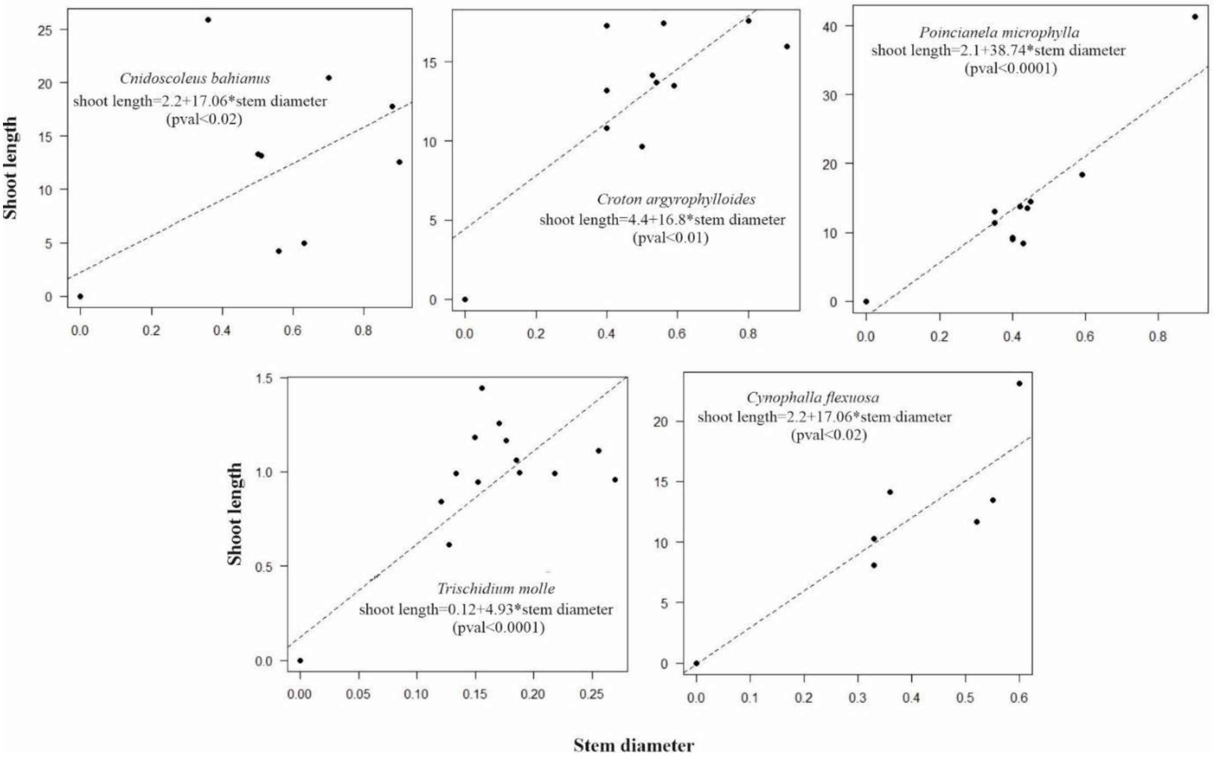

Shoot length
Stem diameter
Cnidoscoleus bahianus
shoot length=2.2+17.06*stem diameter
(pval<0.02)
Croton argyrophylloides
shoot length=4.4+16.8*stem diameter
(pval<0.01)
Poincianela microphylla
shoot length=2.1+38.74*stem diameter
(pval<0.0001)
Trischidium molle
shoot length=0.12+4.93*stem diameter
(pval<0.0001)
Cynophalla flexuosa
shoot length=2.2+17.06*stem diameter
(pval<0.02)
0
5
10
15
20
25
30
40
0.0
0.5
1.0
1.5
0.0
0.2
0.4
0.6
0.8
0.00
0.05
0.10
0.15
0.20
0.25
0.1
0.3
0.5

Fig. 5.

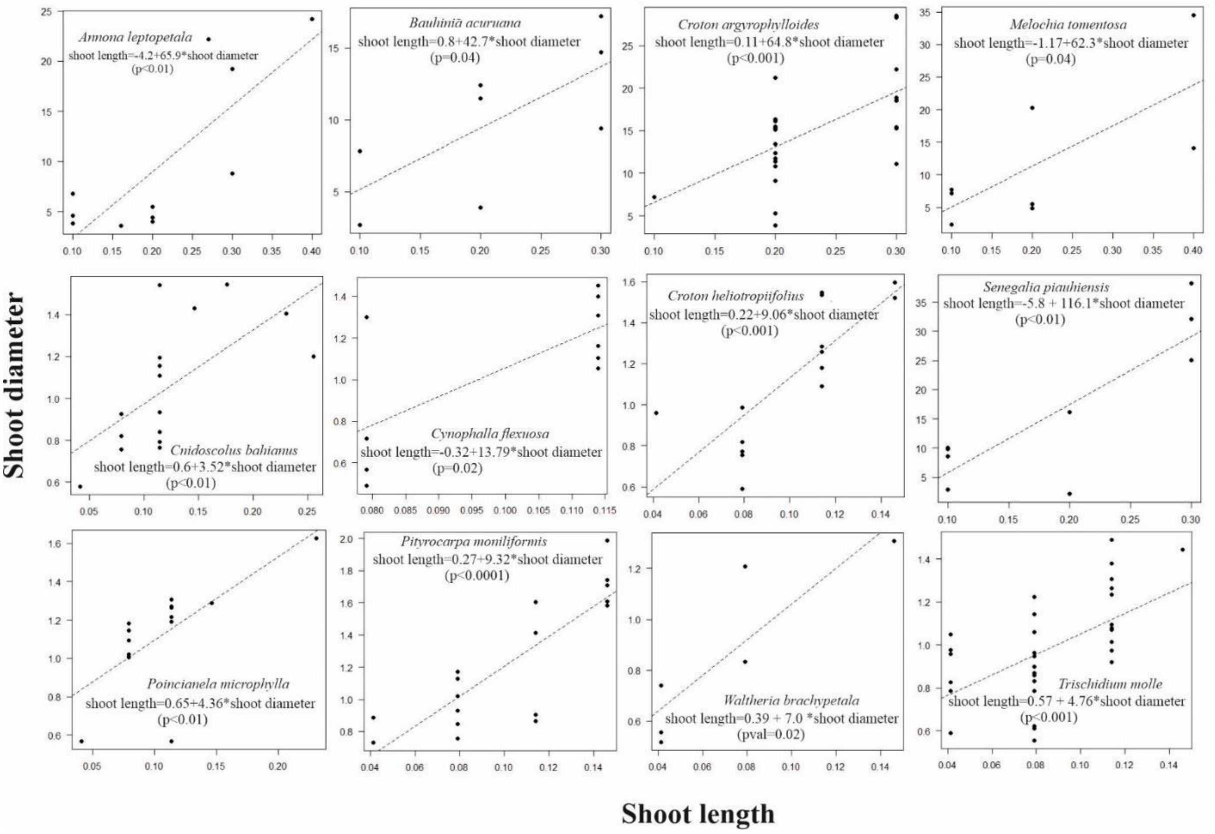
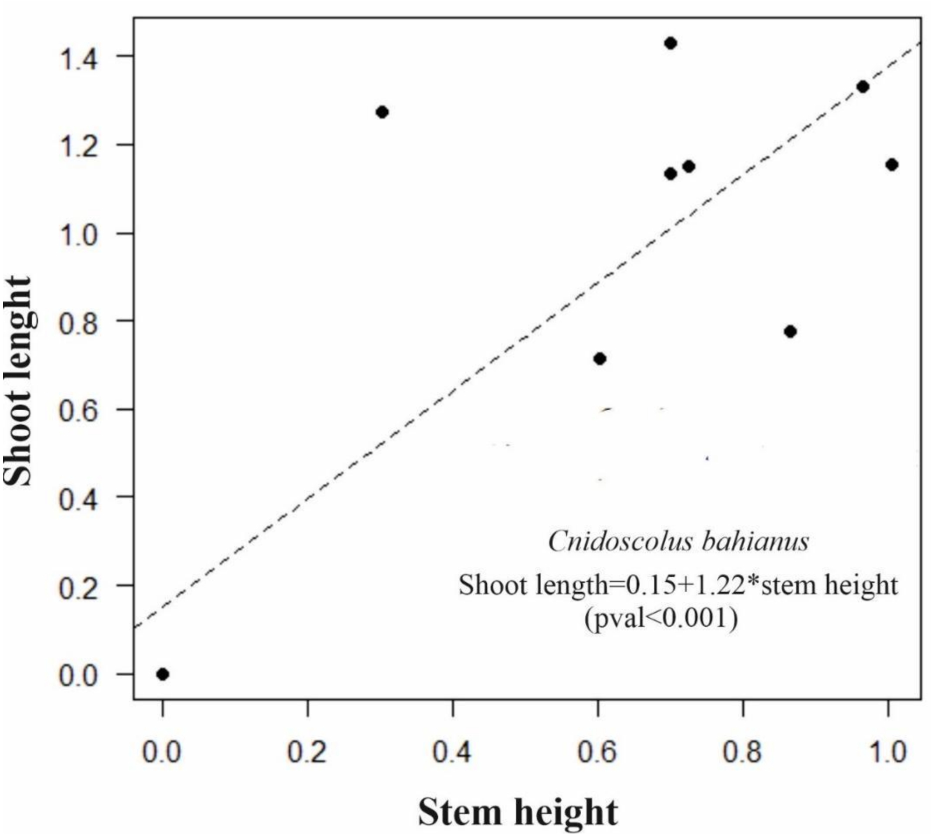

Annona leptopetala
shoot length=-4.2+65.9*shoot diameter
(p<0.01)
Bauhiniā acuruana
shoot length=0.8+42.7*shoot diameter
(p=0.04)
Croton argyrophylloides
shoot length=0.11+64.8*shoot diameter
(p<0.001)
Melochia tomentosa
shoot length=-1.17+62.3*shoot diameter
(p=0.04)
Cnidoscolus bahianus
shoot length=0.6+3.52*shoot diameter
(p<0.01)
Cynophalla flexuosa
shoot length=-0.32+13.79*shoot diameter
(p=0.02)
Croton heliotropiifolius
shoot length=0.22+9.06*shoot diameter
(p<0.001)
Senegalia piauhiensis
shoot length=-5.8 + 116.1*shoot diameter
(p<0.01)
Poincianela microphylla
shoot length=0.65+4.36*shoot diameter
(p<0.01)
Pityrocarpa moniliformis
shoot length=0.27+9.32*shoot diameter
(p<0.0001)
Waltheria brachypetala
shoot length=0.39 + 7.0 *shoot diameter
(pval=0.02)
Trischidium molle
shoot length=0.57 + 4.76*shoot diameter
(p<0.001)
Shoot diameter
Shoot length
5 10 15 20 25
0.10 0.15 0.20 0.25 0.30 0.35 0.40
5 10 15
0.10 0.15 0.20 0.25 0.30
5 10 15 20 25
0.10 0.15 0.20 0.25 0.30
5 10 15 20 25 30 35
0.10 0.15 0.20 0.25 0.30 0.35 0.40
0.6 0.8 1.0 1.2 1.4
0.05 0.10 0.15 0.20 0.25
0.6 0.8 1.0 1.2 1.4
0.080 0.085 0.090 0.095 0.100 0.105 0.110 0.115
0.6 0.8 1.0 1.2 1.4 1.6
0.04 0.06 0.08 0.10 0.12 0.14
5 10 15 20 25 30 35
0.10 0.15 0.20 0.25 0.30
0.6 0.8 1.0 1.2 1.4 1.6
0.05 0.10 0.15 0.20
0.8 1.0 1.2 1.4 1.6 1.8 2.0
0.04 0.06 0.08 0.10 0.12 0.14
0.6 0.8 1.0 1.2
0.04 0.06 0.08 0.10 0.12 0.14
0.6 0.8 1.0 1.2 1.4
0.04 0.06 0.08 0.10 0.12 0.14

Fig.6.


Shoot lenght
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
Stem height
Cnidoscolus bahianus
Shoot length=0.15+1.22*stem height
(pval<0.001)

FINAL CONSIDERATIONS

Natural regeneration represents a good way to understand the functioning of the forests and how they react from previous and current disturbance events. This understanding is even more important in dry forests where harsh abiotic conditions impose ecological filters and limit the growth season of regenerating plant assemblages. In this study, we addressed the effects of chronic anthropogenic disturbances and environmental factors on natural regeneration in a human-modified landscape of Caatinga dry forest. Characterization of the structure and composition of the seed rain, soil seed bank, true seedlings, true saplings and resprouts (Chapter 1) and evaluation of coppicing response of seedling-size resprouts (Chapter 2) were assessed along the human disturbance, aridity, soil fertility and light penetration gradients.

A very low dense and taxonomically impoverished seed rain, soil seed bank and regenerating plant assemblages were observed, with the predominance of resprouts in relation to true recruits. The number and density of viable seeds found in seed rain and soil seed bank indicate that the maintenance and desiccation of seeds should not be neglected, and, the very low abundance of seedlings and saplings revealed that one of the important problems of the regeneration in Caatinga is the persistence of young individuals in the area.

Contrasting effects of chronic anthropogenic disturbances and environmental factors were observed in the regenerating assemblages. Abundance (seed rain, soil seed bank, all regenerating assemblage and resprouts) and species richness (true seedlings) were negatively explained by CAD. Seed rain richness and true sapling abundance were positively and negatively affected by leaf area index respectively, and, interaction between leaf area index and rainfall was positively related to soil seed bank richness. Species composition of soil seed bank, all regenerating assemblages and resprouts were explained only by aridity.

Seedling-size resprouts had a great resprouting capacity as all the 19 species and 144 individuals (74 %) in which experimental coppicing was applied presented new shoots. There is a marked interspecific variation, showing the opposite species-specific tendency and the importance of storage reserves for the maintenance of resprouts following disturbances. Resprouting capacity of some more widely distributed species was related to disturbances and environmental factors.

Given that regeneration is not a simple process as we though, that stochastic factors have a considerable role in this process (Chazdon et al., 2007; Chazdon, 2017; Huanca-Nunez et al., 2021) and that the disturbance and aridity will proceed in the long term, unknown effect on vegetation should attract our intention in order to apply adequate management for the conservation and restauration of the Caatinga.

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APPENDICES

RULES FOR SUBMISSION OF ARTICLES IN THE DESIRED JOURNALS

Chapter 1

Manuscript to be sent to the *Journal of Applied Ecology*

https://besjournals.onlinelibrary.wiley.com/hub/journal/13652664/about/author-guidelines

Chapter 2

Manuscript to be sent to the journal *Forest Ecology and Management*

Guide for authors - Forest Ecology and Management - ISSN 0378-1127 (elsevier.com)