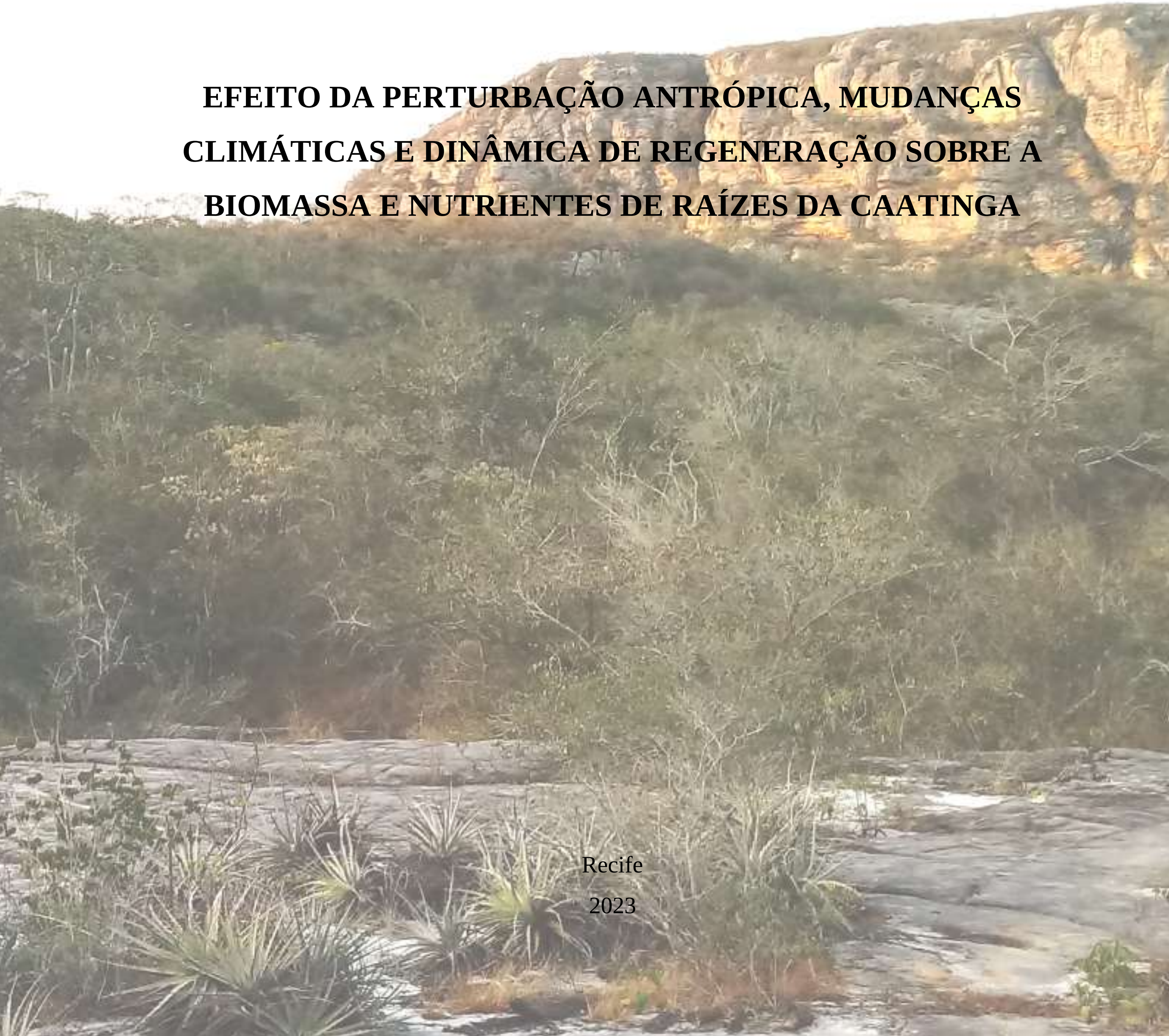
UNIVERSIDADE FEDERAL DE PERNAMBUCO
CENTRO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA VEGETAL

ARTUR GONÇALVES DE SOUZA MENEZES



EFEITO DA PERTURBAÇÃO ANTRÓPICA, MUDANÇAS CLIMÁTICAS E DINÂMICA DE REGENERAÇÃO SOBRE A BIOMASSA E NUTRIENTES DE RAÍZES DA CAATINGA

Recife
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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Biologia Vegetal da Universidade Federal de Pernambuco, como requisito para a conclusão do curso de Doutorado em Biologia Vegetal. Area de concentração Ecologia e Conservação.

Orientador: Marcelo Tabarelli
Coorientadora: Silvia Rafaela Machado Lins

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Aprovado em: 27/02/2023.

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Dedico esta tese à minha amada avó, Carmelita Maria de Souza que nos deixou no dia de minha qualificação, 17 de julho de 2022. Também dedico aos meus familiares, que acompanharam minha batalha.

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“A grandeza das ações humanas é proporcional à inspiração que as produz. Feliz é a

quele que traz dentro de si um Deus, um ideal de beleza a que obedece: ideal de arte, ideal de ciência, ideal de pátria, ideal de virtudes evangélicas. São essas as fontes vivas dos grandes pensamentos e das grandes ações. Todas elas refletem a luz do infinito.”

Louis Pasteur

RESUMO

A redução de biomassa e nutrientes, como carbono (C), nitrogênio (N) e fósforo (P), em florestas tropicais sazonalmente secas (FTSS) agravam mudanças climáticas. A biomassa vegetal é um importante indicador de efeitos de impactos antropogênicos. Apesar de ser pouco estudada, a biomassa de raízes é representativa em FTSS, onde há investimento no incremento de raízes como estratégia de sobrevivência. Contudo, esses sumidouros de C, que também acumulam e nutrientes importantes, têm sido afetados pelas perturbações antrópicas. Então buscamos entender como perturbação antrópica crônica, regeneração natural e redução da precipitação afetam a biomassa vegetal abaixo do solo e o seu conteúdo de nutrientes na Caatinga. Assim, o primeiro objetivo deste estudo é compreender como mudanças climáticas e perturbações antrópicas que não causam perda de habitat influenciam biomassa e nutrientes das raízes, enquanto no segundo capítulo entender como áreas em regeneração natural e que sofreram corte raso da vegetação recupera a biomassa e os nutrientes das raízes. O Parque Nacional do Catimbau, foi a área da Caatinga no Brasil selecionada para o estudo. No 1° capítulo, selecionei 11 parcelas (0,1 ha) de floresta madura e no 2°, 12 parcelas em uma cronossequência de regeneração natural da floresta (entre 10 a 76 anos). Em cada uma parcela foram escavadas três trincheiras (0,7 x 0,7 x 1,0 m). As amostras de solo foram peneiradas, secas, separadas em 3 categorias de raízes (finas, medianas e grossas), pesadas e por fim, foram analisadas as concentrações de nutrientes (N, C e P). O primeiro capítulo apontou biomassa de raízes 14.6±9.2 Mg ha-1. A razão raiz/parte aérea (R/PA) foi de 0.28±0.16. A biomassa de raízes variou significativamente entre as parcelas ($p < 0,05$) e a distribuição radicular variou por classe de tamanho e profundidade do solo, predominando na superfície. A concentração de nutrientes para raízes finas (g kg-1) foi 17.12±3.9 (N), 373.9±71.9 (C) e 0.38±0.08 (P) e para raízes medianas/grossas 14.61±6.4 (N), 358.87±98.5 (C) e 0.29±0.1 (P). Estoques de nutrientes não variaram. A precipitação e a profundidade do solo afetaram mais a biomassa das raízes. Para floresta secundária (2° capítulo), a biomassa abaixo do solo foi de 8.34±4.7 Mg ha-1, e R/PA 0.08±0.08. A concentração de nutrientes (g kg-1) foi 12.49±3.7 (N), 333.61±68 (C) e 0.34±0.06 (P) em raízes finas e 11.71±2.6 (N), 307.43±75 (C) e 0.4±0.28 (P) em raízes medianas e grossas. Houve variação entre os povoamentos de floresta seca em regeneração em relação às raízes de pequeno porte ($p < 0,05$). A biomassa radicular não diferiu significativamente para as classes de tamanho de raízes e predominou nas camadas superficiais do solo (50 cm). De modo geral, efeitos de PAC, precipitação e profundidade do solo foram percebidos para a biomassa de pelo menos uma das categorias de raízes e biomassa total enquanto os nutrientes N e C responderam aos dois primeiros preditores (PAC e precipitação pluviométrica). A degradação florestal e a alteração dos regimes pluviométricos, devem interferir diretamente na capacidade da Caatinga em sequestrar C e manter sua biomassa e nutrientes essenciais.

Palavras-chave: Biomassa abaixo do solo; Florestas tropicais sazonalmente secas; Estoques de nutrientes; Regeneração natural; Semiárido brasileiro.

ABSTRACT

The reduction of biomass and nutrients, such as carbon (C), nitrogen (N) and phosphorus (P), in seasonally dry tropical forests (FTSS) exacerbate climate change. Plant biomass is an important indicator of the effects of anthropogenic impacts. Despite being little studied, root biomass is representative in FTSS, where there is investment in root growth as a survival strategy. However, these C sinks, which also accumulate important nutrients, have been affected by anthropic disturbances. We then sought to understand how chronic anthropic disturbance, natural regeneration and reduced precipitation affect belowground plant biomass and nutrient content in the Caatinga. Thus, the first objective of this study is to understand how climate change and anthropic disturbances that do not cause habitat loss influence biomass and root nutrients, while in the second chapter to understand how areas undergoing natural regeneration and that have undergone clear cutting of vegetation recover biomass and root nutrients. The Catimbau National Park was the Caatinga area in Brazil selected for the study. In the 1st chapter, I selected 11 plots (0.1 ha) of mature forest and in the 2nd, 12 plots in a chronosequence of natural forest regeneration (10 to76 years). In each plot, three trenches (0.7 x 0.7 x 1.0 m) were excavated. The soil samples were sieved, dried, separated into 3 categories of roots (fine, medium and thick), weighed and finally, nutrient concentrations (N, C and P) were analyzed. The first chapter showed root biomass 14.6±9.2 Mg ha-1. The root/shoot ratio (R/S) was 0.28±0.16. Root biomass varied significantly between plots ($p < 0.05$) and root distribution varied by size class and soil depth, predominating at the surface. Nutrient concentration for fine roots (g kg-1) was 17.12±3.9 (N), 373.9±71.9 (C) and 0.38±0.08 (P) and for medium/thick roots 14.61±6.4 (N), 358.87±98.5 (C) and 0.29±0.1 (P). Nutrient stocks did not vary. Precipitation and soil depth affected root biomass the most. For secondary forest (2nd chapter), belowground biomass was 8.34±4.7 Mg ha-1, and R/S 0.08±0.08. Nutrient concentration (g kg-1) was 12.49±3.7 (N), 333.61±68 (C) and 0.34±0.06 (P) in fine roots and 11.71±2.6 (N), 307.43±75 (C) and 0.4 ±0.28 (P) in medium and thick roots. There was variation between dry forest stands in relation to small roots ($p < 0.05$). Root biomass did not differ significantly for root size classes and predominated in intermediate soil stages (50 cm). In general, effects of PAC, precipitation and soil depth were perceived for the biomass of at least one of the root categories and total biomass while the nutrients N and C responded to the first two predictors (PAC and rainfall). Forest degradation and changes in rainfall regimes should directly interfere with the Caatinga's ability to sequester C and maintain its biomass and essential nutrients.

Keywords: Belowground biomass; Seasonally tropical dry forests; Nutrient stocks; Natural regeneration; Brazilian semiarid.

SUMÁRIO

1 INTRODUÇÃO

É bem entendido que as perturbações antrópicas e as mudanças climáticas afetam a biota, e, consequentemente, os ecossistemas e os serviços providos por estes (GARDNER et al., 2009). Por sua vez, essas alterações em ecossistemas estão diretamente ligadas à perda de biomassa vegetal que causa a emissão de carbono (C) para a atmosfera (FEARNSIDE, 2006) e, dessa forma, os estoques de C na vegetação são uma das variáveis que proporcionam o entendimento das mudanças ecossistêmicas, pois a vegetação recobre um terço da superfície terrestre e potencialmente estoca mais de 80% do C orgânico global (HOUGHTON, 1994). Alterações desse tipo nas florestas promovem o empobrecimento do solo com o deplecionamento de nutrientes, afetando desde as atividades agrícolas até a regeneração da vegetação.

A perda de biomassa vegetal pode ser decorrente das perturbações antrópicas agudas, como a queima da vegetação de uma área para a implantação da agricultura ou de pastagens (BARLOW et al., 2016), ou ainda por perturbações crônicas, como a retirada de pequenas porções de madeira e frutos para o uso como fonte de energia e alimento, respectivamente (SINGH, 1998). Assim, em florestas sob o uso antrópico contínuo, a capacidade de aquisição e estocagem de recursos pelos indivíduos vegetais determina seu sucesso competitivo (ERKTAN; MCCORMACK; ROUMET, 2018) e interfere, positiva ou negativamente, na dinâmica da comunidade, tanto em áreas conservadas quanto nas áreas perturbadas. Quando submetidas à perturbação, por exemplo por agricultura, as florestas tropicais perdem em riqueza de espécies e consequentemente, sua capacidade em prover serviços ecossistêmicos como a estocagem de biomassa e nutrientes.

Quando se observam as florestas secundárias com idades próximas a 40 e 50 anos idade, por sua vez, são capazes de suportar uma riqueza de espécies arbóreas semelhantes às de florestas antigas, mas séculos podem ser necessários no caso de biomassa acima do solo (ROBIN L. CHAZDON, 2014). De forma geral, a recuperação dos atributos florestais responde a padrões adicionais, como a perturbação reincidente durante o processo de regeneração. Isso pode aumentar ainda mais o tempo hábil para retorno das condições normais de floresta madura, impondo até mesmo a incapacidade em regeneração natural (aquela sem assistência humana).

Quando observamos a disposição dos nutrientes, o os estoque de C na biomassa vem sendo claramente alterados com o aumento das perturbações antrópicas, que afetam diretamente o incremento, por exemplo, da biomassa abaixo do solo, como a biomassa de raízes

(FREITAS; BARROSO; CARNEIRO, 2008; JACKSON et al., 1996), responsável por estocar mais de 3/4 do C do solo (FREITAS; BARROSO; CARNEIRO, 2008). A despeito da importância da estocagem de biomassa em florestas, os estudos que investigam padrões e processos ecológicos relacionados à biomassa de raízes são escassos em florestas tropicais sazonalmente secas, o que aumenta a necessidade de buscar entender como é a contribuição destes ecossistemas para os estoques de biomassa e nutrientes do solo em um cenário global.

Em ecossistemas tropicais secos, as perturbações antrópicas são intensas, (HIROTA et al., 2011) e esse é o contexto encontrado no maior ecossistema sazonalmente seco da América do Sul, a floresta seca brasileira chamada de Caatinga, que vem sendo transformada em um mosaico de florestas em regeneração, devido ao uso intenso de seus recursos naturais (TABARELLI et al., 2017). Como a Caatinga é marcada pelo sistema agrícola tradicional de corte-e-queima há séculos, torna-se importante a realização de estudos que ajudem a elucidar as mudanças ecossistêmicas provocada por esse uso da terra. Por fim, faz-se necessária a atenção maior ao manejo destes ecossistemas, e a viabilização de políticas de proteção e regulação do extrativismo para retardarem a perda dos serviços ecossistêmicos importantes providos pela Caatinga, bem como o uso sustentável de recursos naturais.

2 REFERENCIAL TEÓRICO

2.1 A perturbação antrópica em florestas tropicais

Tratar das perturbações ocorrentes nos ambientes naturais não é uma tarefa trivial, visto que a dinâmica ocorrente na natureza é intensa e complexa. Quando há a queda causal de uma árvore por exemplo, abre-se uma clareira que, dentre muitas outras, pode proporcionar o efeito de borda. Outro exemplo é a erupção vulcânica que pode gerar perda extensa de hábitat. Esse tipo de perturbação é costumeiramente chamado de natural (CHAZDON, 2012) que causa em pequena ou grande escala alteração de parâmetros de organização do ecossistema, gerando a colonização e proliferação de espécies primárias e diminuição da riqueza e diversidade local. Contudo, o efeito das interferências humanas sobre os ecossistemas, chamadas de perturbações antrópicas (SINGH, 1998), são capazes de modificar drasticamente os padrões de biodiversidade, além de enfraquecer as relações específicas ao romper os ciclos biológicos (CHAZDON, 2003). Essas perturbações também podem variar tanto em intensidade quanto em frequência sendo classificas como agudas e crônicas (SINGH, 1998), que podem alterar de forma distinta as interações e funções biológicas, além de serviços ecossistêmicos.

As perturbações antrópicas a serem classificadas como aguda, geram perda rápida e considerável de biomassa e habitat (BARLOW et al., 2016). Tais perturbações são estudadas há mais tempo, e por isso tem conceitos mais bem definidos causando danos graves aos serviços ecossistêmicos providos. É um exemplo comum a eliminação de floresta para implantação de sistemas agropastoris. O segundo tipo de perturbação antrópica é definido como crônica. Os efeitos que causam ao ecossistema provém de alterações sutis, onde por exemplo, há a remoção da biomassa de forma gradativa que alteram gradativamente estes ecossistemas (SINGH, 1998). Podemos relacionar o corte seletivo de madeira, a caça, o sobrepastejo por animais domésticos e a introdução de espécies exóticas como perturbações crônicas na escala de paisagem (BARLOW et al., 2016; MARTORELL; PETERS, 2005). Em contraste com a perturbação aguda podemos assumir que a crônica frequente atua em pequena escala espacial (RIBEIRO-NETO et al., 2016) muitas vezes sequer é detectado através de método tradicionais, como por sensoriamento remoto (LAURANCE; PERES, 2006) e muito certamente não cessará.

As florestas tropicais, que possuem altas riqueza de espécies, biomassa e produtividade (JORDAN, 1983), vêm se transformando em sistemas agrícolas limitando os habitats e ameaçando a biodiversidade local (LAURANCE et al., 2002). Por isso, os ecossistemas tropicais são tidos como os mais vulneráveis à perda da diversidade biológica (LAURANCE et al., 2011), à redução significativa de biomassa e a desbalanço nos fluxo e estoques de nutrientes (URQUIZA-HAAS; DOLMAN; PERES, 2007). Este cenário é agravado onde a exploração dos recursos naturais é mais intensa, principalmente por haver a concentração de grandes populações humanas (HIROTA et al., 2011). Esta "sobrexploração" é bastante comum em regiões socioeconomicamente mais pobres, com maior dependência de recursos naturais para a subsistência que tipicamente estão localizadas em áreas tidas como florestas tropicais sazonalmente secas (FTSS) (SINGH, 1998). As FTSS são muito ameaçadas e lidam constantemente com perdas de diversidade taxonômica e funcional devido perturbação antrópica crônica (RITO et al., 2017).

2.1.1 Regeneração natural em florestas secas

É um consenso que as florestas tropicais sazonalmente secas (em diante florestas secas) são amplamente distribuídas no globo, enquanto são áreas muito afetadas pelas perturbações em larga escala, como a imposição de agricultura e pecuária (BECKNELL; KISSING KUCEK; POWERS, 2012). O estudo da Organização das Nações Unidas para Agricultura e Alimentação apontaram que no ano até 2010 pelo menos 57% das florestas do mundo já haviam sido convertidas em florestas secundárias (FAO, 2010). Dados alarmantes semelhantes a este reforçam a ideia de que os ecossistemas florestais caminham para uma perda sem precedentes de serviços ecossistêmicos essenciais à subsistência humana. Assim, esses ecossistemas são tidos como mosaicos de florestas maduras e secundárias (i.e. Caatinga *sensu* TABARELLI et al., 2017).

Após o cenário de degradação, o ecossistema entra em processo de regeneração natural (CHAZDON, 2012). Porém, como explica Chazdon (2012), as florestas tropicais estão muito suscetíveis às perturbações rotineiras (como as de ordem natural, i.e. quedas de arvores), sendo assim, comum observar-se a variação de trajetórias de sucessão secundária. Entende-se que a regeneração florestal é um processo de sucessão secundária nas comunidades e nos ecossistemas, em uma área que possuía floresta e foi desmatada e segue uma progressão demarcada por estágios onde florestas apresentam um crescimento gradual da riqueza de espécies e de complexidade estrutural e funcional (CHAZDON, 2012).

Geralmente a regeneração natural é lenta e inconstante, porém, vários fatores podem fazer variar os períodos de sucessão florestal, tais como disponibilidade de água e nutrientes, condições a que foram submetidos os solos durante os ciclos de agricultura e/ou pastejo além da qualidade dos bancos de semente e capacidade de rebrota das espécies (CHAZDON, 2012; CHAZDON et al., 2006). Estudos de Lebrija-Trejos et al. (2011) apontam que fatores abióticos como a sazonalidade hídrica e disponibilidade de luz são decisivos na regeneração de florestas secas. A trajetória de recuperação dos parâmetros ecológicos nem sempre é contínuo, pois enfrenta crescentes níveis de perturbações humanos, que apesar de não acarretar perda e fragmentação de habitat, apresentam impactos nocivos à biota (LAURANCE; PERES, 2006; SINGH, 1998).

Por isso deve-se ter atenção com os ecossistemas que, além do período de agricultura, sofrem rotineiramente com prevalência de distúrbios antrópicos, pois estes podem atrasar ainda mais a recuperação das áreas degradadas. Quando as florestas sucessionais amadurecem, esses novos ecossistemas apresentam uma composição de espécies diferentes com riqueza semelhante, além de um grande potencial em sequestrar C do as florestas primárias (MARÍN-SPIOTTA; OSTERTAG; SILVER, 2007). Porem, esta capacidade em sequestrar carbono certamente se deve a alta taxa de produtividade primária, pois é uma floresta em crescimento. Mas, isso não significa que haverá captação de C emitido por queima de combustíveis fosseis, ora estas florestas secundárias são fruto de emissão de C através do desmatamento.

2.1.2 Caatinga: floresta seca em um cenário de regeneração após perturbações antrópicas

A Caatinga é um bioma exclusivamente brasileiro caracterizando-se de clima semiárido, com vegetação de arbustos e árvores espinhosas, além de uma grande biodiversidade de fauna e flora. Este bioma é fundamental para a região Nordeste do país, não só por sua importância ecológica, mas também por ser o lar de diversas comunidades tradicionais, que dependem dos recursos naturais da caatinga para sua sobrevivência (TABARELLI et al., 2017). Além do mais, representa as florestas tropicais sazonalmente secas (STDF) com grande importância ecológica, mas negligenciada com relação à conservação (LEAL et al., 2005; SZYJA et al., 2019; TABARELLI et al., 2017).

Esta é uma região rica em espécies endêmicas com uma população humana extremamente dependente de recursos naturais para a sobrevivência (SILVA; LEAL; TABARELLI, 2018). Além disso, é um importante corredor ecológico, que liga a Floresta Amazônica ao Cerrado e à Mata Atlântica. A vegetação predominante é majoritariamente formada por floresta seca constituída de um mosaico de caatingas arbóreas e arbustivas, destacando-se os grupos vegetais Cactaceae, Euphorbiaceae e Fabaceae (RITO et al., 2017).

Nesta floresta, a precipitação pluviométrica média anual chega a variar entre 500 e 1400 mm e suas chuvas são concentradas entre os meses de março e julho (SAMPAIO, 1995). A pluviosidade é um fator crítico para a sobrevivência da fauna e flora da Caatinga. As chuvas, que são altamente variáveis e imprevisíveis, podem apresentar períodos de seca prolongados que chegam a durar anos. É bem sabido que há uma tendência de aumento nas temperaturas e redução na pluviosidade da região nos últimos anos, o que pode afetar a distribuição e sobrevivência das espécies (OYAMA; NOBRE, 2004). Além disso é importante monitorar a pluviosidade na região para entender suas variações e impactos na vegetação local. Observa-se que as mudanças climáticas podem afetar o regime de chuvas da região, com possíveis efeitos na produtividade primária (SALIMON; ANDERSON, 2017), o que afeta diretamente a agricultura e a biodiversidade. Essas informações enfatizam a necessidade de se entender melhor os padrões de pluviosidade na Caatinga e aprimorar as medidas de conservação e manejo do ecossistema.

Sua área ocupa cerca de 11% do território brasileiro, estando presente em oito estados do Nordeste e parte de Minas Gerais (ANDRADE et al., 2005). O bioma possui uma vegetação resistente e adaptada às condições de aridez, o que o torna único e valioso em termos de conservação da biodiversidade. Além disso, é responsável por fornecer diversos serviços ecossistêmicos, como a regulação do clima e do ciclo hidrológico, a produção de água, o sequestro de carbono e a manutenção da fertilidade do solo (TABARELLI et al., 2018). Esta é uma das florestas mais importantes do país em termos de provisão de água e regulação do clima, além de contribuir significativamente para a produção de alimentos e outros recursos naturais.

No entanto, a Caatinga enfrenta diversas ameaças, principalmente devido à ação humana. O desmatamento, a conversão da vegetação em áreas de pastagem e agricultura, a exploração predatória dos recursos naturais e as mudanças climáticas são algumas das principais ameaças enfrentadas pela Caatinga (TABARELLI et al., 2017). Estas atividades têm levado a perda da biodiversidade e à desertificação da região. Uma das principais causas do desmatamento é a conversão da vegetação em áreas de pastagem e agricultura, além da exploração predatória dos recursos naturais, como a caça e a pesca (TABARELLI et al., 2018).

Assim como outras florestas tropicais secas, vem sendo rapidamente transformada em um conjunto de paisagens antrópicas, composta por mosaicos formados por áreas intensamente agrícolas, roças abandonadas, florestas em regeneração e algumas poucas florestas maduras, respondendo à agricultura itinerante e à criação de rebanhos que normalmente são alimentados com vegetação nativa (TABARELLI et al., 2017). Neste cenário ecológico emergente e dinâmico, espera-se uma relação complexa entre os humanos e a dinâmica de regeneração da Caatinga (MENEZES, 2018). Torna-se fundamental que sejam adotadas políticas públicas que promovam a conservação da Caatinga, bem como o uso sustentável de seus recursos naturais. Pois, é um patrimônio natural do Brasil e do mundo e sua conservação é essencial para a manutenção da biodiversidade e para o bem-estar humano (SILVA; LEAL; TABARELLI, 2018).

2.2 Produtividade primária bruta, líquida e as mudanças climáticas

A produtividade primária pode ser definida basicamente como sendo a taxa de produção de biomassa por organismos fotossintetizantes em uma área, podendo ser representada em valores de unidade de energia (i.e. $J\ m^{-2}$), matéria orgânica (i.e. $kg\ ha^{-1}\ ano^{-1}$) e carbono (i.e. $g\ C\ m^{-1}\ ano^{-1}$) (BEGON; TOWNSEND; HARPER, 2007). Mas, a produtividade primária requer bem mais do que a fotossíntese por si só, ela necessita dos processos fisiológicos que precedem o processo fotossintético, como a incorporação de nutrientes inorgânicos nos compostos orgânicos do protoplasma celular (LIETH, 1975a). Além de incremento de biomassa, os produtos da fotossíntese são a base fundamental do fluxo de energia entre os organismos vivos e o carbono (C) assimilado que compõe metade da matéria orgânica terrestre (CHAPIN; MATSON; VITOUSEK, 2011).

Portanto, a produtividade primária, energia real ligada à matéria orgânica, é tida como o produto da fotossíntese (LIETH, 1975a). Sabendo disso, seguramente podemos associar as alterações na produtividade primária às mudanças mais gerais no globo como as climáticas que atraem mais atenção (RUNNING et al., 2000). Seguindo este raciocínio acerca das mudanças no clima, segundo dados do IPCC (2001), a quantidade de C concentrado na atmosfera, na forma de CO_2, aumentou cerca de 31%. Isso causou o aumento significativo da temperatura do ar e dos níveis do mar (RAHMSTORF et al., 2007), que, por sua vez, afetam diretamente os ecossistemas terrestres (LIETH, 1975a).

A produtividade primária ainda é dividida em duas outras específicas, a produtividade primária *bruta* (PPB) e *líquida* (PPL). Ambas são importantes para diferentes abordagens ecológicas teórico-práticas, onde as suas definições básicas são: quantidade total de biomassa produzida pela fotossíntese (PPB) e a taxa de biomassa nova produzida e estocada pelos vegetais (PPL) (BEGON; TOWNSEND; HARPER, 2007). A PPB terrestre é tida como o maior fluxo de C do planeta e estimula várias funções do ecossistema como o metabolismo de crescimento dos organismos (BEER et al., 2010). Esse C quando acumulado em biomassa fica disponibilizado para os demais organismos heterótrofos, gerando o fluxo energético dentro dos ecossistemas (SCHOWALTER, 2011). Quando analisada junto à taxa de respiração dos organismos, a taxa bruta de produtividade primária é um dos principais controladores do equilíbrio das trocas de CO_2 entre a terra e a atmosfera (BEER et al., 2010). Isso acentua-se quando fica comprovado que a atividade dos herbívoros depende intimamente das taxas de produtividade primária (MCNAUGHTON et al., 1989).

As florestas tropicais e savanas representam 60% da produtividade primária bruta no planeta (BEER et al., 2010), portanto, com as maiores taxas de PPL globais, chegando à um terço do total (MALHI; DOUGHTY; GALBRAITH, 2011). Dessa forma, esses ecossistemas são de grande importância para a manutenção da vida terrestre, amortização do aquecimento global e desaceleração do efeito estufa. Em termos gerais a produtividade primária está ligada ao bem-estar da humanidade (LIETH, 1975b), e pode balancear parcialmente as emissões de gás carbônico (CO_2) antrópico (BEER et al., 2010).

As mudanças climáticas são as principais pautas científicas da atualidade. Isso se dá pelo fato de que as perdas de grandes porções de florestas e a poluição ambiental alarmam para futuros cenários críticos à existência humana. Estima-se que desde a revolução industrial se lançou na atmosfera mais de 406 Pg C, sinalizando um aumento em torno de 30% da concentração total (LAL, 2004). Lal (2004) ainda fraciona que deste total, 66 % das emissões tiveram origem da queima de combustíveis fósseis e o restante das mudanças de uso do solo. Esperando-se um pior cenário, estipula-se um aumento expressivo da concentração de C na atmosfera até 2200 (figura 3) através de emissões antropogênicas (SCHIMEL et al., 1995).

De forma severa, desde o século XX, alterações no meio ambiente que afetam a capacidade ecossistêmica de prover serviços inerentes à subsistência humana são observadas no planeta Terra (LIETH; WHITTAKER, 1975). Em 2003, por exemplo, observou-se que uma onda de calor causou, para Europa, a redução em 16 gCm^{-2} $mês^{-1}$ (figura 1), equivalente à 30%

da produtividade primária líquida, influenciando diretamente o sequestro de C que vinha acontecendo nos quatro anos antecedentes (CIAIS et al., 2005). Isto pode justificar o aumento da concentração de C na atmosfera que vinha sendo observado (SCHIMEL et al., 1995). Estes resultados podem nortear quanto aos efeitos a longo prazo do aquecimento global, onde as florestas podem mudar de sumidouros para fontes de C (DUFRESNE et al., 2002).

Figura 1. Variação do clima e temperatura observados na França (Hesse) e Itália (San Rossore), em duas florestas, entre os anos de 2002 e 2003. Em **a** observa-se os campos climáticos, enquanto em **b** os fluxos de CO_2 no ecossistema ao longo dos meses. As variações diárias foram excluídas pelo autor com um *fiveday running average*, enquanto os valores de precipitação são as médias mensais. Dados para 2002 em preto e 2003 em azul.

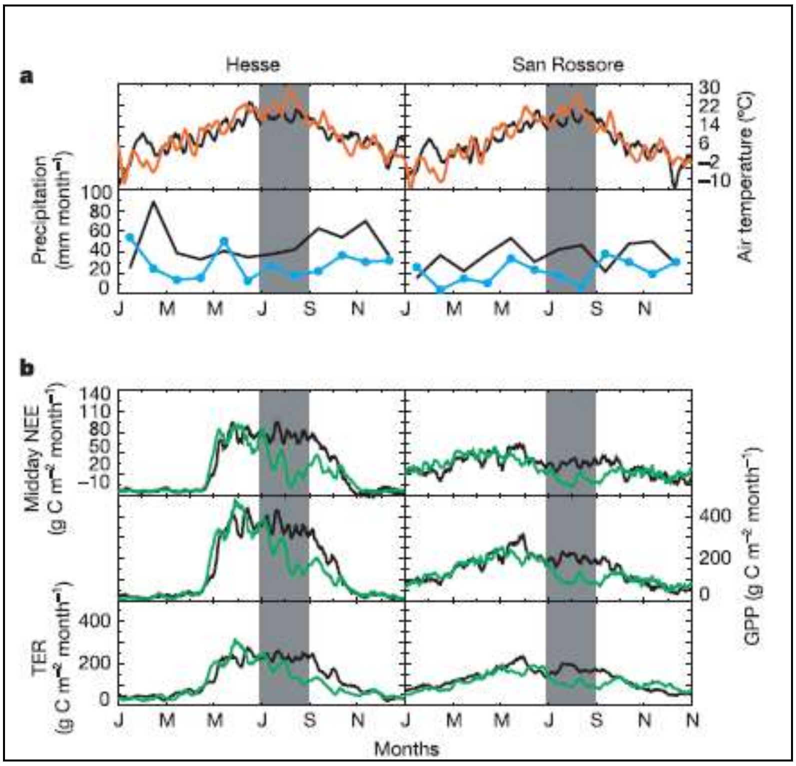

Ilustração pertencente a Ciais et al. (2005).

2.2.1 Biomassa de raízes em florestas tropicais sazonalmente secas

Vários autores tentam classificar a biomassa, mas ainda não há um consenso sobre sua real definição. Há uma definição de que a biomassa é a junção da massa seca vegetal (fitomassa) com a dos animais (zoomassa) (BRIGAGÃO, 1992). Por sua vez, há outra definição que considera a massa seca vegetal como representativa de biomassa (MARTINELLI et al., 1994). Mas a representatividade da fitomassa dentro da biomassa se dá pelo fato da vegetação ser responsável por estocar grande porção do C orgânico do planeta (HOUGHTON, 1994), e por isso há um maior interesse em estimar a biomassa das florestas (RATUCHNE et al., 2016). Em termos globais, estudos estimaram que até o final do século 20 havia mais de 290 Pg de biomassa de raízes no planeta, sendo 31 Pg só em florestas tropicais sazonais (JACKSON; MOONEY; SCHULZE, 1997). Estudos apontam que a biomassa radicular é subestimada em 60% e que um pool global de raízes entre 520 e 540 Pg é aceitável, contendo cerca de 268 Pg de C (ROBINSON, 2007). Para florestas secas Robinson (2007) sugeriu que 123 Pg de C estão somente nas florestas tropicais em geral, por isso assumimos o papel de FTSS em grande relevância no pool global de biomassa e C. Quantificar dos estoques de biomassa em FTSS madura e em regeneração destaca-se, pois envolve a construção de orçamentos globais de C e proporciona a elaboração de políticas locais e ferramentas de gestão projetadas para o sequestro e armazenamento de C.

Muitos estudos estimam a biomassa acima do solo da vegetação, pois é mais facilmente amostrada. Em contrapartida, a biomassa abaixo do solo é mais críptica, o que prejudica a coleta de dados. Historicamente busca-se compreender a biomassa radicular há mais de 280 anos (JACKSON et al., 1996), desenvolvendo-se técnicas para sua difícil amostragem como a escavação para obter a profundidade máxima das raízes (JACKSON et al., 1996; PINHEIRO; COSTA; DE ARAÚJO, 2013). Adicionalmente, técnicas para avaliar o crescimento de raízes (REIS et al., 2006) ou ainda técnicas para estimar a biomassa de raízes por monólitos removidos do solo (ALBUQUERQUE et al., 2015) têm sido desenvolvidas por pesquisadores.

As raízes são importantes pois além de fixarem-na no solo, são responsáveis pela absorção de água e nutrientes para a planta (FREITAS; BARROSO; CARNEIRO, 2008; RATUCHNE et al., 2016). A biomassa radicular de uma floresta, por sua vez, pode representar diferentes proporções em relação à biomassa aérea, sendo influenciada principalmente por fatores climáticos (i.e. regime de chuvas) e antropogênicos (i.e. perturbação) (RATUCHNE et al., 2016). O estudo local em savana brasileira (cerrado) evidencia que diferentes fitofisionomias demonstram que a razão da biomassa vegetal da parte subterrânea e parte aérea viva pode variar, sendo menor em áreas mais abertas e maior em áreas de vegetação mais densa, assim, é responsável por estocar até 76% da biomassa vegetal local (CASTRO; KAUFFMAN, 1998). As florestas tropicais em si apresentam grandes concentrações de biomassa, chegando à 5 kg m^{-2}, sendo maior que outros biomas de vegetação menos densa (i.e. Tundra, desertos e áreas agrícolas) chegando à 1,5 kg m^{-2} (JACKSON et al., 1996). Jackson et al. (1996) ainda evidencia que de modo geral nos biomas menos densos há uma maior razão biomassa de raiz/parte aérea (variando de 4 a 7) do que nas áreas florestais tropicais e agrícolas (0,1 a 0,5). Em buscas, não se encontra de forma clara e sintética, muitos dados sobre os estoques de biomassa de raízes globais nas STDF. Temos exemplos, como os descritos por Meena et al. (2019) em Delhi, Índia que apresenta valores médios em torno de 28 Mg ha^{-1}, e por Jaramillo et al. (2003) em Chamela, México com um valor mais baixo, em torno de 17 Mg ha^{-1}.

Por fim, o maior crescimento da biomassa de raízes se dá nos estágios iniciais do desenvolvimento vegetativo da planta em contrapartida ao período de desenvolvimento reprodutivo (HEAD, 2012). Demonstrando-se um agente determinante para o sucesso ecológico do vegetal (LAUGHLIN, 2014). As raízes, ainda, interagem com outros organismos (principalmente micróbios, fungos e outras plantas) que são responsáveis pela aquisição e armazenamento dos recursos (ERKTAN; MCCORMACK; ROUMET, 2018). Então, fatores como redução de chuvas e o corte e queima diminui drasticamente a biomassa abaixo do solo, colocando em risco toda sua interação com o ecossistema (CASTELLANOS et al., 2001)

2.3 Ciclagem de nutrientes em florestas tropicais

As florestas tropicais são tidas como as mais ricas em nutrientes (VITOUSEK; SANFORD, 1986). Por isso, estudos acerca da concentração de nutrientes na biomassa, bem como a sua ciclagem têm recebido maior atenção nos últimos cem anos (ATTIWILL; ADAMS, 1993). Considerando que a biomassa viva tem relação direta aos estoques e fluxos de nutrientes em ecossistemas, é relevante quantificar a biomassa viva das florestas tropicais (SAMPAIO; SILVA, 2005) (KELLER; PALACE; HURTT, 2001). Além de estimar a biomassa, obter outras informações, como sobre a introdução de espécies exóticas, também são importantes aos estudos de ciclagem de nutriente, uma vez que essas espécies alteram drasticamente os ecossistemas em termos de produtividade, química, morfologia e fenologia (EHRENFELD, 2003).

A biomassa vegetal é composta pelos elementos químicos orgânicos básicos, tais como C (em média 50% da biomassa de uma planta), H (43%) e O (6%), além de outros componentes minerais que somam apenas 1% da massa total divididos em macro e micro nutrientes (LARCHER, 2001). São estes nutrientes o nitrogênio (N), fósforo (P), potássio (K), cálcio (Ca), magnésio (Mg) e enxofre (S) (macronutrientes) e ferro (Fe), manganês (Mn), boro (B), cobre (Cu), zinco (Zn), molibdênio (Mo) e cloro (Cl) (micronutrientes) (RATUCHNE et al., 2016). Dentre estes macro e micronutrientes destacam-se o N, P e K, responsáveis pela regulação de diversas funções orgânicas (RAVEN; EVERT; EICHHORN, 2014).

Dos vários nutrientes encontrados na biomassa e nos solos dos ecossistemas, o N é um dos mais limitantes para a produtividade primária, principalmente em ambientes intensamente degradados, pois o ecossistema tende a perder fluxo de nutrientes entre a vegetação viva e a serapilheira (VITOUSEK; HOWARTH, 1991). Por sua vez, o N pode atuar como fator importante no processo de regeneração natural da floresta (COLETTA, 2010). Em florestas tropicais, por exemplo, um grupo de plantas se destaca na fixação de N, a família Fabaceae que possui associação radicular com bactérias fixadoras de nitrogênio gasoso (N_2), acelerando a colonização e crescimento da floresta nestes ambientes degradados e a recuperação dos níveis de nitrogênio (SIDDIQUE et al., 2008).

A fixação biológica é o mecanismo básico de entrada de nutrientes no planeta. Por exemplo, a fixação de nitrogênio, processo geralmente bacteriano, onde há a transformação do di-nitrogênio em amônia que fica disponível aos vegetais (GALLOWAY et al., 2004). Além da fixação biológica, também existe a antropogênica, que disponibiliza nutrientes (i.e. nitrogênio) para os ecossistemas através da fertilização por adubos químicos (GALLOWAY et al., 2011). Estoques globais de nitrogênio são fortemente influenciados por ações humanas, principalmente em florestas tropicais que possuem muitas espécies fixadoras (BARRON et al., 2009) e por que nestas regiões há mais disponibilidade de nitrogênio gasoso do que em outras (GALLOWAY et al., 2004). Além disso, os estágios iniciais de desenvolvimento de um ecossistema sustentam maiores taxas de fixação de nutrientes que os estágios finais (CREWS; FARRINGTON; VITOUSEK, 2000).

O processo químico da fixação biológica de nitrogênio em microrganismos depende da ação da enzima nitrogenase (redução de acetileno), como sua limitação por retroalimentação pelo excesso do produto da reação no ambiente, ou presença de alguns nutrientes que podem agir como cofatores na reação química (BARRON et al., 2009). Pensava-se que os níveis de nitrogênio afetavam bem menos as florestas tropicais em detrimento de outras, mas estudos recentes demonstraram por exemplo que o aumento de nitrogênio antropogênico gera aumento de nitrogênio em diversos tecidos da planta (GALLOWAY et al., 2011).

Outro nutriente de grande relevância, tanto pela baixa disponibilidade, quanto pela dificuldade em absorver e sua importância para a formação de um organismo vivo é o fósforo (P). Sabe-se que o carbono, nitrogênio e enxofre, por exemplo, podem ser encontrados na forma gasosa, em grande disponibilidade e assimilação mais facilitada, enquanto o P está protegido, mineralizado, e precisa sofre intemperismo para ser disponibilizado (CHADWICK et al., 1999) Um antigo modelo propõe que no início do desenvolvimento do solo, a maior parte do P está na forma de mineral primário, em maioria a apatita, que durante a intemperização, vai liberando outras formas de P (como PO^{3-4}) (WALKER; SYERS, 1976). Walker e Syers (1976) ainda dimensionam que certa quantidade do P é absorvida por plantas e microrganismos, outra parte retorna aos poços inorgânicos (Pi) no solo através da mineralização, enquanto certa quantidade permanece dentro o solo em formas orgânicas (PO). Outros caminhos secundários pouco convencionais podem ser a absorção por minerais secundários do solo, precipitação ou lixiviação em formas orgânicas ou inorgânicas, o que esgotaria gradativamente os *pools* de P total e disponível (WALKER; SYERS, 1976).

A disponibilidade de P em florestas tropicais é fator limitante na provisão de diversos serviços ecossistêmicos (REED et al., 2011). Estas florestas, por armazenarem até um terço de todo o carbono global, tornam-se alvo de maior atenção para a ação de nutrientes sensíveis às mudanças climáticas (YANG et al., 2014). Há evidencias de que a disponibilidade de P, bem como outros nutrientes, no solo pode regular as respostas das florestas tropicais à perturbação antropogênica (como apontam os estudos CLEVELAND; REED; TOWNSEND, 2006; PAOLI; CURRAN; SLIK, 2008). Sendo assim, os esforços científicos para compreender a ciclagem de diversos nutrientes nos mais diversos estratos da floresta são necessários.

2.3.1 Estoque de nutrientes na floresta: o papel de raízes no estoque de nutrientes

A exploração de recursos naturais afeta, em longo prazo, o ciclo dos nutrientes em ecossistemas tropicais, pois este estoque é diretamente relacionado com a biomassa local (ARIAS et al., 2011). A biomassa, por sua vez, é parte fundamental do ecossistema, sendo resultante dos ganhos e das perdas, principalmente, de carbono através dos ciclos bioquímicos (CHAPIN; MATSON; VITOUSEK, 2011). Estima-se que 42% do carbono disponível do planeta esteja estocado na biomassa vegetal (PAN et al., 2011), sendo que, grande parte desse carbono se encontra na biomassa radicular (WARING; POWERS, 2017). No entanto, quantidades expressivas de carbono são devolvidas à atmosfera através do desmatamento e da queima de madeira, contribuindo para o aquecimento global.

Por representar até mais da metade da biomassa vegetal total, as raízes são importantes para o processo de ciclagem de nutrientes, tanto na entrada e estocagem, quanto na devolução de nutrientes ao meio ambiente (POORTER et al., 2012). O desenvolvimento de raízes finas, por exemplo, podem responder à concentração de nitrogênio (N) disponível no solo (CAVELIER, 1992). Ainda as raízes podem responder ao nitrogênio para a absorção de outros nutrientes (P, K e Ca) (FREITAS; BARROSO; CARNEIRO, 2008). Freitas; Barroso; Carneiro (2008) apontam que além disso, o modo e quantidade de absorção de nutrientes afetam tanto o crescimento quanto a longevidade das raízes finas. Um estudo de Jackson; Mooney; Schulze (1997) apresentou valores globais de estoques de nutrientes em raízes, o que enfatizou a importância deste estrato da vegetação para o estoque total de nutrientes nos mais diferentes biomas (Tabela 1).

Elemento	**Nutrientes globais em raízes finas vivas (Pg)**	**Nutrientes globais em raízes finas totais (Pg)**
C	19.9	38.1
N	0.48	0.92
P	0.044	0.085
K	0.12	0.24
Ca	0.17	0.32
Mg	0.054	0.11
S	0.036	0.069

Tabela 1. Valores apresentados por Jackson; Mooney; Schulze (1997) destacando pools globais de nutrientes em raízes finas vivas (Pg) e raízes finas totais (Pg).

Em ecossistemas secos, a biomassa de raízes pode representar também a maior parte da biomassa total – até mais de 70% do total (KAUFFMAN et al., 2003) – o que evidencia mais ainda sua importância no estoque e ciclagem de nutrientes (FREITAS; BARROSO; CARNEIRO, 2008). Para obter nutrientes, as raízes se proliferam nas camadas superficiais do solo, onde têm acesso ao humus e serrapilheira que estão em constante decomposição (FREITAS; BARROSO; CARNEIRO, 2008; JACKSON et al., 1996). Além de nutrientes, as raízes buscam maiores profundidades (mais que 2m), como na Caatinga onde as pivotantes atingem corpos de água subterrânea para se hidratar (figura 2 – observações pessoais do autor em campo). Geralmente, em resposta aos estresses ambientais (falta de recursos ou competição), as raízes podem atingir profundidades superiores à 10 m (VOGT; EDMONDS; GRIER, 1981).

Figura 2. Observações em campo das raízes pivotantes profundas em solo da Caatinga no Parque Nacional do Catimbau, Buíque-PE.

Muitos dos nutrientes contidos na biomassa vegetal retornam ao ambiente através da produção de serrapilheira (ATTIWILL; ADAMS, 1993). Alterações no regime de ciclagem consistem em importantes fatores que contribuem para o desequilíbrio do fluxo energético, alterando a fisiologia dos vegetais e modificando a distribuição das espécies. Podemos citar que os níveis de certos nutrientes, como o nitrogênio, podem influenciar a produção e a regeneração de raízes em vários ecossistemas (VOGT, K. A.; BLOOMFIELD, 1991), fato importante para o funcionamento do organismo vegetal. Isso indica que as modificações no fluxo energético estão ligadas à dificuldade de regeneração natural dos ecossistemas perturbados quando, por exemplo, limitam o estabelecimento das plantas.

2.3.2 Estoque de carbono e a mitigação do efeito estufa

As árvores têm papel fundamental no sequestro de carbono, diminuindo a concentração dos gases do efeito estufa ao estocarem C advindo do CO_2 atmosférico (DANIEL BRIANEZI et al., 2013). Este C tende a ficar alocado na biomassa produzida (SANTOS et al., 2016). Há estimativas que apontam um estoque de 38,1 Pg de C em cerca nas raízes do planeta, sendo e eu florestas tropicais tem maior contribuição nesses estoques (JACKSON; MOONEY; SCHULZE, 1997). Com isso, as florestas tropicais com suas raízes, são responsáveis por grande parte do sequestro de C, como por exemplo as raízes finas que podem contribuir entre 25 e 80% do acúmulo anual de carbono no solo destas florestas (FREITAS; BARROSO; CARNEIRO, 2008). Converter terras degradadas em áreas de restauração, como por meio da implantação de culturas restauradoras, pode reestruturar o ecossistema, quando sequestraria de 50 a 100 kg C ha^{-1} ano^{-1}. Assim, a produção de novas raízes pode representar ainda metade da taxa de produtividade primária local, sendo uma das principais vias de entrada de carbono ao solo (FREITAS; BARROSO; CARNEIRO, 2008). Enquanto isso, a biomassa de raízes vem declinando devido as mudanças no uso do solo (ALBUQUERQUE, 2015), fenômeno esse observado em todo o planeta.

De modo geral, é bem estabelecido que as florestas tropicais sazonalmente secas, como a Caatinga, tem alto potencial de estoque de C (inversamente sua degradação gera perdas consideráveis desse C). Estudos apontam que este ecossistema pode estocar cerca de 5,7 Mg ha^{-1} a 85 Mg ha^{-1} (SAMPAIO; COSTA, 2011; SANTOS et al., 2016). Entretanto, este ecossistema é muito negligenciado quanto à conservação (LEAL et al., 2005) e a maioria das florestas secas permanecem expostas às ameaças da perturbação antrópica (MILES et al., 2006). Por isso que se buscam alternativas de conservação destes ecossistemas secos para evitar o avançar das mudanças climáticas globais.

3 ARTIGO 1: PATTERNS AND DRIVERS OF BELOWGROUND BIOMASS AND NUTRIENTS IN A CAATINGA DRY FOREST

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Patterns and drivers of belowground biomass and nutrients in a Caatinga dry forest

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Abstract

Tropical forests deliver key ecosystem services associated to aboveground biomass. However, information on belowground biomass (i.e. root biomass) is still scarce, particularly in the case of dry forests. In this article, we examine how increasing chronic anthropogenic disturbances (CAD) and decreasing rainfall affect belowground biomass and nutrient stocks at different depths. Our samplings were carried out in the Catimbau National Park, which encompasses the Brazilian seasonally dry forest, called Caatinga. Eleven forest stands were selected and are characterized by different CAD intensities and also for following a precipitation gradient. We also analysed the effects of some biotic metrics, such as annual litter productivity, coarse woody debris accumulation, and biocrust soil cover. In each forest stand, we dug three trenches (0,7 m x 0,7 m x 1 m), and sampled 10 different layers of 10 cm each. The samples were sieved separately, and roots separated by category, dried and weighed. Across the 11 forest stands, belowground biomass ranged from 3.2 Mg ha^{-1} to 29.6 Mg ha^{-1}, averaging 14.6 ± 9.2 Mg ha^{-1}, with belowground in average accounting to less than 1/3 of total forest biomass; i.e. a root to shoot ratio of 0.29 ± 0.1 (mean ± SD). Root biomass was concentrated in the soil superficial layer (< 50 cm deep) and in the large roots (diameter >2.01 cm), but with an immense cross-stand variation. Root nutrient concentration varied little across the stands with small roots exhibiting higher nutrient concentrations. Finally, root biomass responded positively to average annual precipitation, while carbon concentration responded negatively to chronic disturbance and root sizes. Our results suggest that the Caatinga dry forest shows a reduction in root biomass and nutrient concentration and stocks, with predictable scores on landscape spatial scales by a combination of variables and their relationships with environmental vegetation.

Keywords: Below-ground biomass; Anthropogenic disturbance; Semiarid; Carbon, Nitrogen and Phosphorus; Seasonaly tropical dry forest

1 Introduction

A significant increase in the carbon (C) concentration is estimated for the next decades speeding up climate change and all their pervasive impacts on global sustainability (Schmittner et al., 2008). In this context, the role played by natural ecosystem and their services has received increased attention relative to both C sequestration and storage (Abreu et al., 2017) and other nutrients. It has been estimated that 42% of the available C on biosphere is stored in plant biomass (Pan et al., 2011), including both above and below-ground (Waring & Powers, 2017), particularly in the tropical forests, as they respond for most of the C stored in natural ecosystems, especially rain forests (Huang et al., 2021). It is believed on a global scale that belowground biomass (BGB) accounts for 20 to 26% of total biomass, making it a significant carbon reserve for a variety of vegetation types and land use systems (Handavu et al., 2021). In this BGB, we found about 292 Pg of root containing approximately 38.1 Pg of carbon, 0.92 Pg of nitrogen and 0.085 Pg of phosphorus in the fine roots alone (Jackson et al., 1997) This is one of the main reasons tropical forests have been considered an irreplaceable habitat in the context of global sustainable goals, including climate regulation, biodiversity protection and poverty alleviation (Ferraz et al., 2014). Although much of the attention has been given to rain forests, recent reviews have highlighted ecosystem services provided by seasonally dry tropical forests (hereafter dry forests), including climate regulation via C sequestration and storage (Quijas et al., 2019).

There are several differences between dry and rain forests in the context of ecosystem services provision as follow. First, dry forests encompass a wide gradient relative to forest structure and biomass, from low-statured or even scrub vegetation to tall forests (Pennington et al., 2018). Second, a substantial portion of the rain forest is still of old-growth forest with little exposition to local human disturbances across all tropical regions (Barlow et al., 2016). Conversely, most of the dry forest cover globally has been converted into human-modified landscapes, through which high biomass old-growth forest tracts are relatively small and rare (Nanni et al., 2019). Finally, while tropical rain forests can persist as a collection of both forest fragments exposed to little extraction of forest products depending on the income profile of rural populations, remaining dry forest vegetation in human-modified landscapes is converted into successional mosaics due to a disturbance package consisting of slash-and-burn agriculture, exploitation of forest products and livestock production via free-ranging animals; i.e. human-chronic disturbance (sensu Singh, 1998). Accordingly, dry forests are experiencing degradation (Ghazoul & Chazdon, 2017; Songer et al., 2009) and most of them are expected to experience increased aridity due to climate changes (Magrin et al., 2014). In synthesis, the ecosystem services provided by dry forests in human-modified landscapes and its drivers are still to be properly documented, particularly in the case of regulating and support (Calvo-Rodriguez et al., 2017; Sánchez-Azofeifa et al., 2005). This is a key research agenda in the case society wants to benefits from dry forest services by encouraging better agropastoral practices and conservation initiatives able to guarantee forest integrity in human-modified landscapes, since less than 5% of dry forest original cover have set under protected areas (Miles et al., 2006)

Global data indicate that more than half of the world's forests, about 57%, are secondary forests remnants from severe anthropic disturbances (FAO, 2010). The loss of biomass has great potential to impact the nutrients cycling of great importance for the balance of the ecosystem, such as nitrogen (N) and phosphorus (P). Aditionally, big trees play a special role as they account for 50% of the C by tropical forests (Pinho et al., 2020). We also refer to 14.24 Mg ha^{-1} of C associated to aboveground biomass, ranging from 1.86 to 61.3 Mg ha^{-1} in the case of dry forests (Souza et al., 2019). This contribution is not surprisingly since dry forests respond to 40% of tropical forest original cover (Miles et al., 2006). In both cases, forest aboveground biomass and C content (usually 50% of biomass) respond to a myriad of factors including climatic conditions (particularly precipitation and water availability), soil fertility, forest successional status and both natural and human disturbance regimes, such as hurricanes and slash-and-burn agriculture (Moore et al., 2018; Souza et al., 2019). In both cases, the role played by belowground biomass remains uncertainty, although estimates suggest up to 80% of forest biomass stored belowground (Freitas et al., 2008).

The Caatinga dry forest in northeast Brazil has been considered one of the largest blocks of dry forest globally, with a five-century long exposition to human disturbances since the arrival of European settlers (Silva et al., 2017). Slash-and-burn agriculture and livestock production have converted most the original old-growth forest into successional mosaics with regenerating forest stands of varying age (Barros et al., 2021). Moreover, forest stands regardless of the successional status remain exploited for forest products such as firewood, building material and fodder; stands are also freely accessed by livestock, particularly goats feeding on the native vegetation (Arnan et al., 2018; Souza et al., 2019). In this context, precipitation, soil conditions, forest successional status and woody plant species as the main drivers of aboveground biomass (Souza et al., 2019). Finally, Caatinga dry forest usually covers precipitation gradients at both landscape and regional spatial scales, with a tendency of increased aridity as climate changes proceed (Magrin et al., 2014). Thereby, Caatinga dry forest offers an interesting opportunity to investigate dry forest ability to produce and storage biomass/nutrients in human-modified landscapes. We refer not only to biomass as a way to stock C (a key service in the context of climate change), but biomass as nutrients as key products for rural livelihood (Araujo et al., 2021).

Based on what was exposed above, it is reasonable to assume that quantifying the biomass and nutrient stocks in dry forests is important to understand global values, particularly of C, and influence future effective actions for C sequestration (Becknell et al., 2012). This study investigates the belowground biomass of the Caatinga dry forest (hereafter referred to as root biomass) and its nutrient stocks, in order to estimate the forest's capacity to store biomass and nutrients when exposed to anthropogenic disturbances and changes in precipitation. Biomass and nutrient scores (C, N, and P) at various soil depths are provided for eleven forest stands along a gradient of five hundred precipitation and varying intensities of chronic human disturbance. Overall, it was expected (1) biomass and nutrients concentrated in the soil surface layer, (2) biomass and nutrients positively related to precipitation and aboveground biomass, while negatively correlated to human disturbances, (3) a low concentration of both N and P on biomass, regardless of the environmental conditions. Our findings are discussed in the light of drivers for dry forest biomass and forest ability to provide services.

2 Material and methods

2.1 Study area

This study was carried out in the Catimbau National Park, a 607-km2 human-modified landscape in northeast Brazil (Figure 1). This focal landscape is dominated by flat lands with a predominance of nutrient-impoverished sandy soils (Corrêa et al., 2015). Climate is markedly seasonal with an average temperature around 23C and annual precipitation varying from 480 up to 1000 mm^3 $year^{-1}$ across the landscape. Rain concentrates from April to July (Vanderlei et al., 2022). The predominant vegetation type refers to a low-statured seasonally dry forest dominated by multiple-stem shrub and tree species from Euphorbiaceae and Fabaceae families (Rito et al., 2017). A dense layer of weeds (containing a few grasses) is present during the wet season (Vieira et al., 2022). Subsistence farming activities still present into the protected area have converted the old-growth forest into a successional mosaic consisting of crop/pasture fields, regenerating and old-growth forest stands, with aboveground forest biomass ranging from 28.9 to 74.5 Mg ha^{-1} (Souza et al., 2019). Forest stands provide a myriad of products for the rural population from firewood to nutrients for subsistence agriculture and fodder for free-ranging livestock, particularly goats (T. L. d. S. R. Costa et al., 2021; Manhães et al., 2016).

2.2 Biomass and nutrient drivers

Here we considered mean annual precipitation, chronic anthropogenic disturbance, soil depth and aboveground biomass as the explanatory variables for belowground forest biomass and nutrients. Scores for all explanatory were provided by previous published studies in our focal plots in the last five last years. The average annual precipitation for each plot was provided by Rito et al., (2017), and it was obtained through historical data contained in the Wordclim® platform. Our focal plots ranged from 555 to 940 mm year^{-1}. Chronic anthropogenic disturbance refers to an index developed by Arnan et al. (2018), with scores ranging form from 0 (no disturbance) to 100 (maximum disturbance). Briefly, this integrative index combines direct measures of disturbance measured at plot level (e.g. the number of stumps and livestock feaces) with metrics considered proxies of human disturbance pressure such as plot distance to farm holdings (Arnan et al. 2018). According to the scores measured and provided by these authors, the disturbance index for our plots ranged from 2.74 to 58.07. Data on forest aboveground biomass was provided by Souza et al., (2019) with biomass estimated obtained via an allometric equation developed to Caatinga dry forest. Aboveground biomass ranged from 20.9 to 74.5 Mg ha^{-1} across our focal plots.

2.3 Belowground biomass and nutrient stocks

Belowground biomass and nutrient concentration/stocks were recorded in 11 permanent plots of 0.2 ha out of a total of 30 permanent plots previously established in our focal landscape (see Barros et al., 2021; Rito et al., 2017). Plots were located at least 2 km apart each other and were covered by old-growth forest in the sense that there was no record of previous agricultural activities as informed by locals (Souza et al. 2019). Root biomass was obtained by a destructive method, digging three trenches of 0,7 m x 0,7 m x 1 m each (Costa et al., 2014, Figure S1) from July 2020 to March 2021. The excavation was carried out with a metal shovel, while trenches were subdivided into 10 depth intervals of 10 cm each. All root material was carefully sieved in the field using a wooden sieve with a 2 mm metal grid. After being separated from soil sediment, the plant material was packed in individual paper bags. There was no effort to separate live and dead roots or by species. All material was dried in an oven at 60°C until reaching constant mass. Root exudates and materials other than the roots were eliminated from the samples in the laboratory through a screening. Subsequently, the roots were separated and classified into three different categories, according to their diameter: i) <2.0 cm for small-sized roots; ii) between 2.01 cm and 10.0 cm for medium-sized roots; and iii)> 10.01 cm for large roots. Finally, root samples were weighed and subsequently crushed and then sent to a commercial laboratory for phosphorus, carbon and nitrogen content. Briefly, nutrient context followed (Surruge & Haag, 1974). As medium and large-sized roots have a similar function in terms of nutrient stock, we use the sum of these classes together in a single measure for nutrient analyses. To extrapolate our samples for biomass in Mg ha^{-1}, the value (g) collected for each type of root was multiplied by the expansion factor of 1.69 on order to account for those uncollected roots in the base of stems as recommend by reached Albuquerque et al. (2015).

2.4 Data analysis

Due to reduced biomass context, root biomass was collapsed into two categories: social superficial layer (< 50 cm depth) and deep layer (50 -100 cm depth). To compare root biomass, nutrient concentration and stock according to dry forest plots, size class and soil layer, we use one-way ANOVA. Data were log-transformed to comply with the assumptions of normality and homoscedasticity of residuals when necessary. We used Generalized Linear Mixed Models (GLMMs) to examine the influence of aboveground biomass, chronic anthropogenic disturbance (CAD), mean annual precipitation (MAP) and soil depth on root biomass and root nutrient concentration. Accordingly, in our models we accommodate trenches per plot as random factor, while aboveground biomass, CAD, MAP and soil depth were entered as fixed factors. For this, we first assessed the collinearity among predictor variables with the variance inflation factor (VIF) using the “car” package (Fox and Weisberg 2011) in the R software (R Core Team, 2017). All VIF values were lower than 1.5 (ranging from 1.0 to 1.46), suggesting independence among predictors (Chattefujee & Hadi, 2006). All analyses were run using the R environment (R Development Core Team 2017).

3 Results

3.1 Belowground forest biomass and nutrients

Across the 11 forest stands, belowground biomass ranged from 3.23 Mg ha^{-1} to 29.6 Mg ha^{-1}, averaging 14.6 ± 9.2 Mg ha^{-1} (Table 1). It implied much more aboveground than belowground biomass (Table 1), with belowground in average accounting to less than 1/3 of total forest biomass; i.e. a mean root to shoot ratio (R/S) of 0.28 ± 0.1 (mean ± SD). Root biomass varied significantly among plots regarding small-sized roots (ANOVA F= 3.55, P< 0.01), medium-sized roots (ANOVA F= 9.9, P< 0.001), large-sized roots (ANOVA F= 3.16, P< 0.01) and total root biomass (ANOVA F= 5.61, P< 0.001) (Table 2, Figure 2). Moreover, root distribution varied by size class and soil depth with belowground or root biomass concentrated in the superficial soil layer and among large roots. Precisely, large roots support higher biomass than small and medium-sized roots (ANOVA F= 5.85, P< 0.01) (Figure 3) and 75% of the total root biomass in average was in the top 50 cm of soil (Figure S2) with large roots accounting for more one third of the total biomass and concentrated in in the superficial soil layers (Figure S2). In fact, total root biomass (ANOVA F= 25.58, P< 0.001), small-sized roots (ANOVA F= 59.42, P< 0.001), medium-sized roots (ANOVA F= 38.68, P< 0.001) and large-sized roots (ANOVA F= 6.82, P< 0.01) exhibited significantly higher root biomass in superficial than in deep layer (Figure 4).

Moving to nutrient concentration, the N (ANOVA F= 0.94, P=0.52), C (ANOVA F= 0.75, P= 0.66) and P (ANOVA F= 2.14, P= 0.11) root concentrations did not vary significantly among dry forest standings regarding small-sized roots (Figure S3) and medium+large roots (Figure S4). In terms of size class, nutrient concentration ranges from 132.1 to 483.3 g kg^{-1} for C, 8.6 to 29.7 g kg^{-1} for N and 0.24 to 0.59 g kg^{-1} for P regarding small-sized roots, while for large-sized roots these concentrations range from 4.7 to 32.7 g kg^{-1} for N, 139.7 to 476.1 g kg^{-1} for C and 0.08 to 0.55 g kg^{-1} for P across all sites (Table 3). More specifically, small-sized roots support significantly higher concentration of P than medium+large-sized roots (small roots Mean ± SE 0.34 ± 0.05 g kg^{-1}; medium+large roots 0.28 ± 0.09 g kg^{-1}) with a similar tendency to N (small roots Mean ± SE 16.01 ± 0.06 g kg^{-1}; medium+large roots 14.31 ± 0.07 g kg^{-1}) and C (small roots Mean ± SE 366.2 ± 11.42 g kg^{-1}; medium+large roots 354.7 ± 13.35 g kg^{-1}) (Table 3 Figure 5).

Finally, the mean values of nutrient stock in small-sized roots (Mg ha-1) was 0.008±0 (N), 0.16±0.06 (C) and 0.00015±0 (P), while for medium-sized roots size was 0.008±0 (N), 0.17±0.11 (C) and 0.00017±0 (P), and large roots were 0.041±0.09 (N), 0.66±1.2 (C) and

0.00053 ±0 (P) (see Table 4). Although medium+large roots and deep layer support more nutrient stocks than small roots and superficial layer, respectively, these variations among dry forest plots were not significant (Superficial layer: N stock ANOVA F=2.4, P=0.11, C stock ANOVA F= 2.52, P=0.11, P stock ANOVA F=2.14, P=0.14; Deep layer: N stock ANOVA F=0.57, P=0.44, C stock ANOVA F= 0.62, P=0.43, P stock ANOVA F=0.71, P=0.4) (Table 5, Figure S5).

3.2 Root biomass and nutrient drivers

In general, precipitation and soil depth were the most important predictors affecting root biomass, while chronic disturbance and aboveground biomass playing a minor role (Table 2, Figure 6). Precisely, total root biomass, medium-sized and large roots on superficial layer were positively affected by precipitation (Table 2, Figure 6). In terms of nutrients, chronic anthropogenic disturbance affected strong and negatively C concentration regarding both small and large-sized roots, while for both N and P concentration chronic disturbance and aboveground biomass did not significantly affect these nutrients (Table 4, Figure 7).

5 Discussion

Our findings indicate that belowground biomass is a key component of the Caatinga forest biomass as in average it represents one third of the entire forest biomass regardless of the cross-stand variation. Large roots predominate although small and medium-sized roots are also relevant by summing up more than a half of total root biomass. Total belowground biomass concentrates in the soil superficial layer (up to 50 cm deep) across all the stands. Moreover, forest stands tend to exhibit similar scores relative to root-nutrient concentration (C, N, P), but small roots support a higher concentration as compared to other size classes. Belowground or root biomass is highly sensible to precipitation but does not respond to aboveground biomass or chronic disturbance, while root nutrient concentration appears to be less sensible to environmental driver, with exception to C concentration, and accumulate on small roots. In synthesis, the Caatinga belowground biomass across human-modified landscapes is highly variable but it is predictable in some extent, while nutrient concentration occurs more homogenously across forest stands with little sensitivity to environmental drivers but associate to root size.

So far, there is little information on belowground biomass from dry forests, what limits generalizations. Overall, there is an immense variation across tropical dry forest and stands from the same forest relative to both above and belowground forest biomass (J. Castellanos et al., 1991; Souza et al., 2019). Briefly, belowground biomass or root biomass varies between 10 up to 82 Mg ha, with root to shoot ratio ranging from 0.08 to 0.65; i.e. 8-65% of the total tropical forest biomass (Brown et al., 1986; J. Castellanos et al., 1991; Jaramillo et al., 2003; Murphy & Lugo, 1986; Naveenkumar et al., 2017; Raherison & Grouzis, 2005). In general, root biomass represents up to 30% of total biomass in dry forest but less than 15% across humid forests (Sanford & Cuevas, 1996). Alternatively, R/S ratio in dry forest averages 0.17 while it averages 0.08 in humid forests (Naveenkumar et al., 2017; Raherison & Grouzis, 2005) or 8–50% in dry forest vs. 5-33% in wet forests (Roa-Fuentes et al., 2012). Other densely populated semi-arid ecosystems, such as the ridge forests in Delhi (India), had a higher average biomass stock of about 28.4 Mg ha^{-1} and carbon stock of 15.49 Mg C ha^{-1} (Meena et al., 2019). Our mean root biomass when compared with data for dry forest in India and in Chamela, Mexico with 17.1 Mg ha^{-1} (Jaramillo et al., 2003) of root biomass is low.

It appears clearly that the R/S ratio increases with dry conditions (Raherison & Grouzis, 2005) and it has been interpretated as a strategy to cope with low water availability by reducing evapotranspiration and incrementing absorption (Orians et al., 1996). In synthesis, forest biomass responds to water availability (Murphy & Lugo, 1986; Raherison & Grouzis, 2005), particularly in the case of aboveground biomass, as over 80% of variation is explained by mean annual rainfall (Raherison & Grouzis, 2005). However, soil conditions (Colón & Lugo, 2006), leaf-area index (Raherison & Grouzis, 2005) and the abundance of lianas also affect root biomass (Smith-Martin et al., 2020).

The carbon concentration in root biomass in other dry forests is at 39 g kg^{-1} (i.e. Jaramillo et al., 2003), while N ranges from 6.3 g kg^{-1}(Jaramillo et al., 2003) to 12 g kg^{-1} (Lugo & Murphy, 1986). Root carbon concentration also exhibits insignificant differences in relation to root size class or soil depth, but nitrogen depends on root diameter (Jaramillo et al., 2003). Other studies in different types of forests indicate nitrogen and phosphorus are still present in greater concentration in fine roots, with diameter > 2 mm (Gordon & Robert, 2000). However, nutrients accumulate (i.e. stocks or pools) in the superficial soil layer as roots also concentrate in this layer (Jaramillo et al., 2003; Lugo & Murphy, 1986). Finally, nutrient concentration in roots is higher in old-growth as compared to early-successional vegetation (Lugo & Murphy, 1986).

In this context, our findings confirm a stand scale variation in belowground biomass, where roots predominate in the surface layer of the soil and a protagonism of annual precipitation as a main driver of belowground biomass. Although data on nutrients stocks or pools are still missing here, they shall concentrate on the superficial soil layer as pools are directly correlated to biomass distribution across the soil profile. However, we documented a negative impact from chronic disturbance on C concentration and lack of effect by aboveground biomass on belowground biomass and root nutrient concentration, while concentration respond to root size class. Moreover, our scores relative to aboveground biomass and nutrient concentration reaches the lower values of range by dry forests, while R/S ratio fits in the average; i.e. 30% of the whole forest biomass by roots (Albuquerque et al., 2015; Lugo & Murphy, 1986; Murphy & Lugo, 1986; Vitousek, 1984).

Overall, forest biomass should respond positively to increases in soil water and nutrient availability, which may affect forest productivity (Roa-Fuentes et al., 2012). This underlying mechanism is the best explanation for the documented relationship with precipitation, but also the amount of belowground biomass we found (14.6 ± 9.2 Mg ha), as our focal landscape is covered by a nutrient-poor sandy soil (Rito et al., 2017), which is also expected to retain little amount of water due to a coarse granulometry and low content of organic matter typical of tropical sand soils (Kay, 2018). This is consistent with the relative high investment in roots as compared to aboveground biomass documented for Catimbau forest stands by our group (see Vitousek & Sanford, 1986).

Aboveground forest biomass also responds positively to precipitation in the Catimbau landscapes but in this case, it is mediated by woody plant species richness and forest successional status (Souza et al., 2019). In other words, water and nutrient scarcity (1) leads to the development of more conservative plants (i.e. the economic spectrum *sensu* Wright Et Al. (2004), (2) should favour more resource conservative species, and thus (3) increment the R/S ratio across resource gradients (see (Roa-Fuentes et al., 2012). In fact, a reasonable proportion of our local woody species flora has been classified as drought-tolerant by bearing both foliar and wood traits associated with conservative strategies, with precipitation as the major drivers of species assembly at landscape level (Pinho et al., 2019). The opposite strategy associated with more humid habitats was also observed (Pinho et al., 2019).

Low nutrient availability and its concentration on superficial soil layers as well as water content {i.e. data from 30 soils samples across our focal landscapes (Barros et al., 2021; Rito et al., 2017)} also explain root concentration on the superficial soil layers (see Raherison & Grouzis, 2005), with fine roots concentrating the nutrients. Fine roots are considered seasonal and the most productive component of the root system (Ibrahim et al., 2020; Kauffman et al., 2003). Thus, it makes sense physiologically that fine roots exhibit a higher nutrient concentration as compared to other root size class. In this context, it is well known that plants accumulate nutrients and also C on the roots to deal with climate seasonally and seasonal growth (Barros et al., 2021; Piper, 2011).

Chronic disturbance such as firewood and fodder collection might deplete nutrient stocks depending on how intense biomass is harvested and thus explain the CAD effects we documented here. Although our forest stands were classified as old-growth forests; i.e. no record of agricultural activities by locals (Barros et al., 2021; Rito et al., 2017), they are exposed to chronic disturbances including browsing by free-range exotic goats and collection of wood materials (see Specht et al., 2019). Precisely, firewood consumption in our focal landscape achieves in average 154 kg of fire wood a month and per family, while each household raise 22-35 goats in average (Jamelli et al., 2021; Specht et al., 2019), with animal feeding based on native vegetation, from litter to fruits (Formiga et al., 2020; Jamelli et al., 2021). Here we document a potential chronic-disturbance effect on plant nutrient concentration, thus incrementing the long list of chronic disturbance effects, we already documented in the Caatinga dry forest, particularly in the case of plant assemblages (see Barlow et al., 2016; Sfair et al., 2018). Finally, the lack of relationships between above and belowground biomass remains to be investigated. Although these two components of forest biomass correlate positively at large spatial scales, this relationship is highly variable at local and regional scale (Huang et al., 2021). One of the possibilities is a cross-stand variation in the abundance of long-root species such as the tree species *Pityrocarpa moniliformis*, which has been document to develop dense root networks connecting several adults (see Vanderlei et al., 2022) and occurs abundantly at both regenerating and old-growth forest stands in our focal landscape (Barros et al., 2021; Rito et al., 2017).

Caatinga dry forest has been transformed into a successional mosaic (Souza et al., 2019), indicating that soon or later old-growth stands will be incorporated via slash-and-burn agriculture plus chronic disturbances. Note that the Caatinga dry forest is one of the most populated semiarid regions with dense rural populations (Figueirôa et al., 2006). Old-growth stands persist in our focal landscape probably because of a certain level of restriction imposed by protected area regulations. In the Caatinga dry forest, slash-and-burn agriculture is proposed to eliminate most of all aboveground biomass and their nutrients via volatilization and wind erosion of ashes; it may require a century to recover nutrients stocks via forest regeneration (Kauffman et al., 1993). Locals report intensive labour to eliminate roots from native plants in order to reduce plant resprouting and the consequent competition with crops (Vanderlei et al., 2022). This type of land use, which combines two sources of disturbance (i.e. acute and chronic) is expected to reduce root biomass and probably nutrient concentration by depleting soil water and nutrient availability (see Lawrence et al. 2007) and causing root death by fire and weeding operations (Anjos Bittencourt Barreto-Garcia et al., 2021; Jorge Castellanos et al., 2001; Kauffman et al., 2003; Schulz et al., 2016). Such working hypothesis is particularly relevant by (1) considering root concentration and nutrient pools in the superficial soil layer as we documented here, (2) Caatinga depends on resprouting for regeneration (see (Barros et al., 2021; Bezerra et al., 2022; Vanderlei et al., 2022), (3) in dry forests, root biomass not only represent a substantial proportion of total forest biomass, but also affect soil nutrient pools, particularly C (Kauffman et al., 2003), and (4) Caatinga is expected to experience increased aridity and higher exploitation of forest resources associated with climate changes (Tabarelli et al., 2017). Accordingly, our findings and proposed hypotheses deserve attention.

6 Conclusion

In summary, root biomass makes an important contribution to the concentration of nutrients at surface soil levels (i.e. the first 50 cm of the crust). Especially when it comes to small-sized roots, as they are very dependent on biotic and abiotic variations above the ground. Likewise, this soil layer becomes the most sensitive to drastic changes in plant cover through human disturbances (chronic or acute) as well as changes in rainfall patterns caused by natural phenomena (such as global warming). The Caatinga old-growth forest, even composing a mosaic of different phytophysiognomies, are strongly affected by human activities and present a drastic tendency to desertification, because, once lost, the nutrients of these poor soils will be lacking in the remaining plant communities. Efforts to elucidate the roles of subterranean biomass in dry forests such as the Caatinga are generally slow and time and resource consuming, but should occupy more space in the scientific effort to understand nutrient cycling in these ecosystems.

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Table 1. Average description of the plots regarding chronic anthropogenic disturbance (CAD); mean annual precipitation (MAP); above-ground biomass (AGB); belowground biomass in small-sized roots, medium-sized roots, large-sized roots and total root biomass; and roots / shoot ratio (R / S) and mean value more standard deviation (M±SD) in in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

Variables	CAD	MAP mm^3	AGB Mg ha^{-1}	Small-sized		Medium-sized		Large-sized		Total roots	R / S
				Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}	%	Mg ha^{-1}	
Value of study areas	2.08	940	58.5	3.89	15.2	6.41	25.0	15.34	59.8	25.65	0.44
	7.35	653	42.8	4.17	15.5	4.35	16.1	18.44	68.4	26.97	0.63
	15.04	578	64.8	3.65	36.5	2.46	24.6	3.88	38.9	9.98	0.15
	15.68	588	74.5	10.92	36.9	8.50	28.7	10.20	34.4	29.62	0.40
	16.48	591	49.9	4.43	21.5	5.36	26.1	10.78	52.4	20.57	0.41
	27.95	762	36.0	4.00	48.8	2.84	34.6	1.36	16.6	8.20	0.23
	33.02	555	67.1	4.25	50.3	3.48	41.1	0.73	8.6	8.46	0.13
	34.35	647	60.3	3.74	30.5	1.96	16.0	6.54	53.5	12.23	0.20
	45.77	785	28.9	1.82	24.3	3.05	40.7	2.63	35.1	7.49	0.26
	48.27	673	39.3	1.77	54.8	1.46	45.2	0.00	0.0	3.23	0.08
	52.06	913	49.7	3.00	33.6	2.13	23.8	3.82	42.6	8.95	0.18
M±SD	29.09±17	698±134	51.9±16	4.15±2.4	33.4±13	3.8±2.1	29.2±9	6.7±6.1	37.3±21	14.6±9.2	0.28±0.1

Table 2. Results of the Generalized Linear Mixed Models (GLMMs) exhibiting the effects zof aboveground biomass, chronic anthropogenic disturbance (CAD), soil layer and mean annual precipitation (mm) on root biomass sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

Total_roots	Estimate	SE	t value	p	R^2
Inercept	-149.97	64.5	-2.325	0.021	
Aboveground biomass	2.2×10^{-1}	5.85×10^{-1}	0.385	0.708	
Precipitation (mm)	3.21×10^{-1}	5.79 x 10-2	5.54	<0.001	0.24
CAD	-1.77×10^{-1}	4.64×10^{-1}	-0.383	0.701	
Small-sized_roots					
Intercept	16.01	12.26	1.306	0.192	
Aboveground_biomass	-2.39×10^{-1}	0.11	-2.161	0.031	
Precipitation (mm)	9.59×10^{-3}	0.01	0.874	0.383	0.27
CAD	9.99×10^{-3}	0.08	0.114	0.901	
Soil layer	-19.23	2.51	-7.636	<0.001	
Medium-sized_roots					
Intercept	-32.39	12.43	-2.621	0.009	
Aboveground_biomass	-2.23×10^{-2}	0.11	-0.197	0.843	
Precipitation (mm)	7.01×10^{-2}	0.01	6.302	<0.001	0.43
CAD	-4.88×10^{-2}	0.08	-0.546	0.585	
Soil layer	-16.29	2.55	-6.378	<0.001	
Large-sized_roots					
Intercept	-158.42	56.46	-2.81	0.005	
Aboveground_biomass	4.86×10^{-1}	0.511	0.953	0.341	
Precipitation (mm)	2.31×10^{-1}	0.050	4.572	<0.001	0.2
CAD	-2.38×10^{-1}	0.405	-0.589	0.556	
Soil layer	-29.28	11.59	-2.524	0.012	

Table 3. Mean values of concentration (g kg^{-1}) adjusted by standard deviation (M ± SD) to nitrogen (N), carbon (C), phosphorus (P) and carbon / nitrogen ratio (C/N) in areas subjected to different chronic disturbance anthropogenic pressures (CAD) and rainfall regimes in Catimbau National Park, Caatinga natural reserve, a seasonally tropical dry forest (STDF) of northeastern Brazil. Values with (*) do not have data compared to obtain standard deviation. The area with (**) does not have nutrient information for this root category.

Variables	CAD	Rainfall	Small sized root (g kg^{-1})				Large sized root (g kg^{-1})			
			N	C	P	C / N	N	C	P	C / N
Forest stands	2.08	940	20.27±0.7	407.71±22.4	0.39±0.04	20.10±0.4	11.99±1.8	434.31±26.7	0.35±0.20	37.1±7.1
	7.35	653	16.61±2.0	447.10±55.3	0.26±0.03	26.92±0.1	12.37±4.5	347.66±91.9	0.17±0.03	29.0±3.2
	15.04	578	14.58±0.7	346.79±20.4	0.34±0.02	23.82±1.3	14.24±(*)	323.32±(*)	0.45±(*)	22.7±(*)
	15.68	588	11.62±2.6	244.49±97.3	0.37±0.02	20.42±3.7	9.98±4.6	318.44±156.2	0.17±0.08	31.5±1.3
	16.48	591	15.51±1.8	404.54±36.5	0.41±0.02	26.17±1.4	(**)	(**)	(**)	(**)
	27.95	762	16.79±0.5	398.57±31.9	0.42±0.14	23.77±1.9	10.35±(*)	418.05±(*)	0.20±(*)	40.4±(*)
	33.02	555	14.47±1.2	322.35±49.9	0.37±0.02	22.25±1.9	16.40±2.2	412.36±71.4	0.46±0.02	28.1±0.4
	34.35	647	16.59±1.3	435.53±9.9	0.49±0.04	26.42±2	13.34±0.4	238.92±54.0	0.24±0.07	18.0±3.3
	45.72	673	16.30±4.6	343.67±113.2	0.42±0.14	20.89±1.8	24.20±3.2	410.09±93.33	0.41±0.06	16.8±1.1
	45.77	785	24.40±4.5	373.82±38.6	0.34±0.06	15.52±1.7	19.89±18.1	383.08±84.6	0.20±0.06	29.7±16.1
	52.06	913	21.17±1.6	388.27±19.9	0.36±0.02	18.45±1.8	14.82±6.0	303.38±140.44	0.32±0.13	20.1±3.1
M±SD	26.86±16	699±128	17.12±3.9	373.9±71.9	0.38±0.08	21.9±3.3	14.61±6.4	358.87±98.6	0.29±0.13	27.3±7.5

Table 4. Mean values of nutrient stocks (Mg kg^{-1}) for nitrogen (N), carbon (C) and phosphorus (P) in areas subjected to different chronic disturbances, anthropic pressures (CAD) and rainfall regimes in the Catimbau National Park, Caatinga nature reserve of the Caatinga, a Brazilian seasonally tropical dry forest (STDF).

Variables	CAD	Rainfall	Small sized root (Mg ha^{-1})			Medium sized root (Mg ha^{-1})			Large sized root (Mg ha^{-1})		
			N	C	P	N	C	P	N	C	P
Forest stands	16.48	591	0.007	0.18	0.00018	0.008	0.22	0.00021	0.016	0.45	0.00042
	15.04	578	0.005	0.13	0.00013	0.004	0.09	0.00008	0.005	0.13	0.00014
	34.35	647	0.007	0.17	0.00019	0.003	0.09	0.00010	0.011	0.29	0.00035
	45.72	673	0.004	0.08	0.00009	0.003	0.07	0.00006	0.000	0.00	0.00000
	33.02	555	0.006	0.14	0.00016	0.005	0.13	0.00013	0.001	0.02	0.00003
	2.08	940	0.009	0.19	0.00018	0.017	0.35	0.00035	0.042	0.85	0.00083
	7.35	653	0.007	0.18	0.00010	0.005	0.14	0.00008	0.003	0.07	0.00004
	45.77	785	0.019	0.29	0.00028	0.021	0.33	0.00030	0.317	4.38	0.00306
	15.68	588	0.002	0.05	0.00007	0.004	0.07	0.00012	0.003	0.06	0.00010
	27.95	762	0.007	0.15	0.00015	0.005	0.11	0.00011	0.008	0.21	0.00018
	52.06	913	0.011	0.19	0.00018	0.017	0.31	0.00028	0.039	0.77	0.00067
M±SD	26.86±16	699±128	0.008±0	0.16±0,06	0.00015±0	0.008±0	0.17±0,11	0.00017±0	0.041±0,09	0.66±1,2	0.00053±0

Table 5. Results of the Generalized Linear Mixed Models (GLMMs) exhibiting the effects of aboveground biomass, chronic anthropogenic disturbance (CAD) and mean annual precipitation (mm^3) on root nutrient concentration regarding small and large-sized roots sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

Nutrient	Root class	Estimate	SE	t value	p	R^2
N_concentration	a) Small-sized roots					
	Intercept	2.58	0.33	7.82	<0.001	
	Aboveground biomass	3.0 x 10-3	4.0 x 10-3	0.81	0.42	0.18
	CAD	-4.0 x 10-3	2.0 x 10-3	-0.13	0.383	
	Precipitation (mm)	3.0 x 10-3	1.0 x 10-3	1.65	0.09	
	b) Large-sized roots					
	Intercept	3.09	0.39	7.80	<0.001	
	Aboveground biomass	-8 x 10-3	4.0 x 10-3	-1.83	0.06	0.28
	CAD	9 x 10-3	3.0 x 10-3	2.65	<0.01	
	Precipitation (mm)	-3.0 x 10-3	1.0 x 10-3	-1.21	0.22	
C_concentration	a) Small-sized roots					
	Intercept	6.06	0.06	86.8	<0.001	
	Aboveground biomass	-9.49 x 10-4	8.58 x 10-4	-1.01	0.27	0.1
	CAD	-4.50 x 10-3	6.28 x 10-4	-7.16	<0.001	
	Precipitation (mm)	5.92×10^{-5}	4.14 x 10-5	1.42	0.15	
	b) Large-sized roots					
	Intercept	6.1	8.15 x 10-2	74.75	<0.001	
	Aboveground biomass	-3.63 x 10-3	9.04 x 10-4	-4.02	<0.001	0.1
	CAD	-3.13 x 10-3	6.65 x 10-4	-4.76	<0.001	
	Precipitation (mm)	8.83 x 1-5	6.09 x 10-5	1.44	0.14	
P_concentration	a) Small-sized roots					
	Intercept	9.1 x 10-1	1.94	0.5	0.61	
	Aboveground biomass	-8.19 x 10-4	2.57 x 10-2	-0.03	0.97	0.01
	CAD	1.52 x 10-3	2.1 x 10-2	0.07	0.93	
	Precipitation (mm)	-3.22 x 10-6	9.63 x 10-4	-0.003	0.99	
	b) Large-sized roots					
	Intercept	1.67	2.94	0.57	0.56	
	Aboveground biomass	6.33 x 10-3	3.32 x 10-2	0.19	0.85	0.08
	CAD	7.07 x 10-3	2.48 x 10-2	0.28	0.77	
	Precipitation (mm)	-1.61 x 10-4	2.11 x 10-3	-0.07	0.93	

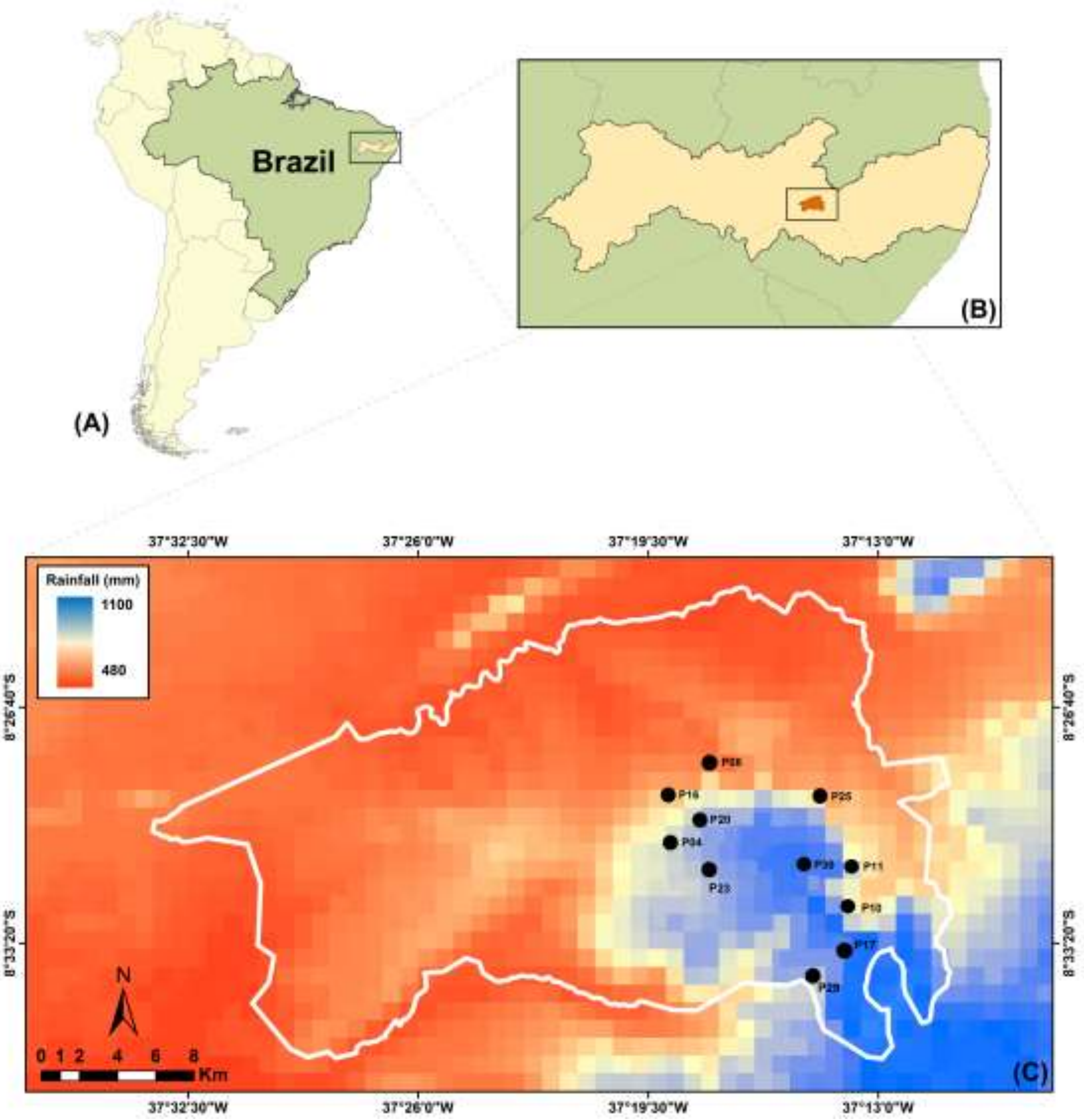

Figure 1. Location of the 11 forest stands (red circles), where we collected all the samples in the Catimbau National Park (PARNA Catimbau), Pernambuco state, Brazil.

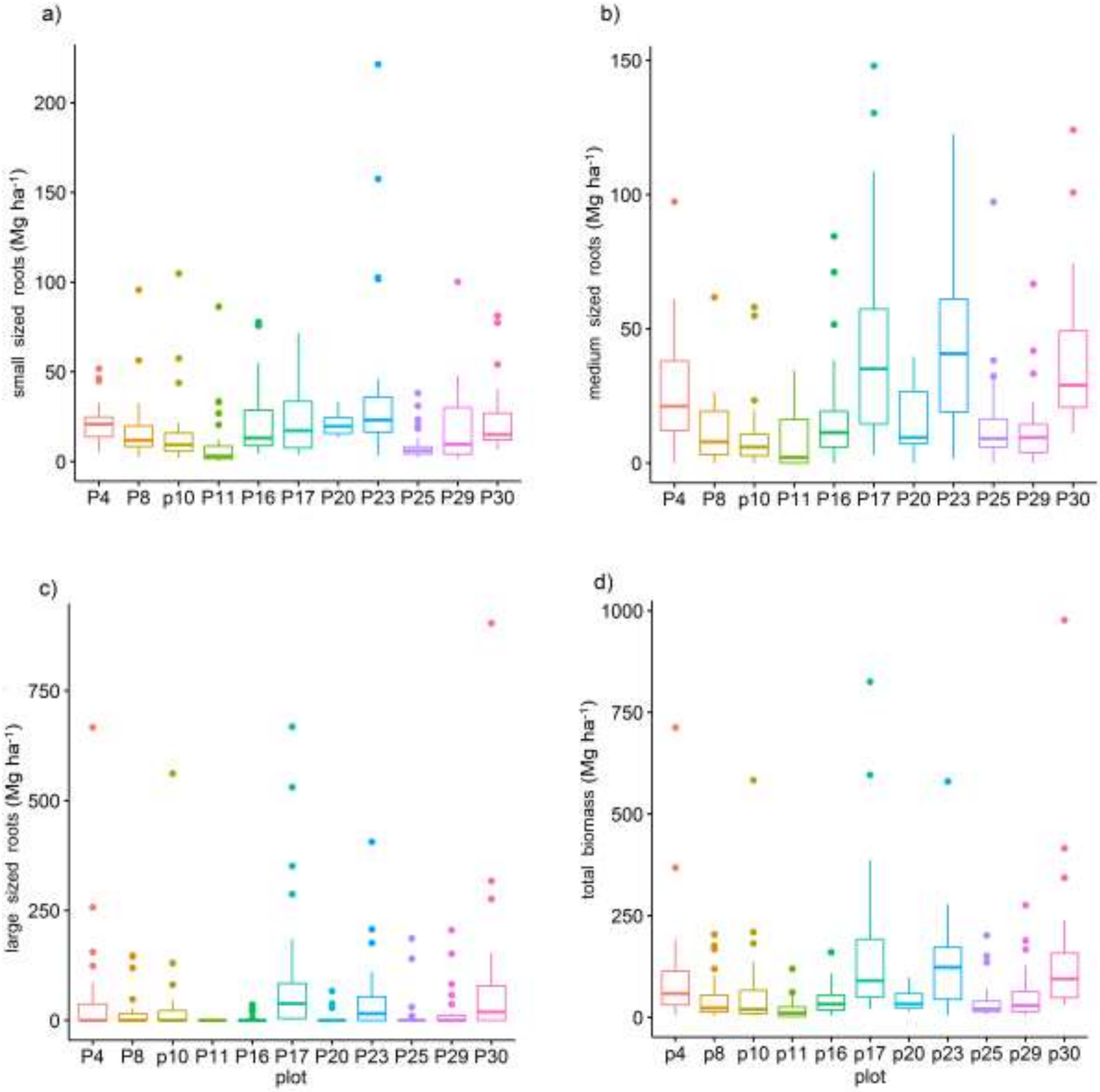

Figure 2. Root biomass according to size class across dry forest satnds in the Catimbau National Park, in Pernambuco, northeastern Brazil

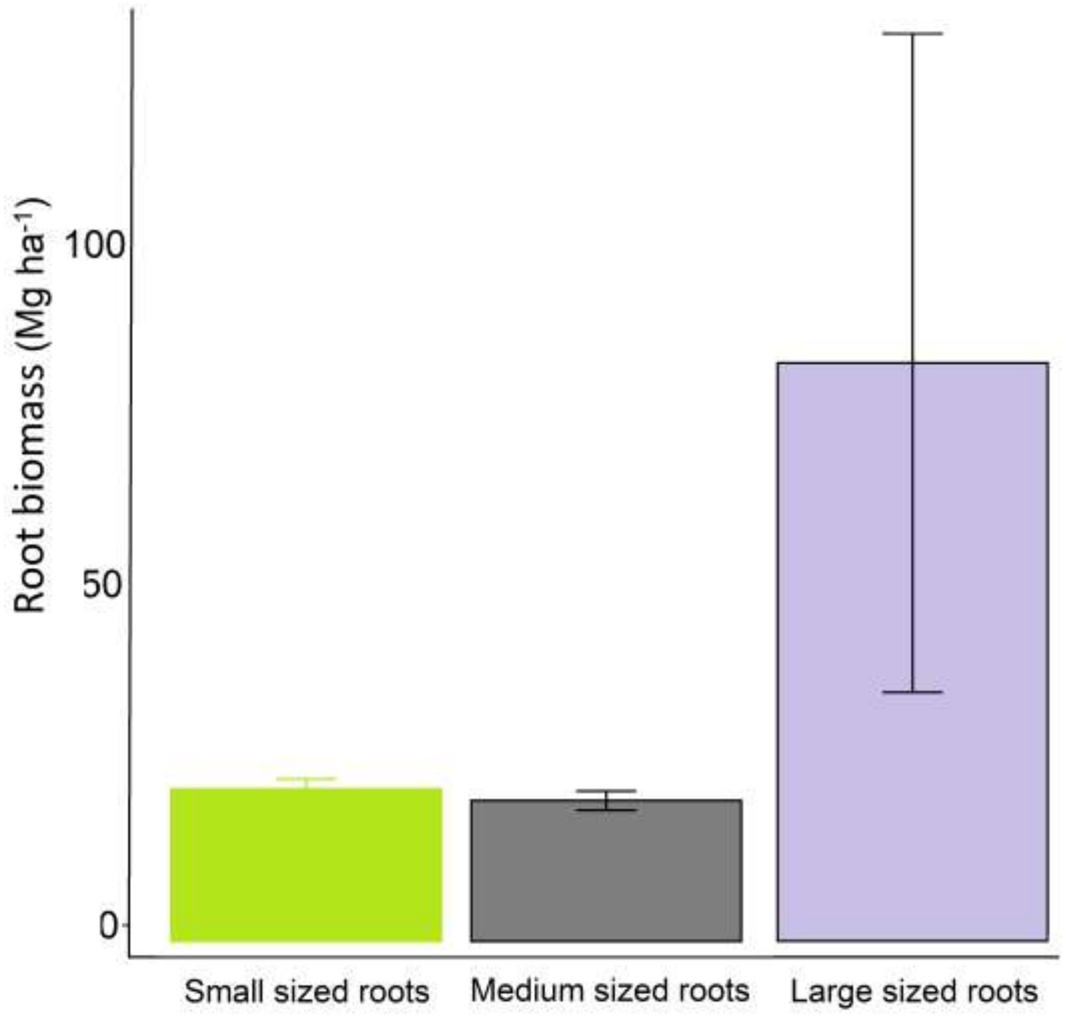

Figure 3. Mean ± SE of small-sized, medium-sized and large-sized root biomass in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

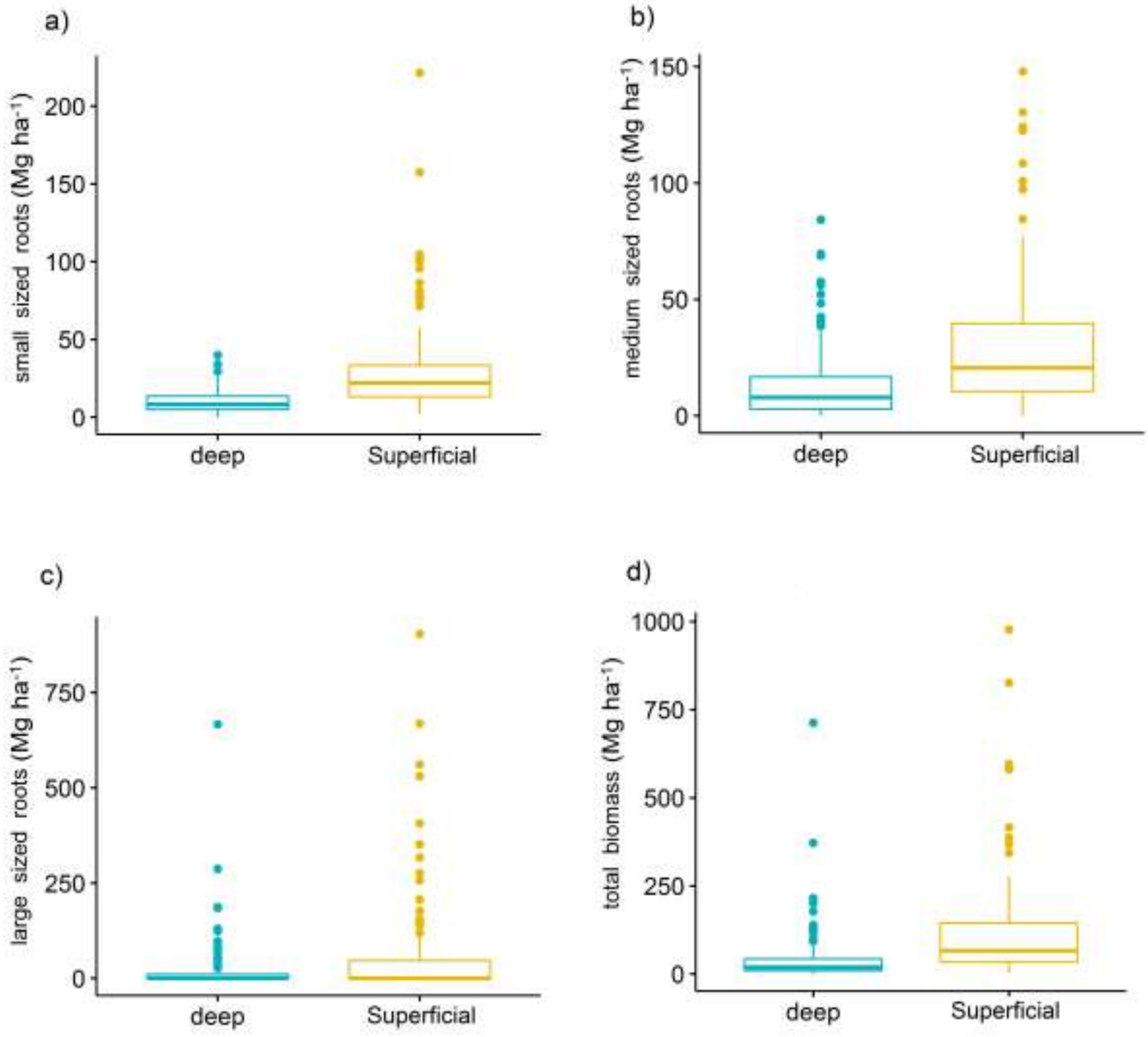

Figure 4. Root biomass according to soil layer in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

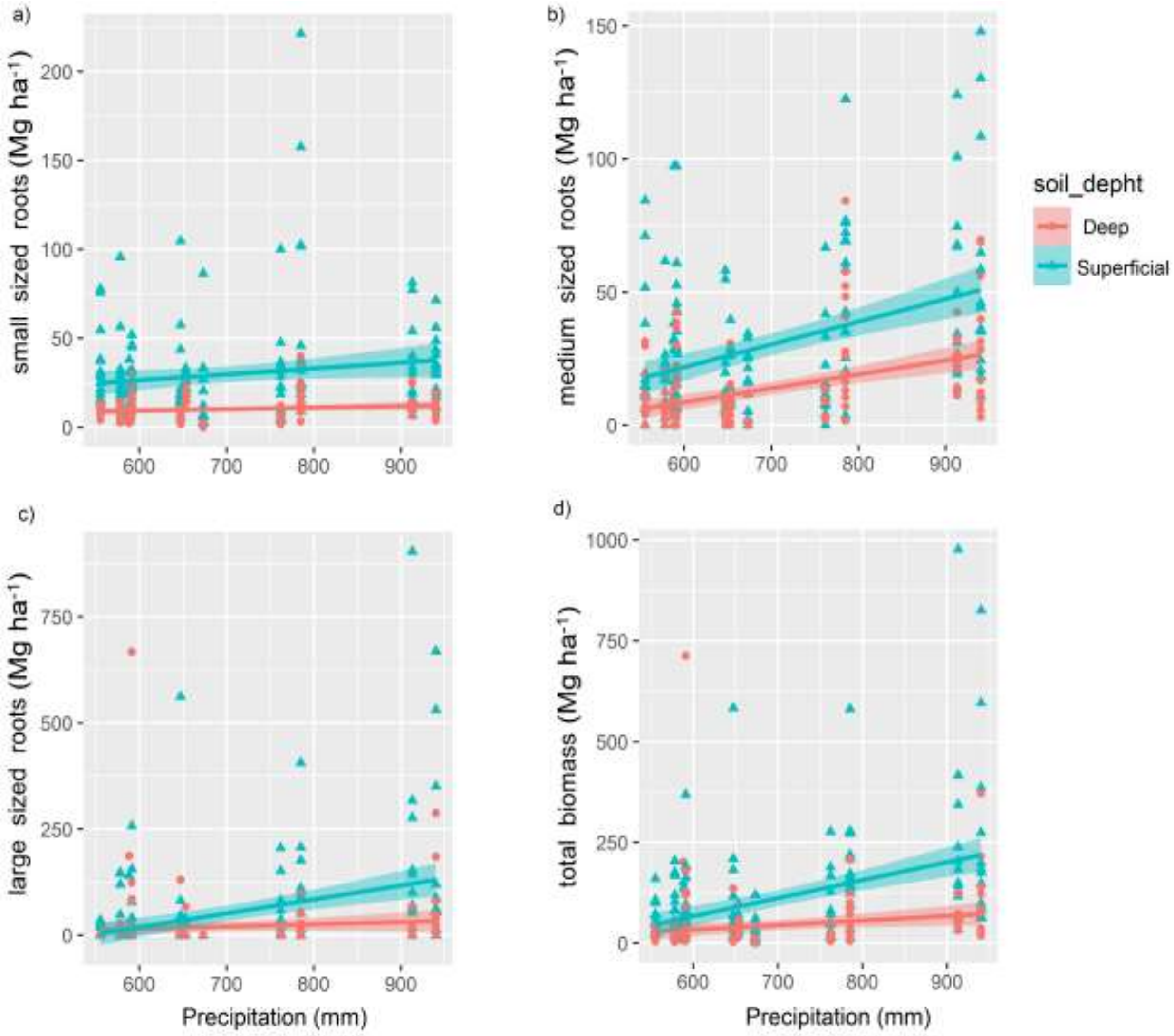

Figure 5. Effect of MAP (mm) on small-sized roots (a), medium-sized roots (b), large-sized roots (c) and total root biomass (d) regarding two classes of soil layer (superficial and deep) in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

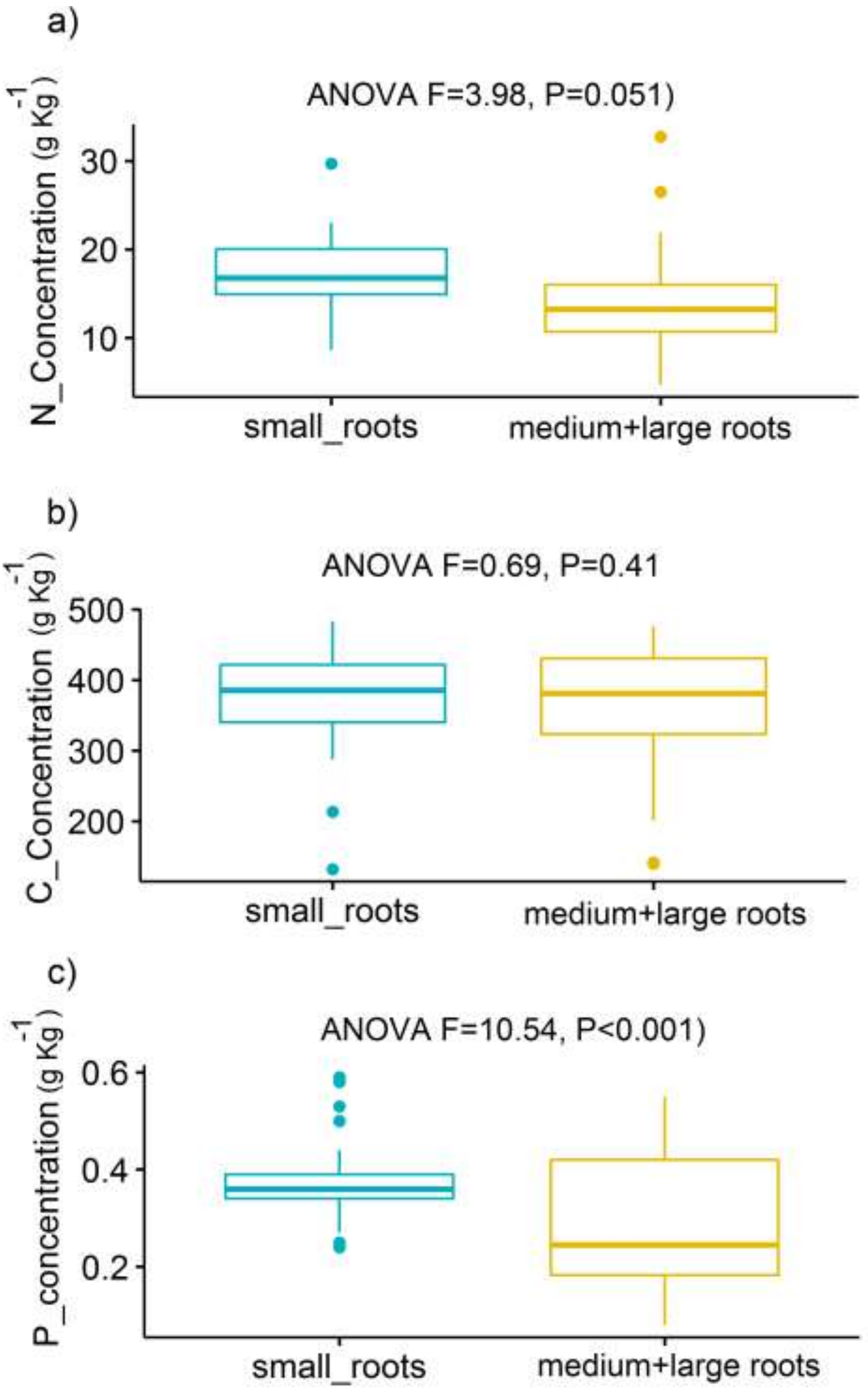

Figure 6. Nutrient concentration (N, C and P) by root size class across dry forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

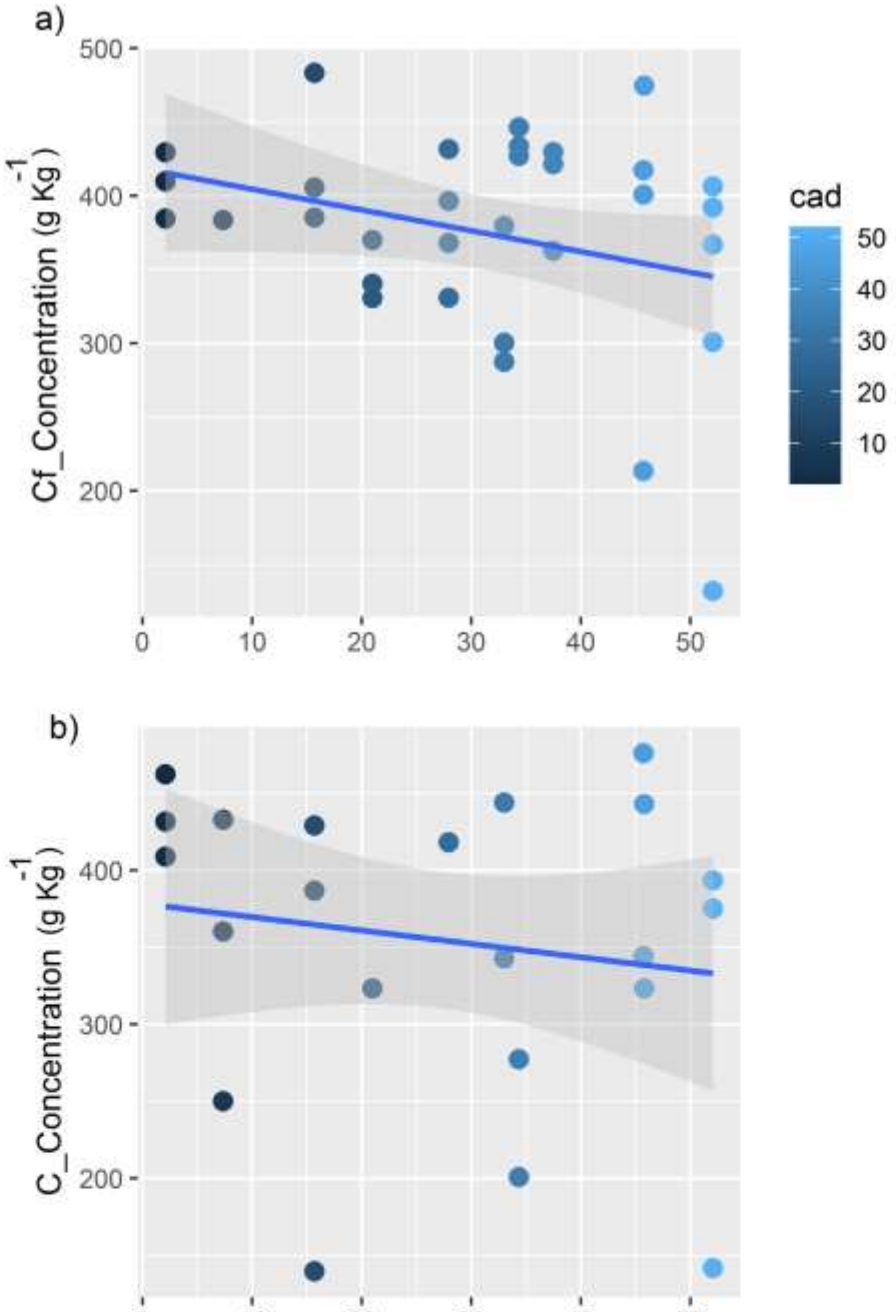

Figure 7. Effect of chronic anthropogenic disturbance (CAD) on root C concentration regarding small (a) and medium+large-sized roots (b) sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

SUPPLEMENTARY MATERIAL

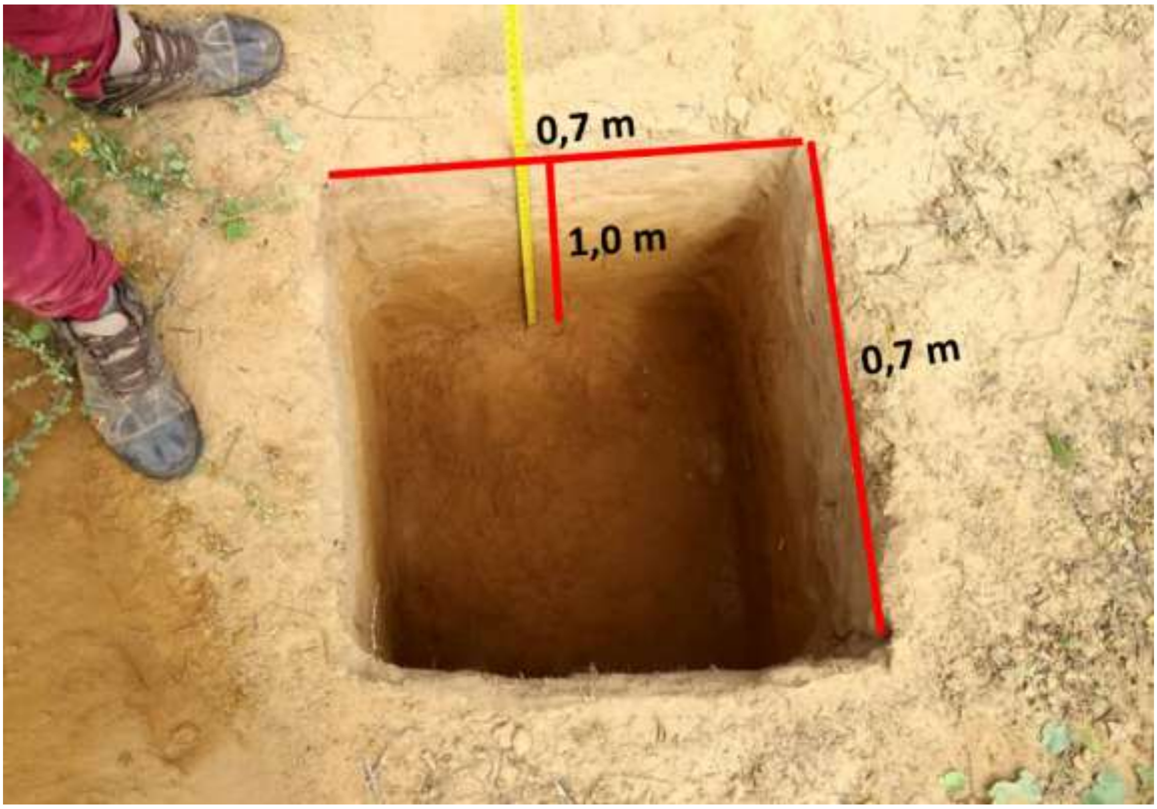

Figure S1. Trench measurement scheme used to obtain root biomass in a Brazilian dry tropical forest based on (COSTA et al., 2014).

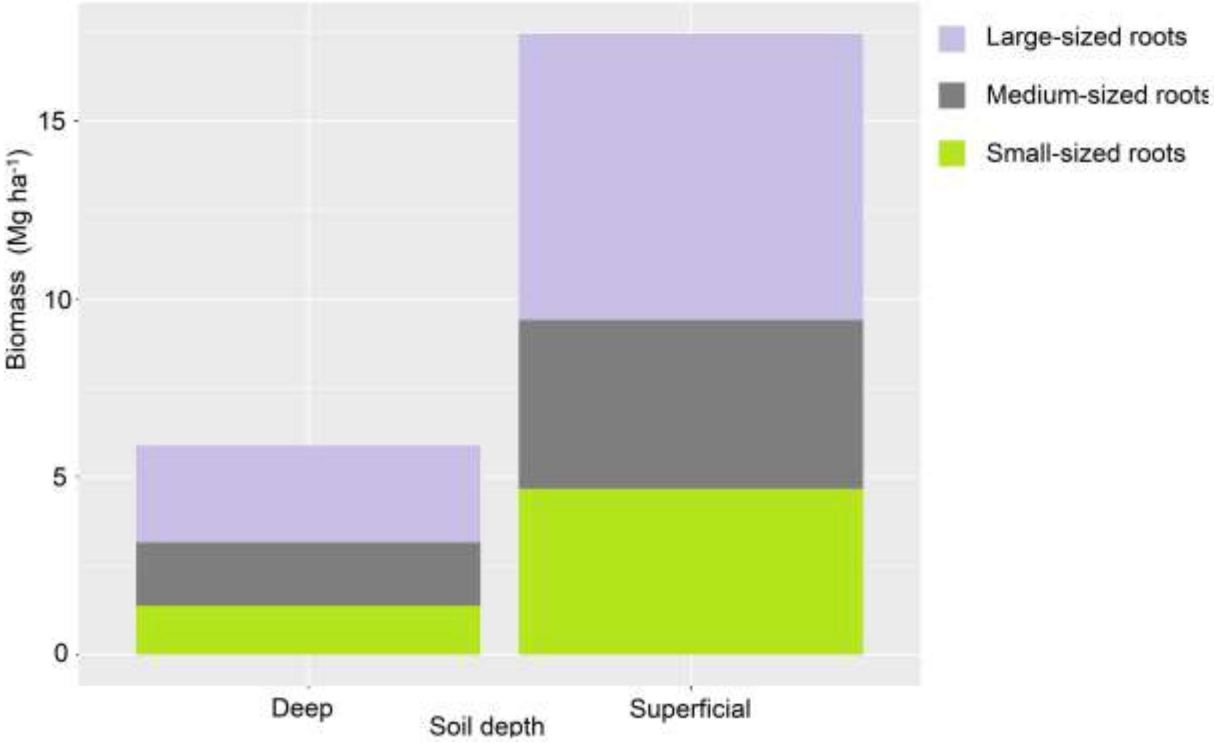

Figure S2. Distribution of root biomass according to size class and soil layer in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

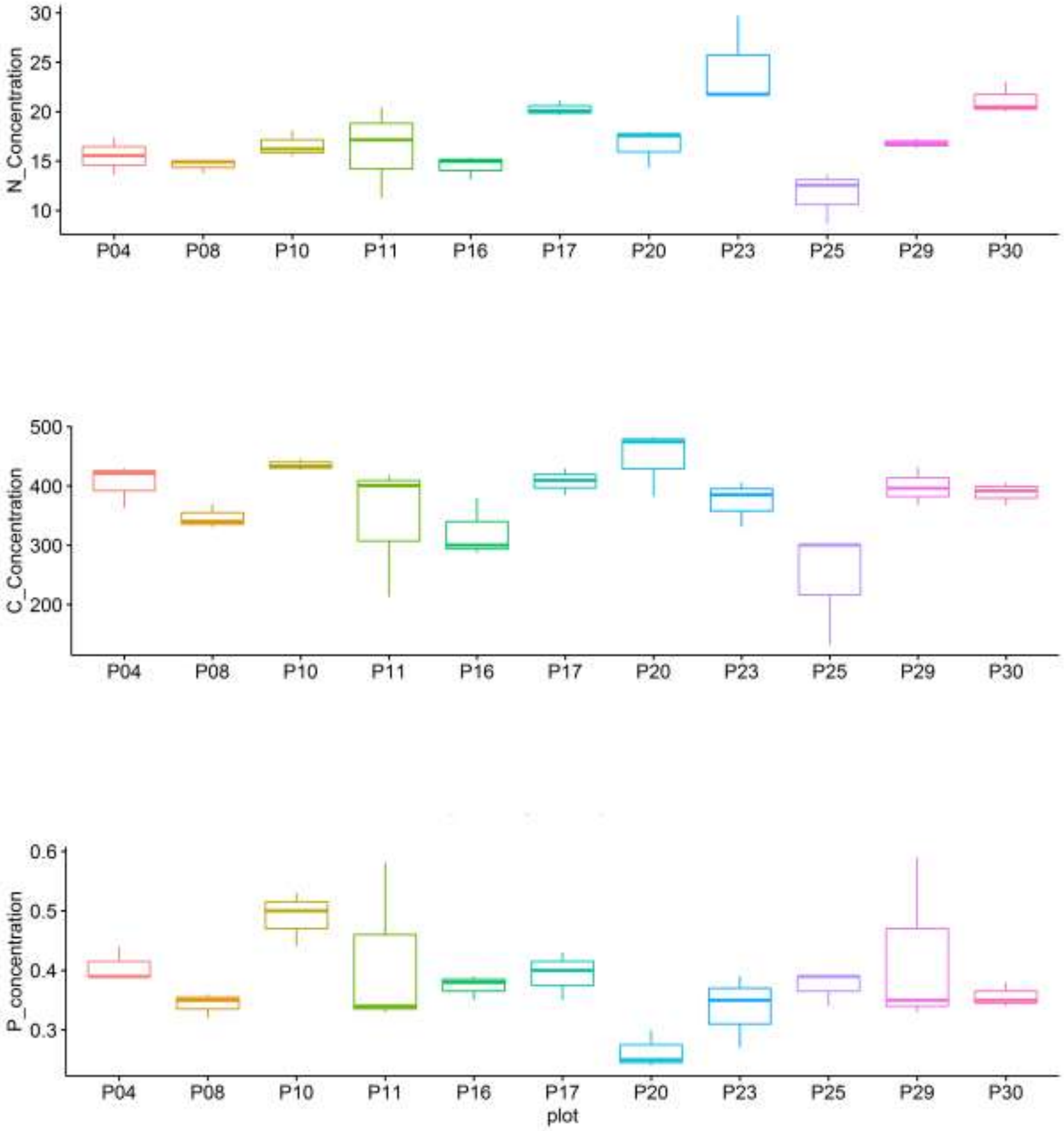

Figure S3. Nutrient concentration (g kg^{-1}) for small-sized roots across dry forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

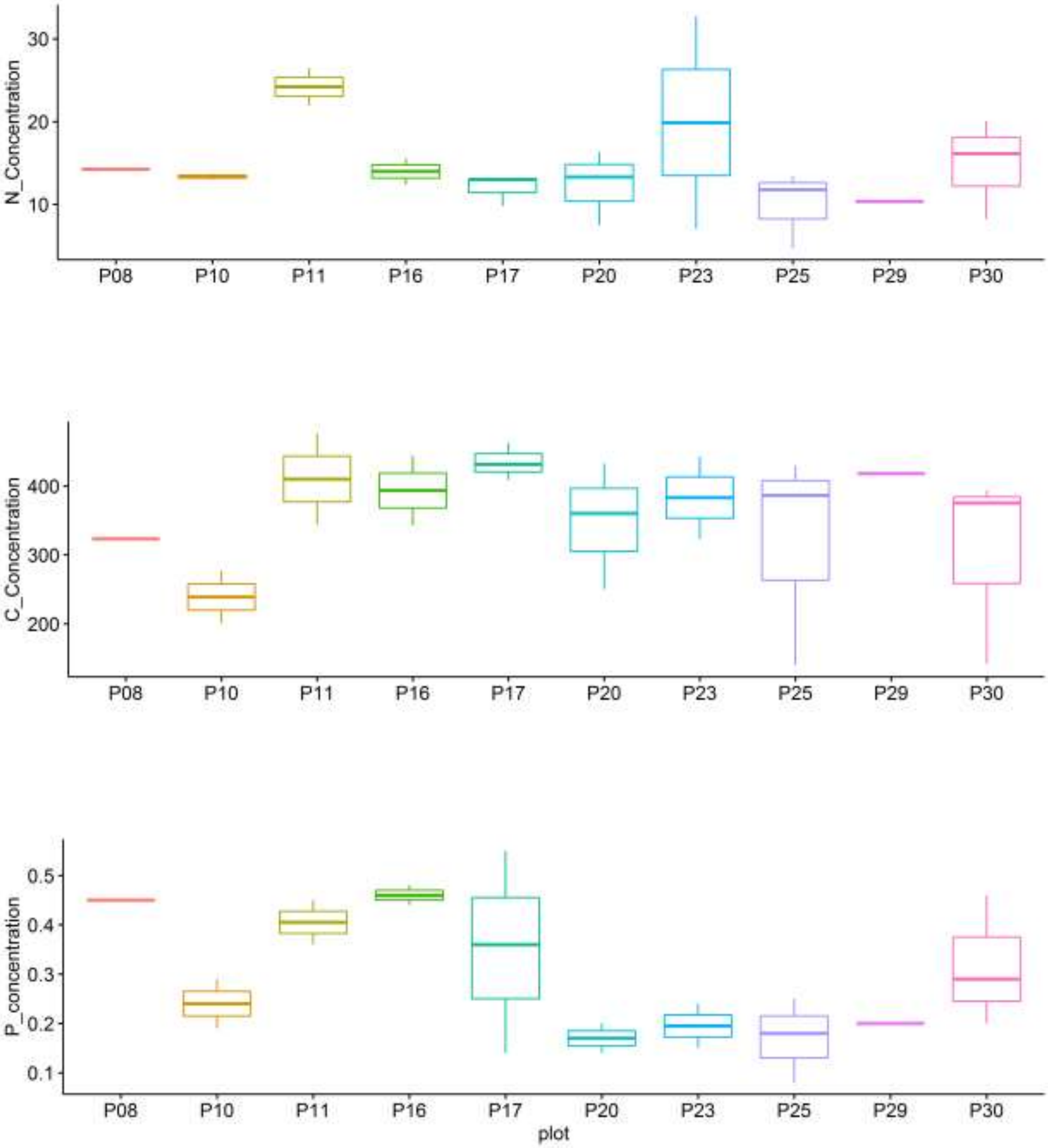

Figure S4. Nutrient concentration (g kg^{-1}) for medium+large-sized roots across dry forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazi

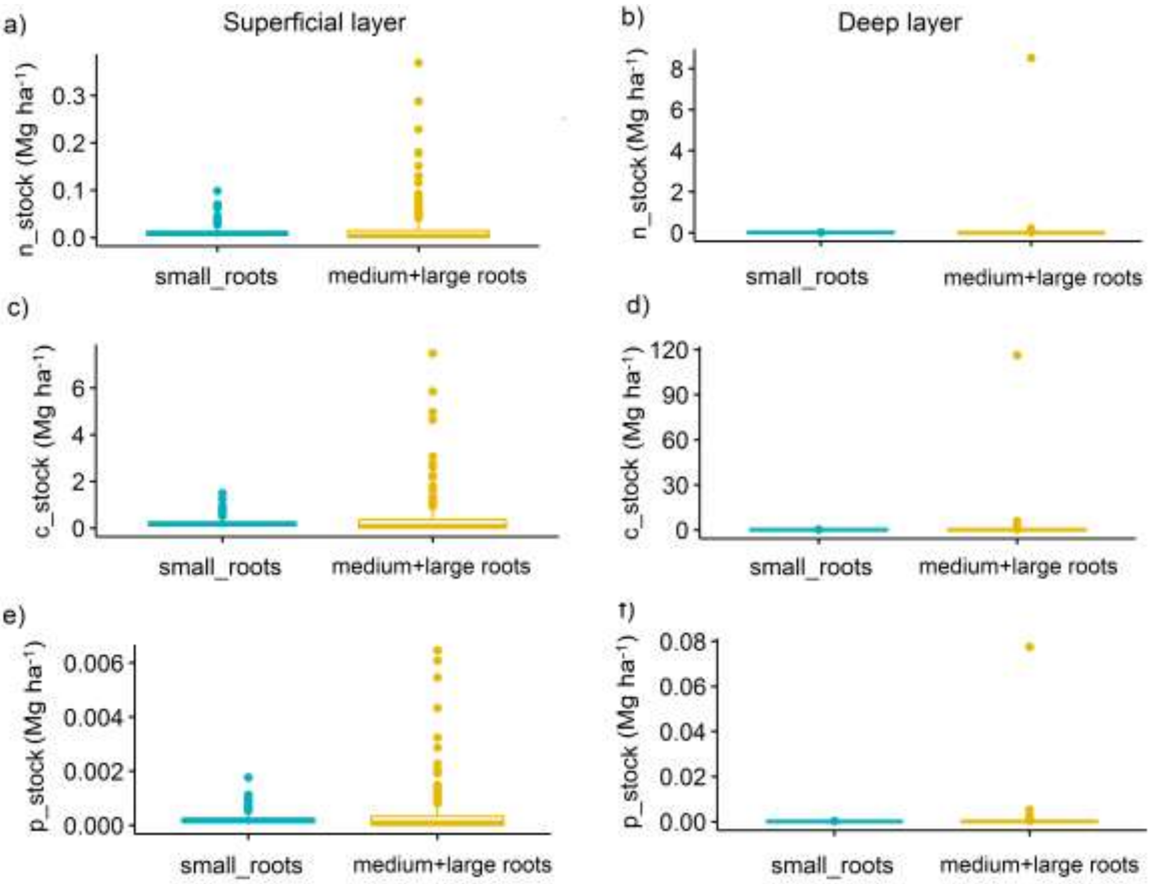

Figure S5. Nutrient stocks according to soil layer (superficial vs. deep) for small and medium+large-sized roots across dry forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

4 ARTIGO 2: CHRONIC-ANTHROPOGENIC DISTURBANCES AND INCREASED ARIDITY ALTER BELOWGROUND BIOMASS AND NUTRIENT CONCENTRATION ACROSS A REGENERATING CAATINGA DRY FOREST

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Chronic-anthropogenic disturbances and increased aridity alter belowground biomass and nutrient concentration across a regenerating Caatinga dry forest

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Abstract

Tropical-forest ability to deliver ecosystem services in human-modified landscapes depends on patterns of forest resilience (i.e. regrowth rate) and its drivers. Here we investigate the stock of belowground biomass and nutrients (C, N, P) in a Caatinga dry forest. Biomass/nutrient estimates were obtained once by a destructive method across old-growth and regenerating forest stands. Scores were examined according to two soil depths and root size with precipitation, aboveground biomass, chronic-anthropogenic disturbances, forest age and successional status as explanatory variables. Root biomass varied from 1.89 up to 17.53 Mg ha^{-1} averaging 8.34 ± 1.7 Mg ha^{-1} across regenerating forest stands. The root to shoot (R/S) achieved 0.92 ± 0.9, with biomass concentrated in the soil superficial layer and among middle and large roots. Regenerating forest stands exhibited significant variation for all class sizes (small-sized roots ANOVA $F = 4.51$, $P < 0.001$; medium-sized roots ANOVA $F = 6.39$, $P < 0.001$; large-sized roots ANOVA $F = 4.11$, $P < 0.001$; total root biomass ANOVA $F = 7.2$, $P < 0.001$). Belowground biomass did not differ between the different classes and did not exhibit successional trends, responding positively to annual precipitation but negatively to aboveground biomass and chronic disturbances. The roots were concentrated in the surface layer of the soil. Nutrient concentration was in the range by dry forests and exhibit higher scores across small roots, but no successional trends. Medium and large roots and deep layer support more nutrient stocks than small roots and superficial layer, respectively. Our results suggest that the Caatinga dry forest covering sand soils has a natural limitation (water and nutrients) to produce and accumulate forest biomass, including root biomass. Forest regeneration benefits from the roots and stumps available across some old fields resulting in relatively high R/S ratio across secondary forests, while it limits the emergence of successional trends related to belowground biomass. Both roots and nutrients concentrate in the superficial soil layer, including middle and large roots targeted by weeding operations. Thereby, the Caatinga belowground biomass and their role relative to forest resilience and provision of ecosystem services appear to be very sensitive to increased aridity and exploitation of forest resources as predicted.

Kyes words: Root biomass; Seasonally tropical dry forest; Secondary Forest; Chronic anthropogenic disturbance; Nutrient cycling

INTRODUCTION

Tropical forests have been considered a key component in support for global sustainability by providing key ecosystem services such as climate regulation, carbon sequestration/storage, soil/watershed protection freshwater provision (Brandon, 2014). For most cases, forest ability to deliver services correlated to forest biomass, what has fueled the academic interest relative to drivers for biomass storage, distribution (above vs. belowground), and recovery rates in response to disturbances and its drivers. This is particularly relevant by considering that tropical forests continue to be incorporated into human-modified landscapes (Gardner et al., 2009; Melo et al., 2013; Wies et al., 2021), through which forest persistence and ecosystem service delivery rely on forest ability to regenerate and thus accumulate biomass at distinct rates as regeneration proceeds (Chazdon et al., 2016).

Patterns of forest recovery or growth rate in response to human disturbance has long been exanimated, particularly in the case of forest regeneration following agriculture and cattle production (Robin L. Chazdon, 2014). Overall, stem abundance and tree species richness tend to recover (i.e. approach the scores by old-growth forest stands) faster than taxonomic composition and aboveground biomass and forest physical structure such as the abundance of large trees (Guariguata & Ostertag, 2001). Although regenerating forest stands aging 40-50 yr old are able to support tree species richness similar to those by old-growth forests, centuries may be required in the case of aboveground biomass (Chazdon et al., 2016). Regardless of forest attribute, recovery rate responds to myriad of drivers, particularly soil water/nutrient content, seed availability, presence of resprout sources and the incidence of additional disturbances (e.g. browsing by livestock) while regeneration proceeds. Land use imposing soil degradation can drastically reduce the recovery rate or forest resilience or even eliminate the possibility of forest regeneration without human assistance.

However, most of the knowledge on forest regeneration have emerged from the rain forests and the aboveground biomass. Much less attention has been given to dry forests and the role played by belowground biomass and its ability to store nutrients. A substantial coverage by dry forests globally has been exposed to a land use combining slash-and-burn agriculture, free-range cattle raising and the extraction of forest products, particularly firewood collection (Powers et al., 2018; Sfair et al., 2018). Slash-and-burn agriculture is a common practice across dry forests, where after the cutting down (slash), the vegetation is burned. Although positive effects can be detected with this archaic method (e.g. elimination of weeds and rapid incorporation of nutrients in the soil), a great variety of negative effects (from disruption of soil seed bank to dispersal limitation) can impact drastically dry forests (Bezerra et al., 2022). In such an extractivism-based land use, forest reliance is essential even to guarantee the nutrient stocks required for crop and fodder production (Blackie et al., 2014). Evidence accumulated so far indicates alarming rates of forest degradation (sensu Ghazoul et al., 2015), with some secondary forest stands supporting a tiny proportion of aboveground forest biomass as compared to old-growth forest stands (Chazdon et al., 2016). The drivers and the role played by belowground biomass remain little investigated regardless the ecological and social relevance by dry forests.

In the last decade, the Caatinga dry forest in northeast Brazil has contributed to a better perspective on dry forest ecology, particularly in the case of forest response to human disturbances (e.g.) and increased aridity as predicted by climatic models (Arnan, Arcoverde, et al., 2018; Rito et al., 2017). It is worth mention the proliferation of disturbance-adapted plant species, reduced forest biomass across the forest mosaics (Souza et al., 2019), and a forest regeneration process depending on resprouts, resulting from a combination of slash-and burn agriculture plus a potential impact by free-range goats and the exploitation of forest products; i.e. chronic disturbances (Barros et al., 2021). All forest attributes also respond to precipitation levels, suggesting that increased aridity shall impact ecological process and sustainability in the human-modified landscapes of this irreplaceable biota (Rito et al., 2017).

The focus of this study is to understand how the regeneration of areas of Caatinga that suffered clear cutting and burning recover biomass and nutrients from the roots. In this paper we examine the Caatinga belowground forest biomass and its nutrient concentration/stock in order to reveal the role played by this biomass compartment and potential drivers. We provided biomass and nutrient scores (N, P, C) from regenerating forest stands (10 to 76 yrs old) in the context of slash-and-burn agriculture and old-growth forests. Forest-stand spatial distribution covers wide gradients relative to both annual precipitation, human-chronic disturbances and aboveground biomass. Our findings are discussed in the light of dry forest potential to produce/store biomass in human-modified landscapes.

MATERIAL AND METHODS

Description of the study area

Sampling was conducted in the Parque Nacional do Catimbau, which is a human-modified landscape covering an area greater than 60,000 ha in northeastern Brazil (see Figure 1). The relief is predominantly flat and mainly composed of sandy soils poor in nutrients (Corrêa et al., 2015). The climate is characterized by marked seasonal variations, with an average temperature of approximately 23°C and annual rainfall ranging from 480 to 1000 mm3 per year across the landscape. The rains are concentrated in the months of April to July (Vanderlei et al., 2022).

The predominant vegetation in the area is a low stature, seasonally dry forest, dominated by multi-stemmed shrubs and tree species from the families Euphorbiaceae, Fabaceae and non-tree Cactaceae (Rito et al., 2017). During the rainy season, a dense layer of herbs and grasses can be found (Vieira et al., 2022). However, subsistence agriculture activities, which still prevail within the protected area, have resulted in the conversion of the ancient forest into a successional mosaic composed of cropland/pasture, regeneration and ancient forest stands. Aboveground forest biomass ranges from 3.71 to 38.54 (Mg ha^{-1}) (Souza et al., 2019). Sampling was carried out in the Parque Nacional do Catimbau, which is a human-modified landscape covering an area of over 60,000 ha in northeastern Brazil (see Figure 1). The relief is predominantly flat and mainly composed of sandy soils poor in nutrients (CORRÊA, CAVALCANTI, & LIRA, 2015). The climate is characterized by marked seasonal variations, with an average temperature of approximately 23°C and annual rainfall ranging from 480 to 1000 mm3 per year across the landscape. The rains are concentrated in the months of April to July (VANDERLEI et al., 2022).

The predictors of biomass and nutrients

In this study, we include several explanatory variables to understand variations in aboveground forest biomass and nutrients, including mean annual rainfall, chronic anthropogenic disturbance, aboveground biomass, forest age, and successional status (vegetation vs. regenerating forest). Previous studies conducted on our focus plots in the last five years preceding this sampling provided scores for all explanatory variables. We obtained the average annual rainfall for each plot using historical data from the

Wordclim® platform, which ranged from 555 to 940 mm yr-1 in our focal plots. The chronic anthropogenic disturbance index ranged from 2.74 to 58.07 in our focal landscape, and we calculated it based on direct measurements at the plot level (e.g., number of stumps and cattle droppings) and metrics considered representative of pressure of human disturbance, such as the distance from the plot to the farm holdings, as previously described by Arnan et al., (2018b). In our focal landscape, the disturbance index ranged from 2.74 to 58.07. We estimated aboveground biomass data using an allometric equation developed for the Caatinga dry forest, as detailed in Souza et al. (2019). Information on forest stand age and successional status was provided by Barros et al. (2021).

Sampling design for biomass and nutrients

Belowground biomass and nutrient concentration/stocks were recorded across a total of 15 0.1-ha permanent plots previously established in our focal landscape (see BARROS et al., 2021; RITO et al., 2017). Plots were located at least 2 km apart each other. Five plots were located into old-growth forest stands, where there were no sign of prior clear-cutting. Additionally, ten plots covered regenerating forest stands (10-76 yrs old). These regenerating forest stands had been previously used for subsistence slash-and-burn agriculture including beans, cassava and maze with the regeneration process without human assistance since abandonment (for more details please see BARROS et al., 2021; SOUZA et al., 2019).

Root biomass was obtained by a destructive method, digging three trenches of 70 cm x 70 cm x 100 cm each (COSTA et al., 2014; Figure S1). The excavation was carried out with a metal shovel, while trenches were subdivided into 10 depth intervals of 10 cm each. All root material was carefully sieved in the field using a wooden sieve with a 2 mm metal grid. After being separated from soil sediment, the plant material was packed in individual paper bags. All material was dried in an oven at 60°C until reaching constant mass. Root exudates and other materials were eliminated from the samples in the laboratory through a screening. Subsequently, the roots were separated and classified into three different categories, according to their diameter: i) <2.0 mm for small-sized roots; ii) between 2.01 mm and 10.0 mm for medium-sized roots; and iii) > 10.01 mm for large-sized roots. To extrapolate our samples for biomass in Mg ha^{-1}, the value (g) collected for each type of root was multiplied by the expansion factor of 1.69 on order to account for those uncollected roots in the base of stems as recommend by reached Albuquerque et al. (2015).

Chemical Analysis

The root samples were dried at 60°C and grounded to fine powder to pass through a 2 mm sieve. Sub-samples of root material were weighed (2 to 3 mg) and sealed in tin capsules. The capsules were introduced into the elemental analyzer Carlo Erba Model 1110 (Milan, Italy) for the determination of total C and N concentrations. Gases are generated following the samples' combustion, then, purified in a chromatography column and introduced into the mass spectrometer for isotopic ratios determinations (IRMS Delta Plus, Finnigan Matt, San Jose, CA, USA). Sugarcane leaves were used as standard material for vegetation material. The δ 15 N and δ 13 C natural abundance is expressed in parts per thousand (‰) as a result of a standard internationally recognized equation: δ 15 N or δ 13 C = (R sample / R standard -1) x 1000...........................(1) where, R is the molar ratio in the sample and standard between 13 C and 12 C or 15 N and 14 N. The standard used for C isotope was Peedee Belemnite (PDB; limestone of the rand Canyon region, USA) and atmospheric air for N isotope. The analytical errors accepted were ± 0.3%, 0.1%, 0.3 ‰ and 0.5 ‰ for C, N, δ 13 C and δ 15 N, respectively. hosphorus concentration in root samples was determined through a wet digestion method, using nitric acid and perchloric acid (4:1 ratio), where 10 mL of the mixture of acids was added to 0.5 g of each sample (Surruge & Haag, 1974). After that, the digests were diluted to 25 mL and the P concentration determined Inductively Coupled Plasma Optical Emission pectroscopy (ICP- OES; Perkin Elmer Modelo Optima 8300 DV).

Data analysis

Due to reduced biomass context, root biomass was collapsed into two categories: social superficial layer (< 50 cm depth) and deep layer (50 -100 cm depth). To compare root biomass and nutrient concentration between regenerating and old-growth dry forest plots, we use one-way ANOVA analyses. We used Generalized Linear Mixed Models (GLMMs) to examine the influence of aboveground biomass, forest age, chronic anthropogenic disturbance (CAD), mean annual precipitation (MAP) and soil depth on root biomass and root nutrient concentration across a chronosequence gradient. Accordingly, in our models we accommodate trenches per plot as random factor, while aboveground biomass, forest age, CAD, MAP and soil depth were entered as fixed factors. For this, we first assessed the collinearity among predictor variables with the variance inflation factor (VIF) using the “car” package (Fox and Weisberg 2011) in the R software (R Core Team, 2017). As age and aboveground biomass are correlated (-0.65), we removed age of your models to reduce the VIF values. In this case, all VIF values were lower than 1.5 (ranging from 1.0 to 1.46), suggesting independence among predictors (Chattefujee & Hadi, 2006). All analyses were run using the R environment (R Development Core Team 2017).

RESULTS

General pattern

Across the chronosequence, root biomass ranged from mean ± SE 1.89 ± 0.33 Mg ha^{-1} to 17.53 ± 2.28 Mg ha^{-1} in regenerating forest stands with 13 and 26 years-old, respectively, with regenerating forest stands exhibited significantly variation for all size class (small-sized roots ANOVA F = 4.51, P<0.001; medium-sized roots ANOVA F = 6.39, P<0.001; large-sized roots ANOVA F = 4.11, P<0.001; total root biomass ANOVA F = 7.2, P<0.001) (Figure 2). Although, old-growth forests showed higher total root biomass (mean ± SE 15.91 ± 1.8 Mg ha^{-1}) than regenerating forest stands (mean ± SE 8.34 ± 1.07 Mg ha^{-1}), this difference was not significant (ANOVA F = 3.43, P=0.06). We found higher R/S (ratio belowground/above ground biomass) ratio across regenerating forest stands than old-growth forests (Table 1). In terms of size class, root biomass did not differ for small-sized roots (mean ± SE, 2.66 ± 1.13 Mg ha^{-1} regenerating forests; 3.18 ± 1.1 Mg ha^{-1} old-growth forests, ANOVA F = 2.63, P= 0.105), medium-sized roots (mean ± SE, 3.09 ± 1.7 Mg ha^{-1} regenerating forests; 4.48 ± 2.3 Mg ha^{-1} old-growth forests ANOVA F= 0.01, P=0.89) and large-sized roots (mean ± SE, 2.51 ± 0.88 Mg ha^{-1} regenerating forests; 8.24 ± 1.8 Mg ha^{-1} old-growth forests, ANOVA F= 1.97, P= 0.161) and total root biomass (mean ± SE, 8.34 ± 1.07 Mg ha^{-1} regenerating forests; 15.91 ± 1.8 Mg ha^{-1} old-growth forests, ANOVA F = 3.43, P=0.06) (Table 1, Figure 2). Regarding the distribution root biomass according to soil layer, root biomass in both regenerating and old-growth dry forest plots was higher in superficial layer than in deep layer for all class size (small-sized roots ANOVA F = 13.84, P<0.001; medium-sized roots mean ANOVA F = 27.45, P<0.001; large-sized roots ANOVA F = 3.28, P=0.07; total root biomass ANOVA F = 18.98, P<0.001) (Figure 3). Regenerating forests did not exhibited significantly variation of root biomass in terms of size class (ANOVA F = 3.28, P=0.07), while large-sized roots across old-growth forests showed significantly higher root biomass than medium and small-sized roots (ANOVA F = 4.46, P<0.05) (Figure 4).

In terms of nutrient concentration, the N (ANOVA F= 16.83, P<0.001) and P (ANOVA F = 6.72, P<0.001) concentration varied significantly among regenerating dry forest stands regarding small-sized roots (Figure S2), while for large-sized roots these nutrients did not show variation (N concentration ANOVA F = 3.91, P=0.08; C concentration ANOVA F = 0.41, P=0.52; P concentration ANOVA F = 1.47, P=0.23) (Figure S3). Moving to size class, nutrient concentration range from 0,68% to 1,8% for N, 21,45% to 41,64% for C and 0,019% to 0,045% for P regarding small-sized roots, while for medium + large-sized roots these concentrations range from 0,71% to 1,53% for N, 20,84% to 40,47% for C and 0,018% to 1,1% for P (Table 2). More specifically, small-sized roots support significantly higher concentration of N than medium + large-sized roots (ANOVA F =5.17, P<0.05) with a similar tendency to C (ANOVA F =0.31, P=0.57) and P (ANOVA F =0.22, P=0.63) across regenerating forest stands (Figure 5).

As for nutrient stocks, their values (M±SD Mg ha^{-1}) for small roots were 0.044±0.02 (N), 1.11±0.5 (C) and 0.0011±0.001 (P), and for medium roots 0.041 ±0.02 (N), 1.03±0.04 (C), and 0.0011±0.001 (P), while for large roots it was 0.043±0.05 (N), 1.03±1 for (C) and 0.0019± 0.003 (P) (table S1). As expected, medium + large roots and deep layer support more nutrient stocks than small roots and superficial layer, respectively (Superficial layer: N stock ANOVA F=12.8, P<0.001, C stock ANOVA F= 8.09, P<0.01, P stock ANOVA F=4.91, P<0.05; Deep layer: N stock ANOVA F=11.86, P<0.001, C stock ANOVA F= 12.14, P<0.001, P stock ANOVA F=3.82, P=0.05) (Table S1 Figure S4).

Root biomass and nutrient drivers across regenerating dry forest stands

In general, all explanatory variables affected root biomass across regenerating forest stands (Table 3). More precisely, chronic anthropogenic disturbance had a drastic and negative effect on medium-sized roots, large-sized roots and total root biomass regarding both superficial and deep soil layer (Figure 6). The annual mean precipitation was a decisive and positive predictor for root biomass regarding large-sized roots (Figure 7), while both soil depth and aboveground biomass had a positive and negative effect, respectively for all size class (Table 3).

Moving to nutrients, annual mean precipitation affected strong and positively N and C concentration regarding small-sized roots as well as N concentration in terms of medium + large-sized roots, while chronic disturbance and aboveground biomass played a minor role (Table 4, Figure 8).

DISCUSSION

Our result suggests that the Caatinga regenerating or secondary forest support a variable amount of root or belowground biomass. Root biomass concentrates in the superficial layer as well as in medium-sized and large roots rather than in the small or fine roots. Moreover, regenerating and old-growth forest stands support similar amounts of belowground biomass and the same pattern of biomass distribution in the space (i.e. high cross-stand variation) and relative to soil profile. However, secondary and old-growth forests differ in terms of the root/shoot ratio, with belowground biomass achieving a higher contribution in the secondary forest. Secondary forest stands exhibit varying scores relative to root nutrient concentration (C, N, P), but they support similar scores as compared to old-growth forest stands; i.e. secondary and old-growth forest support similar nutrient concentrations. However, in both case nutrients are concentrated into the small-sized roots. Finally aboveground biomass and its nutrient concentration is affected by a combination of environmental and forest-stand variables (i.e. aboveground biomass), particularly annual precipitation and chronic disturbance. In synthesis, aboveground biomass and nutrient concentration across the successional mosaics of the Caatinga dry forest are in some extent predictable although the forest successional status does not represent the main driver with exception of the root to shoot investment.

There is little information relative to belowground forest biomass across dry regenerating or secondary forests what impose to discuss our uncovered patterns in the light of the general patterns relative to dry forest biomass (see the syntheses by Guariguata; Ostertag, 2001; Murphy; Lugo, 1986). In general, we assume that until the last century there was around 292 Pg of root biomass globally (Jackson et al., 1997). Furthermore, the average shoot to root ratio was 0.25 and this biomass supported approximately 38 Pg of carbon, 0.92 Pg of nitrogen and 0.085 Pg of phosphorus in fine roots (Jackson et al., 1997). More recent studies indicate that these data are underestimated by 60% and that the global pool of roots exceeds 520 Pg, concentrating more than 280 Pg C (Robinson, 2007). We can minimize the global information gap for root biomass and its nutrients in dry forests by comparing our findings with those from other dry forests. For example, data from dry forest in Dalhe, India averages 28.4 Mg ha^{-1} of root biomass with carbon stock of 15.49 Mg C ha^{-1} (Meena et al., 2019) and in Chamela, Mexico with 17.1 Mg ha^{-1} of biomass (Jaramillo et al., 2003). Also, we found some examples of C concentration values, being 39 g kg^{-1} (i.e. Jaramillo et al., 2003) and N ranging from 6.3 g kg^{-1} (Jaramillo et al., 2003) to 12 g kg^{-1} (Lugo & Murphy, 1986). In fact, there is no information regarding root biomass, nutrient concentration and stocks for dry forests so far. Briefly, dry forest usually supports lower amounts of total forest biomass as compared to humid forests, a higher root to shoot ratio and successional trends; i.e. higher biomass in old-growth forests as compared to secondary forests and positive relationship with stand age, including C stocks (Cavelier et al., 1996; Mora et al., 2018), but no trends related to fine roots and stand age (Powers & Peréz-Aviles, 2013).

In this context, our findings reinforce the notion of low biomass amounts including, aboveground biomass with Caatinga scores probably among the lowest (Souza et al., 2019), but with secondary forest stands supporting in average a high R/S ratios as compared to old-growth forests. In other words, our results indicate higher R/S ratios while forest is regenerating or higher R/S ratios across secondary forest stands in the context of slash-and-burn agriculture. In a global perspective, the R/S for Caatinga exceeds the global average (see Robinson, 2007). Moreover, root biomass concentrates in the soil superficial layer and in the middle-sized and large root as already documented (Jaramillo et al., 2003), but our findings indicate that such a spatial concentration occurs regardless of the forest sucessional status (secondary or old-growth) or forest stand age. Finally, our findings reinforce (1) the range proposed by dry forests relative to nutrient concentration (see Murphy Et Al., 1995), and (2) a protagonism by smalls roots, but similar scores as compared to old-growth forests stands; i.e. no successional trends (see Costa et al., 2014; Vargas; Allen; Allen, 2008). In fact, rather than forest successional, root biomass and nutrient concentrations are sensitive to a myriad of drivers, particularly rainfall, but also chronic-anthropogenic disturbance as we documented here. Precisely, it is probably one of the first evidence suggesting that chronic disturbance negatively affect root biomass in dry forests.

Perhaps the most important patterns to be examined here regarding to potential baseline mechanisms refers to (1) an elevated R/S ration across secondary stands, (2) the lack of successional trends, and (3) the negative impact of chronic disturbances. For the others findings there are reasonable mechanisms proposed in the literature, such as the positive role by water and nutrients for biomass production/productivity in dry forests (see Becknell et al., 2021; Becknell; Kissing Kucek; Powers, 2012; Powers; Peréz-Aviles, 2013), land use effect on soil and roots (Castellanos et al., 2001; Colón & Lugo, 2006) and a higher R/S ratio as water availability reduce (Metcalfe et al., 2008). In this context, the Caatinga regeneration following subsistence agriculture has been advocated to rely on plant resprouting (Barros et al., 2021; Bezerra et al., 2022; Vanderlei et al., 2022; see also Werden et al., 2020) including those considered root suckers as they emerge of roots from native plants able to survive or persist across the crop fields. In the case of our focal landscape, we refer to extensive root systems from clonal plant species such as *Pityrocarpa moniliformis* (Vanderlei et al., 2022). As forest regenerates, above-ground biomass slowly accumulates, what also explain a negative relationship between aboveground biomass and some belowground biomass attributes as we documented here.

However, some farmers try to eliminate stumps and roots from crop fields via weeding, causing the emergence of forest stands with low rate of biomass accumulation (see (Souza et al., 2019), and a great cross-stand variety relative to root biomass. Finally, as regenerating forest stands represent a source of forest products for locals (e.g. firewood, building materials, fodder) and are used as browsing grounds for livestock, such a constant removal of plant biomass, although can stimulate root development, may limit plants ability to accumulate biomass, including in roots. This is particularly relevant in the context of low water and nutrients availability associated to sandy soils, since these two resources affect forest productivity and regeneration (Arroyo-Rodríguez et al., 2016; Moura et al., 2016; Waring et al., 2016).

In synthesis, the Caatinga dry forest covering sand soils has a natural limitation (water and nutrients) to produce and accumulate forest biomass, including root biomass. Forest regeneration benefits from the roots and stumps available across some old fields resulting in relatively high R/S ratio across secondary forests (see Chidumayo, 2014), while it limits the emergence of successional trends related to belowground biomass. Both roots and nutrients concentrate in the superficial soil layer, including middle and large roots targeted by weeding operations. As species survival and regeneration process may be tightly linked to the successful development of superficial, robust rooting systems across tropical dry forests (Vanderlei et al., 2022), the Caatinga belowground biomass and their role relative to forest resilience and provision of ecosystem services appear to be very sensitive to increased aridity and exploitation of forest resources as already predicted (Silva et al., 2017).

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Table 1. Average data of values for each area with different ages (from 10 to 76 years old) in a chronosequence of natural regeneration of the Caatinga and areas old-growth forest, discriminating the average annual precipitation (AAP); chronic anthropogenic disturbance (CAD); belowground biomass (BGB); aboveground biomass (AGB); small sized roots (<2.0 mm), medium sized roots (2.01 to 10.0 mm), large sized roots (> 10.01 mm) and total root biomass (all in Mg ha^{-1}); root/shoot ratio (R/S) and mean value ± standard error (M±SE) in a seasonally dry forest in northeastern Brazil.

Forest type	**Age**	**Small sized (Mg ha^{-1})**		**Medium sized (Mg ha^{-1})**		**Large sized (Mg ha^{-1})**		**BGB**	**R/S**	**AGB Mg ha^{-1}**	**PAC**	**AAP**
		Mg ha^{-1}	**%**	**Mg ha^{-1}**	**%**	**Mg ha^{-1}**	**%**	**Mg ha^{-1}**				
a) Regenerating forest stands	10	2.10	34.77	2.20	36.49	1.73	28.74	6.03	1.11	5.41	33.14	869
	12	3.99	34.61	6.20	53.81	1.33	11.58	11.52	3.1	3.71	25.87	919
	13	1.19	63.11	0.66	34.94	0.04	1.95	1.89	0.31	5.92	20.84	851
	23	4.25	24.23	5.66	32.27	7.63	43.50	17.53	2.01	8.72	35.77	866
	29	3.28	22.21	3.22	21.80	8.27	55.99	14.76	1.05	14.05	31.58	900
	43	1.25	39.97	1.15	36.90	0.72	23.13	3.12	0.08	38.54	3.61	940
	46	3.52	38.77	3.80	41.84	1.76	19.39	9.08	0.47	18.96	23.96	755
	51	2.41	30.10	2.44	30.48	3.15	39.42	8.00	0.48	16.44	16.73	897
	56	2.48	33.86	3.86	52.69	0.99	13.45	7.33	0.39	18.56	15.46	762
	76	2.17	52.48	1.76	42.49	0.21	5.02	4.13	0.27	15.11	48.11	533
	M±SE	2.66±1	37.41±11.7	3.09±1.7	38.37±9.2	2.51±0.8	24.22±16.7	8.34±1.7	0.92±0.9	14.55±9.6	25.51±11.8	829±114
b) Old-growth forest	-	4.17	13.74	7.75	25.51	18.44	60.74	30.36	0.48	63.61	2.08	940
	-	1.58	28.72	2.21	40.33	1.70	30.96	5.49	0.25	22.17	15.68	588
	-	4.63	38.38	3.28	27.21	4.15	34.41	12.07	0.33	36.08	27.95	762
	-	2.21	50.11	2.20	49.89	0.00	0.00	4.41	0.19	22.74	45.72	673
	-	3.32	12.21	6.97	25.62	16.93	62.17	27.22	0.70	39.07	52.06	913
	M±SE	3.18±1.1	28.63±14.4	4.48±2.3	33.71±9.8	8.24±1.8	37.66±2.8	15.91±1.8	0.39±0.18	36.73±15	28.87±1.85	775±135

Table 2. Averages data values of the concentration (g kg^{-1}) of nitrogen (N), carbon (C), phosphorus (P) and the ratio carbon/nitrogen (C/N) in small size (diameter <2,00 cm) and medium+large size roots (diameter > 2,01 cm) in a chronosequence of secondary forest after slash and burn agriculture and old-growth forest areas in northeastern Brazil.

Forest type	**Age**	**Small size root nutrient concentration (g kg^{-1})**				**Medium + large size root nutrient concentration (g kg^{-1})**			
		N	**C**	**P**	**C/N**	**N**	**C**	**P**	**C/N**
a) Secondary forest	10	17.51	416.07	0.34	23.76	13.39	377.84	0.18	31.75
	12	9.82	214.59	0.28	19.97	12.96	266.13	0.19	20.02
	13	12.14	416.42	0.39	34.46	11.12	253.83	0.51	25.78
	23	15.07	380.04	0.32	26.17	13.80	352.98	1.10	26.23
	29	10.98	305.22	0.32	27.48	14.33	404.79	0.72	28.94
	43	14.40	367.15	0.19	26.79	15.39	387.85	0.32	26.27
	46	11.07	296.72	0.31	26.65	7.63	208.43	0.25	27.73
	51	18.98	404.28	0.45	21.45	11.32	230.71	0.23	20.95
	56	8.07	257.79	0.36	32.66	7.11	214.55	0.24	28.54
	76	6.85	277.80	0.41	42.04	10.04	377.22	0.29	38.38
	M±SD	12.49±3.7	333.61±68	0.34±0.06	28.14±6.2	11.71±2.6	307.43±75	0.4±0.28	27.46±4.9
b) Old-growth forest	-	20.27	407.71	0.39	20.11	11.99	434.31	0.35	36.22
	-	11.62	244.49	0.37	21.04	9.98	318.44	0.17	31.92
	-	16.79	398.57	0.42	23.74	10.35	418.05	0.20	40.40
	-	16.30	343.67	0.42	21.09	24.20	410.09	0.41	16.95
	-	21.17	388.27	0.36	18.34	14.82	303.38	0.32	20.47
	M±SD	17.23±3.3	356.5±60	0.36±0.02	20.87±1.7	14.27±5.2	376.85±54	0.29±0.08	29.19±9.04

Table 3. Results of the Generalized Linear Mixed Models (GLMMs) exhibiting the effects of aboveground biomass, chronic anthropogenic disturbance (CAD), soil depth and mean annual precipitation (mm) on root biomass across regenerating dry plots in the Catimbau National Park, in Pernambuco state, northeastern Brazil

Class size	**Estimate**	**SE**	**t value**	**p**	**R^2**
Small-sized roots					
Intercept	-42.68	12.03	-3.547	<**0.001**	
Aboveground biomass	-2.30x 10^{-2}	4.19 x 10^{-3}	-5.487	<**0.001**	
Precipitation (mm)	3.69 x 10^{-4}	4.14 x 10^{-4}	0.891	0.38	0.22
CAD	-5.81 x 10^{-3}	4.06 x 10^{-3}	-1.451	0.157	
Soil depth	7.66 x 10^{-1}	3.2 x 10^{-2}	23.93	<**0.001**	
Medium-sized roots					
Intercept	-55.05	21.71	-2.535	<**0.001**	
Aboveground biomass	-3.14 x 10^{-2}	7.57 x 10^{-3}	-4.155	<**0.001**	
Precipitation (mm)	5.82 x 10^{-4}	1.02 x 10^{-3}	0.485	0.631	0.18
CAD	-1.95 x 10^{-2}	9.49 x 10^{-3}	-2.062	<**0.05**	
Soil depth	9.86 x 10^{-1}	2.96 x 10^{-2}	33.254	<**0.001**	
Large-sized_roots					
Intercept	-4.09	0.52	-7.756	<**0.001**	
Aboveground_biomass	-9.3 x 10^{-1}	1.18	-0.676	0.500	
Precipitation (mm)	8.56 x 10^{-3}	4.35 x 10^{-4}	19.648	<**0.001**	0.11
CAD	-1.36	4.3 x 10^{-1}	-3.145	<**0.01**	
Soil depth	14.99	7.39	2.028	<**0.05**	
Total root biomass					
Intercept	-2.31	2.61 x 10^{-1}	-8.834	<**0.001**	
Aboveground biomass	-2.84 x 10^{-3}	5.68 x 10^{-5}	-50.024	<**0.001**	
Precipitation (mm)	7.39 x 10^{-4}	5.88 x 10^{-4}	1.256	0.219	0.16
CAD	-1.77 x 10^{-1}	4.64 x 10^{-1}	-0.383	<**0.05**	

Table 4. Results of the Generalized Linear Mixed Models (GLMMs) exhibiting the effects of aboveground biomass, chronic anthropogenic disturbance (CAD) and mean annual precipitation (mm) on root nutrient concentration (g kg^{-1}) regarding small and large-sized roots sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

Nutrient	Root class	Estimate	SE	t value	p	R^2
N_concentration (g kg^{-1})	**Small-sized roots**					
	Intercept	1.19	0.75	1.59	0.111	
	Aboveground biomass	1.65×10^{-3}	2.32×10^{-3}	0.71	0.47	0.21
	CAD	-1.84×10^{-3}	7.29×10^{-3}	-0.25	0.82	
	Precipitation (mm)	1.57×10^{-3}	7.62×10^{-4}	2.06	<**0.05**	
	Large-sized roots					
	Intercept	0.51	0.74	0.68	0.49	
	Aboveground biomass	-1.19×10^{-3}	2.31×10^{-3}	-0.51	0.63	0.22
	CAD	1.09×10^{-3}	7.38×10^{-4}	1.47	0.13	
	Precipitation (mm)	2.03×10^{-3}	7.51×10^{-4}	2.67	<**0.001**	
C_concentration (g kg^{-1})	**Small-sized roots**					
	Intercept	5.48	4.42×10^{-1}	38.1	<**0.001**	
	Aboveground biomass	4.47×10^{-4}	2.76×10^{-5}	5.59	<**0.001**	0.11
	CAD	-2.25×10^{-3}	3.39×10^{-4}	-2.98	0.65	
	Precipitation (mm)	5.92×10^{-5}	4.14×10^{-5}	1.42	0.15	
	Large-sized roots					
	Intercept	6.1	8.15×10^{-2}	74.75	<**0.001**	
	Aboveground biomass	-3.63×10^{-3}	9.04×10^{-4}	-4.02	<**0.001**	0.01
	CAD	-3.13×10^{-3}	6.65×10^{-4}	-4.76	0.08	
	Precipitation (mm)	3.91×10^{-5}	1.45×10^{-5}	2.69	<**0.001**	
P_concentration (g kg^{-1})	**Small-sized roots**					
	Intercept	3.87	2.23	0.23	0.81	
	Aboveground biomass	-8.19×10^{-4}	2.57×10^{-2}	-0.03	0.97	0.15
	CAD	1.52×10^{-3}	2.1×10^{-2}	0.07	0.93	
	Precipitation (mm)	-3.22×10^{-6}	9.63×10^{-4}	-0.003	0.99	
	Large-sized roots					
	Intercept	1.67	2.94	0.57	0.36	
	Aboveground biomass	1.33×10^{-3}	1.63×10^{-4}	0.19	0.75	0.14
	CAD	7.07×10^{-3}	2.48×10^{-2}	0.28	0.37	
	Precipitation (mm)	-1.61×10^{-4}	2.11×10^{-3}	-0.07	0.43	

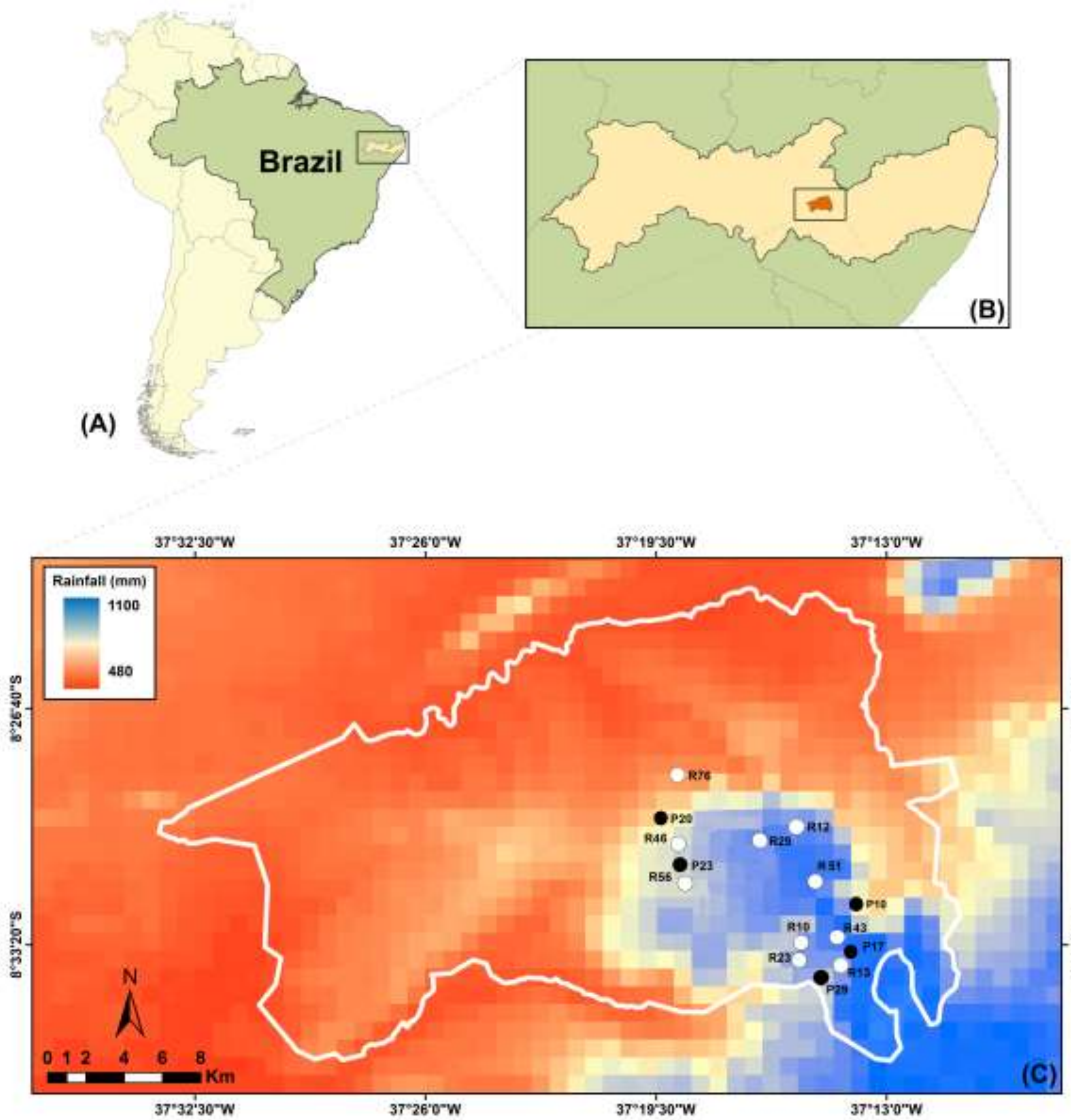

Figure 1. Map of the Catimbau National Park, in Pernambuco state, northeastern Brazil showing the sampling sites in old-growth forests and regeneration areas as well as land-use across the region.

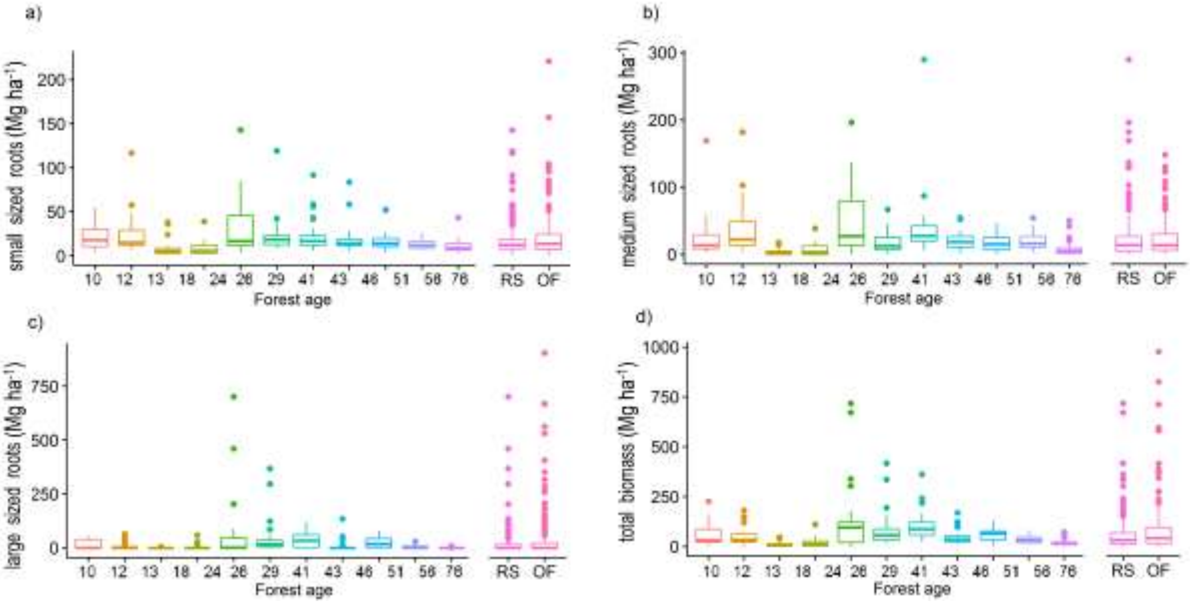

Figura 2. Relationship between forest age and root biomass according to different size class in the Catimbau National Park, in Pernambuco state, northeastern Brazil. RS= regenerating forest stands; OF= old-growth forests.

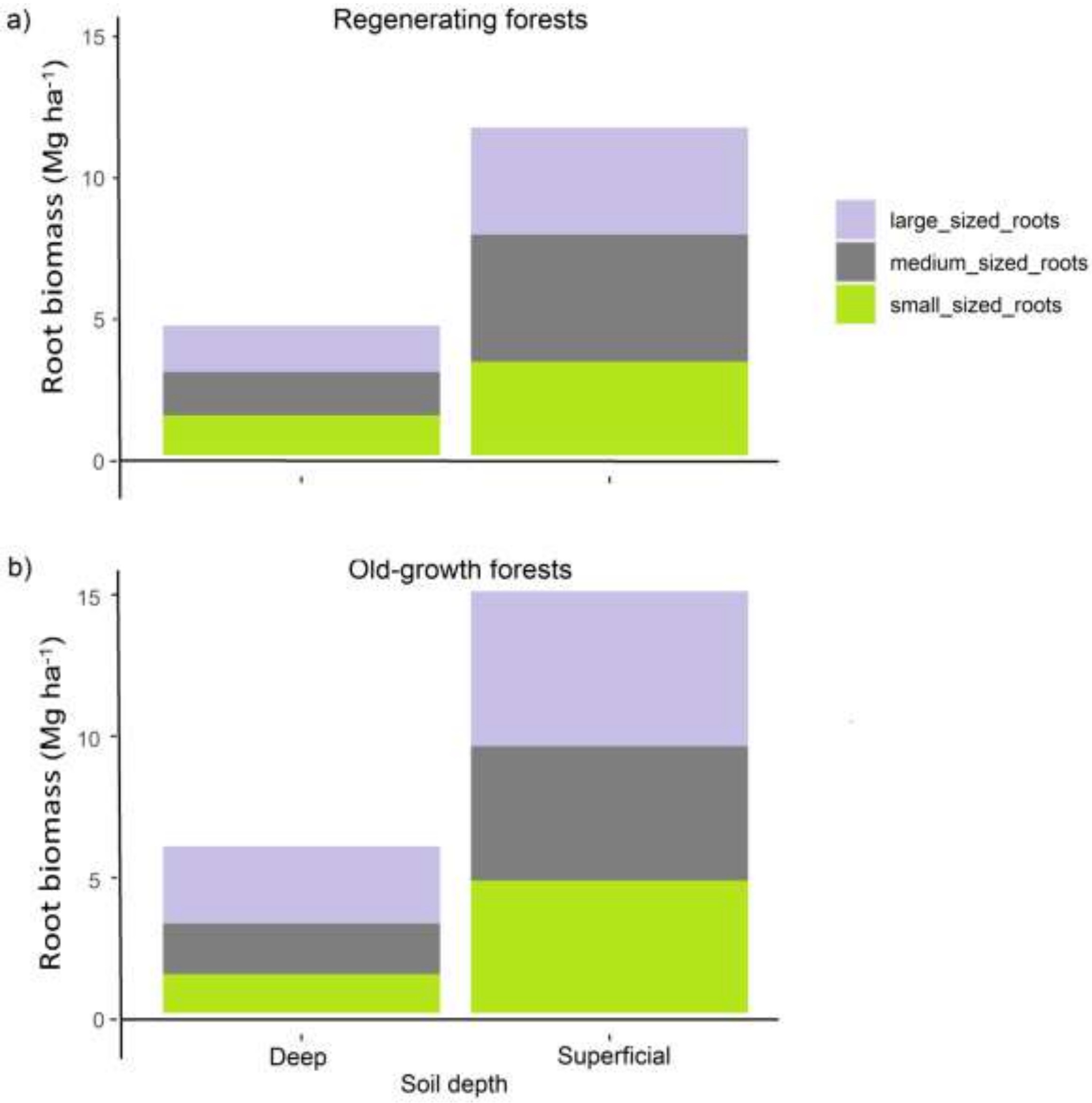

Figure 3. Distribution of root biomass according to size class and soil layer in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

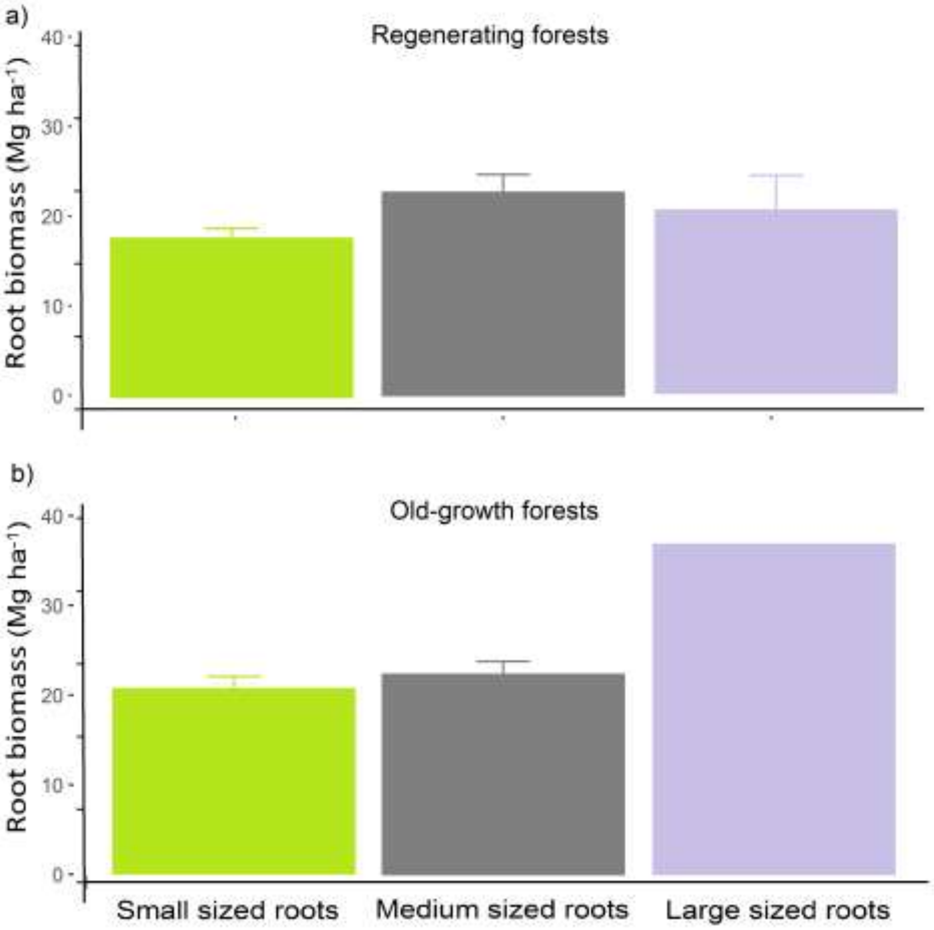

Figure 4. Mean ± SE of small-sized, medium-sized and large-sized root biomass across regenerating forest and old-growth forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

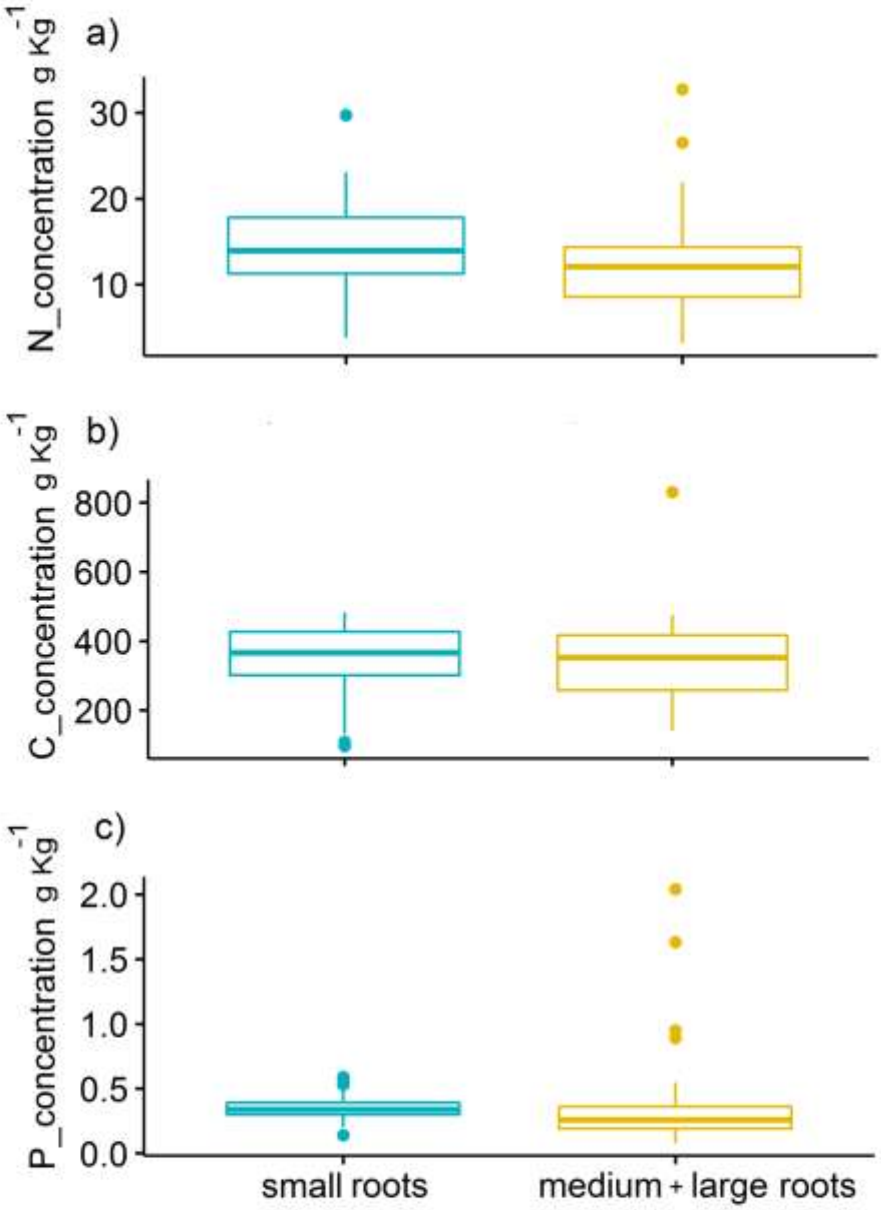

Figure 5. Nutrient concentration (N, C and P) (g kg^{-1}) by root size class across regenerating dry forest stands in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

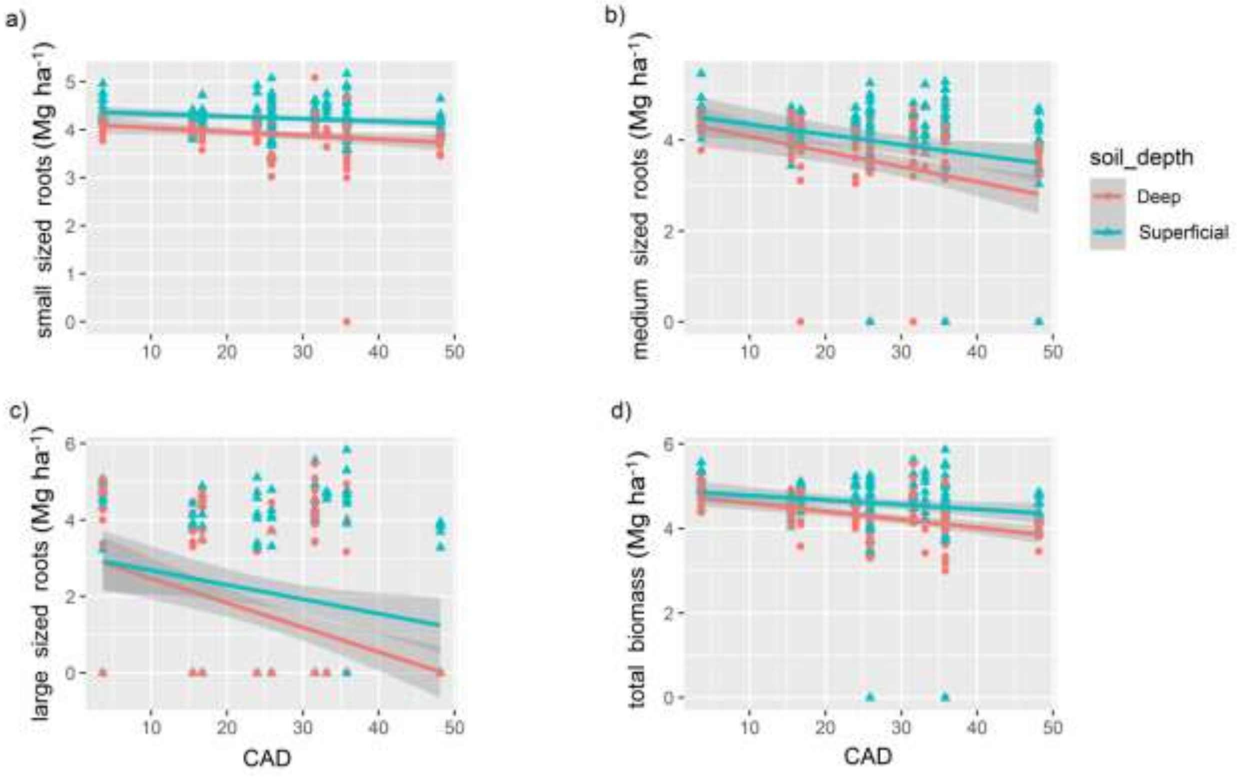

Figure 6. Effect of chronic anthropogenic disturbance (CAD) on root biomass regarding different soil layer across regenerating forest stands sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

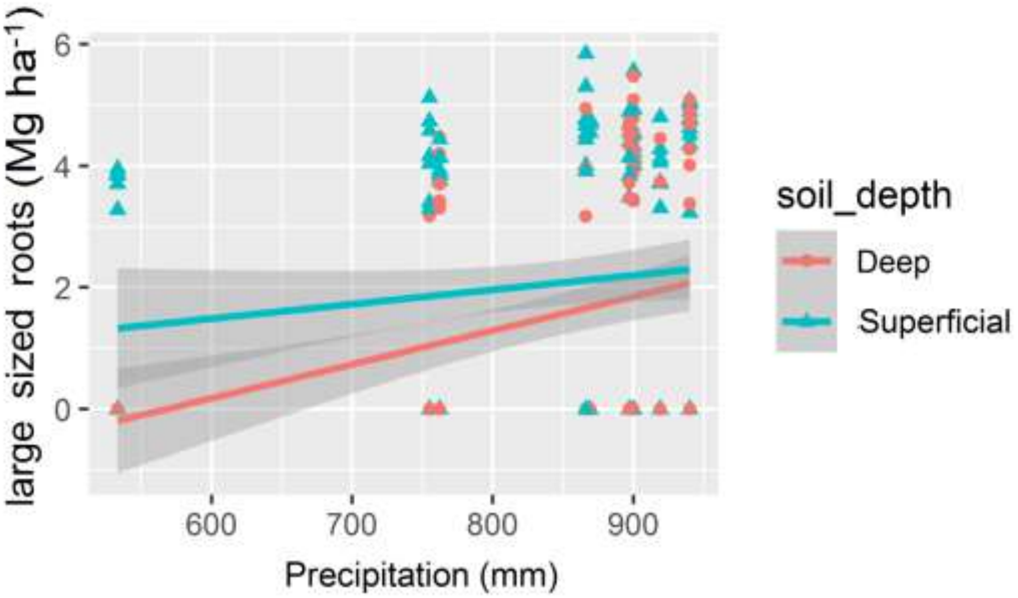

Figure 7. Effect of annual mean precipitation (mm) on root biomass regarding different soil layer across regenerating forest stands sampled in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

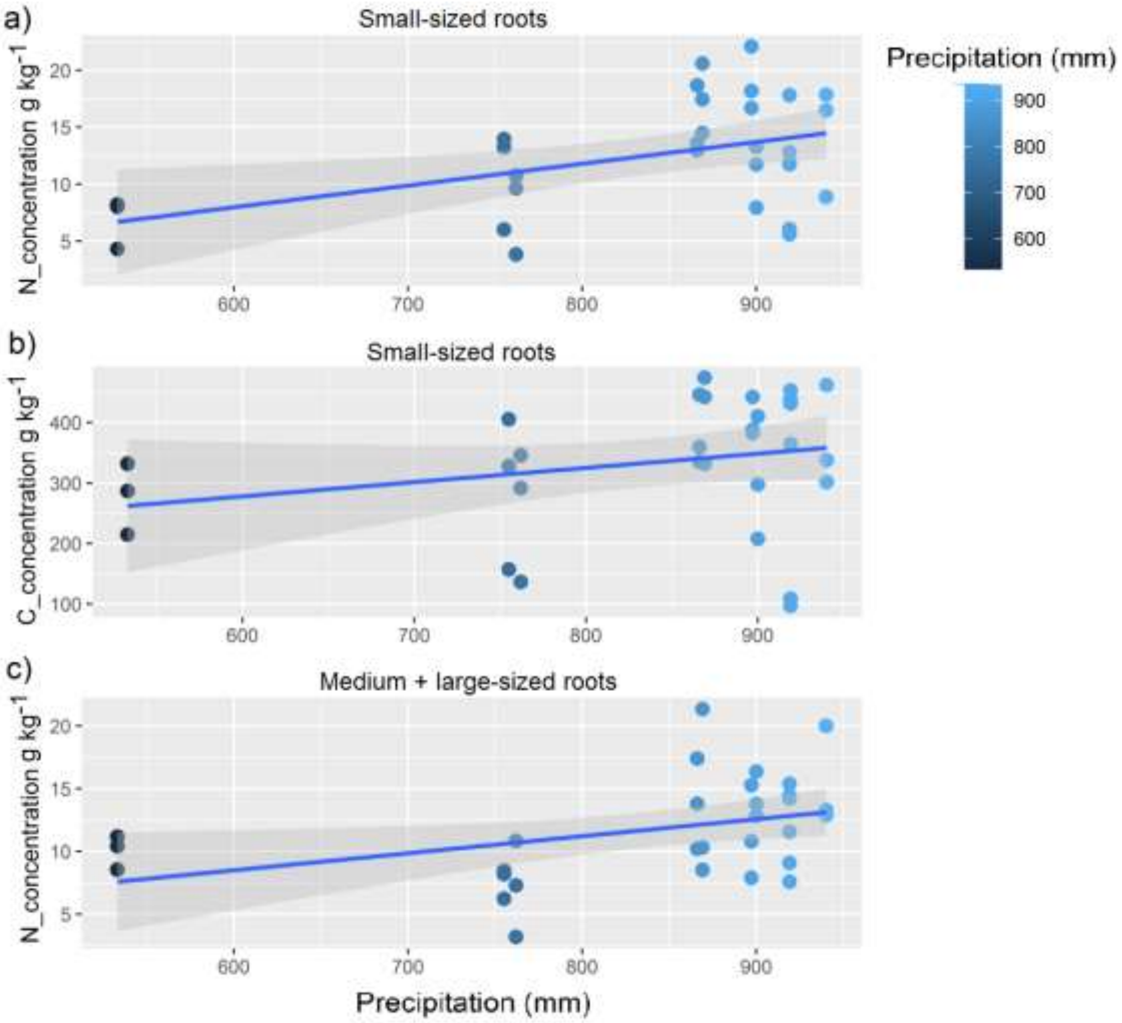

Figure 8. Effect of average annual precipitation (mm) on nutrient concentration of N (a) and C (b) in small-sized roots and on N regarding medium+large-sized roots (c) in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

SUPPLEMENTARY MATERIAL

Table S1. Mean values of values of forest stands with different ages (from 10 to 76 years) in a chronosequence of natural regeneration of the Caatinga, and information on average annual precipitation (AAP); chronic anthropogenic disorder (CAD); underground biomass (BGB); aboveground biomass (AGB); small roots (<2.0 mm), medium roots (2.01 to 10.0 mm), large roots (> 10.01 mm) and total root biomass (all in Mg ha-1); root/shoot ratio (R/S) and mean value ± standard error (M±SE) in a seasonally dry forest in northeastern Brazil. We consider (*) to be less than 0.001 is the standard deviation value.

Age	**Small sized (Mg ha^{-1})**			**Large sized (Mg ha^{-1})**			**Medium sized (Mg ha^{-1})**			**AGB (Mg ha^{-1})**	**CAD**	**AAP**
	N	C	P	N	C	P	N	C	P			
10	0.076	1.82	0.0013	0.057	1.35	0.0007	0.040	0.92	0.0005	5.41	33.14	869
13	0.044	0.94	0.0014	0.064	1.39	0.0009	0.021	0.43	0.0003	3.71	25.87	919
13	0.018	0.62	0.0005	0.016	0.37	0.0007	0.001	0.01	0.0000	5.92	20.84	851
23	0.025	0.60	0.0005	0.021	0.57	0.0014	0.010	0.28	0.0009	8.72	35.77	866
29	0.042	1.16	0.0012	0.055	1.55	0.0027	0.150	3.48	0.0124	14.05	31.58	900
43	0.073	1.78	0.0009	0.076	1.85	0.0015	0.123	3.35	0.0024	38.54	3.61	940
46	0.041	1.13	0.0012	0.028	0.81	0.0009	0.015	0.34	0.0005	18.96	23.96	755
51	0.086	1.82	0.0020	0.054	1.08	0.0011	0.061	1.16	0.0012	16.44	16.73	897
56	0.019	0.60	0.0009	0.016	0.46	0.0006	0.007	0.22	0.0002	18.56	15.46	762
76	0.016	0.60	0.0009	0.021	0.85	0.0006	0.002	0.08	0.0001	15.11	48.11	533
M±SD	0.044±0.02	1.11±0.5	0.0011±(*)	0.041±0.02	1.03±0.04	0.0011±(*)	0.043±0.05	1.03±1	0.0019±0.003	14.55±9.6	25.51±11.9	829±114

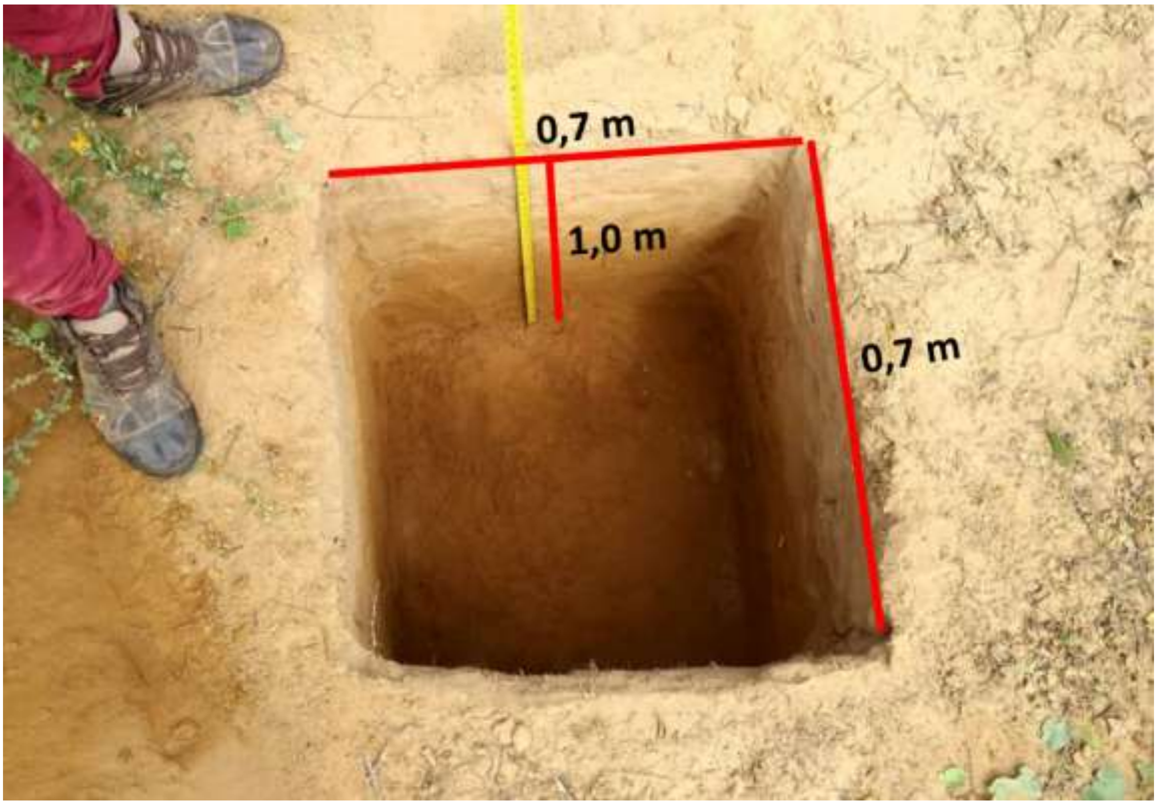

Figure S1. Scheme of measurements of the trench used to collect belowground biomass in the caatinga of Catimbau National Park, Pernambuco Brazil.

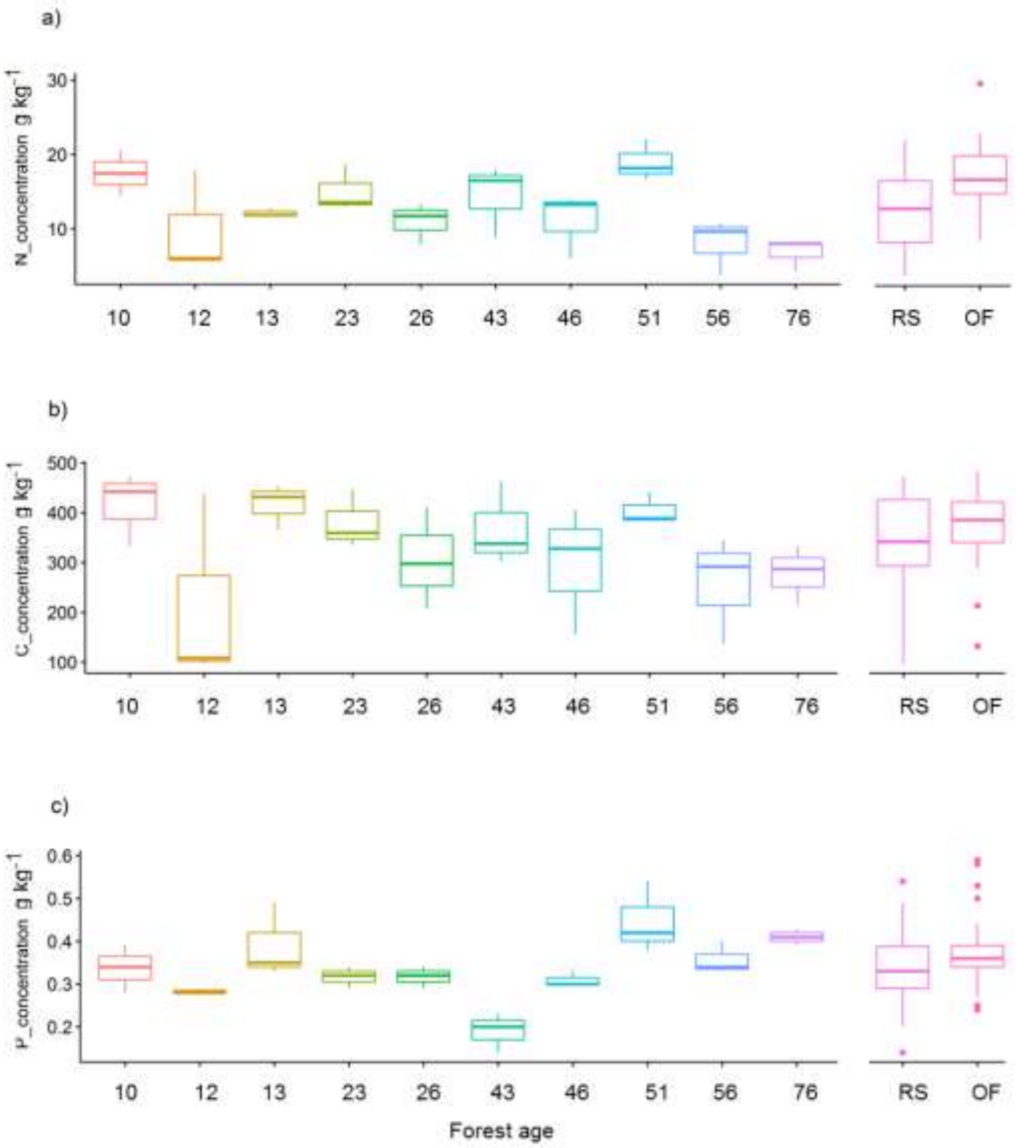

Fig.S2. Nutrient concentration (g kg^{-1}) for small-sized roots across dry forest plots in the Catimbau National Park, in Pernambuco state, northeastern Brazil. RS: regenerating forest stands; OF: old-growth forests.

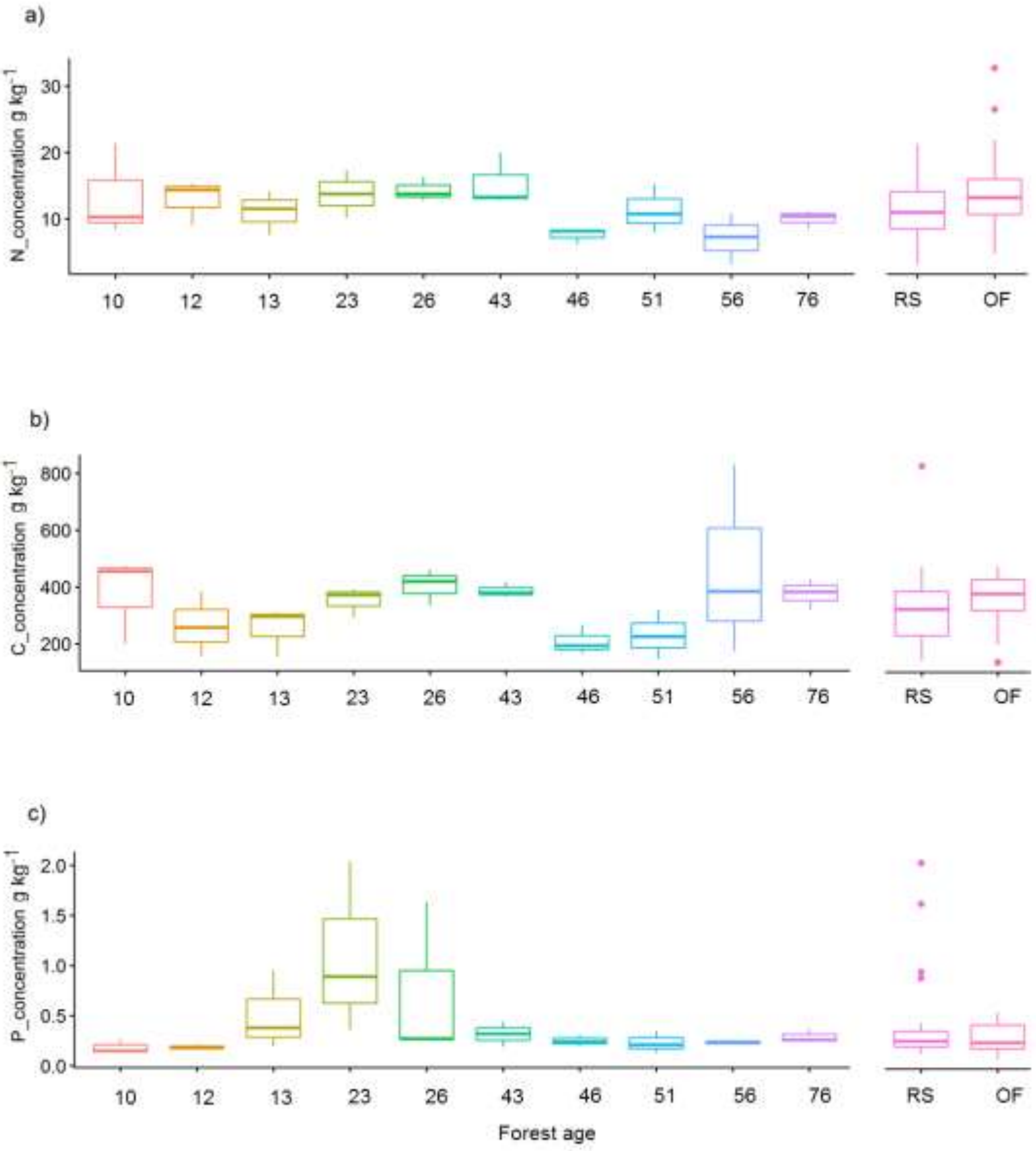

Figure S3. Nutrient concentration (g kg^{-1}) for medium+large-sized roots across dry forest plots in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

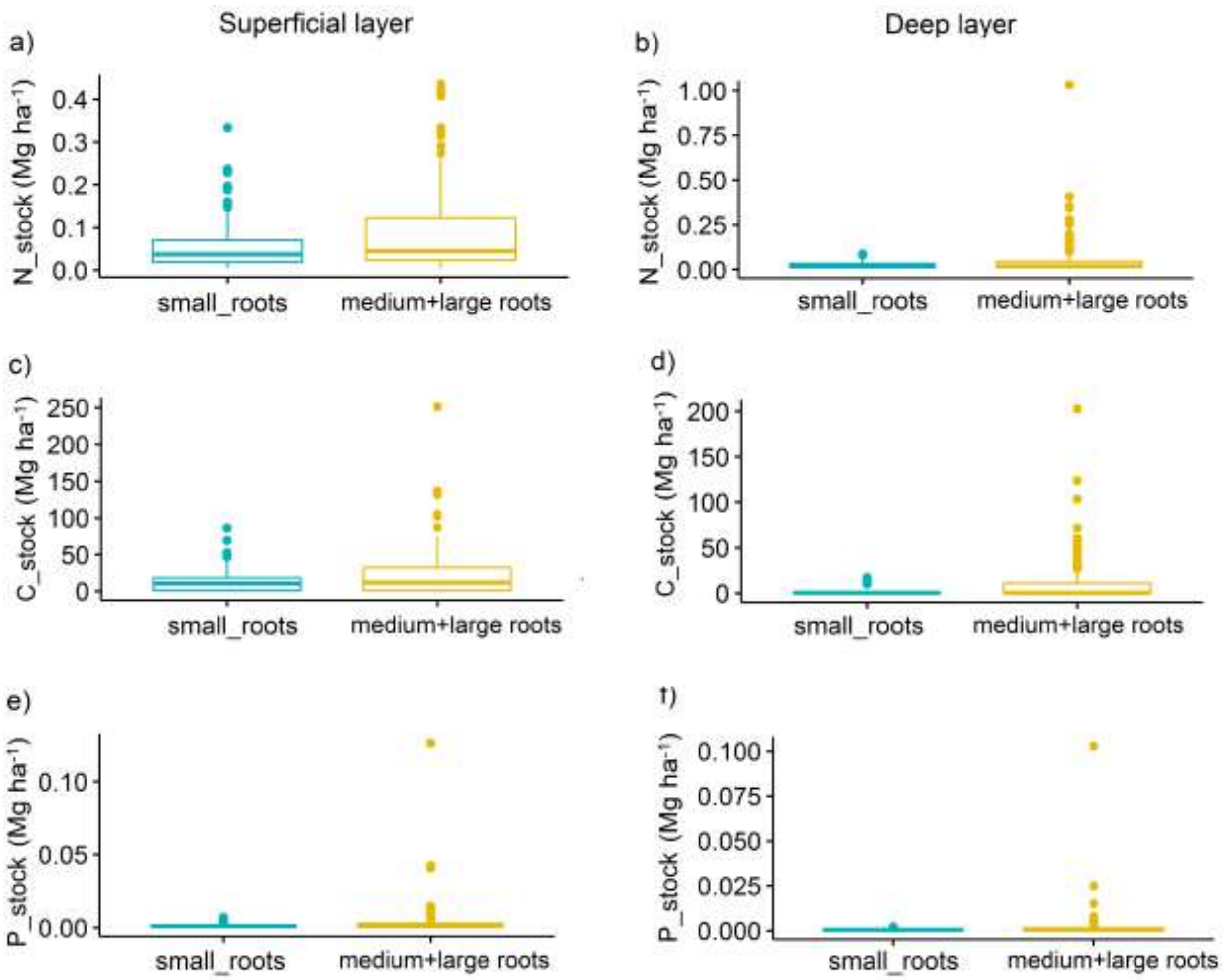

Figure S4. Nutrient stocks according to soil layer (superficial vs. deep) for small and medium+large-sized roots across dry forest plots in the Catimbau National Park, in Pernambuco state, northeastern Brazil.

5 CONSIDERAÇÕES FINAIS

Os achados para biomassa abaixo do solo na Caatinga apresentados em nosso estudo apontam para uma considerável diminuição do estoque de biomassa e concentração de nutrientes com o aumento das perturbações antrópicas crônicas (PAC) e reduções na pluviosidade. Em condições ideais, as áreas atualmente antropizadas deveriam receber menos pressão humana para terem tempo e capacidade de recuperar seus estoques de biomassa e, consequentemente, de nutrientes. Isso é importante porque o sustento das comunidades atreladas a estes ecossistemas será negativamente afetado a partir do desaparecimento da vegetação, e em consequência a desertificação.

Em síntese, em florestas maduras (sem histórico recente de uso do solo para agricultura) e secundárias (após a agricultura de corte e queima) a biomassa de raízes possui contribui muito para a manutenção dos nutrientes (N/C/P) nos primeiros 50 cm da superfície do solo. De forma geral, essa mesma camada do solo é muito propensa a alterações causadas tanto pela instalação de roças, quanto por pressões gradativas (como as causadas pelas PAC) e por mudanças dos regimes de chuva. Por isso, reforçamos que na Caatinga, que está tendenciada à desertificação, uma vez perdidos os nutrientes desses solos pobres, seu retorno às comunidades vegetais remanescentes será extremamente difícil. Então, ressaltamos que, como o previsto, a biomassa subterrânea da Caatinga e seu papel em relação à resiliência florestal e prestação de serviços ecossistêmicos tendem a diminuir com o avançar da aridez e da exploração dos recursos florestais.

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