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RENATO SOARES VANDERLEI

MECANISMOS ECOFISIOLÓGICOS CONTROLADORES E PERFORMANCE DA REBROTA NA CAATINGA

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito parcial para obtenção do título de doutor em Biologia Vegetal. Área de concentração: Ecologia e conservação.

Orientador: Mauro Guida dos Santos

Coorientador: Marcelo Tabarelli

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Área de Concentração: Ecologia e Conservação

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DEDICATÓRIA

À minha família, por tudo, sempre. Aos meus amores, meus amigos e amigas, independentemente da posição geográfica nesse planeta, por serem quem são. Aos meus companheiros de vida acadêmica, pelo compartilhamento de vida. Aos meus orientadores e professores, todos, por cada palavra, gesto, apoio. A mim, suspiro, agradeço, dedico.

AGRADECIMENTOS

Para mim, é impossível iniciar essa sessão de agradecimento sem antes uma reflexão/desabafo/conversa sobre sentimento atual, após 13 anos de vida acadêmica acerca dessa mesma "vida" acadêmica, numa perspectiva "de baixo para cima" de um pós-graduando, de forma extremamente honesta, com todas as inquietações que acompanham.

A gente tende a ter vários objetivos a serem conquistados na vida. Ter um título de doutor nunca foi um objetivo sonhado, perseguido com unhas e dentes. Apesar de estar envolvido em pesquisas desde o ano seguinte do início da graduação em 2010, não lembro em que ponto me explicaram (ou me dei conta) do que era esperado de um "ser cientista" nos moldes "acadêmicos *strictu sensu*", principalmente por ter começado na licenciatura. Leia-se, grosso modo: publicador de artigos, que dependem de financiamento de projetos, que por sua vez dependem de um bom currículo, recursos humanos a serem formados, parcerias, e que resultarão em mais artigos.

Partindo do pressuposto que artigos, por bem ou por o mal, aparentam ser a unidade básica de moeda de troca, o caminho e o conjunto de habilidades para conseguir essa moeda de forma "mais fácil" envolvem, além de todo um desenvolvimento teórico numa área de concentração: um bom conhecimento em língua portuguesa e inglesa, capacidade de sintetizar informações utilizando um método hipotético-dedutivo, habilidades computacionais (organização de dados e, para facilitar a vida, de programação/estatística), habilidades com programas de edição visual (seja para apresentações, figuras, vídeos, ou divulgação em redes sociais), habilidades de relações interpessoais (ninguém faz ciência sozinho) e, preferencialmente, um suporte emocional e de saúde mental considerável. É quase que um funcionário multifacetado, com pouco investimento externo para o desenvolvimento de cada uma dessas habilidades. Tudo isso, em 2023, precisando se manter geralmente longe de casa, tendo que adquirir essas habilidades de forma simultânea ou durante o percurso (caso não tenha a vantagem de ter aprendido parte delas no passado), fora de uma perspectiva de trabalho formal e imerso em bastante instabilidade, num loop de "Profissão? Estudante".

Num mundo ideal de mínima valorização profissional, primeiro um cientista seria tratado como profissão, e teríamos grupos compostos por profissionais que dessem suporte à todas estas etapas da publicação de um artigo: estatísticos, programadores, designers, *social media*. Deveria caber ao ser cientista/pós-graduando se preocupar em preencher lacuna teórica do seu estudo, aos avanços científicos, solução de problemas e em responder "a sua pergunta". Mas, o que geralmente se vê são essas etapas sendo supridas pelos próprios alunos que, de alguma forma, conseguiram adquirir tais habilidades (de graça ou não) e que as incluíram ao “kit pós-graduando”, ao custo de menor investimento de tempo nos próprios trabalhos, maior pressão e num ambiente majoritariamente com pouco suporte financeiro.

Muito comumente, teses acabam num canto, eventualmente sendo consultadas em repositórios, já que podem ser vistas como “produto final para o término de uma etapa”, mas um “produto intermediário” caso os artigos não tenham sido publicados. Quando publicadas, contribuem para uma área de conhecimento, para trabalhos futuros, para *scores* dos programas de pós-graduação. E, a depender da área, objeto de estudo, aplicabilidade, sorte e bastante esforço posterior para superar diversos obstáculos burocráticos (que dependem mais da boa vontade de outrem que da qualidade do seu trabalho), virar uma política pública que pode ajudar diretamente pessoas. Tudo isso, sendo “estudante/bolsista”, uma vez que a “carreira” *per se* só é, de fato, uma carreira profissional reconhecida após uma posição numa instituição pública ou privada. O nível de dedicação e vontade necessários para enxergar todo esse sistema, manter essa engrenagem funcionando E se manter nela para alcançar esta carreira está longe de ser trivial. É louvável. Mas, chegar no final de um doutorado, próximo aos 30 anos (se tudo der certo), ainda sendo “estudante”, com basicamente uma década de dedicação e treinamento é, na minha concepção, extremamente desleal. Gostar de fazer ciência, de pensar ciência, é incrível... o que ✱✱✱✱ é o processo. E isso se reflete no evidente abandono da área por inúmeros pós-graduandos (incluindo diversos colegas) que optam por mudar de área, seja por eventual descoberta de falta de afinidade, seja por necessidade financeira (já que amar o que faz, por si só, não enche barriga), seja por falta de perspectiva do próximo passo, seja por experiências negativas com orientadores. Todas elas, contudo, envolvem tempo, dinheiro, mais investimento, muita reflexão, terapia e instabilidade, mas bastante coragem.

Por muita, muita sorte, eu tive um conjunto de fatores (muitos que nem dependeram de mim) que fizeram isso tudo ser extremamente mais leve. Tive uma base familiar que me permitiu me preocupar somente com meus estudos, passando por apertos financeiros para custear vários cursos extracurriculares que me auxiliaram a marcar várias das habilidades citadas anteriormente ✓. De ser bolsista numa escola que me permitiu adquirir conhecimentos para passar num vestibular de universidade pública. De ter feito cursos que me permitiram me destacar numa seleção de estágio voluntário e ser aceito como potencial membro de um laboratório e, posteriormente, numa seleção para uma graduação sanduíche. De ter um ganho pessoal e profissional imensurável, sem gastar “um real do bolso” para me manter fora do país. De retornar ao país e somar essas experiências ao currículo e começar a trabalhar. De, pouco tempo depois, ser aceito num curso de mestrado numa instituição e Estado diferente (mesmo levando 2 seleções para entrar nela). De ter sido visto como potencial orientando por um chefe de laboratório (na época, desconhecido por mim) e ser aceito no laboratório com um grupo de pesquisa diverso e com recursos para desenvolver as pesquisas necessárias. De, durante diversos anos, ter auxílio financeiro da família para conseguir me manter numa cidade diferente. E, acima de tudo, de todos os fatores operacionais e técnicos, de poder ter olhado para os lados e saber que nunca estive sozinho.

Cada insegurança, desespero, choro, reclamação, raiva, alegria, conquista, perrengue em campo, banho de chuva, mudança, sempre foi acompanhada por pessoas incríveis, de diversas partes do país e do mundo, que contribuíram de alguma forma para eu ser o ser que sou e chegar aonde cheguei. É impossível agradecer nominalmente a cada pessoa, mas cada uma delas colocaram um tijolinho para construir o Renato irmão, filho, amigo, melhor amigo, colega de laboratório, de palestras, de cursos de campo, de academia, de bar, de conversas profundas, de farras até o amanhecer, que tem bastante consciência de quem é, do que é, de onde estou, e que escreve esse agradecimento. E que não se arrepende. A cada um, apesar de tudo, obrigado por me ajudar a ser, muito em breve, o Renato Doutor.

Outro diz
Que se eu estudar engenharia
Mesmo sem ter vocação,
Eu enriqueça.
E eu pergunto
Se esse peste gostaria
Que o prédio que eu fizesse
Lhe caísse na cabeça.

Pra ter um anel no dedo
E um DR no nome
Ser um grande homem
Feliz e famoso
Mudar de repente
Meu comportamento
Tão escandaloso.
(NETO, ACCIOLY, música “Xote universitário”).

RESUMO

Perturbações antrópicas afetam mecanismos de regeneração em florestas tropicais secas. A persistência de plantas via rebrotas e propagação clonal via rametas parecem ser cruciais para a recuperação acelerada da biomassa perdida, mas dependem do armazenamento e eficiência do uso de carboidratos não-estruturais (CNE). Contudo, informações acerca de quais espécies conseguem persistir na Caatinga e de como perturbações antrópicas afetam tanto a persistência quanto os CNE são escassas. Diante disso, avaliamos: 1) como diferentes intensidades de perturbações antrópicas afetam a persistência de espécies lenhosas dominantes via diferentes mecanismos de regeneração e 2) como a perturbação antrópica por corte-e-queima altera suas características bioquímicas e funcionais. O trabalho foi realizado no PARNA Catimbau utilizando 6 espécies lenhosas dominantes. Em campo, foram simuladas perturbações que ocorrem de forma tradicional por populações rurais, sendo elas, o corte de galhos e corte-e-queima (CQ) da vegetação no final da estação seca. Medidas biométricas (i.e., altura, diâmetro no nível do solo, nº de perfílios e biomassa fresca) foram feitas antes e 6 meses depois das perturbações, ao final da estação chuvosa. As frequências dos mecanismos de persistência (i.e., rebrotas e rametas) foram analisadas, além da coleta de amostras de folhas, caules e raízes para análises funcionais e de carboidratos não-estruturais também ao fim da estação chuvosa. De forma geral, a persistência das espécies variou entre 0-80%. 5 das 6 espécies consegue persistir de alguma forma, tanto por rametas quanto por rebrotas. O aumento da intensidade das perturbações estimulou maior número de perfílios, de rametas. Contudo, cerca de 70% da abundância foi perdida após o CQ e apenas 4% da biomassa perdida foi recuperada após 6 meses. As análises de CNE e de características foliares entre árvores controle e indivíduos que persistiram após o CQ indicam que CNE estão mais concentrados em folhas que nos outros órgãos, e que estes indivíduos conseguem alcançar níveis de CNE similares às árvores não perturbadas nestes 6 meses de estação chuvosa. Árvores do grupo controle parece possuir características foliares mais conservativas, enquanto indivíduos que persistiram apresentam estratégia mais aquisitiva com investimento em crescimento e atividades metabólicas. Em síntese, espécies em floresta de Caatinga arenosa conseguem majoritariamente persistir frente a perturbações que removem totalmente sua biomassa acima do solo. Tais perturbações antrópicas parecem estimular clonalidade via rametas e maior emissão de perfílios dos indivíduos que persistem, ao custo de uma alta perda de abundância e eliminação de espécies sem a capacidade de persistir à maior intensidade de perturbação. Os pouco indivíduos que persistem conseguem, no processo de regeneração inicial, rapidamente investir em novo tecido, crescer, iniciar o processo de fotossíntese, e a reabastecer o NSC utilizado, principalmente em raiz, exibindo estratégias de uso de recursos mais aquisitivas antes do início da próxima estação seca.

Palavras-chave: perturbações antrópicas, mecanismos de regeneração, clonalidade, carboidratos não-estruturais, florestas tropicais secas

ABSTRACT

Anthropogenic disturbances lead to aboveground biomass loss and affect forest regeneration patterns in seasonally dry tropical forests. Plant persistence through resprouting and clonal propagation via ramets appears to be crucial mechanisms for accelerated recovery of lost biomass and the continuity of ecosystem service provision. The success of these regeneration mechanisms involves the storage and efficient utilization of non-structural carbohydrates (NSCs) stored in plants. However, information regarding the persistence capacity of Caatinga species and how anthropogenic disturbances affect species persistence and NSCs in plants is limited. Considering this, we assessed: 1) how different intensities of anthropogenic disturbances affect the persistence of dominant woody species through different regeneration mechanisms and 2) how the slash-and-burn anthropogenic disturbance alters their biochemical and functional characteristics. The study was conducted in the Catimbau National Park, using 6 dominant woody species. In the field, disturbances that occur traditionally by rural populations were simulated on 10-15 individuals per species, including branch cutting and slash-and-burn (S&B) of vegetation at the end of the dry season, as typically practiced by the population. Biometric measurements (i.e., height, ground-level diameter, number of shoots, and fresh biomass) were taken before and 6 months after disturbances, at the end of the rainy season. Frequencies of persistence mechanisms (i.e., resprouting and ramet production) were analyzed, along with the collection of leaf, stem, and root samples for functional and non-structural carbohydrate analyses. Overall, species persistence varied strongly between 0-80%. Five out of six species managed to persist to some extent through both ramets and resprouts. Increased disturbance intensity stimulated a higher number of shoots and ramets. However, around 70% of abundance was lost, and only 4% of lost biomass was recovered six months after S&B. Analyses of NSCs and leaf traits between control trees and individuals that persisted after S&B indicate that NSCs are more concentrated in leaves than in other organs, and these individuals are able to attain NSC levels similar to undisturbed trees. Control group trees seem to possess more conservative leaf traits, while persisting individuals exhibit a more acquisitive strategy with investment in growth and metabolic activities. In summary, species in sandy Caatinga forests are largely able to persist in the face of disturbances that completely remove their aboveground biomass. Such anthropogenic disturbances seem to stimulate clonality via ramets and greater shoot production in persisting individuals, at the cost of high abundance loss and elimination of species lacking the capacity to persist higher disturbance intensity. The few persisting individuals can rapidly invest in new tissue during initial regeneration, grow, initiate photosynthesis, and replenish utilized NSCs, primarily in the root, exhibiting more acquisitive resource-use strategies before the onset of the next dry season.

Keywords: anthropogenic disturbances, regeneration mechanisms, plant clonality, non-structural carbohydrates, tropical dry forests

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SUMÁRIO

2. APRESENTAÇÃO

Florestas tropicais representam ecossistemas singulares no contexto da conservação da biodiversidade e na oferta de serviços ecossistêmicos em escala global, tais como a regulação climática e o sequestro de carbono, bem como o fornecimento de recursos florestais para o sustento de populações rurais e tradicionais (BURQUEZ *et al.*, 2005; HOUGHTON; BYERS; NASSIKAS, 2015; PORTILLO-QUINTERO *et al.*, 2015). Contudo, essas mesmas florestas tropicais têm experimentado uma conversão acelerada em paisagens modificadas pelo homem majoritariamente devido a perturbações humanas causadas por diferentes tipos de uso de solo e exploração de recursos florestais (ARROYO-RODRÍGUEZ *et al.*, 2017). Além da perda extensiva de habitat, as florestas remanescentes frequentemente sofrem perturbações decorrentes da agricultura de corte e queima, exploração de produtos florestais como lenha para carvão vegetal e produção de gado (i.e., perturbações antrópicas crônicas (DONS *et al.*, 2015; SINGH, 1998)). Este conjunto de perturbações pode levar à redução da prestação de serviços ecossistêmicos e da resiliência da floresta ao reduzir significativamente sua capacidade de se regenerar.

Florestas tropicais secas não fogem a esse padrão, sendo consideradas as florestas tropicais mais ameaçadas do mundo há, pelo menos, três décadas e meia (JANZEN, 1988; MILES *et al.*, 2006). Nestas florestas, a sazonalidade é uma característica marcante, e a baixa disponibilidade hídrica levam à limitação de regeneração pelo recrutamento de plântulas, uma vez que todas as etapas do recrutamento de plântulas tendem a ser limitadas ao período chuvoso (VIEIRA; SCARIOT, 2006). Perturbações que levam à remoção da biomassa acima do solo resultam em maior exposição do solo e luminosidade, menos umidade, afetando o seu recrutamento (CHATURVEDI *et al.*, 2017; KHURANA; SINGH, 2000, 2004).

No contexto de regeneração, a capacidade de persistir à perda de biomassa tem sido reconhecida como um 'atalho' para uma regeneração mais rápida, uma vez que pula temporariamente o estágio ontogenético mais vulnerável e permite que a recuperação de biomassa recomece a partir de tocos e raízes, progredindo vigorosamente (KENNARD *et al.*, 2002; PAUSAS *et al.*, 2016). Essa persistência depende de reservas de carbono armazenadas (ou seja, carboidratos não estruturais, especialmente nas raízes (BELLINGHAM; SPARROW, 2000), responsáveis por serem fontes de energia direta para suprir a recuperação da biomassa perdida (DIETZE *et al.*, 2014). Esta capacidade de persistir pode se dar através de mecanismos de regeneração como a rebrota a partir de novos perfílios, ou de gerar clones a partir de gemas radiculares (i.e., rametas, sensu JENIK, 1994), apresentando vantagens nos períodos de limitação de água e nutrientes, diferente de plântulas oriundas de sementes, que possuem fonte de reserva limitada (PAUSAS; KEELEY, 2014). Entretanto, pouco se sabe como a dinâmica desses carboidratos ocorre em plantas de florestas secas, e como perturbações antrópicas afetam esta dinâmica.

Dentre as florestas secas no contexto de sazonalidade e múltiplas perturbações simultâneas, temos a Caatinga. Foi reportada a ocorrência do mecanismo de propagação vegetativa por raiz e uma alta proporção de espécies capazes de rebrotar após o corte em espécies dominantes da Caatinga (NOUTCHEU *et al.*, 2023; VANDERLEI *et al.*, 2021). Estes mecanismos comumente relacionados à regeneração da vegetação em ambientes sujeitos ao fogo constante (PAUSAS; KEELEY, 2014), muito embora o fogo não exerça pressão histórica e constante neste sistema. Uma vez que a capacidade de rebrotar ou de propagação vegetativa não ocorre em todas as espécies, perturbações como o corte seletivo de madeira e agricultura de corte e queima podem resultar em alterações nos padrões de regeneração da floresta, incluindo a quantidade de biomassa acima e abaixo do solo e composição futura dela. Nesse contexto, pouco se sabe sobre quais fatores controlam esses mecanismos de regeneração em questão.

Diante disso, é razoável pensar que as espécies conseguem permanecer na Caatinga sob forte ação humana e marcante sazonalidade se beneficiar por conseguirem persistir no sistema de rebrota ou gerar rametas conectados às raízes já estabelecidas. Ainda, diferentes intensidades de perturbação em períodos de baixa e alta disponibilidade hídrica podem afetar o desempenho destes mecanismos em diferentes espécies. Assim sendo, esta tese é dividida em dois capítulos. No primeiro, será avaliado como diferentes intensidades de perturbação antrópica afetam a capacidade de rebrota e propagação clonal através de mecanismos de persistência em espécies dominantes da Caatinga. No segundo capítulo serão analisadas as concentrações de carboidratos não-estruturais e características funcionais das espécies que rebrotaram frente ao corte e queima da vegetação.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 PERTURBAÇÕES E FLORESTAS SECAS

Perturbações são eventos de remoção de biomassa que podem alterar qualquer nível ecológico, ambiental, componente, bem como o status organizacional de um ciclo biológico de organismos (PICKETT *et al.*, 1989), sendo aspectos importantes na seleção natural e em toda a evolução biológica ao modificar o ambiente em que cada ser vivo desempenha suas funções vitais (KREBS, 2001). Mesmo as características biológicas, ecológicas e comportamentais de um organismo, como intensa herbivoria ou alta proliferação em escala local, podem ser uma perturbação para outros organismos, e os efeitos da perturbação podem atingir indiretamente outros componentes do meio ambiente, ecossistemas e processos ecológicos, sendo um fator chave na agenda da ecologia que está relacionado a processos como sucessão e regeneração de um sistema (BATISTI; POETA; FANELLI, 2016).

A origem e a escala de uma perturbação podem variar desde a queda de uma árvore, um furacão ou um período de seca prolongada. Entretanto, não só distúrbios naturais devem ser levados em consideração quando se fala sobre comunidades biológicas. Com o reconhecimento da era do antropoceno (CORLETT, 2014), cresceram as investigações sobre como as atividades humanas têm provocado mudanças em diversos níveis nos ecossistemas, tornando-se indispensável acessar as consequências das perturbações geradas por estas atividades em diferentes níveis de organização biológica, isto é, desde indivíduos à biosfera.

Quando tratamos de perturbações oriundas de ações humanas, podemos separá-las em agudas e crônicas (SINGH, 1998). As perturbações agudas são causadas pela substituição da vegetação natural por outro tipo de uso do solo, como remoção da cobertura vegetal para agricultura, pecuária ou construção de casas (i.e., grande perda de biomassa), resultando em perda e fragmentação de habitat. Já as perturbações crônicas constituem na remoção contínua de pequenas porções de biomassa, tais como extração de lenha, corte seletivo de madeira, caça, criação extensiva de animais domésticos, introdução de espécies exóticas, exploração de produtos florestais não-madeireiros (sensu SINGH, 1998), isto é, que não resultam em perda e fragmentação de habitat.

Os efeitos das ações humanas nas florestas tropicais têm recebido grande destaque nos últimos anos (ARNAN *et al.*, 2018; CHAZDON, 2003; GARDNER *et al.*, 2009). Apesar dessas florestas serem globalmente importantes para a persistência e conservação da biodiversidade, fornecimento de serviços ecossistêmicos e bem-estar humano (MAASS *et al.*, 2005a), populações humanas continuam a converter florestas maduras em paisagens com diferentes usos do solo (ARROYO-RODRÍGUEZ *et al.*, 2017). Esse tem sido particularmente o caso das Florestas Tropicais Sazonalmente Secas (FTSS, (PENNINGTON; LAVIN; OLIVEIRA-FILHO, 2009), que representam cerca de 42% da área das florestas tropicais (MURPHY; LUGO, 1986). O fato de abrigarem cerca de 1 bilhão de pessoas ao redor do mundo que dependem dos seus recursos para sobreviver (SILVA; LEAL; TABARELLI, 2017b) acabou resultando na conversão de aproximadamente 50% da sua área original (MILES *et al.*, 2006). Estudos apontam altas taxas de conversão de áreas de florestas secas, atingindo 60% em algumas áreas do México (TREJO; DIRZO, 2000), 90% no Brasil (SILVA; LEAL; TABARELLI, 2017b) e 95% no Peru (HASNAT; HOSSAIN, 2019). Além da extensa perda de habitat, as florestas remanescentes podem ser frequentemente perturbadas pela agricultura de corte e queima e exploração de produtos florestais (e.g., lenha para carvão e produção de gado) (DONS *et al.*, 2015; SINGH, 1998). Coletivamente, este conjunto de perturbações converteu várias florestas secas em mosaicos com manchas de floresta secundária com diferentes idades e campos agrícolas (PULLA *et al.*, 2015; SOBRINHO *et al.*, 2016). Essa conversão não apenas prejudica a provisão de serviços ecossistêmicos, mas também a resiliência da floresta, levando a trajetórias de intensa degradação (ARROYO-RODRÍGUEZ *et al.*, 2017; MELO *et al.*, 2013), resultando em alguns casos, em áreas em desertificação (PORTILLO-QUINTERO *et al.*, 2015; TABARELLI *et al.*, 2017a).

No Brasil, a floresta seca da Caatinga é considerada a maior e mais diversa floresta tropical sazonalmente seca da América do Sul, com uma área de 912,529 km² que abriga mais de 28 milhões de pessoa e cerca de 5 mil espécies animais e vegetais (SILVA; LEAL; TABARELLI, 2017b). Este ecossistema vem sendo modificado drasticamente por atividades humanas desde o início da colonização europeia no século XVI (COIMBRA-FILHO; CÂMARA, 1996). De forma semelhante a outras florestas secas ao redor do mundo, a população rural que reside nesta região é majoritariamente pobre e depende intrinsecamente dos recursos oferecidos pela floresta para a sua subsistência (SUNDERLAND *et al.*, 2015). Com isso, práticas como agricultura de corte e queima, pecuária e outras perturbações antrópicas crônicas, como extração de produtos florestais madeireiros e não madeireiros, têm transformado florestas maduras em paisagens modificadas pelo homem, caracterizadas por pastagens, áreas de cultivo agrícola e áreas de floresta secundária com diferentes idades de abandono pelo homem (TABARELLI *et al.*, 2017b). Atualmente, cerca de 65% do território da Caatinga já foi modificado por ações humanas e atualmente 94% da sua área possui algum grau de risco de desertificação (SILVA; LEAL; TABARELLI, 2017b).

As perturbações antrópicas não só têm levado à perda de biodiversidade em escalas locais, regionais e globais (FAHRIG, 2003; FISCHER; LINDENMAYER, 2007; SAGAR; RAGHUBANSHI; SINGH, 2003), como as perturbações antrópicas crônicas possuem um efeito sinergético com outro fator intrínseco dessas florestas: a sazonalidade (RITO *et al.*, 2017): em ambientes com menor disponibilidade hídrica, o efeito das perturbações antrópicas tende a ser mais acentuado, enquanto o oposto ocorre onde há mais água disponível. Estudos realizados na Caatinga têm observado 1) empobrecimento taxonômico, funcional e filogenético de comunidades de plantas e formigas (OLIVEIRA *et al.*, 2016; RIBEIRO *et al.*, 2015, 2019), 2) redução no processo de dispersão de sementes (LEAL; ANDERSEN; LEAL, 2014), 3) menor proteção de plantas contra herbívoros (LEAL; ANDERSEN; LEAL, 2015) e 4) assembleias de plântulas taxonomicamente e funcionalmente pobres (VANDERLEI *et al.*, 2022). Ainda, a perda de biomassa acima do solo pode resultar em áreas mais expostas e, consequentemente, maior limitação no recrutamento de plântulas lenhosas devido ao aumento de temperatura e dessecação de sementes (LIEBERMAN; LI, 1992).

2.2 MECANISMOS DE REGENERAÇÃO FRENTE A PERTURBAÇÕES

A regeneração natural de uma floresta é um processo vital para a manutenção de um ecossistema, sendo classicamente atribuído de forma primordial ao recrutamento de plântulas. Esse recrutamento representa um gargalo demográfico para a comunidade arbórea e necessita do cumprimento de algumas etapas sequenciais (KHURANA; SINGH, 2001): primeiramente, a chegada de diásporos, que podem ser autóctones[1] ou alóctones[2], ou a presença de diásporos viáveis no banco de sementes. Após a chegada, estando em condições bióticas e abióticas favoráveis, ocorre a germinação. E, mesmo após a plântula emergir, a mesma precisa desenvolver um conjunto de características que a auxilie para lidar com as diferentes pressões resultantes das interações bióticas e

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[1] autóctone: oriundo de uma fonte local.

[2] alóctone: oriundo de uma fonte externa.

abióticas (e.g., competição, herbivoria, dessecação e disponibilidade de recursos), fazendo com que espere-se que poucas plântulas se tornem árvores jovens mesmo em locais favoráveis e pouco perturbados (SWAINE, 1996). Consequentemente, a regeneração de uma floresta é considerada "saudável", ocorrendo de forma contínua e com bom potencial de recrutamento, quando sua estrutura populacional segue um padrão de maior abundância de plântulas e indivíduos com menores diâmetros, seguido de um menor número de indivíduos com maior porte/mais largos (i.e., uma distribuição em formato de uma curva J reversa – *reverse J-shape curve*) (Fig. 1) (BIRHANU; BEKELE; DEMISSEW, 2018; GEBEYEHU *et al.*, 2019). Esta estrutura é comumente associada às florestas naturais com limitadas perturbações externas (TEKETAY, 2005).

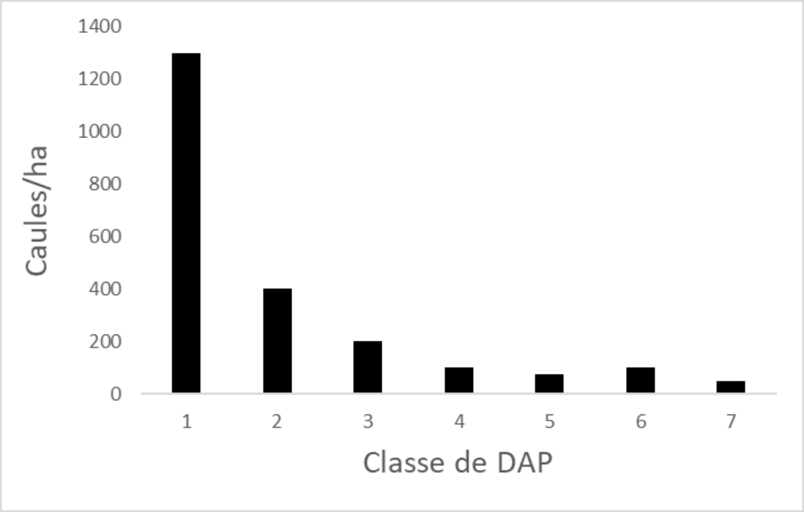

Figura 1. Exemplo de distribuição de uma estrutura populacional de uma floresta fictícia seguindo o padrão de uma curva J reversa. Adaptado de (BIRHANU; BEKELE; DEMISSEW, 2018; GEBEYEHU *et al.*, 2019), onde se tem a distribuição da densidade de espécies lenhosas entre as classes de diâmetro a altura do peito (DAP) (1=2,5-10cm, 2=10,1-20 cm, 3=20,1-40 cm, 4=40,1-60 cm, 5=60,1-80 cm,6=80,100 cm,7=>100cm).

O interesse evolvendo a regeneração natural tem aumentado ao passo que ações antrópicas, resultantes de diferentes formas de uso da terra, e mudanças climáticas vêm ganhando mais destaque e importância (BOUCHER *et al.*, 2020; WALCK *et al.*, 2011). O aumento da conversão de florestas maduras em secundárias tem sido alvo de estudos com o objetivo de entender o papel das mesmas na manutenção de processos e serviços ecossistêmicos e da conservação da biodiversidade (CHAZDON *et al.*, 2009). Esse processo de conversão, usualmente sendo fruto de atividades que removem a cobertura vegetal, levam à maior exposição do solo e altas temperaturas por tempo prolongado (especialmente em florestas secas). Com isso, há uma cascata de fatores que culminam numa regeneração natural mais lenta, como a redução da umidade e alterações nas condições nutricionais do solo (i.e., sucessão presa), microclima menos favorável para a chegada de sementes (e.g., menos habitats para animais dispersores) e maior dessecação de sementes e plântulas (CHATURVEDI *et al.*, 2017). Devido ao aumento do uso de terra para fins agropecuários e de subsistência (e.g., agricultura de corte-e-queima e criação de animais), somados aos movimentos migratórios de populações rurais após a exploração de áreas previamente florestadas (FOOD AND AGRICULTURE ORGANIZATION, 2016), grande parte das florestas remanescentes ao redor do planeta são florestas secundárias (CHAZDON, 2003; POORTER *et al.*, 2016). Ou seja, se a tendência é termos cada vez mais áreas em regeneração, compreender os padrões de sucessão da floresta secundária e sua resiliência se faz essencial para antecipar e aumentar seu potencial para conservação da biodiversidade e fornecimento de serviços ecossistêmicos (CHAZDON, 2003; FOOD AND AGRICULTURE ORGANIZATION, 2016; SOUZA *et al.*, 2019).

Ao tratar de mudanças climáticas, especialmente em florestas secas, o cenário da regeneração natural por meio do recrutamento de plântulas aparenta ser mais preocupante. Nessas florestas, a germinação de sementes ocorre via pulsos diretamente proporcionais à duração e intensidade da estação chuvosa (i.e., maior disponibilidade hídrica) (VIEIRA; SCARIOT, 2006). Nos cenários futuros previstos de aumento de temperatura e diminuição de precipitação (IPCC, 2014), somados à exploração de recursos naturais cada vez mais constante, as condições necessárias para a germinação e sobrevivência de plântulas tendem a ser cada vez mais restritas, exigindo ajustes/escapes para mitigar os efeitos negativos da baixa disponibilidade de água, maior luminosidade e temperatura. Nestas condições, é de se esperar que sejam necessários ajustes ecofisiológicos e funcionais para garantir a perpetuação das espécies, como defesas físicas e químicas contra herbivoria e competição (i.e., alelopatia), além de maior armazenamento e eficiência no uso de recursos. Neste sentido, outros mecanismos de regeneração e persistência de espécies através de diferentes mecanismos de propagação e reprodução assexuada, como a capacidade de rebrota após o corte ou de propagação clonal por raízes, podem ser cruciais para garantir a resiliência da floresta, podendo representar maior importância relativa quando comparado ao recrutamento de plântulas (GARIGLIO *et al.*, 2010; JENIK, 1994; KENNARD *et al.*, 2002).

2.2.1 Mecanismos de persistência de espécies

2.2.1.1 Capacidade de rebrota e propagação vegetativa

A "capacidade de rebrota" se refere à habilidade de algumas plantas de formar novos brotos após a destruição de tecidos vivos devido a perturbações que resultaram na perda parcial ou total de biomassa (PAUSAS *et al.*, 2016), sendo comum em diversos ambientes e tipos de plantas ao redor do planeta (PAUSAS; KEELEY, 2014; VESK; YEN, 2019). Este mecanismo de regeneração representa uma maneira eficiente de recuperar a biomassa perdida, uma vez que as gemas utilizam nutrientes já presentes em partes da planta como fontes nutricionais (e.g., raízes, troncos ou caules) (BELLINGHAM; SPARROW, 2000). A presença de espécies capazes de rebrotar pode representar um "atalho" para a regeneração da floresta, com implicações desde o nível de indivíduo ao do ecossistema como um todo (EVERHAM III; BROKAW, 1996).

Retomar o crescimento a partir de tocos (ou outras partes pré-existentes) pode ser uma alternativa de regeneração mais acelerada em relação às plântulas jovens, que representam o estágio ontogenético mais vulnerável às pressões bióticas e abióticas (ENGELBRECHT *et al.*, 2006; KENNARD *et al.*, 2002). Não depender diretamente do processo de germinação significa, a princípio, evitar filtros bióticos e abióticos até o estabelecimento e crescimento da plântula. Desta forma, em cenários de limitação de germinação e estabelecimento de plântulas lenhosas, esta capacidade de rebrotar pode ser mais vantajosa por ter acesso a sistemas radiculares/troncos previamente estabelecido que ajudam na persistência das espécies, diferente de plântulas oriundas de sementes, que possuem apenas a reserva da semente para o crescimento inicial (PAUSAS; KEELEY, 2014).

Após um evento de perturbação que resulta em perda de biomassa aérea, as espécies que conseguem rebrotar podem dar início a este processo a partir de diferentes partes (i.e., tocos, raízes ou ramos), a depender do dano sofrido (KENNARD *et al.*, 2002). Em ambientes sob constante perturbação, como a ação do fogo em ecossistemas mediterrâneos e na região do Cerrado brasileiro (PAUSAS; KEELEY, 2014; VIEIRA; SCARIOT, 2006), as plantas desenvolveram estratégias para lidar com estas perturbações, seja por meio de sementes mais resistentes ao fogo, gemas protegidas abaixo do solo ou órgãos subterrâneos de reserva para armazenar nutrientes (PAUSAS; KEELEY, 2014). Algumas, ainda, apresentam formas de propagação clonal via raízes gemíferas, gerando rametas (GARIGLIO *et al.*, 2010; JENIK, 1994) que crescem conectados à planta-mãe, com integração clonal (i.e., a capacidade das plantas clonais de transferir produtos fotossintéticos, água e sinais entre os rametas interligados para ajustar e se adaptar ao estresse ambiental (DONG-WEI; YUAN-YUAN; XIAO-YONG, 2007). Embora esse mecanismo seja comumente relacionado a ambientes onde o fogo é um fator constante (JENIK, 1994; SAHA; HOWE, 2003), estudos preliminares têm observado a capacidade de propagação por gemas de raízes em espécies dominantes na Caatinga, ecossistema cujo fogo não atua como um fator limitante e evolutivo. Ou seja, não só o uso do fogo não ocorre com frequência, mas também a flora da Caatinga teoricamente não é adaptada ao fogo (SILVA; LEAL; TABARELLI, 2017b). Contudo, foram observadas espécies que apresentavam uma rede de rametas conectadas a indivíduos adultos e entre si através do sistema radicular em roças destinadas à agricultura de corte e queima (Fig. 2a-2b), de floresta madura (Fig 2c-2d) e em propriedades rurais (Fig. 2e).

Figura 2. Espécie *Pityrocarpa moniliformis* (Benth.) Luckow & R. W. Jobson (Fabaceae) em (a) uma área de plantação de macaxeira, exibindo uma árvore com diversas raízes laterais superficiais e (b) múltiplos rametas conectados entre si

dominando uma área após corte e queima da vegetação; (c) rametas de *Croton argyrophyllus* Kunth e *Cnidoscolus bahianus* (Ule) Pax & K.Hoffm (Euphorbiaceae) conectadas à adultos por raízes em florestas maduras; (e) rametas de *Cenostigma pyramidale* (Tul.) Gagnon & G.P. Lewis (Fabaceae) conectados por raiz em uma propriedade rural.

Num sistema tão modificado pelo homem como o da Caatinga, estes mecanismos de persistência podem ser cruciais para garantir a sobrevivência das espécies, recuperação da biomassa, manutenção dos serviços ecossistêmicos e resiliência da floresta. Uma vez que existe um conjunto de fatores que causam a perda da biomassa adulta e de plântulas (i.e., escassez hídrica, herbivoria, corte-e-queima da vegetação), as espécies que conseguem rebrotar e/ou se propagar de forma vegetativa ganham uma nova chance de superar tais condições adversas, tendo maiores chances de sobrevivência pós-perturbação e permanência no ambiente (MOREIRA; TORMO; PAUSAS, 2012). Em áreas de roça, há relatos de árvores da espécie *P. moniliformis* que continuam rebrotando após 16 anos de ciclos anuais de corte e queima. Esta estratégia pode não apenas garantir a persistência das espécies, mas também aumentar sua área de dominância ao emitir rametas ao longo de raízes laterais superficiais, com relatos de mais de 900 metros de extensão (VANDERLEI *et al.*, 2021). Desta forma, uma vez que rebrotas tendem a crescer mais rápido que plântulas (BOND; MIDGLEY, 2001; KENNARD *et al.*, 2002; PAUSAS; KEELEY, 2014), é de se esperar que elas possam potencialmente alterar o ambiente ao seu redor ao promover uma recuperação mais acelerada da cobertura vegetal, garantir maior sombreamento e melhores condições microclimáticas. Consequentemente, o processo de recrutamento por meio da facilitação pode também ser auxiliado, resultando numa regeneração natural mais acelerada.

Apesar da capacidade de persistir soar como um processo apenas vantajoso para um ecossistema, é importante ressaltar que uma floresta com regeneração dominada por propagação vegetativa (i.e., baixa frequência de reprodução sexuada) traz diversas implicações potencialmente negativas. Primeiramente, não são todas as espécies que conseguem persistir via rebrotas ou rametas. Neste sentido, se imaginarmos uma floresta totalmente devastada, certamente parte das espécies será eliminada. Segundo, existe uma grande lacuna sobre o conjunto de fatores que controlam a capacidade de persistir (e.g., posição e quantidade de gemas radiculares, quantidade e acesso à reservas de nutrientes, tipo de perturbação (MIRANDA *et al.*, 2020; POORTER *et al.*, 2010; VESK; YEN, 2019)), portanto ter a capacidade de persistir via diferentes mecanismos não necessariamente significa que todos os seus indivíduos o farão. Terceiro, do ponto de vista ecológico, a capacidade de rebrotar após perturbações resulta em alterações estruturais das plantas, sendo comumente mais baixas, com mais perfílios (VESK; YEN, 2019; WARE *et al.*, 2022a). Ainda, populações predominantemente dominadas por propagação vegetativa podem ter o seu potencial evolutivo e adaptação local das espécies reduzidas, com mutações que reduzem a fertilidade podem levar à disfunção sexual (BARRETT, 2015; DONG; YU; ALPERT, 2014).

Embora a capacidade de rebrota ou de possuir raízes gemíferas não seja algo novo para espécies da Caatinga (GARIGLIO *et al.*, 2010; SAMPAIO; SALCEDO; KAUFFMAN, 1993), informações precisas acerca deste mecanismo entre as espécies da sua flora são escassas. Existe uma série de questões a serem investigadas, como qual a velocidade de recuperação da biomassa perdida; como é essa resposta ao longo do tempo e entre estações, e como esta capacidade persistir através de diferentes mecanismos se comportará frente à maior intensidade de perturbações antrópicas e mudanças climáticas. Ainda, existem diversas lacunas sobre como estes mecanismos afetam a reprodução sexuada e diversidade genética das espécies a longo prazo, uma vez que há uma demanda conflitante (i.e., *trade-off*) entre armazenar recursos, investir energia para persistir no ambiente (i.e., manutenção da geração atual) ou em atributos reprodutivos para uma nova geração (i.e., garantir diversidade genética que permita a continuidade da população em condições abióticas e bióticas futuras). Sabe-se que perturbações alteram substancialmente esta demanda conflitante, a depender de suas frequências e intensidades (BELLINGHAM; SPARROW, 2000), juntamente com as condições locais de fertilidade e umidade (IWASA; KUBO, 1997). Desta forma, se faz crucial entender os fatores que controlam estes mecanismos de persistência.

2.2.1.2 – Dinâmica de carboidratos não-estruturais e mecanismos de persistência

As plantas adquirem carbono por meio do processo de fotossíntese, sendo grande parte deste destinada para fins metabólicos (e.g., respiração), outra para construção da estrutura física da planta (i.e., biomassa) e parte exportada para o meio ambiente (DIETZE *et al.*, 2014). Uma menor quantidade é retida em forma de carboidratos não-estruturais (em inglês: *non-structural carbohydrates*; daqui em diante

NSC), sendo eles principalmente o amido e os açúcares solúveis (DIETZE *et al.*, 2014). Enquanto o amido é um composto de reserva mais recalcitrante, os açúcares solúveis desempenham funções metabólicas mais imediatas, como demandas de respiração e defesa, e substratos para transporte de metabólitos (e.g., sacarose; Fig. 3) (DIETZE *et al.*, 2014; MARTÍNEZ-VILALTA *et al.*, 2016a). Os NCS são os primeiros fotossintatos produzidos pelas plantas (LIU *et al.*, 2018) e, dentre suas variadas atuações, podemos citar ajustes fisiológicos (HARTMANN; TRUMBORE, 2016) e adaptações a períodos de escassez hídrica (LIU *et al.*, 2018). Contudo, mais importante para esta tese, os estoques de NCS são intrinsecamente ligados e responsáveis pela recuperação da biomassa após perturbações, como corte da vegetação, herbivoria e resistência à seca (O'BRIEN *et al.*, 2014)(IWASA; KUBO, 1997; LATT; NAIR; KANG, 2001; O'BRIEN *et al.*, 2014).

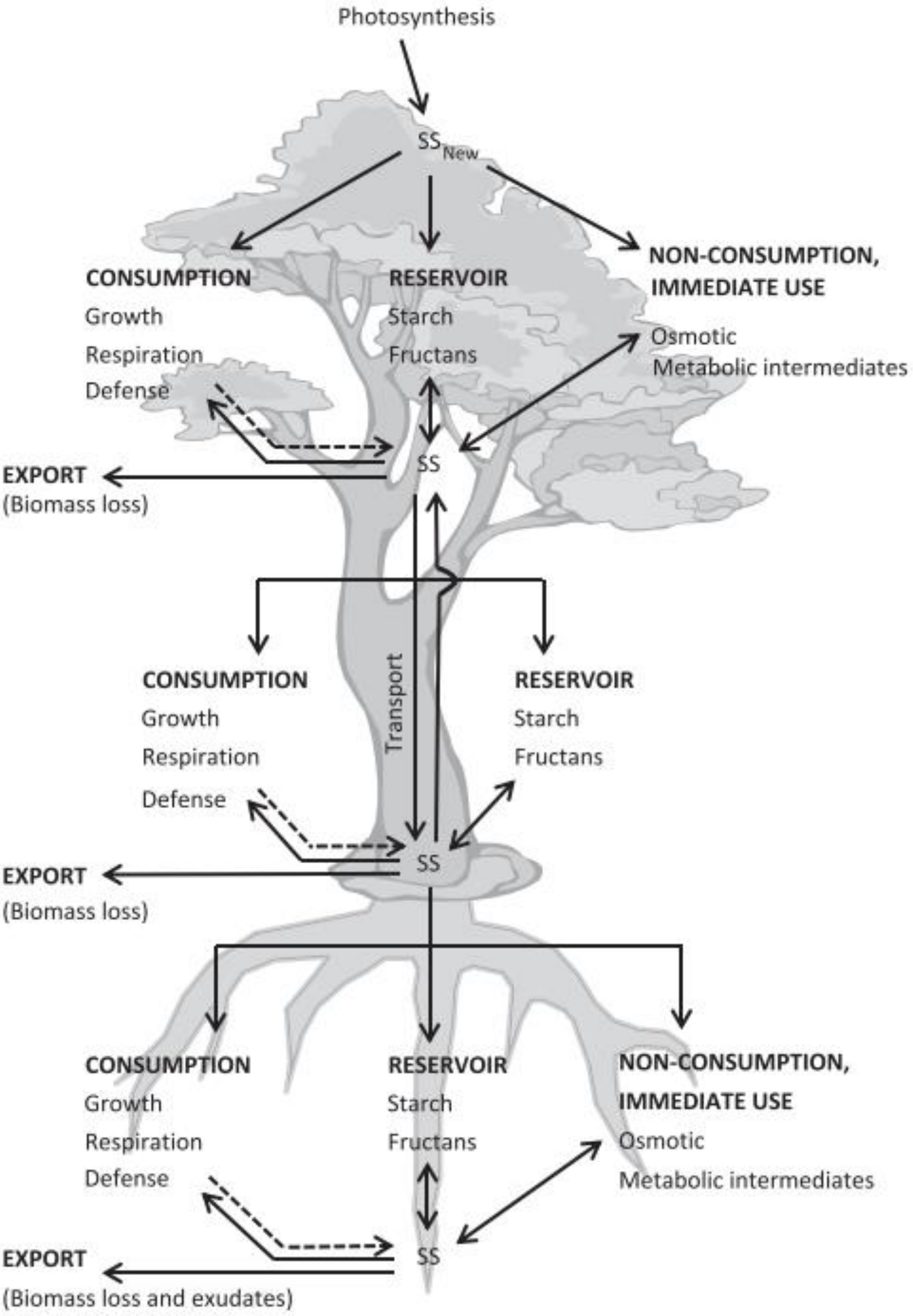

Figura 3. Diagrama conceitual que mostra os principais papéis e funções de diferentes carboidratos não estruturais (NSC) em diferentes órgãos da planta. *SS* indica açúcares solúveis e SS_{New} indica os açúcares solúveis recém-assimilados. Figura presente em (MARTÍNEZ-VILALTA *et al.*, 2016a).

Em plantas lenhosas, os carboidratos se acumulam durante os períodos de excesso de produção e tendem a se esgotar quando a sua taxa de utilização excede a taxa de produção (KOZLOWSKI, 1992). A concentração de NSC tende a variar entre os órgãos das plantas: 1) maiores concentrações de NSC, especialmente de açúcares solúveis, são encontradas em folhas, uma vez que os mesmos são importantes para o processo de osmoregulação (DIETZE *et al.*, 2014); 2) maiores concentrações de amido em raízes (KELLER; LOESCHER, 1989), para uso futuro e; 3) concentrações mais baixas de NSC nos caules, onde a proporção relativa de tecidos lignificados e não vivos tende a ser mais alta (MARTÍNEZ-VILALTA *et al.*, 2016a).

O armazenamento e alocação de NSC ocorre de forma diferenciada em plantas que rebrotam em contraste às que não rebrotam: enquanto em espécies rebrotadoras, parte dos recursos produzidos são armazenados em órgãos subterrâneos para manter e proteger as gemas e dar suporte ao rápido crescimento após uma perturbação (PAUSAS *et al.*, 2016; SCHWILK; ACKERLY, 2005), as não-rebrotadoras alocam seus recursos para outras funções, como crescimento rápido e fins reprodutivos (PAUSAS; KEELEY, 2014). Contudo, mesmo em situações de partes aéreas de tamanhos similares, as rebrotadoras tendem a ter uma maior proporção raiz:parte aérea, tendo maior acesso a fontes de água (SCHWILK; ACKERLY, 2005). A diferença, então, pode se dar nas estratégias de alocação dos carboidratos durante a produção de biomassa acima do solo, especialmente nas estruturas foliares (LI *et al.*, 2016).

Embora a capacidade e vigor de rebrota (i.e., quantidade de biomassa rebrotada) dependam intrinsecamente das reservas de NSC, ambos variam entre espécies, entre estações do ano e em relação à diferentes tipos de perturbação (LATT; NAIR; KANG, 2001; PAUSAS *et al.*, 2016). Em florestas secas, há estudos que relatam um comportamento dos ciclos de NCS semelhante ao de zonas temperadas (LATT; NAIR; KANG, 2001), embora regiões tropicais tendam a apresentar menores concentrações de NSC (MARTÍNEZ-VILALTA *et al.*, 2016a). Ainda, embora as informações sobre esta dinâmica em florestas secas seja escassa (LATT; NAIR; KANG, 2001), alguns estudos indicam mudanças nos padrões de alocação de NSC nos diferentes órgãos da planta (i.e., raiz, caule e folha) de acordo com a sazonalidade (MARTÍNEZ-VILALTA *et al.*, 2016a) e mudanças na disponibilidade hídrica (SANTOS *et al.*, 2021).

Tratando-se das rebrotas, elas tendem a ser mais vigorosas se as árvores forem cortadas durante os períodos em que o crescimento é cessado, contendo altos níveis de NSC (BLAKE, 1983; MARTÍNEZ-VILALTA *et al.*, 2016a). A reposição do amido começa logo após as suas concentrações atingirem o mínimo, levando cerca de três meses para que a planta primeiro invista em folhas, supra suas necessidades fotossintéticas e, daí, inicie o processo de armazenamento (LATT; NAIR; KANG, 2001). É importante ressaltar que plantas lenhosas raramente acabam com seus estoques de NSC, ao menos que estejam sob condições extremas (naturais ou artificiais) que levem à morte (HARTMANN; ZIEGLER; TRUMBORE, 2013; MARTÍNEZ-VILALTA *et al.*, 2016a; SEVANTO *et al.*, 2014). Em outras palavras, a frequência e intensidade de perturbações podem levar a cenários críticos para a recuperação da biomassa perdida.

Em relação à persistência por propagação clonal por rametas, especialmente sobre suas relações com NSC, é importante ressaltar que as informações são oriundas majoritariamente de trabalhos com espécies não-lenhosas ou voltados para fins econômicos; quando lenhosas, de porte arbustivo; quando árvores, poucos são os estudos realizados em regiões de florestas secas (BARRETT, 2015; COSTA *et al.*, 2021; DONG *et al.*, 2015; DONG; YU; ALPERT, 2014; DONG-WEI; YUAN-YUAN; XIAO-YONG, 2007; FAHRIG *et al.*, 1994; JENIK, 1994; JIAO *et al.*, 2020; KLIMEŠOVÁ; DOLEŽAL, 2012). A planta clonal é capaz de produzir descendentes com o mesmo genótipo da planta mãe por meio de reprodução assexuada em condições naturais e apresentam diferenças em relação a plantas não clonais em muitos aspectos, como crescimento próprio, metabolismo e reprodução com integração de recursos, e plasticidade morfológica (DONG; YU; ALPERT, 2014; JIAO *et al.*, 2020).

Sabe-se que NSC em plantas clonais apresentam diferenças em relação à tipos distintos de solo, com respostas variadas a depender da espécie (LIANG, 2019), e que diferenças nas funções fisiológicas e capacidades metabólicas de vários componentes da planta também podem refletir a estratégia de alocação de NSC nas plantas e seu mecanismo de adaptação sob estresse ambiental (NEWELL; MULKEY; WRIGHT, 2002). Desta forma, são necessário estudos adicionais para entender como padrões na distribuição de NSC se comportam em plantas clonais, se os mecanismos já conhecidos para herbáceas/plantas não-lenhosas podem ser extrapolados para espécies lenhosas / arbóreas (e.g., integração clonal, sendo a habilidade das plantas clonais de transportar substâncias e/ou sinais entre os rametas conectados para ajustar e se adaptar a vários estresses ambientais), e como essas espécies regulam a distribuição de NSC entre diferentes rametas/frente à perturbações.

2.2.1.3 – Perturbações, persistência e carboidratos não-estruturais

Podemos pensar em diversos tipos de perturbações que podem reduzir a biomassa acima do solo e alterar as concentrações de NSC, como déficit hídrico, herbivoria, defoliação e corte e queima. Frente ao déficit hídrico, pode-se observar uma diminuição no conteúdo de amido e, às vezes, um aumento no açúcar (KRAMER, 1983). De fato, existe uma relação positiva entre as maiores concentrações de NSC antes da seca e a sobrevivência da planta durante a seca (O'BRIEN *et al.*, 2014). Ainda, plantas que rebrotam podem sofrer menos falha hidráulica por possuírem maiores sistemas radiculares capazes de evitar cavitação (PAUSAS *et al.*, 2016). Contudo, quanto maior a e mais intensa for a duração do déficit hídrico, maiores os riscos de limitação de carboidratos e de falha hidráulica (PAUSAS *et al.*, 2016). Caso haja uma perturbação/perda de biomassa acima do solo, o novo caule emitido passa a ser mais vulnerável à falta de água que uma planta não perturbada por dois motivos: 1) tais caules possuem condutância estomática mais alta e um xilema mais vulnerável à cavitação (PRATT *et al.*, 2014); 2) como a única fonte de carboidrato após a perda da biomassa acima do solo são as raízes, os mesmos devem ser mobilizados para repor essa biomassa perdida até que o crescimento da rebrota gere fotossintato excedente. Se durante este processo a captação de CO_2 for limitada pela restrição estomática devido à seca, os carboidratos podem ser esgotados, levando à mortalidade do indivíduo (MCDOWELL *et al.*, 2008; PAUSAS *et al.*, 2016; PRATT *et al.*, 2014).

É importante frisar dois pontos: 1) parte dos fotossintatos produzidos por plantas adaptadas à herbivoria é investido em forma de defesas físicas ou químicas contra os herbívoros (DIETZE *et al.*, 2014); 2) podemos pensar no processo de herbivoria, de forma geral, como uma defoliação/perturbação menos severa, uma vez que usualmente seu efeito é relacionado aos insetos. Quando tratamos de herbívoros de maior porte, como caprinos e gado, este efeito passa a ser mais acentuado especialmente em plântulas ou em rebrotas em estágio inicial de crescimento, uma vez que estes animais podem consumir sua parte aérea (LINS *et al.*, 2022; MENEZES *et al.*, 2020). A Caatinga, por sua vez, abriga mais de 9 milhões de caprinos introduzidos pelos europeus para pastar predominantemente na vegetação nativa (IBGE, 2006). Neste sentido, em casos em que há alta intensidade de pecuária extensiva que resultam em defoliação total de indivíduos, o consumo constante dessas rebrotas pode levar à morte dos indivíduos

(LINS *et al.*, 2022)por esgotamento de NSC (PAUSAS; KEELEY, 2014), especialmente em condições menos favoráveis de recursos para reposição.

Uma vez que o tipo e frequência da perturbação influenciam diretamente a capacidade de rebrota e, consequentemente a quantidade de NSC necessários para recuperar a biomassa perdida (KENNARD *et al.*, 2002), podemos considerar a agricultura de corte e queima como uma perturbação de alta intensidade, especialmente pela maneira que este processo milenar é realizado. A agricultura de corte e queima, especialmente em florestas secas que apresentam limitação de recursos e períodos sazonais, tende a ser realizada de forma anual, com baixo intervalo de descanso da terra (i.e., período de pousio) (SOBRINHO *et al.*, 2016). A vegetação acima do solo é comumente cortada, amontoada e queimada (i.e., coivara). Desta forma, a exportação contínua de nutrientes do solo realizada pelo corte e queima da vegetação, somada ao pouco tempo para a recuperação dos nutrientes perdidos, podem ter um efeito sinergético negativo na regeneração e sobrevivência de espécies, inclusive daquelas que possuem a habilidade de rebrotar.

Ao adicionar o fogo ao contexto, temos um uma situação ainda mais adversa, pois o fogo causa impactos adicionais à remoção de biomassa devido às altas temperaturas, podendo ser letal para as gemas das plantas (PAUSAS *et al.*, 2016), além de alterar as condições nutricionais do solo (e.g., menos serapilheira no ambiente) e espécies que possam interagir positivamente com as plantas (PAUSAS *et al.*, 2016). Desta forma, a maioria das plantas que rebrotam após o fogo também tem a probabilidade de rebrotar depois de outros tipos de distúrbios, mas o oposto não é necessariamente verdadeiro, havendo evidências de menor capacidade de rebrota após o fogo do que após o corte (VESK; WARTON; WESTOBY, 2004). Adicionalmente, rebrotas de plantas queimadas podem apresentar maior cavitação devido ao estresse hídrico, maior esgotamento das reservas de carboidratos e maior mortalidade do que plantas não queimadas da mesma espécie (PRATT *et al.*, 2014).

2.2.2 Persistência, Caatinga e o futuro: lacunas teóricas

Primeiramente, é crucial ressaltar que os padrões descritos na literatura são majoritariamente oriundos de estudos realizados em florestas úmidas e temperadas. Estudos em florestas tropicais sazonalmente secas, embora tenham aumentado no decorrer dos anos, tomam por referência e comparativos tais padrões previamente citados. Uma vez que cada formação vegetal/ecossistema apresenta suas próprias características, esforços para desenvolver métodos e obter descrições e padrões mais assertivos para as florestas secas são essenciais para o avanço científico acerca dessas florestas, além de auxiliar diretamente em tomadas de decisão sobre conservação e políticas públicas.

Este cenário reflete na Caatinga que, embora seja a maior FTSS da América do Sul, esteja exclusivamente em solo brasileiro, seja considerada uma das *Wilderness* com altos índices de endemismo (SANTOS, 2011) e abrigue aproximadamente 30 milhões de pessoas em seu território (SILVA; LEAL; TABARELLI, 2017b), tem sido historicamente negligenciada (SANTOS, 2011). Apenas 1% dos seus 912,529 km² está sob proteção integral (KOCH; ALMEIDA-CORTEZ; KLEINSCHMIT, 2017). Estudos recentes têm buscado padrões para entender e descrever o funcionamento ecológico da fauna e flora da Caatinga, especialmente frente a perturbações antrópicas e variação de disponibilidade hídrica (ARNAN *et al.*, 2018; KNOECHELMANN *et al.*, 2020; RIBEIRO *et al.*, 2019; RITO *et al.*, 2017; SIQUEIRA *et al.*, 2017; SOUZA *et al.*, 2019; TRINDADE *et al.*, 2020; ZORGER *et al.*, 2019).

O atual modelo rudimentar de agricultura de corte-e-queima envolve o uso da terra com a remoção da biomassa aérea da vegetação e, tradicionalmente, a retirada dos tocos remanescentes seguido de queima (HAUSER; NORGROVE, 2013). Seguindo o raciocínio de que plantas armazenam NSC quando há produtos carbono excedente, e que isso ocorre em condições ambientais favoráveis (DIETZE *et al.*, 2014; MARTÍNEZ-VILALTA *et al.*, 2016b) podemos assumir num exercício de pensamento que, quando este corte-e-queima é realizado no começo da estação seca, rebrotas mais vigorosas podem ser geradas por haver, em teoria, maiores concentrações de NSC recém armazenados. Contudo, este modelo com o uso contínuo da terra resulta numa cascata de fatores que podem explicar o atual risco de desertificação da Caatinga, sendo eles: maior exposição do solo a altas temperaturas e por tempo prolongado, o que influencia na menor capacidade de germinação de sementes devido às condições ambientais; lixiviação e menor produtividade do sistema pela exportação de nutrientes; baixo período de pousio para novos ciclos de agricultura; esgotamento dos mecanismos de regeneração e sua persistência e, lento ou travado processo de regeneração natural (BEZERRA *et al.*, 2022; CHATURVEDI *et al.*, 2017; KENNARD *et al.*, 2002; SILVA; LEAL; TABARELLI, 2017a).

Atualmente, a Caatinga é considerada um sistema socioecológico de importância global e tem uma alta densidade de pessoas em situação de pobreza que exploram a floresta para sua subsistência e sobrevivência, gerando perturbações antrópicas que levam ao abandono da terra e reduzem a sua produtividade (SILVA; LEAL; TABARELLI, 2017b). Desta forma, esta região necessita de investigações rápidas e eficazes para gerar melhores práticas de manejo e uso do solo, manutenção da biodiversidade, restauração ecológica e garantia da provisão dos bens e serviços para o bem-estar humano (TABARELLI *et al.*, 2017a). De forma agravante, relatórios sobre mudanças climáticas indicam que a Caatinga é uma área de alta vulnerabilidade, com modelos climáticos que preveem redução de 22% na precipitação, aumento da temperatura de até 6,7 °C e maior frequência de secas até meados de 2100 (MAGRIN *et al.*, 2014); além de maior perturbação humana (PBMC, 2013). Neste sentido, plantas que conseguem rebrotar ou se propagar de forma vegetativa parecem ser favorecidas neste cenário de fatores que dificultam (retardando ou inibindo) a regeneração por sementes. Contudo, as informações sobre quais espécies são capazes de rebrotar ou de se propagar vegetativamente, a generalidade desses mecanismos e sua importância real para a regeneração natural e resiliência florestal (i.e., efeitos na biodiversidade, velocidade de recuperação da cobertura vegetal, estoque de carbono) são pouco conhecidas, mas com investigações em andamento (BARROS *et al.*, 2021; NOUTCHEU *et al.*, 2023; SAMPAIO; SALCEDO; KAUFFMAN, 1993; VANDERLEI *et al.*, 2021). Estas informações são cruciais para indicar potenciais espécies para restauração ecológica, recuperação mais acelerada da cobertura vegetal, ou ainda indicar quais espécies serão mais vulneráveis às perturbações. Ainda, embora a capacidade de rebrotar possa afetar a reprodução sexuada de espécies ao potencialmente acumular alelos deletérios (WIENS *et al.*, 1987), resultando em menor quantidade de sementes (LAMONT; WIENS, 2003) e mais sementes abortadas (MENEY; DIXON; PATE, 1997), estas habilidades de persistir no ambiente podem ser a única forma de garantir regeneração da cobertura florestal/recuperação da biomassa, a resiliência do sistema e a provisão de processos e serviços ecossistêmicos, evitando o colapso do mesmo e garantindo a subsistência das populações humanas dependentes da floresta.

3. Capítulo 1: Human disturbances reduce tree abundance and stimulate woody plant resprouting and clonal growth in a tropical dry forest

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Human disturbances reduce tree abundance and stimulate woody plant resprouting and clonal growth in a tropical dry forest

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Abstract

In environments under chronic human disturbance, the persistence of woody plants via both resprouting of new shoots and clonal growth via new root suckers can increase survival and fitness. However, the relative frequency and importance of these mechanisms following disturbance remain poorly explored. Here we simulated both wood extraction (partial aboveground biomass (AGB) removal) and slash-and-burn (complete AGB removal plus burn) practices in situ and compare their effects versus controls after six months on the persistence (resprouting from new shoots and clonal growth via new root suckers), biomass, and structure (height, diameter at ground level, and number of stems) of six dominant tree species (n=210). Tree regeneration following slash-and-burn varied from 0-80% across species. Half regenerated exclusively via clonal growth, one via resprouting, and one via both mechanisms. Increased disturbance intensity (control < wood extraction < slash-and-burn) resulted in at least fivefold more root suckers produced. Nevertheless, slash-and-burn led to the apparent mortality of nearly 70% of trees (i.e., absence of living aboveground tissue after six months). For those trees that did show evidence of regeneration, initial biomass recovery was nearly 5%, mainly from resprouting of new shoots. Our findings support the presence of persistence mechanisms after human disturbances in a relatively high proportion of woody plant species in the Caatinga dry forest. In the context of limited seed germination and seedling recruitment, resprouting and clonal growth may have a more significant role in regeneration dynamics than previously thought. Regeneration ability must be considered when choosing species for restoration purposes, especially in disturbed landscapes.

Keywords: Clonality, Forest regeneration, Plant persistence, Resprouting, Tropical dry forest, Vegetative propagation

1. INTRODUCTION

Resprouting and clonal growth via root suckers are different types of vegetative propagation that have been identified as critical mechanisms for regeneration dynamics in vegetation types where natural disturbances such as fire constantly remove the aboveground biomass (Buisson et al., 2018; Clarke et al., 2012; Jenik, 1994; Pausas et al., 2016). However, human disturbances such as wood extraction, coppicing, and slash-and-burn practices can also trigger these mechanisms (Kammesheidt, 1999; Kennard et al., 2002; Moola and Vasseur, 2008; Noutcheu et al., 2023; Vanderlei et al., 2021). Despite the prevailing focus on seed and seedling banks as the primary sources of natural regeneration, disturbances in tropical dry forests can lead to changing microclimates and, consequently, decreased seed germination and seedling recruitment due to desiccation (Chaturvedi et al., 2017; Lieberman and Li, 1992). Thus, there is growing evidence that vegetative-based regeneration, rather than seedling recruitment, holds equal or greater importance, particularly after disturbances in tropical dry forests (Bond and Midgley, 2001; Buisson et al., 2018; Clarke et al., 2012; Kammesheidt, 1999; Kennard et al., 2002). Nevertheless, the impact of both natural and human factors on the frequency of this phenomenon and regeneration dynamics in dry environments remains poorly understood. In this context, vegetative propagation may have a greater influence on forest regeneration than has been explored so far.

Plants use dormant buds or bud-forming tissues to regenerate after biomass loss (Pausas et al., 2018; Klimešová et al., 2018). Here, we refer to “resprouting” as regeneration from undamaged buds located either in the stem, root collar, or taproot of the disturbed tree, typically generating multi-stemmed individuals (Bellingham and Sparrow, 2000; Moreira et al., 2012; Pausas et al., 2016). As “clonal growth”, we refer to root suckers emerging from root buds connected via a root network, which can be produced at a spatial distance from the mother plant, and then grow into independent, genetically identical individuals (Jenik, 1994, Vanderlei et al., 2021). These spatially separated individuals can share compounds and signals (i.e., clonal integration; Dong-Wei et al., 2007), potentially leading to horizontal expansion (see Fig. 1). When facing natural or anthropogenic disturbances that remove their biomass, plants utilizing both mechanisms mobilize non-structural carbohydrates (hereafter NSC), stored either in the remaining biomass or in roots, to the dormant buds (Dietze et al., 2014; Klimešová et al., 2018; Moreira et al., 2012). Although both mechanisms can generate new tissue from root buds, they differ in their processes and outcomes: disturbances that damage buds (e.g., fire) are likely to reduce plant resprouting where buds are located (Pausas et al., 2016), whereas plants exhibiting clonal growth via buds in roots can produce root suckers that are distant from the original site of establishment and disturbance sources (Bond and Midgley, 2003). Finally, recurrent cycles of biomass removal can limit or even extinguish the ability to reproduce vegetatively (Barros et al., 2021; Buisson et al., 2018; Pausas et al., 2016; Pausas and Keeley, 2014; Shibata et al., 2016; Vanderlei et al., 2021).

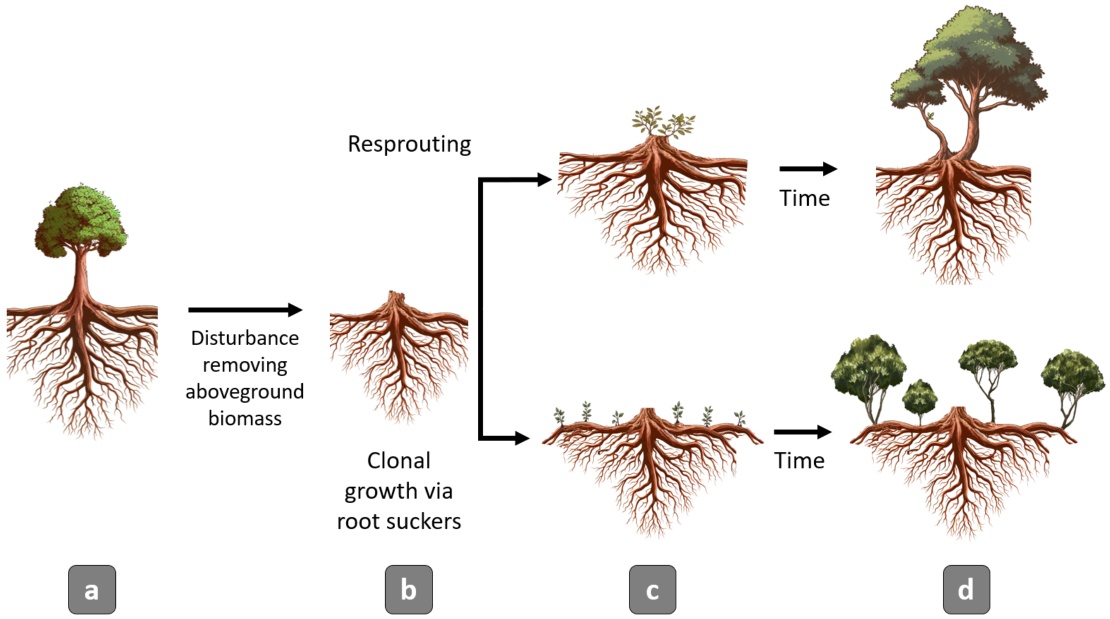

Figure 1. Conceptual framework of the plant vegetative propagation mechanisms following disturbances that completely remove aboveground biomass. Here, we present an undisturbed tree (a) that has its aboveground biomass removed and persists (b) via either resprouting (at the top) or clonal growth via root suckers (at the bottom) mechanisms. (c) Resprouting results in new shoots from stumps/root collar, whereas clonal growth results in root suckers from root buds along horizontal roots that spread

from the original site of establishment and disturbance sources; (d) after some time, resprouting is expected to generate multi-stemmed, shorter individuals, whereas new root suckers can grow, share nutrients via the connected root network, and potentially grow into independent adults.

Tropical dry forests (hereafter TDFs) are globally important ecosystems for the provision of ecosystem services and human well-being (Maass et al., 2005), yet they face a set of diverse and often simultaneous disturbances (Murphy and Lugo, 1986; Sunderland et al., 2015). With approximately 1 billion forest-dependent people relying on forest product exploitation for livelihoods, mature TDFs have been converted into mosaics of secondary forests and areas for agriculture and livestock breeding (Pulla et al., 2015; Silva et al., 2017; Singh, 1998). In this scenario, species without persistence mechanisms are likely to be removed selectively from frequently disturbed environments (Miller and Kauffman, 1998), limiting taxonomic, functional, phylogenetic, and genetic diversity (Almeida-Rocha et al., 2020; Pausas and Keeley, 2014). In disturbed forests, pre-disturbance plant structural characteristics (e.g., number of stems and height) are often found to be related to survival/persistence in a range of ecosystems (Grady and Hoffmann, 2012; Hoffmann et al., 2009; Mostacedo et al., 2022; Su et al., 2020). These structural characteristics may reflect higher aboveground biomass and pools of NSC, which can increase persistence success. After disturbances, the persisting flora may present changes in their structure and function by increasing their number of stems (i.e., multi-stemmed trees; Bellingham and Sparrow, 2000; Vesk and Yen, 2019), potentially gaining more carbon (Ware et al., 2022) and leading to a shorter stature and slower litter decomposition rates (Bellingham and Sparrow, 2009).

The Brazilian Caatinga dry forest, which is the largest and most diverse TDF in South America, has a similar socioecological context to other TDFs worldwide. It supports approximately 30 million forest-dependent (i.e., rural people; Silva et al., 2017). The region likely has been occupied as long as humans have been in South America, but it has been more intensely modified by human activities since the beginning of European colonization in the 16th century (Coimbra-Filho and Câmara, 1996). Harsh dry seasons and anthropogenic practices negatively impact the Caatinga ecosystem (Rito et al., 2017a), resulting in 1) reduced aboveground biomass, carbon storage, and wood provision; 2) taxonomic, functional, and phylogenetic impoverishment of plant and ant communities (Oliveira et al., 2016; Ribeiro et al., 2015); and 3) diminished seed dispersal (Leal et al., 2014). In this scenario, Caatinga regeneration dynamics combine low tree density, taxonomically impoverished seed rain and banks, and seedling assemblages particularly sensitive to both rainfall and human disturbances (Bezerra et al., 2022; Lins et al., 2022; Paula et al., 2023; Trindade et al., 2020; Vanderlei et al., 2022). Meanwhile, resprouting from new shoots and root sucker production have been observed in Caatinga woody plant species following human-imposed disturbances with varied responses (Figueirôa et al., 2006; Gariglio et al., 2010; Noutcheu et al., 2023; Vanderlei et al., 2021), including early resprouting in disturbed woody seedlings (Noutcheu et al., 2023; Vanderlei et al., 2021). However, the generality of these mechanisms, how fast individual and stand biomass recover, and their relative importance for Caatinga resilience facing different disturbances is still under a slow-paced investigation (Figueirôa et al., 2006; Barros et al., 2021; Vanderlei et al., 2021). The combination of social and environmental variables that favor vegetative persistence over seed germination offers an excellent opportunity to investigate how anthropogenic and abiotic factors affect dry forest regeneration.

Here, we examine the regeneration (i.e., resprouting via new shoots or clonal growth via new root suckers) and structural changes of six woody plant species in response to experimental treatments with varying intensity of disturbance that simulate common practices by forest-dependent people in our study region. We also examine the potential use of structural characteristics of individuals (e.g., height, number of stems, and diameter at ground level) as predictors of fresh aboveground biomass (AGB) and post-disturbance persistence. Specifically, we investigate: 1) how the ability to persist via either new shoots or root suckers varies among species; 2) how increasing intensities of disturbances affect resprouting via new shoots or clonal growth via new root suckers; 3) how disturbances affect the number of stems in individuals that persist via different mechanisms; 4) whether structural characteristics can be significant predictors of pre-disturbance AGB and 5) whether structural characteristics can be significant predictors of successful persistence. Reducing uncertainty in all five of these areas will improve the ability to manage wooded ecosystems in the Caatinga for tree species conservation and essential ecosystem services provision.

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted in the Catimbau National Park (hereafter Catimbau NP), northeast Brazil. The park consists of predominantly flat sandy soils, composed of approximately 70% quartzite sandy soils, 15% lithosols, and 15% planosols (Rito et al., 2017a), which are commonly utilized for agriculture and livestock purposes in the Caatinga region. The mean annual temperature in the area is 23 °C, and the average annual rainfall is 700 mm, with a historical concentration between January and July. Including the surroundings of the park, altitudes vary between 370 and 1068 m (Cavalcanti and Corrêa, 2014). During the dry season, surface soil temperatures can exceed 65 ºC under direct sunlight. The woody vegetation is dominated by the Euphorbiaceae and Fabaceae families (Rito et al., 2017b). Despite being an officially protected area since 2002, there are nearly 300 families who have lived within the Catimbau NP area since its inception (because of not being compensated to move). These low-income families rely on land and forest resources for their livelihood and income, reflecting a socioeconomic context similar to other dry forests globally (Pulla et al., 2015). Common practices in the area include wood extraction via branch and stem removal and slash-and-burn agriculture. Concurrently, the year-round collection of forest products plus intensive goat farming (Lins et al., 2022; Ribeiro et al., 2015) add to the set of disturbances that have changed the area into a human-modified landscape with a mosaic of arable fields, areas under regeneration (following land abandonment) and old-growth forest stands (Albuquerque et al., 2017; Souza et al., 2019).

2.2. Experimental design

2.2.1. Species selection

We selected six tree species that are abundant in the landscape and represent > 30% of the relative abundance of the adult flora within the 600 km² park area (Rito et al., 2017b). The species belong to the families Fabaceae: (1) *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson), (2) *Bauhinia acuruana* Moric; Euphorbiaceae: (3) *Croton argyrophylloides* Müll.Arg., (4) *Jatropha mutabilis* (Pohl) Baill, (5) *Cnidoscolus bahianus* (Ule) Pax & K.Hoffm; and Erythroxylaceae (6): *Erythroxylum revolutum* Mart.

2.2.2. Trees selection and treatments

Over a 12.3-ha area (centered on 8°33'04"S, 37°14'31"W), we performed an active search, selecting between 30 to 45 individuals for each species. We selected individuals with height ≥ 1 m and diameter at ground level (DGL) ≥ 2 cm. Multi-stemmed individuals were only included if at least one stem was within the measurements; in this case, we counted all stems and summed their DGL up. All individuals were at least five meters apart, and we carefully dug around the stem and down to 30 cm deep to identify and avoid clonal stems/root suckers connected via horizontal roots.

We placed the individuals into three treatments: partial aboveground biomass (AGB) removal (to simulate wood extraction), complete AGB removal followed by burning (to simulate slash-and-burn disturbance, hereafter "slash-and-burn" treatment), and a control group (of undisturbed trees). They were assigned to the treatments in the order they were encountered in the field, rotating across the treatments, such that the nearest neighbor trees of a given species were never assigned to the same treatment. Thus, for each species, individuals belonging to each experimental group and the control were spatially interspersed across the landscape. The six tree species themselves were also spatially interspersed across the landscape, with no clear topographic or edaphic variation within the landscape restricting the distribution of individual species. The individuals submitted to the partial AGB removal had 1/3 of their stems or their total crown cut (the latter when they did not have multiple stems), simulating the process of wood extraction commonly practiced by the local population for firewood and fencing. In the slash-and-burn treatment, individuals were first cut near ground level (Fig. 2a). Then, the biomass was piled up on top of each stump and burnt (Fig. 2b), which simulates how local communities engage in slash-and-burn agricultural practices. We applied the treatments in situ at the end of the dry season (for *J. mutabilis* and *C. bahianus* in November and December of 2019 and for the other four species in December 2020), which represents the period of the year when the rural population commonly "prepares fields" for sowing and planting. Prior to experimental treatment, all individuals were measured for their diameter at ground level (DGL; cm), height (m), and number of stems. For individuals in the complete AGB removal treatment, we also weighed the entire fresh AGB. Since cutting, drying, weighting, and burning the AGB had to be done in separate moments with the presence of the fire brigade, the process of drying the AGB prior to weighing and burning was not possible due to the low staff availability and to limitations in accessing the National Park imposed by COVID-19 pandemic restrictions and in using fire, particularly during the dry season.

After six months, at the end of the subsequent rainy season, we assessed tree structure again, including the number and frequency of new shoots and/or root suckers by carefully digging around each individual, and repeating all the measurements for each individual (i.e., height, DGL, and number of stems; Fig. 2c). For the slash-and-burn treatment only, we also cut and weighed the fresh AGB of any new shoots/root suckers. It is reasonable to believe that the six-month rainy period is marked by increased water availability, potentially more shading, and better microclimatic conditions, therefore potentially enhancing the chance to emit new shoots/root suckers.

Figure 2. Images of a *Cnidoscolus bahianus* tree undergoing the slash-and-burn treatment: (a) the previously marked and measured tree was cut near the ground level using a scythe; (b) then its biomass was piled up on the top of its stump and set on fire; and (c) the persistence via new shoots and/or root suckers of each individual was examined six months later, after an intervening rainy season.

2.2.3. Clonal growth via root suckers following disturbances

To explore whether the chosen species can propagate via new root suckers (see Jenik, 1994; Klimešová et al., 2018) and whether this mechanism is triggered by disturbances, we searched for any potential root sucker (i.e., woody individuals from the same species) within a 2.5 m radius of each tree, before and after all the treatments. If both the adult and individual were from the same species, we carefully removed soil to check if there was any lateral root connecting the individual to the focal tree.

2.3. Data analysis

Prior to the analyses, we examined if height, diameter at ground level (DGL), and the number of stems of the selected trees were different among treatments at the start of the experiment using Generalized Linear Mixed Models (GLMMs; *lmer* function and *lme4* package; Bates et al., 2015), with treatment as a fixed effect and species as a random effect. We then used both Generalized Linear Models (GLMs; *glm* function and *stats* package; Development Core Team, 2023) and GLMMs to answer our questions, using different model families according to each data type (see Table S1). We assessed the normality and heteroscedasticity of residuals both visually and using the *DHARMa* package (Hartig, 2022), log-transforming some variables to improve normality and homoscedasticity (Crawley, 2015). We also checked for overdispersion and zero-inflation in count data models using the *performance* package (Lüdecke et al., 2021), adjusting the model family as needed. When statistical differences were found between species or treatments, we performed post hoc Tukey tests using the *glht* package (Hothorn et al., 2008). R-squared values were obtained using the *rsq* package (Dabao, 2023). All analyses were performed using the R software v 4.1.3 (Development Core Team, 2019). All the models are described in Table S1.

We assessed how the ability to persist via either new shoots or root suckers varied among species using a binomial GLMM with treatment as a random effect, where 0 indicates that an individual did not produce new shoots or root suckers and 1 indicates the individual did. To examine how increasing intensities of disturbance (i.e., undisturbed, partial AGB removal, and slash-and-burn) affect clonal growth via new root suckers, we compared a) the number of individuals that produced new root suckers among treatments using a Poisson GLMM with treatment as a fixed effect and species as a random effect, and b) the number of new root suckers produced among treatments also using a Poisson GLMM with treatment as a fixed effect and species as a random effect. To assess how disturbances affect the number of stems from either resprouting or clonal growth, we compared a) the number of stems before and after this disturbance using a Poisson GLMM with time (before and after disturbances) as a fixed effect and individuals identity nested within species as random effect, and b) the number of stems after disturbances using a Poisson GLMM with mechanism (i.e., resprouting or clonal growth) as a fixed effect and species as a random effect.

Regarding the structural characteristics, we first investigated whether height, DGL, and the number of stems before the disturbances can be significant predictors of pre-disturbance aboveground biomass using GLMMs with species as a random effect.

Then, we ran separate GLMs for each species with the same structure (i.e., AGB ~ height + DGL + nº of stems) to assess their different responses. Finally, we ran a binomial GLMM to test if any of the structural characteristics, including fresh AGB, could be used to predict the regeneration of the surviving individuals following slash-and-burn, with species as a random effect.

3. RESULTS

3.1. Structural characteristics

The height, diameter at ground level (DGL), number of stems, and fresh aboveground biomass (AGB) (the latter only assayed in slash-and-burn treatment) varied substantially across individuals, ranging from 1 - 4.2 m, 2.03 - 31.78 cm, 1 - 11 stems, and 0.4 - 20.9 kg, respectively (Table 1). Trees selected for each treatment did not differ in structural characteristics before biomass removal (height: $\chi^2 = 0.71$, $df = 2$, $p = 0.70$; DGL: $\chi^2 = 1.56$, $df = 2$, $p = 0.45$; number of stems: $\chi^2 = 1.88$, $df = 2$, $p = 0.39$; df = degrees of freedom). For trees harvested in the slash-and-burn treatment, all structural characteristics were good non-destructive predictors for estimating fresh AGB under field conditions ($p < 0.0001$, $r^2 = 0.71$), with DGL being the most accurate predictor (DGL: $r^2 = 0.32$, height: $r^2 = 0.23$, number of stems: $r^2 = 0.11$). When analyzing individual species separately, some characteristics did not explain variation in fresh AGB (Table S2). Unexpectedly, all the *P. moniliformis* "tree" individuals across all treatments were actually found to be adult-sized root suckers with no taproot (Fig. 3), but with similar structural characteristics compared to the other species.

Table 1. Species, number of individuals, mean and standard error (SE) values for the height (m), diameter at ground level (cm), number (**Nº**) of stems, and fresh aboveground biomass (kg).

	Height (m)	**DGL (cm)**	**Nº of stems**	**AGB (kg)**
	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Bauhinia acuruana (30)	2.22 ± 0.36	7.15 ± 3.88	3.40 ± 1.80	2.58 ± 2.04
Cnidoscolus bahianus (45)	2.31 ± 0.80	5.10 ± 2.76	1.50 ± 1.11	3.86 ± 2.02
Croton argyrophylloides (30)	2.68 ± 0.60	10.8 ± 6.33	4.1 ± 2.70	8.04 ± 5.82
Erythroxylum revolutum (30)	2.37 ± 0.49	10.29 ± 5.13	6.60 ± 2.60	6.41 ± 5.99
Jatropha mutabilis (45)	1.68 ± 0.48	4.06 ± 1.18	1.00 ± 0.00	2.98 ± 2.34

Pityrocarpa moniliformis (30)	3.04 ± 0.45	6.36 ± 3.09	1.50 ± 1.70	8.45 ± 3.76

Figure 3. *Pityrocarpa moniliformis* adult-sized root suckers with diameter at ground level > 3 cm and height > 2 m (a, c), without taproots (b, d).

3.2. Persistence mechanisms among treatments

Five out of the six species exhibited at least one of the persistence mechanisms (i.e., resprouting via new shoots or clonal growth via new root suckers; Table S3, Fig. 4). Overall, 32 of 210 trees across all treatments (15.2%) exhibited one of the persistence mechanisms, and this response varied among the species ($\chi^2 = 31.82$, $df = 5$, $p < 0.001$). When analyzing the treatments separately, only 2 of 70 trees from the control group produced root suckers (2.85%). Meanwhile, the partial removal triggered both mechanisms in seven trees (10%), with more than twice as many producing new root suckers versus new shoots (5 vs 2). Among the trees under the slash-and-burn treatment, 32.8% persisted after the disturbance, with similar frequency of both mechanisms (12 via new shoots vs 11 via root suckers).

Following slash-and-burn, the persistence ratio (i.e., the proportion of individuals that persisted via any or both mechanisms) varied between 0-80% across species (Table 2). *C. bahianus* was the species with the highest persistence ratio, whereas none of the *J. mutabilis* individuals persisted. Regarding the relative importance of each mechanism, three of the species persisted exclusively via clonal growth, one via resprouting, and one via both mechanisms. For the latter, two *C. argyrophylloides* trees submitted to the partial AGB removal exhibited both mechanisms. When comparing undisturbed and disturbed trees, disturbances increase the number of root suckers, increased disturbance intensity (control < partial ABG removal < complete AGB removal) resulted in at least two-fold more trees producing root suckers (2 < 5 < 11) ($\chi^2 = 5.91$, df = 2, $p = 0.02$) and fivefold more root suckers produced (2 < 6 < 31) ($\chi^2 = 25.17$, df = 2, $p < 0.001$; Fig 5).

Figure 4. Individuals that exhibited persistence mechanisms following the partial biomass removal (i.e., PBR; to simulate wood extraction) and complete aboveground removal followed by burning (i.e., SLAB; to simulate slash-and-burn practices). (a) What was thought to be a *Croton argyrophylloides* seedling was actually a root sucker (b) connected via a root to a remaining stump of an individual previously submitted to the SLAB treatment (d); (c) *Bauhinia acuruana* individual producing new shoots after SLAB; (e) *C. argyrophylloides* tree producing new shoots following PBR; (f) *Erythroxylum revolutum* root suckers following SLAB; (g) *Cnidoscolus bahianus*

individual following SLAB; (h) *Pityrocarpa moniliformis* root suckers following SLAB.

Table 2. Species responses to slash-and-burn treatment. The table shows the total number (nº) of trees per species, the number of individuals that persisted after the treatment and by which mechanisms they persisted (i.e., via new shoots or clonal growth via new root suckers), and the mean number of new shoots and new root suckers per individual only using the ones that persisted, followed by their respective minimum and maximum numbers.

Species	**Nº of trees**	**Persisted**	**Via resprouting**	**Via root suckers**	**Mean nº of new shoots (min-max)**	**Mean nº of new root suckers (min-max)**
Bauhinia acuruana	10	1	1	0	5	-
Cnidoscolus bahianus	15	12	11	1	4.2 (1-7)	1
Croton argyrophylloides	10	5	0	5	-	2.2 (1-7)
Erythroxylum revolutum	10	1	0	1	-	4
Jatropha mutabilis	15	0	0	0	-	-
Pityrocarpa moniliformis	15	4	0	4	-	3.75 (1-8)

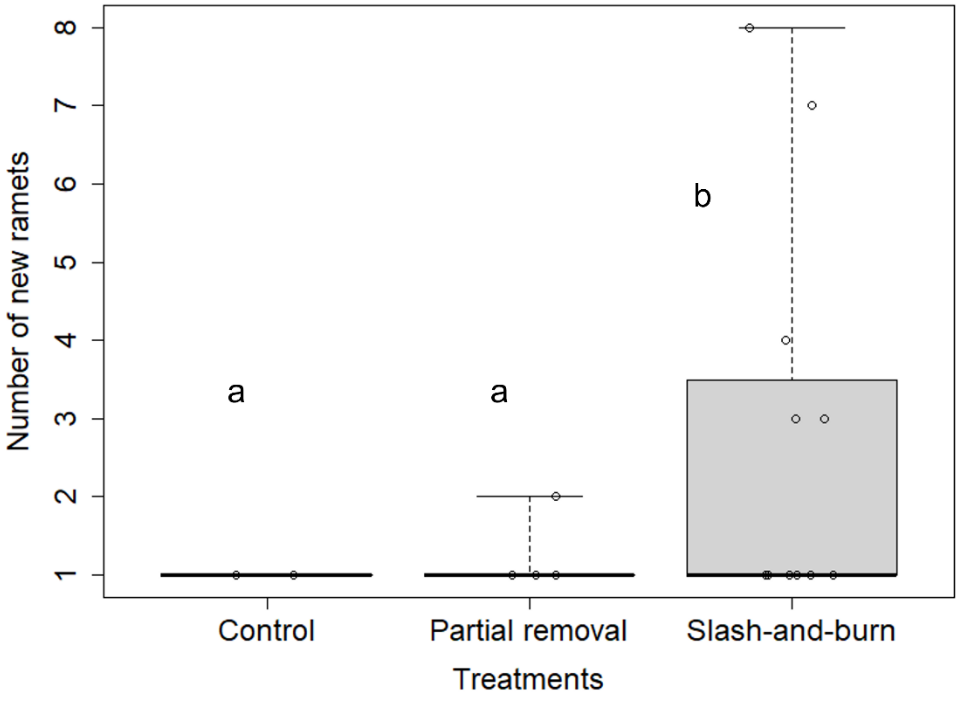

Figure 5. Number of new root suckers among the treatments following each treatment. Different letters indicate statistical differences ($p < 0.05$).

The number of stems more than doubled after the slash-and-burn ($\chi^2 = 22.29$, *df* = 1, *p* < 0.001, Fig. 6a). When comparing both persistence mechanisms, new root suckers exhibited over 50% more stems than new shoots ($\chi^2 = 4.09$, *df* = 1, *p* = 0.04, Fig. 6b). Nevertheless, of the total 357.6 kg of fresh biomass removed, 5.5% (~ 20kg) was recovered by the end of the following rainy season, with the most significant share (90%) represented by new shoots of *C. bahianus* (Fig. S1). Finally, none of the aboveground structural characteristics or fresh aboveground biomass pre-treatment proved to be good predictors of persistence success (p values > 0.05, r^2adj = 0.39, Table S4).

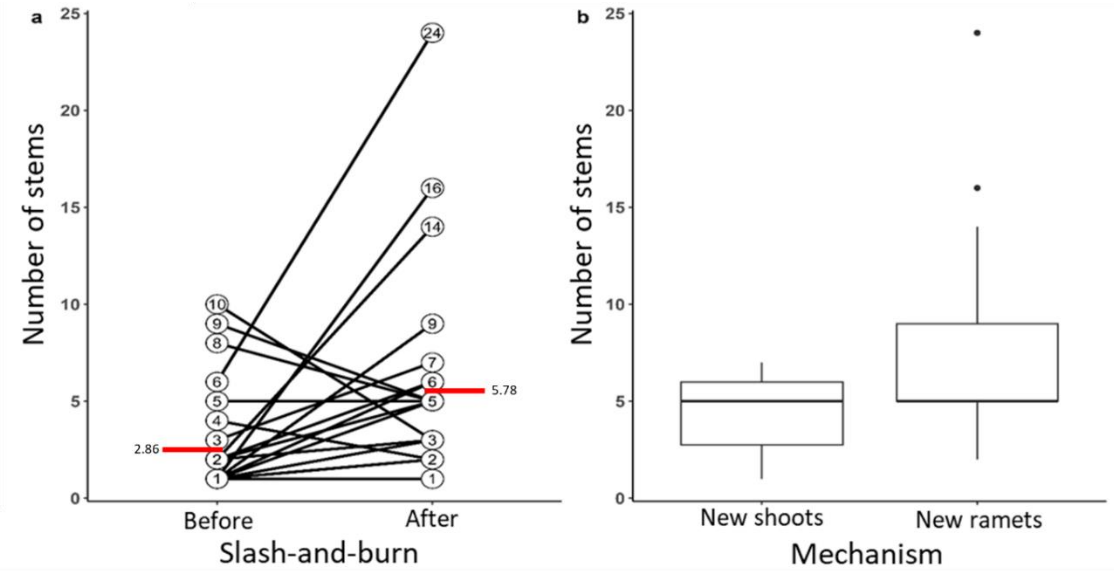

Figure 6. Comparison between the number of stems of individuals before and after the slash-and-burn treatment (mean values indicated with red lines) (a) and the number of stems between individuals that regenerated via new shoots or new root suckers after slash-and-burn (b).

4. DISCUSSION

Our results suggest that most of the currently dominant woody species in a Caatinga dry forest can persist in the environment via different mechanisms after biomass removal treatments that mimic human-induced disturbances. These human disturbances stimulate both plant resprouting via new shoots and clonal growth via root suckers. More species rely on clonal growth than exclusively resprouting, although both mechanisms have similar relative importance regarding the number of persisting individuals after slash-and-burn. Higher disturbance intensity increases the frequency of clonality, and the two mechanisms can simultaneously occur in the same tree under intermediate disturbance, although it is rare. Despite the widespread abilities of species to persist, the slash-and-burn treatment led to a drastic reduction of the initial aboveground regeneration, with a putative mortality of nearly 70% of individuals in six months. The tree species that survived complete aboveground biomass (AGB) removal show an increased number of stems via both persistence mechanisms, becoming multi-stemmed trees if they were not already. A greater number of new stems were produced as clonal root suckers versus shoots from the core rootstock, but the latter strategy is almost entirely responsible for the initial aboveground biomass recovery. Surprisingly, none of the structural characteristics predict the ability to persist following disturbances.

While resprouting and clonal growth are observed in fire-prone and human-disturbed ecosystems (Bond and Midgley, 2003; Espelta et al., 2003; McDonald, 2010; Mostacedo et al., 2022; Pausas and Keeley, 2014; Saha and Howe, 2003), data on these mechanisms are still limited for dry forest ecosystems where fire is not common (Dexter et al., 2018). Our findings support the hypothesis of widespread persistence in Caatinga woody species under increasing disturbance regimes, validating previous findings about multiple persistence mechanisms across Caatinga species (Araújo et al., 2007; Gariglio et al., 2010; Sampaio et al., 1993; Vanderlei et al., 2021). Despite addressing a small but highly abundant subset of the Catimbau flora (six species), the observed reliance on vegetative propagation may potentially explain their dominance within the landscape (Rito et al., 2017a). It highlights the need for further studies exploring these mechanisms, preferably with increased sample size to allow improved considerations and drier AGB, since some of our non-significant results (e.g., structural characteristics predicting persistence success) may be due to limited sample size. Furthermore, this propagation strategy may also account for their extensive occurrence under different environmental and human pressures across the 850.000 km² Caatinga region (Caruzo et al., 2020; Loiola and Costa-Lima, 2015; Maya-Lastra., C.A.; Torres, D.S.C.; Cordeiro, I.; Silva, 2020; Queiroz, 2020; Vaz, 2020).

Several perspectives emerge from combining the persistence across species, driven by human disturbances, and the historical situation of the Caatinga, which has received limited scientific attention and insufficient legal protection (DeAlbuquerque et al., 2012; Lessa et al., 2019; Santos, 2011; Teixeira et al., 2021). Firstly, it reinforces the role of human disturbances in driving forest regeneration and structural changes (Chaturvedi et al., 2017; Chazdon, 2003; Gardner et al., 2009). Secondly, it highlights the importance of clonal growth as a regeneration strategy in woody plant species in human-modified landscapes, expanding the existing knowledge predominantly focused on herbaceous species and shrubs (Fahrig et al., 1994; Klimešová et al., 2018; Ott et al., 2019). And thirdly, given the current evidence on plant resprouting and clonal growth in this ecosystem (Barros et al., 2021; Noutcheu et al., 2023; Sampaio et al., 1993; Vanderlei et al., 2021), it is reasonable to expect that unexplored Caatinga species may also rely on these mechanisms, particularly clonal growth, given the physical effort required for field excavation and the lack of studies exploring belowground structures *in situ*, such as root buds.

The ability to persist is traditionally considered a binary trait (e.g., resprouters vs non-resprouters; Moreira et al., 2012; Pausas et al., 2016). However, factors beyond intrinsic persistence capacity also influence persistence success. In other words, not every tree of a species that can persist after a disturbance will automatically do so, nor do their structural characteristics necessarily reflect their persistence ability. Non-structural carbohydrates (NSC) storages are crucial for producing new shoots and root suckers, and disturbance levels and seasonal changes that influence the above and belowground NSC pools likely impact persistence success (Mondal and Sukumar, 2015; Nzunda et al., 2008; Würth et al., 2005). For instance, high-intensity disturbances like fire can damage aboveground buds and stimulate additional root buds (de Rouw, 1993; Pausas et al., 2018). In this sense, both NSC and water reserves stored in root systems (O'Brien et al., 2014) facilitate aboveground biomass maintenance and recovery via resprouting and new root suckers' formation from remaining buds (see Clarke et al., 2010; Hayashi and Appezzato-da-Glória, 2009), especially during the dry season (Pausas et al., 2016). Furthermore, distinct responses to the slash-and-burn simulation among the three Euphorbiaceae species in our study (i.e., *C. bahianus* via both mechanisms, *C. argyrophylloides* via clonal growth, and *J. mutabilis* complete apparent mortality) reinforce how diverse strategies can exist even within evolutionary clades (Bond and Midgley, 2003). It may also indicate the different survival strategies between single and multi-stemmed trees in disturbed ecosystems (Su et al., 2020; Ware et al., 2022). A combination of environmental, physiological, evolutionary, and anthropogenic factors, plus disturbance intensities, may drive variation in woody plant persistence.

A considerable proportion of the Caatinga flora resprouts (see Araújo and Tabarelli, 2002; Figueirôa et al., 2006; Noutcheu et al., 2023; Sampaio et al., 1993), and the implications for forest regeneration and resilience in the socio-ecological context of constant use of forest resources has been recently explored (see Barros et al., 2021; Noutcheu et al., 2023; Sobrinho et al., 2016; Souza et al., 2021; Vanderlei et al., 2021). Still, very little is known about the extent of clonal growth among Caatinga woody species and its ecological and genetic implications (Araújo et al., 2007; Vanderlei et al., 2021), especially considering the impoverished seed rain, banks and seedling assemblages sensitive to human disturbances, intense herbivory by goats, and rainfall patterns (Bezerra et al., 2022; Lins et al., 2022; Paula et al., 2023; Ribeiro et al., 2015; Vanderlei et al., 2022). The persisting flora is characterized by the dominance of disturbance-adapted species that represent multi-stemmed, shorter trees, and root suckers that may accumulate more carbon, persist longer, and have a slower turnover than single-stemmed trees (Bellingham and Sparrow, 2009; Ware et al., 2022). While these regeneration dynamics may indicate forest resilience, species lacking the ability to persist are typically excluded from disturbed sites, thus leading to biotic homogenization. Therefore, the interplay of factors favoring plant persistence while disfavoring seed germination and seedling recruitment highlights the crucial role of plant persistence in dry forest regeneration.

In synthesis, the Caatinga dry forest supports a relatively high proportion of woody plant species able to persist after disturbances via multiple mechanisms. These persisting tree species play important ecosystem-level roles in forest regeneration, resilience, dominance, and diversity. Nonetheless, human disturbances that completely remove aboveground biomass may drastically reduce species abundances by potentially reducing buds' viability and excluding species without any persistence mechanism. Vegetative persistence (rather than via seedling) may also lower genetic diversity, with implications for ecosystem functioning, such as population stability and primary production (Dong-Wei et al., 2007). Given the importance of different regeneration mechanisms for dry forests under different types of natural and human disturbances in distinct parts of the world (Pausas et al., 2016), and considering the millions of hectares of dry forests exploited yearly for the livelihood of local populations (Sunderland et al., 2015), not to mention imminent climate change (Magrin et al., 2014), assessing the generality of persistence mechanisms across the flora of human-disturbed landscapes is necessary to improve conservation strategies, ecological restoration, and understand the future of tropical dry forests.

5. CONCLUSION

Human disturbances affect regeneration mechanisms of dry forest species, with some demonstrating the ability to persist through resprouting and clonal growth. However, it is important to note that not all species exhibit this capacity for persistence. Disturbances involving the complete removal of aboveground biomass followed by burning result in a significant decline in plant abundance. Nevertheless, among the persisting individuals, there is a notable increase in shoot production, particularly through clonal growth. While structural characteristics can serve as indicators for estimating fresh aboveground biomass, they do not necessarily correlate with the ability to persist. These findings underscore the need for careful consideration of the diverse responses and varying persistence mechanisms exhibited by dry forest species in the face of human-induced disturbances. Future studies should focus on assessing belowground structures, physiology, and how disturbances affect bud numbers and viability.

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Human disturbances reduce tree abundance and stimulate woody plant resprouting and clonal growth in a tropical dry forest

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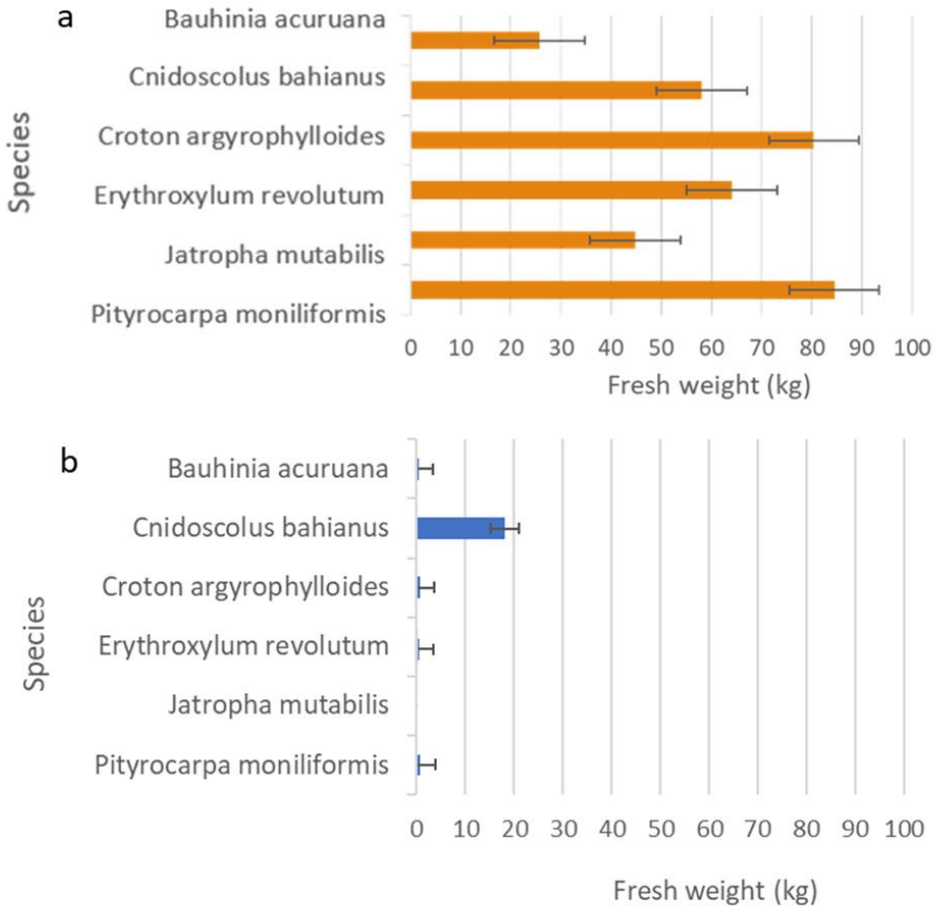
SUPPLEMENTARY FIGURES

Figure S1. The sum of fresh aboveground biomass for each species before (orange) and after (blue) the slash-and-burn disturbance treatment.



SUPPLEMENTARY TABLES

Table S1 – Models used to answer each question, using generalized linear model (glm) or mixed models (lmer / glmer).

1) how the ability to persist via either new shoots or root suckers varied among species: - glmer(persistence_binary~species+(1|treatment), family=binomial(link="logit"), where: persistence_binary = 0 for individuals that did not produce new shoots or root suckers and 1 for individuals who produced new shoots or root suckers;
2) how increasing intensities of disturbance affect clonal growth via new root suckers a) the number of individuals that produced new root suckers among treatments - glmer(ind_rootsucker~treatment+(1|species), family=poisson(link="log"), where: ind_ rootsucker = number of individuals that produced at least one root sucker; b) number of new root suckers produced among treatments: - glmer(root_suckers~treatment+(1|species), family=poisson(link="log")), where root_suckers= number of new root suckers produced;
3) how disturbances affect the number of stems between both resprouting and clonal growth: a) - glmer(n_stems~status+(1|species/id), family=poisson(link="log"), where: n_stems = number of stems, status = pre- and post-disturbances; b) - glmer(stems_post~mechanism+(1|species), family=poisson(link="log")), where: stems_post = number of root suckers after slash-and-burn treatment, mechanism = root suckers or new shoots from resprouting.
4) whether structural characteristics can be significant predictors of pre-disturbance aboveground biomass: - lmer(log(agb_pre) ~ height_pre + dgl_pre + stems_pre + (1|species)); and a mixed liner model for each separate species: glm(agb_pre ~ height_pre + dgl_pre + stems_pre), where: agb_pre = abovegorund biomass, dgl = diameter at ground level, stems = number of stems
5) whether structural characteristics can be significant predictors of successful persistence: - glmer(persistence_binary~ height_pre + dgl_pre + agb_pre + stems_pre + (1|species), family=binomial(link = "logit")

Table S2. Multiple regression values between the predictor variables height (m), diameter at ground level (DGL) (cm), and number of stems and the fresh aboveground biomass of the trees prior to the experiments. χ^2, p and adjusted r^2 values are given.

	Predictor	**$\chi 2$**	***p value***		**r^2_{adj}**	**Slope value**	**Confidence intervals**	
							2.5%	**97.5%**
All species	Height (m)	32.95	< 0.0001	***	0.69	0.34	0.19	0.49
	DGL (cm)	31.009	< 0.0001	***		0.65	0.43	0.86
	Nº of stems	10.275	0.0021	***		-0.39	-0.65	-0.13
Bauhinia acuruana	Height (m)	1.7478	0.2343		0.93	0.59	-0.27	1.44
	DGL (cm)	54.3335	0.0003	***		2.58	1.89	3.26
	Nº of stems	6.9227	0.0390	*		-1.48	-2.58	-0.37
Cnidoscolus bahianus	Height (m)	3.97	0.0715		0.91	0.44	0.01	0.87
	DGL (cm)	15.81	0.0021	**		1.77	0.89	2.64
	Nº of stems	3.31	0.0957			0.96	-0.07	1.98
Croton argyrophylloides [1]	Height (m)	0.7678	0.3808		0.84	-1.51	-4.87	1.86
	DGL (cm)	0.3955	0.0653			2.53	-0.16	5.21
	Nº of stems	0.4583	0.4984			2.11	-4.01	8.23
Erythroxylum revolutum	Height (m)	3.5863	0.1071		0.90	1.99	-0.06	4.03
	DGL (cm)	7.1628	0.0367	*		3.56	0.95	6.17
	Nº of stems	0.2795	0.6160			-0.77	-3.63	2.09
Jatropha mutabilis	Height (m)	6.6467	0.0242	*	0.83	1.12	0.26	1.98
	DGL (cm)	17.3861	0.0013	**		5.31	2.81	7.81
	Nº of stems	NA	NA				NA	NA

Pityrocarpa moniliformis	Height (m)	19.5371	< 0.0001	***	0.88	3.66	2.03	5.28
	DGL (cm)	18.4337	< 0.0001	***		3.65	1.98	5.32
	Nº of stems	9.1817	0.0024	**		-2.29	-3.77	-0.81

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[1] *Croton argyrophylloides* presented high multicollinearity among its variables (VIF > 15). We then used a stepwise function to choose the best model. DGL proved to be the best predictor with lowest AIC; $\chi2=60.05$, $p<0.0001$, $r^2adj=0.86$. Slope = 1.56 (2.5% = 2.29, 97.5% = 3.85).

Table S3. The total number of individuals per species and treatment, frequency of each persistence mechanism (i.e., resprouting via shoots and clonal growth via ramets) in each treatment, and combined frequency of persistence mechanisms after six months of the disturbances. The number of trees used for each treatment was exactly 1/3 of the total number of individuals.

Species	**Nº of individuals**	**Control group**		**Partial removal**		**Slash-and-burn**		**Persistence mechanism's frequency**
		Via shoots	Via ramets	Via shoots	Via ramets	Via shoots	Via ramets	
Bauhinia_acuruana	30	0	0	0	0	1	0	1
Cnidoscolus_bahianus	45	0	0	0	0	11	1	12
Croton_argyrophylloides	30	0	1	2	4	0	5	12
Erythroxylum_revolutum	30	0	0	0	0	0	1	1
Jatropha_mutabilis	45	0	0	0	0	0	0	0
Pityrocarpa_moniliformis	30	0	1	0	1	0	4	6
Total	210	0	2	2	5	12	11	32

Table S4. Results of the generalized linear mixed model (glmm) used to understand whether structural characteristics pre-disturbances can be significant predictors of successful persistence: glmer(persistence_binary~ height_pre + dgl_pre + agb_pre + stems_pre + (1|species), family=binomial(link = "logit"), where: persistence_binary = 0 for individuals that did not produce new shoots or root suckers and 1 for individuals that produced new shoots or root suckers, agb_pre = abovegorund biomass (kg), dgl_pre = diameter at ground level (cm), stems_pre = number of stems of the trees prior to the experiment. VIF (Variance Inflation Factors), χ^2, *p*, slope and 95% confidence intervals, and r^2 value of the model are given.

Predictor	VIF	***χ2***	***p value***	**Slope value**	**Confidence intervals**		***r²***
					2.5%	**97.5%**	
Height_pre	1.79	0.34	0.55	0.33	-0.61	1.27	0.39
DGL_pre	9.07	0.12	0.72	-0.29	-1.99	1.42	
AGB_pre	4.81	0.22	0.63	0.08	-0.26	0.41	
Stems_pre	4.09	0.49	0.48	0.59	-1.01	2.18	

4. Capítulo 2: Changes in non-structural carbohydrates dynamics and leaf functional traits in tropical dry forest woody species after slash-and-burn disturbance

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Impacts of slash-and-burn disturbance on non-structural carbohydrates, structure, and leaf traits in regenerating woody dominant species in a tropical dry forest

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Abstract

Plants can cope with disturbances by persisting via different regeneration mechanisms, such as resprouting and clonal growth. Non-structural carbohydrates (NSC) play a crucial role in this process, supporting biomass recovery and guaranteeing the continuity of the ecosystem services provision. However, the effect of human-induced disturbances in NSC dynamics of regenerating tropical dry forest species and their trade-offs between growth and storage remain poorly explored, particularly in non-fire-prone ecosystems. In this study, we investigate how the slash-and-burn disturbance affects soluble sugars (SS) and starch concentrations in different plant organs and leaf traits, also addressing their relationships with plant structural characteristics. We used data from an experiment that simulated slash-and-burn practice *in situ* using six abundant species, comparing its effects between undisturbed trees (n=70) and regenerating individuals (n=23) six months after the disturbance. Soluble sugars exhibit greater variability among plant organs and with few differences between treatments. Higher SS concentrations are observed in leaves and stems when compared to roots, whereas there are minimal disparities in starch concentrations. Plants with high NSC do not necessarily persist, as evidenced by the NSC values *Jatropha mutabilis* but zero persisting individuals. Regenerating individuals can rapidly attain NSC concentrations in stems and roots comparable to those of adult, undisturbed trees after a six-month rainy period, producing leaves with more acquisitive resource-use traits (e.g., thinner leaves with lower dry matter content) and similar leaf area, specific area, succulence, and construction cost. Our findings underscore the role of starch in roots as a crucial source for initial post-disturbance biomass increment and leaf trait development. Integrating these findings enhances our understanding of the ecophysiological mechanisms driving plant persistence and regeneration in disturbed dry forests. We also highlight the need for further exploration into the underlying processes governing post-disturbance NSC dynamics to support forest resilience.

Key-words: Slash-and-burn agriculture, Land-use, Leaf functional traits, Regeneration dynamics, Vegetative propagation, Resprouting, Root suckers.

1. Introduction

Human disturbances have caused striking changes in tropical forests worldwide, leading to significant changes in vegetation cover due to biomass loss (Fahrig, 2003; Fischer & Lindenmayer, 2007; Sagar et al., 2003) and converting old-growth forests into human-modified landscapes with various forms of land use (Arroyo-Rodríguez et al., 2017). This has been particularly the case of tropical dry forests (*sensu* (Pennington et al. 2009), which are home to about 1 billion people around the world who rely on the forest's resources for survival (Silva et al., 2017) using traditional methods of subsistence such as slash-and-burn agriculture (Curtis et al., 2018). This practice involves cutting down trees at the soil level and then burning the plant biomass, leading to increased soil exposure, and consequently disrupting soil seed banks, seed germination, and seedling recruitment (Bezerra et al, 2021; Chaturvedi et al., 2017; Lieberman and Li, 1992), severely impacting the forest regeneration. In this context, some species can persist in the environment and regenerate via different mechanisms, such as resprouting via new shoots and clonal growth via root buds, but the effects of this practice on the structure and physiological aspects of the regenerating individuals remain unexplored.

Plants use part of the carbon produced via photosynthesis as non-structural carbohydrates (hereafter NSC), mainly soluble sugars (SS) and starch (Dietze et al., 2014). Soluble sugars represent an immediate substrate for metabolic functions, such as respiration and defense demands (DIETZE et al., 2014; MARTÍNEZ-VILALTA et al., 2016a), while starch is a reserve, long-term compound that is less mobile and needs to be converted in SS for use. NSC can be dynamically partitioned among leaves, stems, and roots according to the plant's needs (Basu et al., 2016). For instance, during favorable environmental conditions and water availability periods, plants allocate a significant portion of NSC to leaves for increased photosynthetic activity and carbohydrate production, while storing part of the NSC in their roots to support future growth. When facing intense disturbances that completely remove the aboveground biomass and, consequently, the photosynthetic tissue, species that possess the ability to persist use the stored NSC as the main energy source for sustaining metabolic processes and supporting the development of new tissues at periods of negative carbon source–sink balances (Chapin et al. 1990). The NSC are mobilized to the dormant buds to initiate biomass recovery (Dietze et al., 2014; Klimesova et al., 2018; Moreira et al., 2012), and here we refer to the production of new shoots and root suckers either from buds located in the root collar or in roots. In this context, plant growth, survival, and the characteristics of new leaves and stems can be related to how well plants are able to use these stored compounds (Piper, 2011).

An initial regeneration dominated by persisting plants offers advantages over seed germination, particularly in environments with frequent disturbances and in highly seasonal (Buisson et al., 2018; Kammesheidt, 1999; Kennard et al., 2002). Successful seed germination relies on suitable environmental conditions, such as temperature and moisture, but seedlings represent the most vulnerable ontogenetic stage in a plant's life (Engelbrecht et al., 2006). In contrast, regrowing from an existing root system with stored non-structural carbohydrates (NSCs) enables rapid biomass recovery and ecosystem functions (Du et al., 2020), especially in water-limited periods. Regenerating plants are expected to 1) use stored NSCs to grow new tissue from buds, 2) rapidly produce leaves to initiate photosynthesis and maintain metabolic processes, and 3) replenish carbohydrates to prepare for potential future disturbances (Palacio et al., 2012). Root suckers have additional advantages, including sharing substances and signals among connected clones through roots (i.e., clonal integration (Dong-Wei et al., 2007) and producing root suckers away from the mother plant, along the root-network (Jenik, 1994). These characteristics are crucial for plant survival by increasing the available pool of nutrients and spatially spreading the initial colonization away from disturbance sources. However, not all species can persist, leading to a selection of those able to cope with continuous disturbances and a potential taxonomic homogenization of communities. Additionally, individuals that persist after aboveground biomass loss may exhibit changes in functional characteristics such as changes in leaf traits and construction cost (Peña-Rojas et al., 2005) and increased number of stems (i.e., multistemmed trees).

Similar to several dry forests across the world under human disturbances and seasonal water variation, the Brazilian Caatinga has a flora adapted to the variation in water availability (Dantas et al., 2020; Pinho et al., 2019; Santos et al., 2021) and biomass removal (Sfair et al., 2018), even across different ontogenetic stages (Trindade et al., 2020; Vanderlei et al., 2021, 2022). Persisting in the environment via different mechanisms apparently has a significant contribution in terms of survival, the dominance of plant species, and Caatinga forest regeneration and resilience (Barros et al., 2021; Gariglio et al., 2010; Sampaio et al., 1993; Vanderlei et al., 2021). This importance is likely to increase in the context of slash-and-burn agriculture, since a) Caatinga is not a fire-prone ecosystem, thus its flora is not expected to be adapted to fire (de Queiroz et al., 2017) and b) there is a drastic impoverishment of the soil seed bank following the slash-and-burn agriculture (Bezerra et al., 2022). Recurrent cycles of biomass removal can limit or even extinguish the ability to persist (Barros et al., 2021; Buisson et al., 2018; Pausas et al., 2016; Shibata et al., 2016; Vanderlei et al., 2021), and NSC dynamics may play a crucial role in this process. However, changes in NSC dynamics, use of resources, and how they relate to plant structure in early regeneration following disturbances (particularly *in situ*) have been poorly explored in woody plants and in non-fire-prone ecosystems. This lack of information originates not only from the historic scientific neglect of tropical forests but also from the time, cost, and effort necessary for studies *in situ* followed by biochemical laboratory analyses. Thus, the socio-ecological context of the Caatinga dry forest composed of several species able to regenerate via different mechanisms and constant biomass removal by different sources (wood extraction, livestock, goat breeding) offers an excellent opportunity to investigate these questions.

Given the importance of NSC for regulating plant metabolic processes in TDF and in the process of initial regeneration and growth following disturbances, assessing their partition within the plant's organs and their dynamics is crucial for elucidating their role in forest resilience. Here we aim to understand how intense human disturbances and plant structural characteristics affect NSC partition and leaf traits in regenerating individuals. First, we address (1) how non-structural carbohydrates (soluble sugars and starch) are partitioned in leaves, stems, and roots of (a) undisturbed trees and (b) regenerating individuals in dominant woody Caatinga dry forest species. Then, investigate (2) how the slash-and-burn disturbance affects leaf traits and NSC dynamics in different organs, and (3) whether and how NSC concentrations across organs are correlated with leaf traits and structural characteristics of plants during initial regeneration.

2. Material and Methods:

2.1 – Study area

The study took place in the Catimbau National Park (8º24'00" S; 37º14'40" W), a 607-km² Caatinga dry forest in northeast Brazil. This region is characterized by sandy soils covering a relatively flat topography (RITO *et al.*, 2017), facilitating land use for livestock and agricultural purposes. The average annual temperature is 23 °C, and the annual rainfall varies from 480–1100 mm per year, showing pronounced seasonality. The forest is predominantly composed of small-statured vegetation and mainly dominated by the Euphorbiaceae and Fabaceae families (RITO; TABARELLI; LEAL, 2017). The collection of forest products (e.g., firewood and fodder) and browsing by free-ranging, exotic goats are an intrinsic part of the landscape (ARNAN *et al.*, 2018; MENEZES *et al.*, 2020), since the Catimbau supports about 300 families that use the forest resources for subsistence (SPECHT *et al.*, 2019). Additionally, traditional practices such as slash-and-burn agriculture are carried out by the local population in order to meet their needs for livelihood, consequently playing a considerable role in changing the forest landscape (ALBUQUERQUE *et al.*, 2017; SOUZA *et al.*, 2019).

2.2 - Experimental design

2.2.1 – Slash-and-burn experiment

We used a partial data from an experiment performed *in situ* by Vanderlei et al. (2024). Six abundant species in the landscapes of Catimbau National Park were selected, representing > 30% of the relative abundance of the adult flora within the 600 km² park area (Rito et al., 2017b). The species belong to the families Fabaceae (2): *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson), *Bauhinia acuruana* Moric; Euphorbiaceae (3): *Croton argyrophylloides* Kunth, *Jatropha mutabilis* (Pohl) Baill, *Cnidoscolus bahianus* (Ule) Pax & K.Hoffm; and Erythroxylaceae (1): *Erythroxylum revolutum* Mart (Table S1).

In the experiment, 20 to 30 individuals of each species (n=140) were assigned equally into two groups: complete AGB removal followed by burning (to simulate slash-and-burn disturbance, hereafter “slash-and-burn” treatment), and a control group (of undisturbed trees). All individuals had height ≥ 1 m and diameter at ground level (DGL) ≥ 2 cm and were at least five meters apart. They were carefully dug around their stems and down to 30 cm deep to identify and avoid clonal stems/root suckers connected via horizontal roots. In the slash-and-burn treatment, individuals were first cut near ground level, then their biomass was piled up on top of each stump and burnt, simulating how local communities engage in slash-and-burn agricultural practices. The treatment *in situ* was applied at the end of the dry season (for

J. mutabilis and *C. bahianus* in November and December of 2019 and for the other four species in December 2020), which represents the period of the year when the rural population commonly “prepares fields” for sowing and planting.

After six months, at the end of the subsequent rainy season, the number and frequency of individuals regenerating via resprouting of new shoots and clonal growth via root suckers was counted. Also, tree structural characteristics of both undisturbed trees and regenerating individuals were assessed (i.e., diameter at ground level (DGL; cm), height (m), and number of stems). We used this data from the 6-month period after the slash-and-burn treatment (i.e., the initial regeneration after one rainy season). Tree persistence following the slash-and-burn treatment greatly varied among species, with five out of the six species persisting via either resprouting or clonal growth. 23 out of the 75 slash-and-burned trees persisted, generating 12 resprouts and 20 new root suckers (see Table S1). We then used these persisting individuals to collect data for the functional and non-structural carbohydrates analyses. For more information on the experiment and results, see Vanderlei et al. (2024).

2.2.2 – NSC analyses

We measured non-structural carbohydrates (NSC) in leaves (fully expanded, from the edge to the crown area), branches (close to the branches, with similar thickness), and coarse roots. Samples were collected between 8 am and 12 pm. To halt enzymatic activity, samples were microwaved (3 minutes per 100 g of sample) following the method described by Quentin et al. (2015), then promptly frozen and stored at -20°C. Soluble sugars (SS) were extracted by macerating 25 mg of tissue in an 80% ethanolic suspension, according to Farrar (1995). Starch quantification utilized the insoluble fraction obtained from the ethanol extraction of soluble carbohydrates. Starch was hydrolyzed using 10 units of amyloglucosidase (Sigma-Aldrich), incubated for 1 hour in a 95°C thermal bath. SS and starch concentrations, measured as glucose equivalents, were determined at 487 nm using a double-beam spectrophotometer (Geneses 10S UV-Vis, Thermo Scientific, Waltham, USA), following the method outlined by Dubois et al. (1956).

2.2.3 – Leaf functional measurements

In order to understand whether and how the slash-and-burn affects leaf functional characteristics, we also collected fully expanded and healthy leaves from up to 5 individuals per species (trees and regenerating individuals) to measure 6 leaf functional traits from both the control group and persisting individuals in the field according to Pérez-Harguindeguy et al. (Pérez-Harguindeguy et al. 2013). We measured the following traits: (1) leaf area (LA; mm²); (2) specific leaf area (SLA; the ratio of leaf area to leaf dry mass; m²/kg); (3) leaf dry matter content (LDMC; the ratio of leaf dry mass to fresh mass, mg/g); (4) leaf thickness (Lth; mm) and; (5) leaf succulence (LS; the ratio of leaf water content to leaf area; mg/cm²), and leaf construction cost (see Table S2). The construction cost of leaves was calculated using the nitrogen content in the ash resulting from the heat of combustion (Hc) of the dried material using the following equation determined by (Williams, K., Percival, F., Merino, J., Mooney 1987) et al (1987): $CC = [(\Delta Hc\ 0.06968-0.065)\ (Ash-1) + 7.5\ (kN / 14.0067)] / GE$, where GE is the growth efficiency, estimated at 0.87 according to (Penning de Vries, F.W.T., Brunsting, A.H.M., Van Laar 1974) et al. (1974).

2.3 – Data analysis

We used Generalized Linear Models (GLMs, *glm* function, *stats* package) and Generalized Linear Mixed Models (GLMMs, *lmer*/*glmer* functions, *lme4* package) to test our hypotheses. We assessed the normality and heteroscedasticity of residuals both visually and using the *DHARMa* package, transforming continuous data when necessary (Crawley, 2015). When statistical differences were found between species or organs, we performed post-hoc tests using the *emmeans* package, which allowed us to observe each pairwise combination between the variables and factors. All analyses were performed using the R software v 4.1.3 (Development Core Team, 2019).

We first assessed how NSC concentrations (both soluble sugars and starch) in undisturbed trees vary among their organs (leaves, stems, and roots) using glmm with species as random effect (i.e., SS/starch ~ organ + (1|species)). Then, we investigated the differences between NSC concentrations across species using an interactive glm (i.e., SS/starch ~ species*organ). To assess how NSC are partitioned among the organs in regenerating individuals, we also performed a glmm with species as random effect. To examine how the slash-and-burn practice affects NSC concentrations in different organs, we compared each organ (leaves, stems, and roots) of undisturbed trees and regenerating individuals using a glmm with species as a random effect (i.e., SS/starch ~ treatment + (1|species)). Then, we explored how leaf traits (LA, SLA, LTH, LDMC, LS, LCC) change among treatments using different glmms for each leaf trait with species as random effect (i.e., leaf trait ~ treatment + (1|species)). Finally, we ran a Pearson's correlation among NSC in different organs, structural characteristics (i.e., height, diameter at ground level, nº of stems, and fresh biomass weight), and leaf traits from regenerating individuals to explore their potential relationships and then we performed glmms to assess (1) how structural characteristics modulate NSC changes in each organ, and (2) how these NSC potentially affect leaf traits. The species *J. mutabilis* was removed from comparisons among treatments since none of its individuals persisted.

3. Results

3.1 – NSC partition among species and organs in undisturbed trees

Overall, the partition of soluble sugar varied among organs and across species, with higher concentrations in leaves, followed by stems, and roots (χ^2=1.73, df=2, p<0.001, r^2=0.65). Undisturbed trees had SS leaf concentration averages three times higher than the stems (1386 ± 956 and 397 ± 217 mg g^{-1} DW, respectively; z=7.21, p<0.001), and nearly 7.5 times the root values (189 ± 128; t=4.08, p=0.001), whereas SS in stems was twice as high than the concentration in roots (z=5.51, p<0.001) (Figure 1a, Table 1). Differences among organs explain most of the variation (r^2m=0.59), whereas species explain nearly 6%. Across the examined species, *J. mutabilis* displayed the highest average soluble sugar concentration in leaves, while *C. bahianus* exhibited the lowest average concentration (Fig. S1a). *E. revolutum* exhibited the highest average soluble sugar concentration in stems, whereas *B. acuruana* had the lowest (Fig. S1b). In roots, *E. revolutum* also had the top values, while *C. bahianus* represented the bottom one (Fig. S1c, Tables S4, S5).

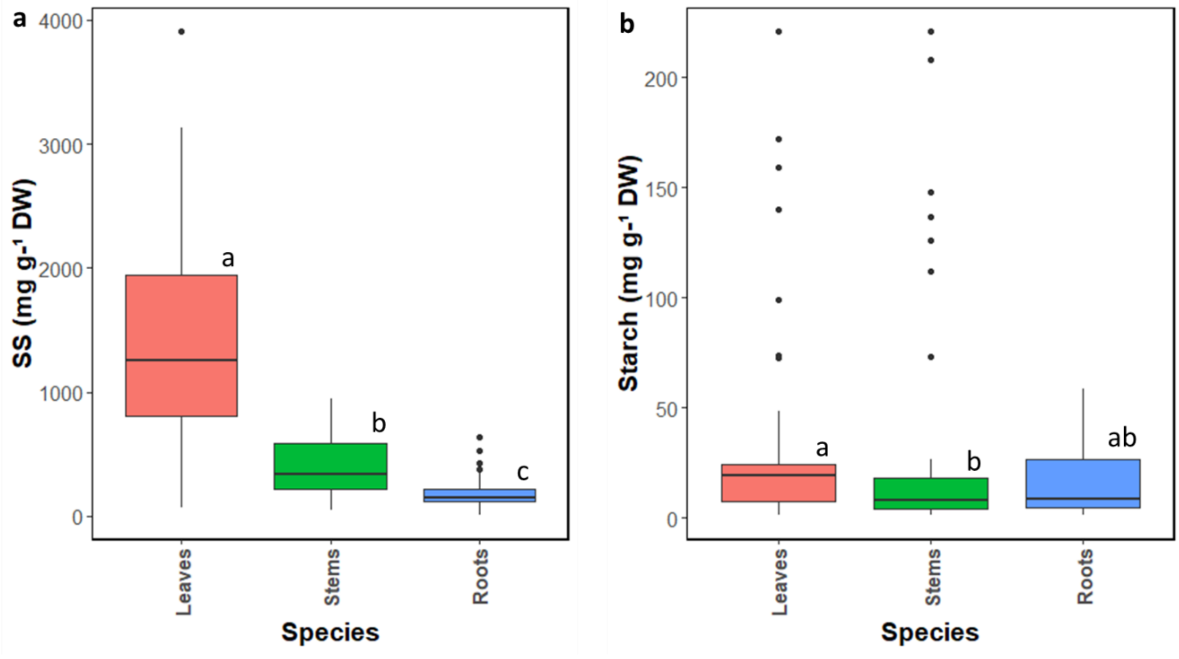

Figure 1. Soluble sugars (a) and starch (b) concentrations (mg g^{-1} DW) in leaves, stems, and roots of undisturbed individuals in a Caatinga dry forest, Brazil. Different letters indicate statistical differences between treatments.

Table 1. Mean ± sd, minimum, and maximum average numbers of soluble sugars (SS) and starch concentrations (mg g^{-1} DW) in leaves, stems, and roots of undisturbed individuals in a Caatinga tropical dry forest, Brazil.

Organs	**Mean ± sd**	**Minimum**	**Maximum**
SS			
Leaves	1386 ± 956	72.1	3906
Stems	397 ± 217	47.1	947
Roots	189 ± 128	5.03	633
Starch			
Leaves	35.8 ± 51.6	1.2	221
Stems	31.1 ± 55.4	1.23	221
Roots	16.5 ± 16.6	0.965	58.3

Starch partition across organs varied differently from SS, with similar average concentration in leaves and in stems (35.8 ± 51.6 and 31.1 ± 55.4 mg g^{-1} DW, respectively; z=2.33, p=0.052), and twice as much of root concentration (16.5 ± 16.6; z=2.65, p=0.02), but no differences between stems and roots (z=0.36, p=0.92) (Figure 1b, Table 1). Despite these significant results, the differences among organs only explain about 0.03% of the variation (r^2c = 0.03), which is considerably accentuated across species (r^2m=0.39). Starch values highly fluctuated across species and organs, but a similar overall pattern was observed for leaves, stems, and roots, respectively: *J. mutabilis* showed the highest average starch concentrations in all three organs, while *C. bahianus* notably exhibited the lowest averages (Fig. S1a-c, Tables S6, S7).

3.2 – NSC partition following slash-and-burn disturbance

Moving to the regenerating individuals, the average soluble sugar concentration in leaves (743.87 ± 673.71) did not differ from stems (434.12 ± 237.07; t=1.916, p=0.14), but both leaves and stems had concentrations were at least four and two times higher than in roots (182.62 ± 104.26 mg g^{-1} DW), respectively (t=5.278, p<0.001, and t=3.330, p<0.004) (Figure 2a, Table 2). Starch average values did not differ among organs (χ^2=4.32 df=2, p=0.11) (Figure 2b, Table 2). When comparing concentrations between treatments, regenerating individuals had similar SS concentrations in stems and roots than undisturbed trees (χ^2=2.14, df=1, p=0.14, r^2=0.48 and χ^2=0.22, df=1, p=0.63, r^2=0.28), but with lower leaf values (χ^2=5.73, df=1, p<0.01, r^2m=0.08) (Fig. 3a). Meanwhile, no differences were observed regarding the starch concentrations among organs from both treatments (Fig. 3b), with a strong indication of species differences influencing the concentration of both NSC types (please see Fig. S2a-b).

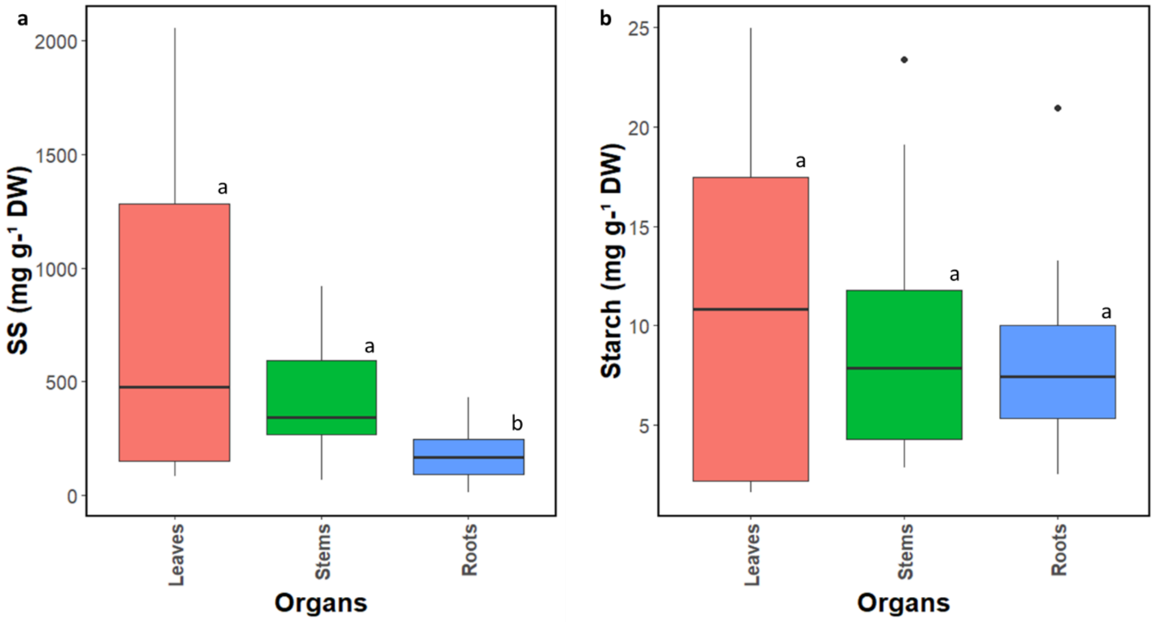

Figure 2. Soluble sugars (a) and starch (b) concentrations (mg g^{-1} DW) in leaves, stems, and roots of regenerating individuals in a Caatinga dry forest, Brazil. Different letters indicate statistical differences between treatments.

Table 2. Mean ± sd, minimum, and maximum average numbers of soluble sugars (SS) and starch concentrations (mg g^{-1} DW) in leaves, stems, and roots of regenerating individuals in a Caatinga tropical dry forest, Brazil.

Organs	**Mean ± sd**	**Minimum**	**Maximum**
SS			
Leaves	742.87 ± 673.71	85.65	2054.36
Stems	434.12 ± 237.07	66.81	918.10
Roots	182.63 ± 104.26	12.04	431.75
Starch			
Leaves	11.44 ± 7.87	1.59	24.97
Stems	8.82 ± 5.51	2.86	23.37
Roots	7.89 ± 4.36	2.51	20.97

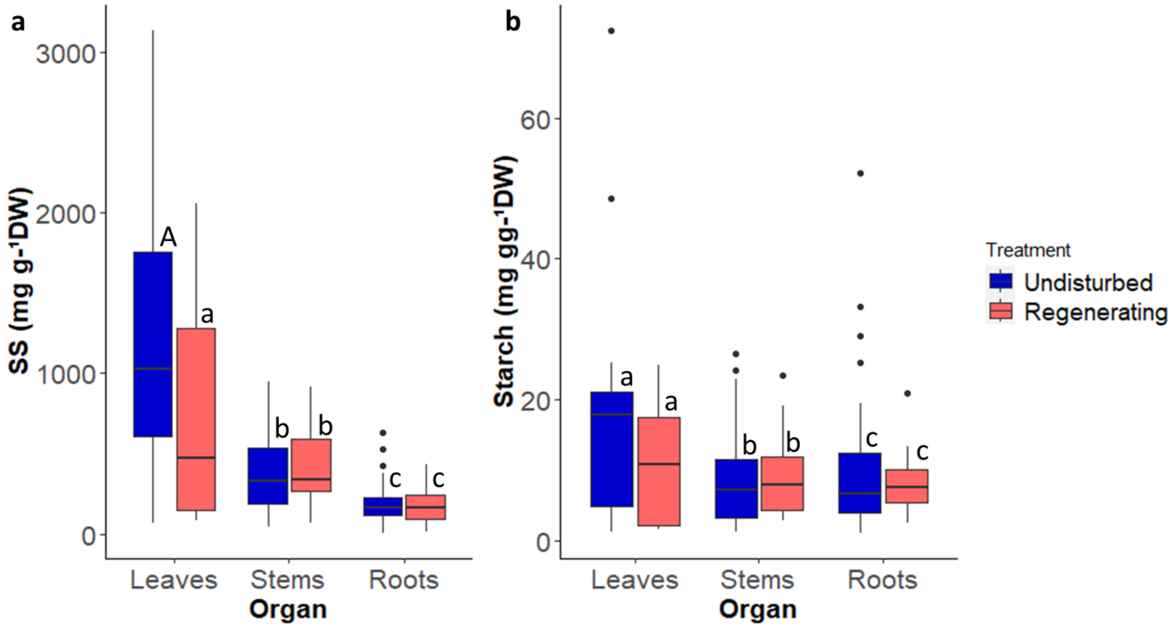

Figure 3. Soluble sugars (a) and starch (b) average concentration values (mg g^{-1} DW) between treatments and among organs. Same letters with distinct cases (uppercase and lowercase) indicate statistical differences between treatments.

3.3 – Leaf functional traits, treatments, and NSC

Overall, when comparing the averages of leaf traits between treatments, undisturbed trees showed higher values than regenerating individuals for two out of the six analyzed traits: leaf thickness (0.28 ± 0.09 and 0.20 ± 0.07 mm, fig. 4c) and LDMC (391.15 ± 66.18 and 314.35 ± 49.33 m^2 kg, fig. 4d), respectively (Fig. 4a-f; Table S8). Differences across species apparently play an important influence on the results (See Table S8, S9) despite the low number of persisting individuals (Table S1). Correlations indicate some positive and negative trends among NSC in leaves, stems, roots, and structural characteristics (Table SX). Consequently, a few significant relationships appear between SS and starch in different organs, structural characteristics, and leaf traits, as follows: (1) SS in roots and number of stems (-), leaf area (-), and leaf succulence (-); (2) starch in leaves and number of stems (+), (3) starch in roots and height (-), diameter at ground level (-), leaf area (-) and leaf succulence (-) (see tables S11, S12).

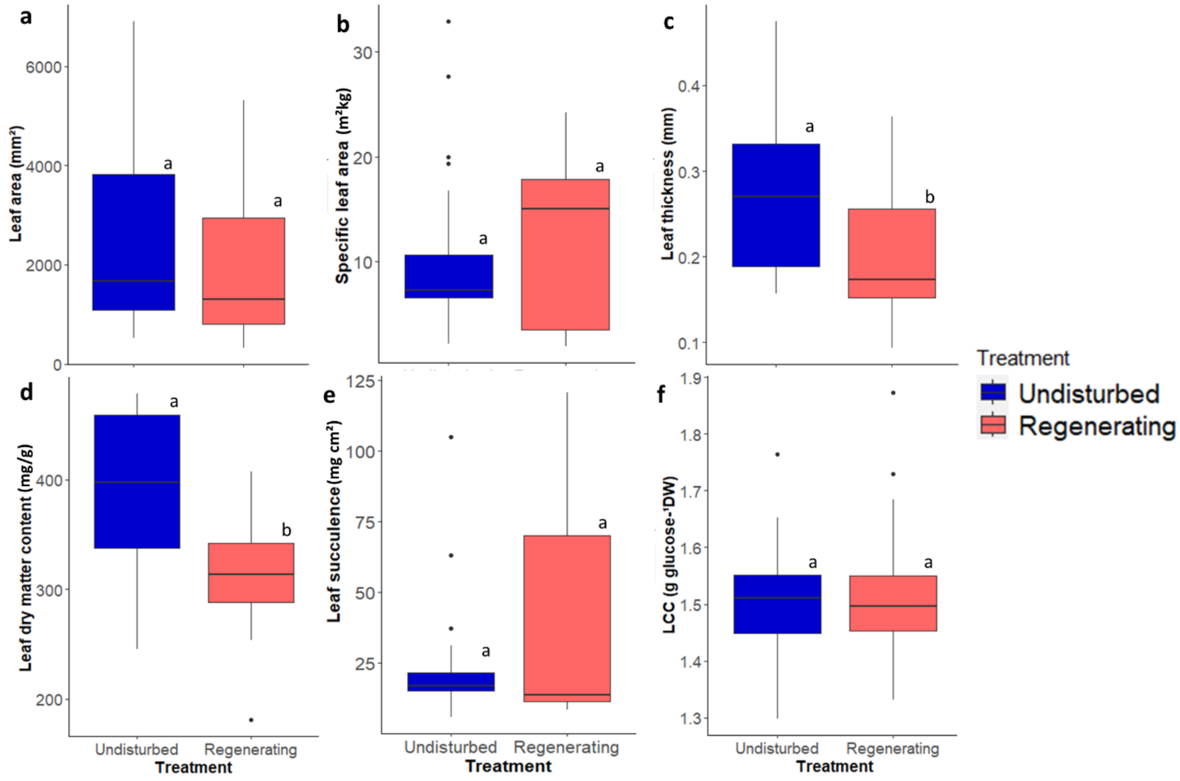

Figure 4. Leaf area (mm^2) (a), specific leaf area (m^2 kg) (b), leaf thickness (mm) (c), leaf dry matter content (mg/g) (d), leaf succulence (mg/cm^2) (e), and leaf construction cost (g gucose^{-1} DW) (a) average values in both undisturbed trees and regenerating individuals. Different letters indicate statistical differences ($p < 0.05$).

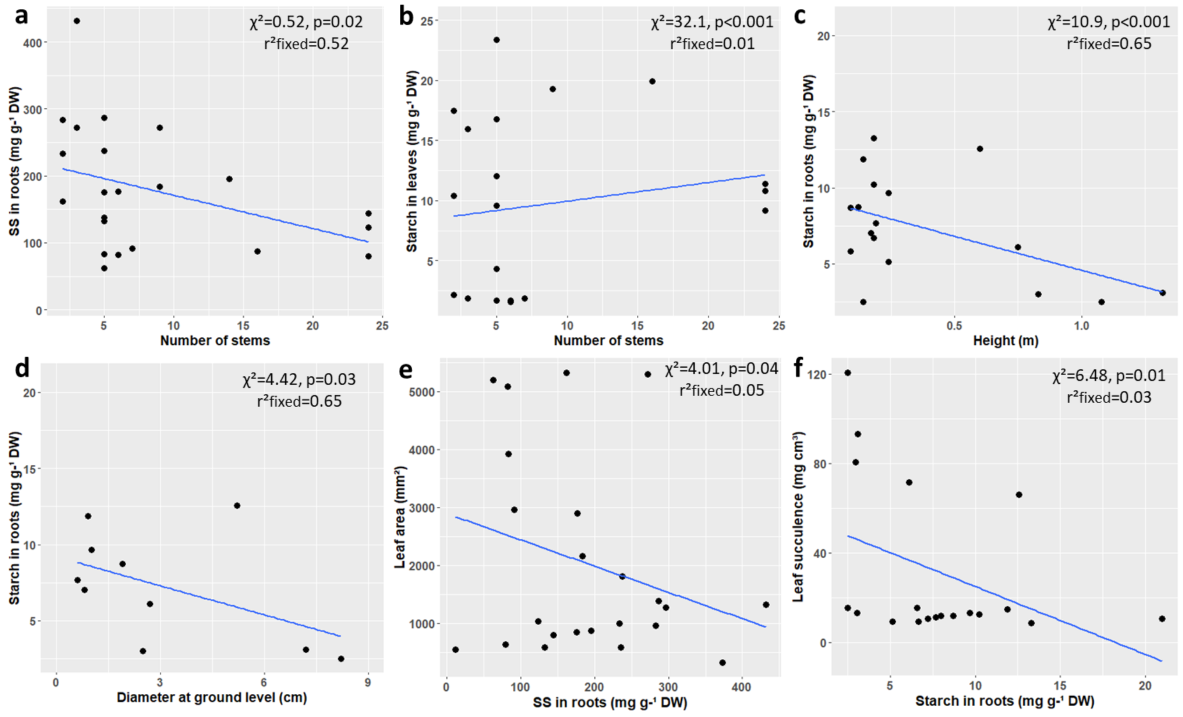

Figure 5. Changes in (a) soluble sugars (SS) in roots and (b) starch in leaves (mg g^{-1} DW) as a function of the number of stems, in starch in roots and (c) height (m) and (d) diameter at ground level (cm), and responses of (e) leaf area (mm²) and (f) leaf succulence (mg cm³) against SS in roots. Only statistically significant relationships are show.

4. Discussion

Our results suggest that concentrations of soluble sugars (SS) exhibit greater variability among plant organs compared to starch levels, with a significant variation across species. Specifically, there is a consistent pattern of higher SS concentrations observed in leaves and stems when compared to roots, a pattern observed in both undisturbed trees and regenerating individuals. Conversely, there are minimal disparities in starch concentrations among these organs. However, the sole high accumulation of NSC does not guarantee plant persistence, as evidenced by the increased SS and starch reserves found in *J. mutabilis* but zero persisting individuals. Surprisingly, individuals able to persist after slash-and-burn disturbance can rapidly attain NSC concentrations in stems and roots comparable to those of adult, undisturbed trees after a six-month rainy period. Regenerating individuals also display leaves with more acquisitive resource-use traits such as thinner leaves with lower dry matter content. Despite this, leaf area, specific area, succulence, and construction cost remain similar to leaves from undisturbed trees. Furthermore, relationships between structural characteristics, leaf traits, and NSC concentrations among regenerating individuals highlight the role of starch in roots as the main source of nutrients after slash-and-burn practice related to initial biomass increment (e.g., height and diameter at soil level) and certain leaf traits. In synthesis, six months after having the aboveground biomass completely removed and burnt, individuals able to persist can use NSC stored in roots to regenerate via different mechanisms, produce leaves with similar characteristics as of undisturbed trees to rapidly initiate the photosynthetic activity, and apparently replenish part of the used resources to equal the levels of NSC concentrations in stems and roots. These patterns enhance the understanding of the ecophysiological mechanisms behind plant persistence in regenerating individuals during initial plant regeneration after disturbances.

The role played by different regeneration mechanisms (e.g., resprouting and clonal growth) is known to be crucial for rapid biomass recovery in fire-prone and human-disturbed ecosystems (Bond & Midgley, 2003; Mostacedo et al., 2022; Saha & Howe, 2003). However, not only data on these mechanisms are limited in dry forests where fire is not a natural driver (Dexter et al., 2018), but the underlying processes that guarantee their success and support forest resilience (including NSC dynamics) remain largely unexplored (Piper & Paula, 2020). Our findings reinforce the notion of NSC mediating plant persistence and plant regrowth following disturbances (Hartmann & Trumbore, 2016; Reed & Hood, 2023; Würth et al., 2005). The patterns of higher concentrations in leaves, lower variability in starch concentrations, and species-specific responses regarding carbon dynamics are in accordance with previous studies (Baião et al., 2023; Cho et al., 2022; Poorter et al., 2010; Reed & Hood, 2023). In this context, despite addressing a small but abundant subset of species in our focal landscape, our observations contribute to the limited understanding of post-disturbance NSC remobilization, especially *in situ*, to mediate dry forest regeneration under human disturbances. As our study focused on broader responses across species, and their response to the slash-and-burn practice (i.e., the number of regenerating individuals) was not predictable, we also highlight the need for further explorations on the key ecophysiological factors driving plant persistence, biomass regeneration, and resource allocation preferably with increased sample sizes to account for intraspecific variances.

Considering that soluble sugars have fast mobilization and play immediate roles in the maintenance of metabolic activities (Dietze et al., 2014), differences in concentrations among organs likely arise from specific needs for regulation due to abiotic changes. Starch, in turn, is expected to be osmotically inert, and fluctuations in undisturbed trees may be related to situations that demand remobilization (e.g., defoliation and emission of new leaves, partial aboveground disturbance and growth of new tissue from using stem resources) (Nzunda et al., 2008). Given the known importance of NSC for plant persistence and the low number of regenerating individuals found in our study, we can ponder some aspects that elucidate these patterns: (1) as plant regrowth rely on active, healthy buds to emit new shoots, slash-and-burn practices not only completely remove the aboveground biomass but also may directly damage and make buds unviable (Pausas et al., 2016), thus leading to the lack of new tissue production even in the presence of sufficient stored NSC, (2) stored carbon in belowground organs become the main source of NSC after complete aboveground biomass removal, but they may not be promptly available or accessible for remobilization (Martínez-Vilalta et al., 2016; Millard et al., 2007), (3) different and frequent disturbance regimes determine allocation strategies (Shibata et al., 2016), and plants facing constant biomass loss may not be able to replenish the NSC reserves used for constant regrowth, hence limiting or impeding plant persistence (Moreira et al., 2012; Pausas & Keeley, 2014), and (4) regardless of the amount of NSC stored, environmental conditions, or type of disturbance, a tree will not persist if the species does not have the ability to do so, which apparently is the case with *J. mutabilis*.

Notwithstanding the potential reasons that led to plant mortality following the slash-and-burn disturbance, interesting insights arise from the individuals who successfully persisted. As water shortage directly limits carbon investment (i.e., new tissue formation) (Würth et al., 2004), the first six months of regeneration which comprise the rainy period following slash-and-burn disturbance not only potentially result in more shading and better microclimatic conditions but also appear to be crucial for the fast investment in new plant tissue in regenerating individuals. Biomass burning may promote the rapid incorporation of nutrients into the soil and the elimination of weeds (Hauser and Norgrove, 2013; Ribeiro-Filho et al., 2015, 2013), potentially supporting an increased nutrient absorption to aid biomass recovery. The negative relationships between NSC in roots and structural characteristics not only highlight the trade-off between investing in biomass at the expense of carbon storage (Dietze et al., 2014; Shibata et al., 2016) but also the necessary balance to quickly grow biomass and acquire resources for sustaining the plant maintenance costs and avoiding reserve depletion (Moreira et al., 2012). Additionally, the observed characteristics of acquisitive resource-use strategies regarding leaf traits in regenerating species emphasize their ability to (1) use the previously stored carbon reserves in the root system to invest in fast regrowth, (2) efficiently make use of the environmental conditions to produce new leaves meet their demands for photosynthetic activity during the initial regeneration, and (3) take advantage of the potential carbon surplus to replenish NSC reserves (Martínez-Vilalta et al., 2016), consequently reaching concentration levels similar to adult, undisturbed trees.

The prompt reallocation of stored NSC to fuel new growth holds significant implications for both forest regeneration and the provisioning of essential ecosystem services after disturbances. The Caatinga dry forest, like other dry forests worldwide, faces a combination of factors that reduce seed viability, germination, and seedling recruitment (Bezerra et al., 2022; de Paula et al., 2023; Lins et al., 2022), leading to impoverished seedling assemblages and an increased reliance in different regeneration mechanisms, such as resprouting and clonal growth (Barros et al., 2021; Noutcheu et al., 2023; Vanderlei et al., 2021, 2022). This, in turn, aids in the faster vegetation recovery, microclimatic conditions, and restoration of critical ecological functions such as carbon sequestration and soil health, especially considering that the Caatinga is not a fire-prone ecosystem. This rapid biomass recovery and carbon production/storage may be crucial to endure the next dry season and/or any of the set of disturbances that may lead to another cycle of aboveground biomass loss (e.g., grazing by goats, new slash-and-burn cycles, livestock trampling). The Caatinga woody flora exhibits the co-occurrence of distinct strategies associated with water and/or nutrient use, including softwood species with soft leaves, such as *J. mutabilis*, and hardwood species with either conservative (i.e., *C. argyrophylloides*) or acquisitive leaves; Pinho et al., 2019), which likely explain the species-specific NSC partition and leaf trait patterns. Although these regeneration dynamics may indicate forest resilience, it is reasonable to expect that the exclusion of species not able to persist and drastic putative tree mortality following the slash-and-burn disturbances may lead to functionally poor and taxonomically impoverished regenerating forests. Moreover, the persisting flora is expected to be characterized by the dominance of disturbance-adapted species that represent multi-stemmed, shorter trees (Bellingham & Sparrow, 2009; Palacio et al., 2012; Vanderlei et al., 2024; Ware et al., 2022), altering the forest structure.

In synthesis, plants able to persist after slash-and-burn disturbance in this Caatinga dry forest seem to present changes in NSC dynamics, leaf functional traits, and resource-use strategies for rapid investment in aboveground biomass to meet their photosynthetic demands and regain NSC storage during initial regeneration. Despite the general patterns, these responses seem to be potentially mediated by the species-specific characteristics, therefore they should be taken into consideration. The recovery of NSC concentrations among the persisting individuals may both support the initial accelerated biomass increment and provide forest resilience and, consequently, guarantee the provision of ecosystem services. However, the drastic reduction in carbon availability (i.e., tree abundance) and carbon uptake, plus the potential impoverishment of regenerating forests should be strongly kept in mind. We suggest further *in situ* studies, preferably comparing NSC pools before and after disturbances to help unveil the mechanisms potentially controlling plant persistence in human-modified landscapes.

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Impacts of slash-and-burn disturbance on non-structural carbohydrates, structure, and leaf traits in regenerating woody dominant species in a tropical dry forest

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SUPPLEMENTARY MATERIAL

Figure S1. Soluble sugar (a) and starch (b) concentration values (mmol kg^{-1} DW) in leaves, stems, and roots among species. Distinct letters indicate significant differences between species ($p < 0.05$).

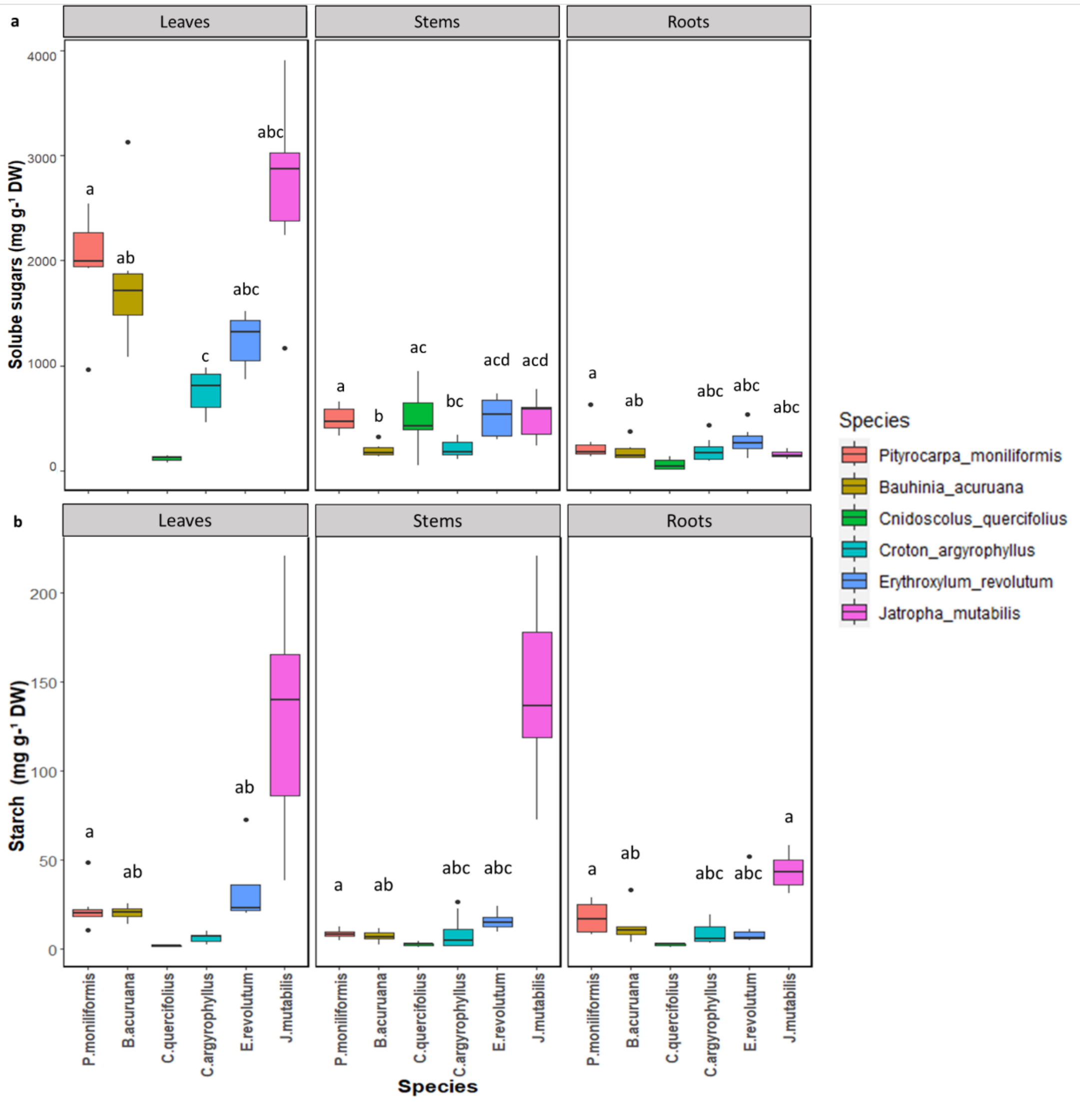
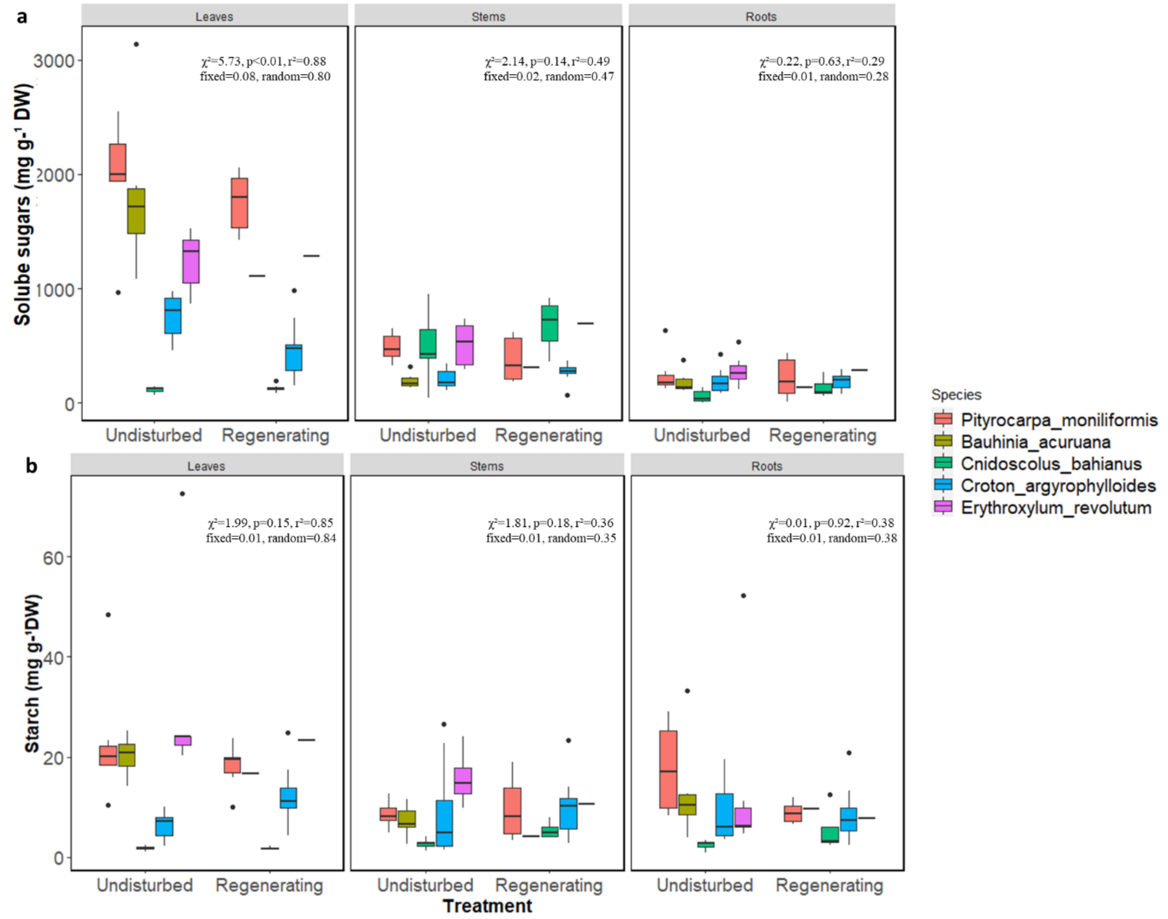


Figure S2. Soluble sugars (a) and starch (b) average concentrations (mg g^{-1} DW) across organ and species in both undisturbed and regenerating individuals in a Caatinga dry forest, Brazil.



TABLES

Table S1. Species name, family, plant habit, dispersal syndrome, and deciduity of the six species used in this study. Information was compiled from Flora do Brasil and personal databases.

Species	Plant Habit	Dispersal Syndrome	Family	Deciduity
Bauhinia acuruana Moric	Tree/shrub	Autocoric	Fabaceae	Deciduous
Cnidoscolus bahianus (Ule) Pax & K.Hoffm	Tree/Shrub	Autocoric	Euphorbiaceae	Deciduous
Croton argyrophylloides Müll.Arg.	Shrub	Autocoric	Euphorbiaceae	Evergreen
Erythroxylum revolutum Mart.	Tree/shrub	Zoocoric	Erythroxylaceae	Evergreen
Jatropha mutabilis (Pohl) Baill	Tree/Shrub	Autocoric	Euphorbiaceae	Deciduous
Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	Tree/shrub	Autocoric	Fabaceae	Deciduous

Table S2. Species responses to the slash-and-burn treatment. The table shows the total number of individuals per species, the number of individuals that regenerated after the disturbance and by which mechanisms they persisted (i.e., resprouting via new shoots or clonality via new ramets), and the mean number of new shoots and new ramets followed by their respective minimum and maximum numbers.

Species	**Nº of trees**	**Persisted**	**New shoots**	**New ramets**	**Mean nº of new shoots (min-max)**	**Mean nº of new ramets (min-max)**
Bauhinia acuruana	10	1	1	0	5	-
Cnidoscolus bahianus	15	12	11	1	4.3 (1-7)	1
Croton argyrophylloides	10	5	0	5	-	2.2 (1-7)
Erythroxylum revolutum	10	1	0	1	-	4
Jatropha mutabilis	15	0	0	0	-	-
Pityrocarpa moniliformis	15	4	0	4	-	3.75 (1-8)
Total	70	23	12	11	12	20

Table S3. Functional traits included in the study, description of the functional role, and references used.

Measured trait	**Abbreviation**	**Functional role**	**Reference**
Leaf thickness (mm)	Lth	Construction costs, leaf life span, photosynthetic rates per unit leaf area, against mechanical and herbivore damage and gas exchange.	Popma and Bongers, 1991, Reich et al., 1991; Díaz et al., 2004; Loranger and Shipley, 2010.
Leaf Dry Matter Content (mg/g)	LDMC	Level of assimilative compounds and transfer conductance to CO_2, construction costs, nutrient retention, tolerance against water limitations and mechanical and herbivore damage.	Poorter and Garnier, 1999; Niinemets, 2001; Garnier et al., 2004; Poorter and Markesteijn, 2008.
Specific Leaf Area (mm^2/mg)	SLA	Light capture economics, net assimilation rate, relative growth rate, leaf life span and photosynthetic capacity.	Reich et al., 1997; Poorter and Garnier, 1999; Poorter and Bongers, 2006; Sterck et al., 2006.
Leaf Area (mm^2)	LA	Light intercepting area, dry matter production, respiration, leaf cooling and gas exchange.	Bazzaz and Picket, 1980; Popma et al., 1992.
Leaf Succulence (mg /cm^2)	LS	Variation in resource availability and leaf water content.	Pérez-Harguidenguy et al., 2013.
Leaf construction cost (g glucose DW^{-1})	LCC	A quantifiable measure of energy invested by a plant to construct biomass. Can be related to resource utilization efficiency reflecting the integral efficiency of light energy conversion	Singh et al., 2012; Williams et al, 1987; Lambers and Poorter, 1992

Table S4. Average, standard deviation, minimum, and maximum soluble sugar concentration (mg g^{-1} DW) values among species and organs.

Species	Leaves		Stems		Roots	
	Average	StDev	Average	StDev	Average	StDev
Bauhinia acuruana	1.81	0.65	0.20	0.06	0.19	0.09
Cnidoscolus bahianus	0.12	0.03	0.50	0.28	0.06	0.05
Croton argyrophylloides	0.76	0.20	0.21	0.09	0.20	0.12
Erythroxylum revolutum	1.24	0.26	0.51	0.19	0.29	0.13
Jatropha mutabilis	2.69	0.92	0.50	0.20	0.15	0.04
Pityrocarpa moniliformis	1.99	0.50	0.49	0.12	0.25	0.17
Average	1.39	0.96	0.39	0.21	0.19	0.12
Minimum	0.07		0.04		0.07	
Maximum	3.91		0.95		0.005	

Table S5. Significant statistical differences from the pairwise comparison between the soluble sugar concentration (mg g^{-1} DW) of each species and their respective organs (leaves, stems, and roots).

Organ	Pairwise comparison			z	p
Leaves	*Pityrocarpa moniliformis*	-	*Cnidoscolus bahianus*	-3.75	0.029
	Pityrocarpa moniliformis	-	*Croton argyrophylloides*	11.721	<0.001
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	11.33	<0.001
	Bauhinia acuruana	-	*Croton argyrophylloides*	3.72	0.004
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	-7.97	<0.001
	Cnidoscolus bahianus	-	*Erythroxylum revolutum*	-9.76	<0.001
	Cnidoscolus bahianus	-	*Jatropha mutabilis*	-12.46	<0.001
	Croton argyrophylloides	-	*Jatropha mutabilis*	-5.19	<0.001
	Erythroxylum revolutum	-	*Jatropha mutabilis*	-3.07	0.031
Stems	*Pityrocarpa moniliformis*	-	*Bauhinia acuruana*	3.79	0.003
	Pityrocarpa moniliformis	-	*Croton argyrophylloides*	3.64	0.005
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	-3.84	0.003
	Bauhinia acuruana	-	*Erythroxylum revolutum*	-3.94	0.002
	Bauhinia acuruana	-	*Jatropha mutabilis*	-3.85	0.003
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	3.72	0.004
	Croton argyrophylloides	-	*Erythroxylum revolutum*	-3.80	0.003
	Croton argyrophylloides	-	*Jatropha mutabilis*	-3.71	0.004
Roots	*Pityrocarpa moniliformis*	-	*Cnidoscolus bahianus*	6.07	<0.001
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	4.85	<0.001
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	-5.24	<0.001
	Cnidoscolus bahianus	-	*Erythroxylum revolutum*	-6.68	<0.001
	Cnidoscolus bahianus	-	*Jatropha mutabilis*	-4.04	0.001

Table S6. Average, standard deviation, minimum and maximum starch concentration (mg g^{-1} DW) values among species and organs.

Species	Leaves		Stems		Roots	
	Average	StDev	Average	StDev	Average	StDev
Bauhinia acuruana	20.28	3.80	7.36	3.21	13.20	10.31
Cnidoscolus bahianus	1.87	0.46	2.67	1.00	2.48	0.87
Croton argyrophylloides	6.28	2.68	9.00	9.94	9.22	6.70
Erythroxylum revolutum	34.84	25.19	15.69	4.88	13.56	17.17
Jatropha mutabilis	129.00	62.44	146.26	52.26	43.68	10.60
Pityrocarpa moniliformis	22.93	12.01	8.58	2.60	17.91	9.14
Average	36.1	17.18	31.41	12.28	16.04	8.78
Minimum	1.87		2.67		2.48	
Maximum	129.00		146.26		43.68	

Table S7. Significant statistical differences from the pairwise comparison between the starch concentration (mg g^{-1} DW) of each species and their respective organs (leaves, stems, and roots).

Organ	Pairwise comparison			t.ratio	p
Leaves	*Pityrocarpa moniliformis*	-	*Cnidoscolus bahianus*	7.52	<0.001
	Pityrocarpa moniliformis	-	*Croton argyrophylloides*	4.17	0.001
	Pityrocarpa moniliformis	-	*Jatropha mutabilis*	-5.40	<0.001
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	7.16	<0.001
	Bauhinia acuruana	-	*Croton argyrophylloides*	3.78	0.003
	Bauhinia acuruana	-	*Jatropha mutabilis*	-5.78	<0.001
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	-3.75	0.004
	Cnidoscolus bahianus	-	*Erythroxylum revolutum*	-7.57	<0.001
	Cnidoscolus bahianus	-	*Jatropha mutabilis*	-12.71	<0.001
	Croton argyrophylloides	-	*Erythroxylum revolutum*	-4.67	0.000
	Croton argyrophylloides	-	*Jatropha mutabilis*	-9.75	<0.001
	Erythroxylum revolutum	-	*Jatropha mutabilis*	-3.49	0.009
Stems	*Pityrocarpa moniliformis*	-	*Cnidoscolus bahianus*	3.64	0.006
	Pityrocarpa moniliformis	-	*Jatropha mutabilis*	-8.86	<0.001
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	3.16	0.025
	Bauhinia acuruana	-	*Jatropha mutabilis*	-9.34	<0.001
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	-3.92	0.002
	Cnidoscolus bahianus	-	*Erythroxylum revolutum*	-5.53	<0.001
	Cnidoscolus bahianus	-	*Jatropha mutabilis*	-12.50	<0.001
	Croton argyrophylloides	-	*Jatropha mutabilis*	-8.99	<0.001
	Erythroxylum revolutum	-	*Jatropha mutabilis*	-6.97	<0.001
Roots	*Pityrocarpa moniliformis*	-	*Cnidoscolus bahianus*	5.64	<0.001
	Bauhinia acuruana	-	*Cnidoscolus bahianus*	5.02	<0.001
	Bauhinia acuruana	-	*Jatropha mutabilis*	-3.59	0.007
	Cnidoscolus bahianus	-	*Croton argyrophylloides*	-4.24	0.001
	Cnidoscolus bahianus	-	*Erythroxylum revolutum*	-5.31	<0.001
	Cnidoscolus bahianus	-	*Jatropha mutabilis*	-8.96	<0.001
	Croton argyrophylloides	-	*Jatropha mutabilis*	-5.02	<0.001
	Erythroxylum revolutum	-	*Jatropha mutabilis*	-3.65	0.005

Table S8. Average, standard deviation, minimum and maximum values of each functional trait per treatment (i.e., undisturbed trees and regenerating individuals after slash-and-burn), followed by their respective glmm results (i.e., χ^2, p, r^2 adjusted for the entire model and for both fixed (treatment) and random (species) effects). LA = Leaf Area (mm^2), SLA = Specific Leaf Area, LTH = Leaf thickness, LDMC = Leaf Dry Matter Content, LS = Leaf Succulence, LCC = Leaf Construction Cost.

Traits	Undisturbed			Regenerating			χ^2	p	r^2 adj		
	Avg ± sd	Min	Max	Avg ± sd	Min	Max			Model	Fixed	Random
LA (mm^2)	2671 ± 1889	527	6912	2318 ± 1779	580	5323	2.51	0.11	0.61	0.00	0.61
SLA (m^2/kg)	9.61 ± 6.46	2.14	33	12.4 ± 8.1	1.86	24.7	1.05	0.30	0.65	0.00	0.65
LTH (mm)	0.27 ± 0.08	0.15	0.47	0.21 ± 0.7	0.09	0.36	8.94	0.002	0.59	0.09	0.50
LDMC (mg/g)	402 ± 84.2	246	713	313 ± 38.4	253	407	13.36	< 0.001	0.37	0.25	0.12
LS (mg /cm^2)	21.7 ± 17.4	5.87	105	40.1 ± 39.6	8.42	121	1.68	0.19	0.71	0.02	0.69
LCC (g glucose DW^{-1})	4837 ± 277	4268	5668	5323 ± 443	4759	6027	17.02	< 0.001	0.47	0.28	0.19

Table S9. Average, standard deviation, minimum and maximum values of each functional trait per species in each treatment (i.e., a) undisturbed trees and b) regenerating individuals after slash-and-burn). LA = Leaf Area (mm^2), SLA = Specific Leaf Area, LTH = Leaf thickness, LDMC = Leaf Dry Matter Content, LS = Leaf Succulence, LCC = Leaf Construction Cost.

a)

Undisturbed	LA (mm^2)		SLA (m^2/kg)		LTH (mm)		LDMC (mg/g)		LS (mg /cm^2)		LCC (g gluc DW^{-1})	
Species	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev
Bauhinia acuruana	1441.07	404.54	9.35	4.80	0.36	0.10	421.20	40.68	16.85	4.01	1.56	0.03
Cnidoscolus bahianus	4122.25	1367.54	5.10	2.16	0.31	0.03	343.04	57.00	36.94	22.53	1.48	0.03
Croton argyrophylloides	971.22	304.85	19.43	9.58	0.17	0.01	336.10	18.88	13.64	8.21	1.48	0.19
Erythroxylum revolutum	1622.57	575.28	7.60	1.13	0.34	0.08	450.92	27.37	16.21	0.73	1.41	0.11
Pityrocarpa moniliformis	4598.48	1443.48	7.37	2.19	0.25	0.03	449.13	32.91	17.44	2.96	1.50	0.03
Average	2551.12	819.14	9.77	3.97	0.29	0.05	400.08	35.37	20.22	7.69	1.49	0.08
Minimum	971.22	304.85	5.10	1.13	0.17	0.01	336.10	18.88	13.64	0.73	1.41	0.03
Maximum	4598.48	1443.48	19.43	9.58	0.36	0.10	450.92	57.00	36.94	22.53	1.56	0.19

b)

Regenerating	LA (mm^2)		SLA (m^2/kg)		LTH (mm)		LDMC (mg/g)		LS (mg /cm^2)		LCC (g gluc DW^{-1})	
Species	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev	Avg	StDev
Bauhinia acuruana	580.00	0.00	11.21	0.00	0.22	0.00	407.48	0.00	12.97	0.00	1.87	0.00
Cnidoscolus bahianus	4381.15	1022.83	2.94	0.69	0.29	0.04	290.78	22.17	88.08	19.58	1.48	0.03
Croton argyrophylloides	992.38	348.82	19.40	3.16	0.15	0.02	319.66	29.99	11.34	2.04	1.59	0.15
Erythroxylum revolutum	1382.93	0.00	15.72	0.00	0.17	0.00	363.64	0.00	11.14	0.00	1.46	0.00
Pityrocarpa moniliformis	1137.86	733.15	15.02	2.02	0.16	0.02	300.60	76.99	16.93	5.31	1.51	0.04
Average	1694.87	420.96	12.86	1.17	0.20	0.02	336.43	25.83	28.09	5.39	1.58	0.05
Minimum	580.00	0.00	2.94	0.00	0.15	0.00	290.78	0.00	11.14	0.00	1.46	0.00
Maximum	4381.15	1022.83	19.40	3.16	0.29	0.04	407.48	76.99	88.08	19.58	1.87	0.15

5 CONSIDERAÇÕES FINAIS

Diante do exposto, contribuímos com mais um tijolo no grande campo da ecologia. Contudo, ainda existem diversas lacunas a serem preenchidas em relação aos temas abordados. Por fim, sugerimos que estudos futuros foquem em investigações relacionadas à: capacidade de persistência de diferentes espécies ainda não exploradas, velocidade de regeneração de plântulas oriundas de semente vs rebrotas e rametas, como diferentes mecanismos de regeneração afetam a biodiversidade no processo de regeneração e suas possíveis interações (i.e., facilitação, competição), se a disponibilidade de NSC antes de perturbações indicam um possível sucesso em espécies que sabidamente persistem, como se dá o compartilhamento de nutrientes entre rametas de espécies lenhosas conectados, quais as implicações da redução de regeneração de sementes na recuperação e provisão de serviços ecossistêmicos na Caatinga.

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ANEXO A – Regras para submissão na revista Applied Vegetation Science

APPLIED VEGETATION SCIENCE
AUTHOR GUIDELINES

Sections

1. Aims and Scope
2. Manuscript Categories
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10. 1. AIMS AND SCOPE

Applied Vegetation Science publishes studies of plant communities that are relevant for human interaction with vegetation, including topics such as conservation, management and restoration of plant communities and natural habitats, effects of global change on plant communities, and the planning of semi-natural and urban landscapes. The journal also publishes vegetation classification and survey studies of international interest. Papers on plant communities which do not fit to this scope (do not have an applied aspect and are not vegetation classification or survey) should be directed to our associate journal, the *Journal of Vegetation Science*. The journal does not publish articles on the ecology of a single species, except for studies framed in the community context, especially of species that play a key role in structuring plant communities (e.g. stand dominants). Papers based on remote sensing and papers on ecosystem functions of vegetation can be considered if they focus on species or functional diversity or composition of plant communities.

2. MANUSCRIPT CATEGORIES

Article Types

Research Article. This category includes description of vegetation patterns or processes, experiment, simulation, theory, description of a new method, or any combination of those. The length of these papers should be up to 8000 words, including References but excluding electronic Supplementary Information. The submission of longer papers can be accepted on the basis of sound explanation given in the cover letter. Shorter papers can be managed and published faster. Online supplementary files may be used for less essential text, tables or figures.

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Acknowledgements

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- Wilson, J.B., Sykes, M.T. & Peet, R.K. (1995) Time and space in the community structure of a species-rich limestone grassland. *Applied Vegetation Science*, 6, 729–740. https://doi.org/10.2307/3236444

Book

- van der Maarel, E. & Franklin, J. (Eds) (2013) *Vegetation Ecology*, 2nd edition. Chichester: Wiley-Blackwell.

Book chapter

- Peet, R.K. (2000) Forests and meadows of the Rocky Mountains. In: Barbour, M.G. & Billings, W.D. (Eds), *North American Terrestrial Vegetation*, 2nd edition. Cambridge: Cambridge University Press, pp. 75–122.

Internet document

- Oksanen, J., Blanchet F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2017) *Vegan: community ecology package. Version 2.4-5*. Available at https://cran.r-project.org/web/packages/vegan/index.html [Accessed 21 January 2018]
- Euro+Med (2019) *Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity*. Available at http://ww2.bgbm.org/EuroPlusMed/query.asp [Accessed 31 March 2019]

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