

**UNIVERSIDADE FEDERAL DE ALAGOAS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
Programa de Pós-Graduação em Diversidade Biológica e
Conservação nos Trópicos**

ADRIANA DOS SANTOS COSTA

**CORRELATOS AMBIENTAIS E ANÁLISES MACROECOLÓGICAS DE SEMENTES
E FOLHAS DAS ESPÉCIES LENHOSAS NO SEMIÁRIDO TROPICAL**

MACEIÓ-ALAGOAS

Setembro/2020

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Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde da Universidade Federal de Alagoas, como requisito para obtenção do título de Doutora em **CIÊNCIAS BIOLÓGICAS**, na área da Biodiversidade.

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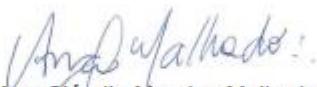
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Orientação: Dr^a Ana Cláudia Mendes Malhado

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Pesquisadora externa: Dr^a Fernanda Alves-Martins

*À minha família querida, que sempre me deu apoio
e motivação para a realização dos meus sonhos e
metas, grata por todo carinho recebido.*

Dedico

In memoriam

*De minha avó, mãe, Irene Conceição Costa pelo
acolhimento, zelo, conselhos, força e
direcionamentos para a minha vida durante sua
existência.*

*Eu sou eu mesmo (a) divêrjo de todo mundo. Eu
quase de nada não sei. Mas desconfio de muita
coisa.*

Guimarães Rosa, em Grande Sertão: Veredas

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Resumo

A sobrevivência e distribuição das espécies vegetais nas condições ambientais extremas dos ambientes semiáridos é fortemente dependente de características associadas à resistência à seca. O peso das sementes e o tamanho das folhas pode ser particularmente importante, uma vez que são traços capazes de responder a várias condições ambientais sobretudo em ambientes estressantes, como aqueles com grande restrição hídrica. O objetivo da nossa pesquisa é descrever a biogeografia funcional e fornecer a primeira avaliação biogeográfica do peso das sementes e da área foliar em condições climáticas e edáficas do bioma Caatinga no nordeste do Brasil. Nós utilizamos dados do peso de sementes de 277 espécies lenhosas e o tamanho de folhas de 192 espécies de plantas lenhosas da Caatinga. Modelos de equações estruturais (SEM) foram utilizados para testar efeitos diretos e indiretos entre o peso da semente e as condições climáticas, incluindo temperatura, precipitação, sazonalidade climática, e compactação do solo e as associações das propriedades do solo e o tamanho médio das folhas. Dados de ocorrência de espécies foram recuperados 510 022 registros de ocorrência de espécies de Angiospermas na Caatinga a partir dos portais de dados GBIF e SpeciesLink em novembro de 2016. Nossos resultados indicam que os maiores pesos de sementes de espécies lenhosas na Caatinga são principalmente uma adaptação ao solo compactado, distribuição desigual de chuvas e altas temperaturas. A associação mais forte foi entre o peso da semente e a compactação do solo, com temperatura média do trimestre mais seco e aridez influenciando diretamente a compactação do solo (influenciando indiretamente o peso da semente). Verificamos que 67 % da variação do pH do solo da Caatinga é explicado pela aridez e existe uma relação positiva entre a tamanho das folhas e a disponibilidade de minerais catiônicos do solo. Embora a relação entre a área foliar e disponibilidade de minerais catiônicos seja mais forte que o tamanho médio das folhas e o pH do solo, essa relação pode refletir diferentes estratégias de tolerância à seca. Discutimos que o pH do solo pode ser reconhecido como um fator importante na distribuição de plantas em florestas tropicais. No geral, o esforço de amostragem em toda a Caatinga mostrou cobertura geográfica heterogênea; como indicado pelas grandes áreas do bioma que permanecem sob coleta. Concluímos que às variáveis ambientais favorecem a adaptação de sementes maiores e que as propriedades físico-químicas do solo exercem influência direta sobre o tamanho das folhas.

Palavras-chave: Aridez, Sazonalidade, Compactação, florestas secas, Vegetação, banco de dados

Abstract

The survival and distribution of plant species in the extreme environmental conditions of semiarid environments is strongly dependent on characteristics associated with drought resistance. The weight of the seeds and the size of the leaves can be particularly important, since they are features capable of responding to various environmental conditions, especially in stressful environments, such as those with great water restriction. The aim of our research is to describe functional biogeography and to provide the first biogeographic assessment of the weight of seeds and leaf area in climatic and edaphic conditions of the Caatinga biome in northeastern Brazil. We used seed weight data for 277 woody species and the leaf size of 192 woody plant species in the Caatinga. Structural equation models (SEM) were used to test direct and indirect effects between seed weight and climatic conditions, including temperature, precipitation, climatic seasonality, and soil compaction and associations of soil properties and average leaf size. Species occurrence data were retrieved 510 022 records of occurrence of species of Angiosperms in the Caatinga from the data portals GBIF and SpeciesLink in November 2016. Our results indicate that the highest weights of seeds of woody species in the Caatinga are mainly an adaptation to compacted soil, uneven distribution of rain and high temperatures. The strongest association was between seed weight and soil compaction, with average temperature of the driest quarter and aridity directly influencing soil compaction (indirectly influencing seed weight). We found that 67% of the pH variation of the Caatinga soil is explained by aridity and there is a positive relationship between leaf size and the availability of cationic minerals in the soil. Although the relationship between leaf area and availability of cationic minerals is stronger than the average leaf size and soil pH, this relationship may reflect different drought tolerance strategies. We argue that soil pH can be recognized as an important factor in the distribution of plants in tropical forests. Overall, the sampling effort across the Caatinga showed heterogeneous geographic coverage; as indicated by the large areas of the biome that remain under collection. We conclude that the environmental variables favor the adaptation of larger seeds and that the physical-chemical properties of the soil have a direct influence on leaf size.

Keyword: Aridity, Seasonality, Compaction, dry forests, Vegetation, database

Lista de figuras

Capítulo 1 **pág.**

Figura 1-Resumo de <i>trade-off</i> em plantas em ambientes áridos, resultando na perda e manutenção das folhas e os mecanismos envolvendo demandas conflitantes (Garcia et al. 2017).	17
Figura 2-Distribuição das florestas tropicais, úmidas e savanas no mundo (Pennington et al.2018)	21

Capítulo 2 **pág.**

Figura 1-Geographical coverage of records of Magnoliopsida and Liliopsida (a and b) and woody species (c and d) retrieved from GBIF and SpeciesLink in November 2016, in the Caatinga, Northeast Brazil....	40
Figura 2-Structural Equation Model describing the relationship between seed-weight and environmental, vegetation and soil predictors.	42

Capítulo 3 **pág.**

Figura 1-Structural Equation Model (SEM)- relationship between the effect of aridity and physicochemical properties of the soil in leaf size. In our model, aridity influences soil pH, and cation exchange affect leaf size.	73
Figura 2-Spatial distribution of mean annual temperature and aridity in the Caatinga.	74
Figura 3-Percentage of simple and compound leaves occurring in the Caatinga.	74
Figura 4-Life size categories (Raunkier 1931) in the different Caatinga ecoregions.	75
Figura 5-Proportion of leaf types across the taxonomic families of the Caatinga woody plant.	75
Figura 6-Proportion of leaf types in four Ecoregions – ADF: Atlantic Dry Forest, CAA: Caatinga, CRMS: Campos rupestres montane savanna, PCF: Pernambuco Costal Forests.	76

Lista de Tabelas

<u>Capítulo 1</u>	<u>pág.</u>
Tabela 1-Hipóteses do significado adaptativo do tamanho da sementes.....	18
Tabela 2-Hipóteses dos significado adaptativo do tamanho de folhas	19
<u>Capítulo 2</u>	<u>pág.</u>
Tabela 1-Eletronic Supplementary Material Table S2.....	48
Tabela 2-Description of environmental variables usedin this study Table S2	59
Tabela 1-Descriptive statistics of environmental variables used in this study.....	61
<u>Capítulo 3</u>	<u>pág.</u>
Tabela 1-Direct and indirect effects of environmental variables and physical-chemical properties of the soil on the leaf size of woody plants in the Caatinga.....	73
Tabela 2-Eletronic Suplementary Material Table S1.....	77

Sumário

Apresentação.....	12
1- Revisão da literatura	14
1.1- Trade-offs em sementes e folhas	14
1.2- Funções e correlações ambientais do peso das sementes	18
1.3- Padrões biogeográficos do tamanho de folhas.....	19
1.4- Florestas tropicais secas.....	20
1.5- Caatinga.....	23
Capítulo I	27
2- Manuscript published in the Plant and Soil	27
2 .1-Introduction	29
2.2- Methods	31
2.2.1- Study area	31
2.2.2- Species data	31
2.2.3- Selection of woody species in the Caatinga.....	32
2.2.4- Seed size data collection	32
2.2.5- Accounting for uneven sampling effort	33
2.2.6- Environmental data.....	34
2.2.7-Data Analysis.....	34
2.3- Results	35
2.3.1-Geographical and taxonomic coverage of seed weight	35
2.3.2- Environmental effects on seed weight	35
2.4-Discussion.....	36
Electronic Supplementary Material S1	44
Tabela 1-Eletronic Suplementary Material Table S2.....	48
Tabela 2-Description of environmental variables used in this study Table S2.....	59
Tabela 3-Descriptive statistics of environmental variables used in this study.....	61
Capítulo II.....	62
3.1-Introduction	62
3.2-Methods	65
3.2.1-Study area	65
3.2.2-Selection of woody species.....	65
3.3-Database Construction.....	66

3.3.1-Digital Imagens of dry herbarium specimens	66
3.3.2-Metrics of leaves.....	66
3.3.3- Environmental variables and data analysis	67
3.4-Results	68
3.4.1- Characterization of leaves.....	68
3.4.2- Leaf Metrics.....	68
3.4.3-Leaf size and environmental variables.....	68
3.5- Discussion.....	69
Conclusão	85
Referências	87

Apresentação

Mais da metade das florestas secas tropicais no mundo são localizadas na América do Sul, e são definidas no sentido amplo como um tipo de vegetação tipicamente dominada por árvores decíduas. No Brasil, estas florestas são concentradas no Nordeste do país, ocupa uma área de cerca de 844.453 quilômetros quadrados, o equivalente a 11% do território nacional (MMA, 2020). A região possui uma vegetação conhecida localmente como Caatinga que é constituída predominantemente por árvores e arbustos que perdem suas folhas em determinadas épocas do ano. Nos últimos anos o conhecimento sobre a biodiversidade da Caatinga tem crescido e comprovou-se que é uma região semiárida rica em espécies. Até momento, já foram listados milhares de espécies vegetais para a Caatinga e vários outros grupos de plantas vasculares, peixes répteis, anfíbios, pássaros e mamíferos foram apontados para a região. Tudo isso, além do elevado nível de endemismo nas ecorregiões biodiversas que a constituem.

A Caatinga, assim como as demais florestas secas, sofre com os distúrbios humanos crônicos e agudos e com às mudanças climáticas globais. Os distúrbios crônicos provocados pelas ações moderadas vem se acumulando em grandes impactos ecológicos. Outra ameaça importante é referente as mudanças climáticas, visto que pesquisas recentes indicam que 94% da região Nordeste brasileira está sob moderada a elevada susceptibilidade à desertificação (VIEIRA et al., 2015) e que as zonas semiáridas podem ser as mais vulneráveis às secas de longo prazo no futuro (RAMMIG; MAHECHA, 2015). Assim podemos concluir que a vulnerabilidade da Caatinga está associada às mudanças ecológicas e climáticas que podem refletir nos ecossistemas e nas suas espécies. Dessa forma, através do uso das ferramentas espaciais aplicadas à biogeografia tentamos descrever e explicar a distribuição das características morfológicas das espécies lenhosas da Caatinga e suas possíveis relações com os fatores ambientais que podem identificar padrões funcionais dessas características e ajudar no entendimento das ameaças à Caatinga a desertificação e ao desmatamento.

Sabemos que os traços morfológicos das espécies vegetais são amplamente utilizados para identificar padrões gerais da distribuição de plantas ao longo de gradientes ambientais na vegetação. Nesse presente estudo, selecionamos folhas e sementes por serem considerados, em termos funcionais, os órgãos vegetais mais importantes das plantas e por possuir vários atributos funcionais que podem funcionar como respostas adaptativas quando condicionados a diferentes ambientes. Para atender essa abordagem foi construído um banco de dados inédito para a Caatinga, como potencial de testar as hipóteses e responder aos objetivos do trabalho.

Dessa forma, o objetivo geral deste trabalho foi utilizar a Biogeografia funcional para descrever e explicar a distribuição de características funcionais nas árvores da Caatinga com o intuito de suprir a deficiência Raunkiær no conhecimento sobre os traços das espécies e suas funções (HORTAL et al., 2015) e indicar os padrões das características funcionais de folhas e sementes que poderão limitar a distribuição geográfica de determinados táxons.

O presente trabalho está dividido em três capítulos:

- I) **Revisão da literatura**, apresenta ao leitor a discussão atual sobre relação entre atributos e variáveis ambientais.
- II) **Capítulo 2 – apresentado em formato de artigo científico: Environmental correlates of seed weight of tropical semi-arid woody species**, amplia o conhecimento sobre a biogeografia da sementes da Caatinga, permitindo assim um melhor entendimento da influência do clima para a adaptação funcional de sementes de espécies lenhosas da Caatinga.
- III) **Capítulo 3 – proposta de artigo científico: Macroecological analysis of physiological activity of Neotropical semi-arid woody species**, faz uso da abordagem biogeográfica para tentar compreender as relações iniciais entre o tamanho de folhas e as propriedades do solo da Caatinga.

1.REVISÃO DA LITERATURA

1.1- *Trade-offs* em sementes e folhas

Os *trade-offs* são considerados uma característica fundamental das estratégias ecológicas e tem como uma de suas possíveis traduções para o português a expressão “demandas conflitantes” (SOUZA, 2015; ZANELATO, 2012), ou seja, toda vez que um organismo destina recursos a um fim, esse recurso fica indisponível para outro fim (BEGON et al.2007). Processos evolutivos preveem *trade-off* entre dormência da semente, peso da semente e dispersão espacial da semente, e esses processos podem evoluir em respostas a condições ambientais desfavoráveis (REES, 1993).A alocação diferencial de recursos ocorre entre crescimento, armazenamento e reprodução (BARRERE et al., 2019; VILELA et al., 2008) e tem um efeito definido entre a quantidade e o tamanho das sementes (FIGUEIREDO et al., 2015).

Os mecanismos que operam dentro do modelo de *trade-off* entre o tamanho vs. número das sementes demonstram mudanças no tamanho das sementes pronunciada pela disponibilidade de recursos (VENABLE, 1992), e consiste na premissa entre produzir uma menor quantidade de sementes grandes contra uma maior quantidade de sementes pequenas em espécies de plantas que abrangem várias formas de crescimento e uma variedade de hábitos (LEISHMAN, 2001). O *trade-off* tamanho vs. número de sementes pode ser interpretado ecologicamente de diferentes formas, e atua também como um fator determinante no processo de competição vs. colonização, por permitir que sementes de tamanho grande proporcione uma maior capacidade competitiva nos locais de estabelecimento das mudas (TURNBULL et al.; 1999).Estudos abrangentes consideraram traços relevantes de tolerância ao estresse e os diferentes níveis de fecundidade capazes de explicar o *trade-off* entre fecundidade vs. tolerância ao estresse encontrados em espécies que co-ocorrem com diferentes tamanhos de sementes em ambientes estressantes (VILLELLAS; GARCÍA, 2013)

A limitação de recursos pode afetar o *trade- off* tamanho/ número de sementes entre anos de alto e baixo investimento reprodutivo em espécies tropicais arbóreas (MENG et al., 2014; SOUZA et al.; 2015). Além disso, existem correlações genéticas entre o tamanho das sementes e traços vegetativos, a exemplo dos genótipos de sementes pequenas capazes de produzir mais sementes no total porque atrasam a floração, produzem folhas mais longas, constroem uma roseta maior e, portanto, acumulam mais recursos (PAUL-VICTOR; TURNBULL, 2009). A relação número/peso da semente pode se correlacionar com outros traços da planta como o número dos

diásporos produzidos, altura das espécies e a capacidade de propagação lateral (ŠERÁ, 2008). A massa da semente e os traços de reprodução das sementes são correlacionados com o tamanho da planta (PIERCE et al., 2014) e positivamente relacionados com as defesas foliares (KRAFT et al., 2015).

Sementes maiores podem exigir plantas maiores em ambientes competitivos criando uma correlação entre plântulas e crescimento adulto e taxas de sobrevivência (REES; VENABLE, 2007). A existência de *trade-off* entre a redução da dormência das semente e o aumento da longevidade de plântulas adultas também foram testadas, essa redução parece ser generalizada nas comunidades vegetais de plantas temperadas (REES, 1993). Há evidência que o tamanho das semente é resultante da seleção estabilizadora (RIDLEY, 2007), mantém a constância do tamanho médio das sementes no curso do processo evolutivo, mas também sujeito a seleção natural (SILVERTOWN, 1989). HAIG (1989) acrescenta que ambientes diferentes tem sementes de diferentes tamanhos no qual estaria de acordo com a evolução de uma “estratégia condicional” que consiste no tamanho da semente como uma resposta ao ambiente parental. Portanto, a variação no tamanho das sementes entre ambientes é compatível com a seleção estabilizadora no tamanho das sementes dentro de um ambiente.

Os *trade-off* tamanho de semente vs. número podem ser correlacionar com padrões de distribuição espacial, temporal e abundancia das espécies (GUO et al., 2000). A produção de muitas sementes pequenas pode ser uma resposta adaptativa para aumentar a dispersão (MOLES; WESTORBY, 2004). A associação entre tamanho da semente e habitat sombreado na flora britânica revelou que espécies associadas a habitats sombreados tendem a ser maior que as sementes de espécies associadas a espécies de habitat abertos (HODKINSON et al., 1998). Sementes de tamanho maior oferece maiores vantagens no estabelecimento de mudas até a reprodução entre as espécies anuais, e fornece estratégias de apostas em ambientes temporalmente imprevisíveis (METZ et al., 2010). A variabilidade no padrão de distribuição espacial da massa média das sementes em ambientes na zona temperada pode ser explicado pelo ph e umidade do solo, considerados relevantes por modelar a composição de traços de plantas sob mudanças do uso da terra e clima (TAUTENHAHN et al., 2008). A massa da semente ideal depende de uma relação entre a massa da semente e a umidade do solo aliado à suscetibilidade à predação e infestação de sementes, além da quantidade e previsibilidade da queda de chuva (VOLIS; BOHRER, 2013).

Os *trade-offs* também são observados em folhas, e a relação significativamente negativa (isometria) entre o tamanho de folhas vs. número é amplamente conservada nas plantas e pode

resultar na troca de alocação de recursos de biomassa em espécies lenhosas (YANG et al.,2008). Os *trade-offs* isométricos são considerados um princípio fundamental da teoria da estratégia de ecologia evolutiva (KLEIMAN; AARSSEN, 2007) porque pode levar a adaptação local (HEREFORD, 2009). O *trade-off* pode ser alométrico (desproporcionalidade) em populações de espécies herbáceas, plantas com folhas menores, que tem tamanhos corporais geralmente menores, apresentam uma intensidade de folheação maior devido a necessidade de maximizar adaptabilidade (SCOTT; AARSSEN, 2012). A relação tamanho de folhas e vs. número por unidade de galho anual pode estar relacionado com a perda de água e o tamanho das folhas, ou seja, quanto menor a folha mais rápida é a perda de água para espécies arbóreas de folhas simples desenvolvidas em ambientes quentes (WANG et al., 2019).

As plantas em resposta a seca utilizam os *trade-offs* para manter os benefícios para a manutenção da área foliar em locais com déficit hídrico, os indivíduos que tenham menor área foliar minimizam a perda de água e o aquecimento por radiação (BARKER;CARADUS, 2001). O *trade-off* entre a capacidade fotossintética máxima e a resistência em condições desfavoráveis tem levado as folhas resistir ao estresse ambiental, marcado pelo maior investimento na construção da folha do que na função fisiológica (ZHANG et al., 2017). Adaptações evolutivas e *trade-offs* fisiológicos podem explicar variações nos traços morfológicos das folhas sob diferentes estratégias de crescimento em espécies de leguminosas lenhosas decíduas tolerantes a seca em habitat semiáridos e áridos (QIN et al.,2018). O *trade-off* entre a queda vs. manutenção das folhas é visto como uma necessidade para economia de água, perda de carbono e nutrientes em compensação da perda de água e carbono e manutenção de nutrientes, além de funcionar como um escape rápido para fuga de herbívoros (Fig.1,GARCIA et al.; 2017).

Trade-off

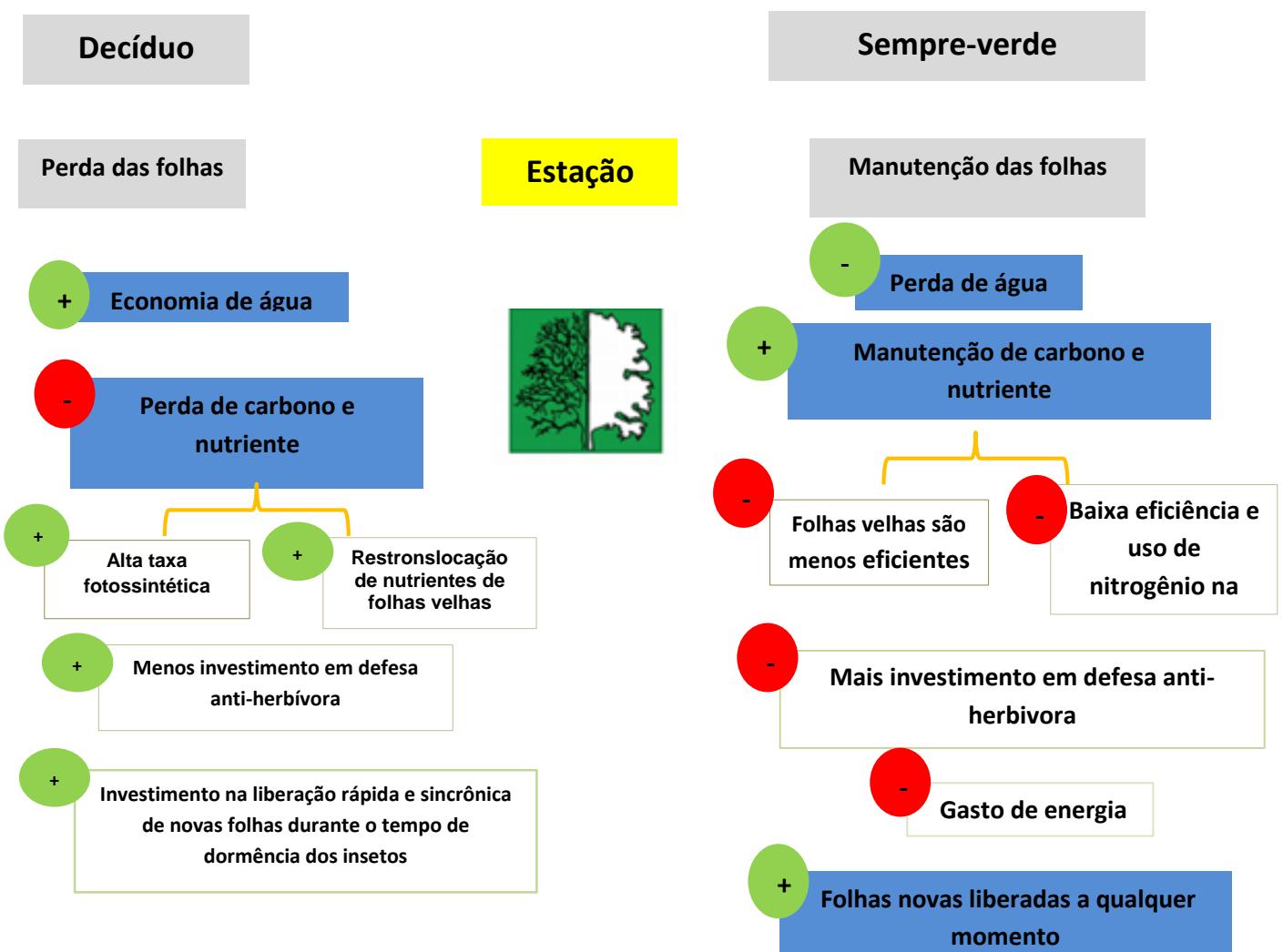


Figura 1-Exemplos de *trade-offs* em plantas em ambientes áridos, resultando na perda e manutenção das folhas e os mecanismos envolvendo demandas conflitantes (Garcia et al. 2017).

1.2- Funções e correlações ambientais do peso das sementes

A massa da semente é um traço que ocupa uma posição central na ecologia de uma espécie, pois liga a ecologia da reprodução e o estabelecimento de plântulas com crescimento vegetativo (LEISHMAN et al., 2000). Existem muitas correlações conhecidas entre os traços das sementes, estratégias reprodutivas e as condições ambientais. Um dos traços mais estudados é o tamanho e peso da semente. O padrão mais geral é: as sementes são maiores em ambientes mais secos (MALHADO et al., 2015a). De acordo com BAKER (1972), o aumento no peso da semente é uma resposta adaptável, pois diferentes circunstâncias ambientais exigem diferentes respostas das sementes a essas condições, a exemplo o aumento do peso das sementes em habitat cada vez mais seco (xérico) devido ao aumento da espessura do revestimento de semente.

Outro padrão bem conhecido e estudado é referente à correlação entre a massa da semente e a correlação com a fertilidade do solo (Tabela 1).

Tabela 1-Hipóteses do significado adaptativo do tamanho da sementes.

Hipóteses	Local	Referências
A massa das sementes é positivamente correlacionada com a fertilidade do solo.	Alemanha (Zona temperada)	(TAUTENHAHN et al., 2008)
A massa das sementes é negativamente correlacionada com a fertilidade do solo.	Amazônia (Floresta tropical úmida)	(TER STEEGE et al., 2006)
Tamanho grande da semente é uma vantagem em ambientes sombreados.	Reino Unido (Flora Britânica)	(HODKINSON et al., 1998)
A sobrevivência de mudas na sombra aumenta com o tamanho das sementes.	México (Floresta tropical úmida)	(IBARRA-MANRÍQUEZ et al.; 2001)
Sementes grandes e com capacidade de germinação precoce geram mudas com competitividade alta.	Inglaterra (Campo)	(GRIME et al., 1981)
Sementes maiores produzem mudas mais vigorosas que suportam melhor danos físicos e bióticos.	México (Floresta tropical úmida)	(IBARRA-MANRÍQUEZ et al., 2001)
Sementes grandes são uma adaptação para a maior altura da planta.	Peru (Floresta tropical úmida)	(KELLY, 1995)
Espécies florestais maduras possuem sementes maiores do que espécies pioneiras.	Peru (Floresta tropical úmida)	(KELLY, 1995)
Sementes maiores possuem bancos de sementes menos persistentes.	Europa e América do Norte (Flora Europeia e Americana)	(VERHEYEN et al., 2003)
Em ambientes susceptíveis a incêndios, sementes maiores têm mais vantagem de estabelecimento.	Austrália Ocidental (Flora do Mediterrâneo)	(HANLEY et al., 2003)
Existe uma forte correlação entre o tamanho da semente e a morfologia funcional dos cotilédones.	México (Floresta Tropical úmida)	(IBARRA-MANRÍQUEZ et al., 2001)

Outro padrão bem conhecido e estudado é referente à correlação entre a massa da semente e a correlação com a fertilidade do solo (Tabela 1).

1.3- Padrões biogeográficos do tamanho de folhas

Folhas é um traço extremamente importante para as plantas capazes de expressivas plasticidades morfológicas em respostas a diferentes condições ambientais (ROZENDAAL et al., 2006). Dentre as proposições defendidas por GIVNISH (1987) sobre a forma das folhas destaca-se a que árvores com folhas compostas são mais comuns em habitats áridos e semiáridos. Um conjunto de hipóteses tem sido amplamente testado na literatura sobre a forma das folhas (Tabela 2).

Tabela 2-Hipóteses dos significado adaptativo do tamanho de folhas

Aspectos	Padrão Macrogeográfico	Referências
Forma da Folha	Alta proporção de árvores com folhas oblongadas no Norte e Nordeste da Amazônia. Região Central e Noroeste contém uma alta proporção de árvores com folhas relativamente estreitas.	(MALHADO et al., 2009a)
Tamanho da Folha	Parcelas ao Noroeste da Amazônia possuem uma maior proporção de folhas de tamanho grande ($> 20,25 \text{ cm}^2$) do que parcelas de outras regiões; O Norte e o Sudoeste da Amazônia exibem uma menor proporção de árvores com folhas grandes (folhas grandes são menos abundante), já o Noroeste e a Amazônia Centro-Oriental exibem uma maior proporção de árvores com folhas grandes (folhas grandes são mais abundantes).	(MALHADO et al., 2009a)
Tamanho da folha e fertilidade do solo	No Noroeste da Amazônia não foi encontrado qualquer correlação significativa entre o tamanho da folha e a fertilidade do solo. No Sudoeste da Amazônia, ao contrário, houve uma correlação negativa entre as proporções de árvores com folhas grandes e fertilidade do solo	(MALHADO et al., 2009b)
Tamanho da folha e fertilidade do solo	Presença forte de árvores com folhas compostas no Norte da região do que em outras regiões. Regiões Centrais e Leste da Amazônia com mais árvores com folhas compostas do que o Sul e Oeste da região.	(MALHADO et al., 2009b)
Presença de árvores com folhas compostas	Claro agrupamento de gêneros e árvores com folhas compostas em regiões de floresta da Venezuela e Guiana e baixa frequência em áreas no Sul da Amazônia. Embora haja também variações consideráveis dentro de cada região, por exemplo, são encontrados parcelas com baixa quantidade de árvores com folhas compostas na região do Escudo das Guianas.	(MALHADO et al., 2010)

Presença da Ponta de Gotejamento	<p>Árvores e espécies com pontas de gotejamento foram mais prevalentes na Amazônia Central – Leste do que em outras regiões. Pontas de gotejamento também foram associadas com espécies arbóreas que têm alturas máximas e diâmetro de tronco menor. A proporção de espécies e indivíduos com as pontas de gotejamento foi mais fortemente correlacionada com a precipitação do trimestre mais chuvoso do que com a precipitação total anual ou a duração da estação seca;</p> <p>Rebelo & Williamson (1996) demonstraram que as pontas de gotejamento são mais prevalentes nas comunidades de árvores provenientes de solos de argila, propensos a erosão, em comparação com os solos arenosos da Amazônia Central, mais resistentes à erosão.</p>	(MALHADO et al., 2012)
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Fonte: (OLIVEIRA-NETO, 2014)

1.4- Florestas tropicais secas

A florestas secas são responsáveis por quase metade das áreas tropicais e subtropicais do mundo, abrangendo grandes áreas da África, América Latina e Ásia Pacífico (Center for International Forestry Research, O'NEILL et al., 2014). Nos trópicos, metade do clima é sazonalmente seco (Figura 2), e desempenham um importante papel no padrão de distribuição das florestas tropicais (PENNINGTON et al., 2018). As florestas tropicais secas são reconhecidas por possuir um tipo de vegetação tipicamente dominado por árvores caducas (pelo menos 50% das árvores presentes são consideradas decíduas), e incluem outros tipos de vegetação associadas que podem ser incluídos na matriz da vegetação de floresta tropical, como savanas, florestas costeiras, florestas de galerias e manguezais (SÁNCHEZ-AZOFÉIFA et al., 2005). As florestas secas são tipos de vegetação dominadas por plantas lenhosas, principalmente árvores, cuja copa cobre mais de 10% da superfície do solo em climas com estação seca de três meses ou mais, ou seja, áreas caracterizadas por secas frequentes, inundações ocasionais e vulnerabilidade geral à variabilidade climática (CHIDUMAYO; MARUNDA, 2010).

BLACKIE et al., (2014) fundamentados nos estudos da (FAO, 2001) define as florestas tropicais secas como aquelas que possuem clima tropical, com chuvas de verão, período seco de 5 a 8 meses e a precipitação anual com variação de 500 a 1500 mm. Ainda de acordo com Blackie e colaboradores, as florestas tropicais incluem as florestas de Miombo, florestas do Sudão, Savanas (África), Caatinga e Chaco (América do Sul), e Florestas decíduas secas de Dipterocarpaceaes (Ásia). As florestas secas neotropicais, se estendem por 519.597 Km², e 39%

ocorrem na América do Norte e Central, 51% na América do Sul e 9% nas Ilhas do Caribe. O México contém a maior extensão, 181.461 Km² (38% do total), das florestas secas neotropicais e, correspondentemente, apresenta um maior número de eco regiões das florestas secas do que qualquer outro país neotropical (PORTILLO-QUINTERO; SÁNCHEZ-AZOFÉIFA, 2010). Das 24 360 espécies de plantas vasculares encontradas no México, 10 235 (42%) são endêmicas (SOSA et al., 2018). As florestas secas da América Central apresentaram riqueza de espécies semelhantes quando comparadas com outras florestas neotropicais (GILLESPIE et al., 2000). BUCHER (1982), classificou o Chaco (Argentina) e a Caatinga (Brasil) como “savanas áridas” da América do Sul. Entretanto, a Caatinga é considerada a maior região de floresta seca tropical da América do Sul (SILVA et al., 2017)

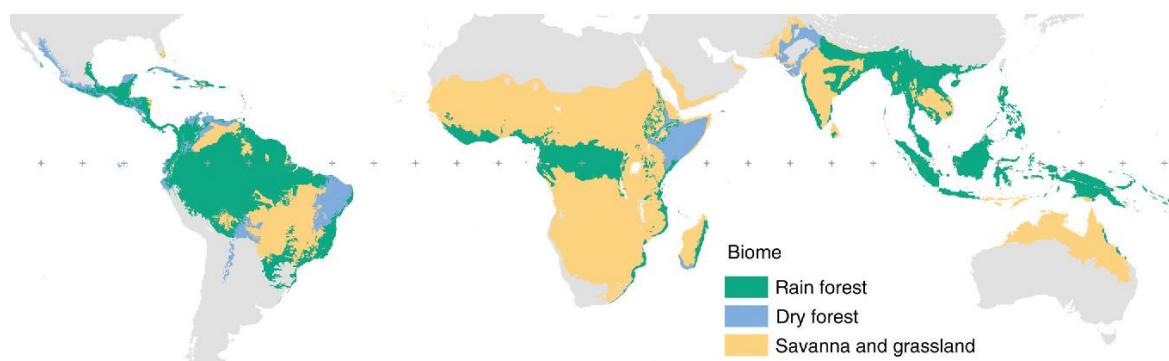


Figura 2-Distribuição das florestas tropicais, úmidas e savanas no mundo (Pennington et al.2018)

Nas florestas tropicais secas certos traços (traços funcionais) das plantas são comumente medidos (ou seja, características de folhas, características de caule e características regenerativas) pois essas características permitem responder a várias condições ambientais (CHATURVEDI; RAGHUBANSHI, 2013). Condições ambientais como mudanças no clima, escassez de água no solo, falta de minerais, que podem ser evidenciadas através de adaptações morfológicas (espinhos, tecidos suculentos, tricomas) ou adaptações fisiológicas (regulação do potencial da água, concentração de nutrientes, etc (SINGH; VERMA, 2020). As florestas tropicais são ambientes sazonais ideal para estratégias adaptativas de germinação de sementes durante a transição entre estações secas e chuvosas (MARTINS et al., 2019). Sementes de muitas espécies lenhosas nas florestas tropicais secas permanecem adormecidas durante a estação seca e emergem com chuvas (RAY; BROWN, 1994). As sementes permanecem no chão da floresta até

a próxima estação chuvosa, quando encontra condições favoráveis para germinação e crescimento (CECCON et al., 2006). As florestas secas tropicais são caracterizadas por um número relativamente alto de espécies arbóreas com sementes pequenas, secas e dispersas pelo vento (SCARIOT; VIEIRA, 2006). A variação no tamanho e formas das sementes em espécies de árvores tropicais secas reflete o polimorfismo com o maior sucesso de colonização em uma ampla gama de situações ambientais (KHURANA; SINGH, 2001). A estrutura das florestas secas tropicais podem ser amplamente determinada pelas categorias de tamanho das sementes, isto é, a massa da semente, a frequência e a abundância podem indicar que indivíduos de espécies de sementes pequenas são mais amplamente distribuídos do que aquelas de espécies de sementes grandes (KHURANA ET AL., 2006). Estudos sobre o peso das sementes por forma de vida em florestas tropicais secas mostram diferenças significativas nas médias de peso das sementes entre árvores, arbustos e ervas (do maior para o menor) semelhante aos observados em estudos na zona temperada (ROCKWOOD, 1985).

Além disso, nas florestas tropicais sazonalmente secas as folhas pequenas de espécies arbóreas tendem a ser menos sensíveis às mudanças na disponibilidade de água do que espécies com folhas grandes (GARCÍA-CERVIGÓN et al., 2020). A deciduidade foliar durante a estação seca, períodos em que as árvores provavelmente sofrem severos estresses de água, está fortemente correlacionados com a variação da disponibilidade de água no subsolo (BORCHERT, 1994). Diferenças fenotípicas sazonais encontradas em folhas podem ser respostas adaptativas, pois as folhas produzidas imediatamente antes da estação seca provavelmente experimentam maior disponibilidade de luz durante a vida útil devido à redução da cobertura de nuvens durante a estação seca (KITAJIMA et al., 1997). Variações nos regimes de precipitação em florestas tropicais sazonalmente secas afetam os traços foliares capaz de promover mudanças na aquisição e na abertura ciclo do nitrogênio na planta (ROA-FUENTES e.t al., 2015). Os traços foliares (área foliar, peso foliar, área foliar específica e teor de clorofila) sofrem variabilidade entre locais e refletem a plasticidade fenotípica, levando à adaptação às condições locais no ambiente seco tropical (PANDEY et al., 2009; PANDEY et al., 2013).

As variações dos traços anatômicos lenhosos em árvores tropicais, entre indivíduos da mesma espécie e dentro dos locais, podem ser maior que as variações entre espécies e locais (FICHTLER; WORBES, 2012). Traços foliares xeromórficos são comumente considerados adaptações estruturais que reduzem a perda de água (p.ex. espessura, cutícula, estômatos submersos, papilas e tricomas epidérmicos, papilas estomáticas e estômatos dispostos em sulcos profundos) e sua presença em plantas fósseis é frequentemente usado para indicar aridez

paleoambiental (HAWORTH;MCELWAIN, 2008). *Traits* folhas-caules estão intrinsecamente relacionados, por exemplo, espécies com madeira de baixa densidade, flexível, quebrável, hidraulicamente eficiente, mas cavitacionalmente vulnerável perdem suas folhas rapidamente em resposta à seca e apresentam baixa massa foliar por área e teor de massa seca (MARKESTEIJN et al., 2011; MÉNDEZ-ALONZO et al., 2012). Em geral, os traços das folhas adultas nas florestas tropicais secas diferem em relação a tolerância a sombra quando comparado as florestas tropicais úmidas (POORTER, 2009).

1.5- Caatinga

O nome Caatinga significa “floresta branca” na língua Tupi, fazendo menção à penetração da luz até o solo quando as árvores estão desfolhadas durante a estação seca (FERNANDES; QUEIROZ, 2018; PRADO, 2003). A Caatinga apresenta uma alta heterogeneidade espacial e temporal na dinâmica da vegetação em virtude, principalmente, de fatores climáticos (SILVA et al., 2017), é reconhecida como o maior núcleo contínuo de Florestas e Arbustais Tropicais Sazonalmente Secos da América do Sul (DE QUEIROZ et al., 2017; FERNANDES; QUEIROZ, 2018). Segundo (GIULIETTI et al., 2004) a vegetação da Caatinga é constituída por um conjunto de características tais como: a) vegetação submetida a um clima quente e semi-árido, circundado por clima mais úmido; b) possui espécies que apresentam adaptações à deficiência hídrica (caducifólia, herbáceas anuais, suculência, acúleos e espinhos, predominância de arbustos e árvores de pequeno porte, cobertura descontínua da copa) e c) a existência de espécies endêmicas. A vegetação da Caatinga muda previsivelmente em resposta à precipitação e fertilidade do solo e são mediadas por traços funcionais, ou seja, espécies com combinação de características particulares tendem a responder de maneira semelhante a uma combinação de fatores (PINHO et al., 2019a). A produtividade da vegetação da Caatinga está intimamente ligada à variabilidade da precipitação (SALIMON; ANDERSON, 2018), e cerca de 70% da precipitação anual retorna à atmosfera (PINHEIRO et al., 2016). A precipitação tem um efeito mais forte na assembleia de espécies, quando comparados aos distúrbios humanos agudos (por exemplo, perda da floresta) e crônicos (sobrepastoreio extração de lenha) sobre espécies lenhosas da vegetação da Caatinga brasileira (RITO et al., 2017).

OLIVEIRA-FILHO et al., (2006) afirmam que períodos crescentes de escassez de água, com aumento da fertilidade do solo e temperatura marcam a transição das florestas semidecíduas (Floresta úmida) para as caducifólias e depois para as formações semiáridas, tanto para as Caatingas (tropicais) quanto as Chaco (subtropicais). A flora lenhosa da Caatinga exibe uma ampla variação de traços inter e intraespecíficos, isto é a variação intraespecífica dos *traits*

explica pelo menos um terço da variação total. Essa variação não é distribuída aleatoriamente dentro das comunidades, mas varia de acordo com as condições de precipitação e intensidade de perturbação (ZORGER et al., 2018). Além disso, inventários florísticos recentes revelam a formação de dois principais grandes grupos florísticos na região, classificados de acordo com os tipos de solos existentes, que constituem a Caatinga Cristalina e a Caatinga Sedimentar (Costa et al. 2015). A descrição de novas biorregiões descritas na Caatinga contribuem para uma melhor compreensão dos padrões biogeográficos nos neotrópicos (COLLI-SILVA et al., 2019).

Velloso e colaboradores (VELLOSO et al., 2002) identificaram oito ecorregiões para a biota Caatinga e as definiram como: “é uma unidade relativamente grande de terra e água delineada pelos fatores bióticos e abióticos que regulam a estrutura e função das comunidades naturais que lá se encontram”. Nesse sentido cada ecorregião pode ser vista como uma unidade biogeográfica (DINERSTEIN et al., 1995). As definições das ecorregiões na Caatinga proporcionaram um levantamento geoambiental para auxiliar na criação das Unidades de Conservação na região (FREIRE, 2015). Entretanto, apenas 5% do território da Caatinga é coberto por Unidades de Conservação Federal, e com poucas coleções da flora amostrada (MAGDALENA et al., 2019). Atualmente algumas ecorregiões apresentam menos de 1% de sua área protegida por unidade de conservação na Caatinga (TEIXEIRA, 2018). Mesmo assim, (MORO et al., 2016) através de comparações fitogeográficas da Caatinga tendo por base dados florísticos e fitossociológicos classificaram nove tipos de ecoregiões na região. Recentemente, (SILVA et al.;2017) propõem um novo mapa das ecorregiões da Caatinga diferindo de (VELLOSO et al., 2002) que consiste na retirada da ecorregião Campo Maior e acréscimo de uma nova ecorregião denominada de São Francisco-Gúrgéia, devido destacada singularidade dentre as ecorregiões estudadas.

Os estudos realizados na escala de paisagem, apoiam as unidades de paisagem como preditoras da distribuição, abundância, riqueza e diversidade de plantas lenhosas da Caatinga (SILVA et al., 2003). Padrões de composição florísticas de famílias botânicas (por exemplo, Boraginales, Boraginaceae *s.l*) estão relacionados às Ecorregiões e aos substratos oriundos do embasamento cristalino e bacias sedimentares (SILVA-MATOS et al, 2020; VIEIRA et al., 2015). As ecorregiões da Caatinga são ricas em espécies endêmicas, ou seja, que não são encontradas em nenhuma outra região do mundo (TABARELLI et al., 2018). Ecorregiões tais como o Raso da Catarina (PE e BA) e Chapada Diamantina (BA) destaca-se pelo expressivo número de espécies vegetais endêmicas (AMORIM; BAUTISTA, 2016; VARJÃO et al.; 2013, VALENTE et al., 2013). Novos registros taxonômicos das espécies vegetais são frequentemente

descritos nas ecorregiões (CARNEIRO-TORRES et al., 2011) e ajudam a elevar o número de táxons endêmicos ao Brasil e exclusivos para a Caatinga (SILVA et al., 2018; LIMA et al., 2019). A singularidade da biodiversidade das ecorregiões da Caatinga está associada a fauna local, a exemplo de algumas espécies de angiospermas associadas a abelhas nos estratos herbáceo e lenhoso (TROVÃO et al., 2009). Três ecorregiões da Caatinga refletem o padrão de endemismo de lagartos (dunas paleoclimáticas do rio São Francisco, Chapada Diamantina e Raso da Catarina), enquanto outras duas ecorregiões da Caatinga (Depressões Sertanejas e Planalto da Borborema) apesar de demonstrarem alguma heterogeneidade no clima e na geomorfologia, não influenciam a fauna de lagartos (MESQUITA et al., 2017).

A Caatinga vem ao longo dos anos sofrendo com a perda da biodiversidade e degradação ambiental no Brasil (BUSTAMANTE; METZGER, 2019). As perturbações antrópicas, como a extração da madeira e pressão de animais (pastejo de cabras e gado), associado a variáveis ambientais (solo e precipitação) tem afetado a vegetação da Caatinga (SFAIR et al., 2018). Milhões de pessoas vivem na Caatinga e utilizam seus recursos para atender as suas necessidades em termos de subsistência e necessidades adicionais (ALBUQUERQUE et al., 2017). A utilização recorrente das “queimadas” como técnica agrícola de limpeza para o manuseio do solo pelos agricultores e o desmatamento tem contribuído para extinção de várias espécies da fauna e flora (TAVARES, 2018). Essas práticas agrícolas tradicionais de corte-e-queima e cultivo itinerante intensificados na região nos últimos três séculos tem reduzido significativamente a densidade e a diversidade do banco de sementes do solo da Caatinga (MAMEDE; DE ARAÚJO, 2008). A regeneração da Caatinga é afetada pelo uso histórico da terra, achando-se incapaz de se recuperar completamente após períodos curtos do abandono da terra, isto é., pousio, e sofre alterações no perfil estrutural, taxonômico e funcional das assembleias de plantas (SOBRINHO et al., 2016). O pastoreio pesado principalmente de caprinos e bovinos tem reduzido significativamente o estoque de carbono orgânico no solo (SCHULZ et al., 2016). Os estoques de carbono e a atividade microbiana em solos das florestas secas da Caatinga são fortemente influenciados pelos tempos de corte das florestas e refletem perdas significativas de carbono associado a esse tipo de manejo (ARAÚJO FILHO et al., 2018).

Além disso, o consumo de folhas e taxas de herbivoria por formigas cortadeiras são maiores nas áreas mais perturbadas com maior consumo foliar durante a estação seca (SIQUEIRA et al., 2018). Folhas, flores, frutos e sementes são recursos alimentares importantes durante a estação seca na Caatinga (ARAÚJO FILHO et al., 1998). A remoção da biomassa associada a degradação ambiental da Caatinga vem a favorecendo a formação dos processos de

desertificação nas áreas mais suscetíveis na região (FIGUEIREDO et al., 2012). Estudos recentes indicam que a perda cobertura vegetal na Caatinga aumentaram no período de 2000-2017, sobretudo em áreas de pastagem, e essa expansão foi mais acentuada devido à seca severa que ocorreu em 2011 (TOMASELLA et al., 2018). Devido à forte relação entre clima e vegetação, cenários de mudanças climáticas atuais e futuras evidenciam que as regiões ocupadas pela Caatinga podem não suportar altos índices de aridez (RODRIGUES et al., 2015). A redução das chuvas correlacionada a aridez favorece a mastigação de folhas por herbívoros na Caatinga (ANDRADE et al., 2020). Modelos térmicos descreve que a redução precipitação, mais que a temperatura, irá afetar a germinação e o recrutamento de espécies endêmicas da Caatinga (OLIVEIRA et al., 2019; DANTAS et al., 2019). Enfim, ampliação da área de distribuição da Caatinga pode ocorrer, sendo mais resistentes que outras biotas, mas nesse meio tempo a região também seria afetada pelas perdas de seus enclaves de florestas fechada e espécies endêmicas ou habitat-específico (ZANINI et al., 2017; SIMÕES et al., 2020).

Capítulo I

2- Manuscript published in the Plant and Soil

Title: Environmental correlates of seed weight of tropical semi-arid woody species

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Electronic Supplementary Material Table S2

2- Title: Environmental correlates of seed weight of tropical semi-arid woody species

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Abstract

Aims: The survival and distribution of plant species in the extreme environmental conditions of semi-arid regions is strongly dependent on traits associated with drought resistance. Seed weight may be particularly important, since larger seeds are predicted to promote survival in harsh environments, especially those of low soil moisture. Here, we test this hypothesis using data on the seed weight of 277 woody plant species in the semi-arid Caatinga biome of northeast Brazil.

Methods: We used Structural Equation Models (SEM) to test for associations between seed weight and biophysical conditions, including temperature, precipitation, climatic seasonality, soil-vegetation interaction and soil compaction.

Results: Species occurrence data were geographically biased due to large areas of the biome that remain under-collected. The strongest statistical association was between seed weight and soil compaction, with mean temperature of the driest quarter and aridity directly influencing soil compaction (and indirectly influencing seed weight).

Conclusions: We conclude that the larger seeds of woody species in the Caatinga are primarily an adaptation to compacted soil, uneven distribution of rainfall and high temperatures, intrinsic conditions of the Caatinga biome.

Keywords: Arid and Semi-arid, Dry forest, Seasonality, Compaction, Rainfall, Vegetation

Acknowledgements

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2 .1-Introduction

Seed weight is one of the most studied functional traits in ecology, being easy to measure and strongly influencing survival and distribution (STEARNS, 1992). Indeed, the size of a seed influences almost all aspects of plant regeneration and pattern establishment (MOLES, 2018), including the size of the seedling (HENRY; WAYNE, 1982). Consequently, seed weight is predicted to vary considerably across environmental gradients especially those related to stress (CHAPIN III; AUTUMN; PUGNAIRE, 1993). In general, small-seeded species produce more seeds per unit area of the canopy per year (JAKOBSSON; ERIKSSON, 2000) and more per unit above-ground dry biomass per lifetime (AARSSEN; JORDAN, 2001). Smaller seeds are also more likely to have dormancy (DE CASAS et al., 2017) and to have higher survival in the soil (THOMPSON; BAND; HODGSON, 1993), but also to produce smaller seedlings with lower survivorship (BERGHOLZ et al., 2015; LEBRIJA-TREJOS et al., 2016). Larger seeds, in contrast, are predicted to produce larger seedlings with higher survivorship reviewed in Moles (2018); MOLES and WESTOBY(2004) and establishment, especially on compacted soils where there may be mechanical barriers that impede the penetration of the radicle (SHELDON, 1974).

In addition to its direct selective significance under different environmental conditions, seed mass has been observed to co-vary with tree height and wood density, creating complex selective trade-offs that are currently poorly understood (MOLES; WESTOBY, 2006). The complex ecological costs and benefits of small versus large seeds and the physiological trade-offs associated with either strategy generate enormous variation within and between species and assemblages along environmental gradients (e.g. DeMALACH and KADMON 2018; METZ et al.,2010). Nevertheless, several patterns have emerged at different spatial scales that provide insights into the adaptive significance of seed size under different environmental conditions. For example, species from wet and warm environments tend to be characterized by larger seeds (e.g. MALHADO et al., 2015). Overall, there are also clear relationships with rainfall at large spatial scales, with larger seeds associated with areas with high

rainfall such as tropical forests (FOSTER, 1986). The strength of this relationship is strongly related to the length of the environmental gradient, with studies using shorter gradients often finding weak or even negative relationships (CORNWELL AND ACKERLY 2009 ;COSTA -SAURA C et al., 2016; DUBOIS et al. 2013; ŠÍMOVÁ et al. 2015; SIMPSON ET AL. 2016; STROMBERG AND BOUDELL 2013). Pronounced seasonality (precipitation and temperature) also tends to be associated with lower seed masses (MURRAY et al., 2004).

Geographic patterns of seed weight size variation and their biophysical drivers have generally been less studied in semi-arid areas, despite the pronounced gradients in water stress, temperature and soil surface characteristics. Soil surface properties may be particularly important determinants of seed mass, through their influence on processes such as runoff, infiltration, seed germination, and seedling establishment (MAESTRE et al., 2003). The semi-arid Caatinga of northeast Brazil is well-suited to studies of climatic effects on seed weight, being characterized by strong environmental gradients, high spatio-temporal variation in precipitation and temperature (AB SÁBER, 1974) and high levels of plant endemism (BRAZILIAN FLORA GROUP, 2015; QUEIROZ et al., 2017). In the mosaic of dry forest and scrub vegetation found in the Caatinga (SILVA; LEAL; TABARELLI, 2017), a significant part of the Caatinga's flora is made up of non-woody species (MORO et al., 2016b). Nevertheless, woody species are well represented in botanical collections (MORO et al., 2015) and many have the unusual ability to remain dormant in the seed bank for several years until there is sufficient moisture for germination. Smaller-seeded dry tropical forest species, which are generally dispersed by wind, are more widely distributed in comparison with larger-seeded species (KHURANA; SAGAR; SINGH, 2006).

The objective of this study was to test the hypothesis that larger seeds are associated with more compacted soils in the semi-arid Caatinga biome, northeast Brazil. Our hypothesis is based on the fact that compacted soils are characterized by decreased porosity and correspondingly increased mechanical impedance (COLOMBI et al., 2016). Soil compaction therefore limits

germination by reducing the availability of microsites and by making it more difficult for new roots to penetrate the surface layer (Chambers and MacMahon 1994; Sheldon 1974). Even when a seedling is established, soil compaction can negatively influence root development by decreasing oxygen availability and increasing soil strength (BASSETT; SIMCOCK; MITCHELL, 2005), once again favoring larger seedlings (from larger seeds). Soil compaction itself, is influenced by several climatic variables (e.g. precipitation, aridity, vegetation cover) that we would predict to be statistically associated with larger seeds in the Caatinga. We test this hypothesis using structural equation models and distributional data from 277 woody plant species.

2.2- Methods

2.2.1- Study area

The study area was defined by the geographic limits of the Caatinga, the largest semi-arid tropical ecoregion in South America, as mapped by the Brazilian Institute of Geography and Statistics (IBGE, 2004). The Caatinga has a semi-arid climate with gradients in rainfall, distinct soil types and a distinct soil-water gradient (MORO et al., 2016b). The biome covers more than 912,529 km² of northeast Brazil and experiences a seasonal climate, with a highly variable dry season lasting from 6-11 months each year. Most areas typically receive less than 1,000 mm of annual precipitation, with some areas receiving less than 500 mm per year (IBGE 2002; NIMER 1972, 1989). The soils tend to be either shallow, clayey, rocky and fertile, usually being classified as lithosols, regosols and non-calcic brown soils, or deep, sandy with low fertility, classified as latosol, podzolic and quartz sand soils (SAMPAIO, 1995).

2.2.2- Species data

We retrieved 510,022 records of species occurrence of Angiosperms collected in the Caatinga from the data portals GBIF and SpeciesLink on November 2016. From both data portals, were retrieved

only records which specimens had original geographic coordinates. We applied a protocol to evaluate data consistence to these records. We aimed to exclude records with: 1) implausible geographic coordinates, 2) missing and/or implausible date of collection, 3) invalid species names based on the Taxonomic Name Resolution Service software (TNRS) version 4.0 (BOYLE et al., 2013) and 4) duplicate records that originate from different data providers. This filtering led to a database containing 225,735 records of plants collected in the Caatinga between 1818 and 2016 (see Electronic supplementary material S1 for details on data filtering).

2.2.3- Selection of woody species in the Caatinga

We compiled a single list of plant species registered for the Caatinga using data from Moro et al. (2014) and Siqueira-Filho et al., (2012); these studies represent a recent and relatively complete compilation of plants belonging to this biome. We standardized plant names originally present in MORO et al., (2014) AND SIQUEIRA-FILHO et al., (2012) by submitting all names to the TNRS in May 2017. We then selected only ‘accepted’ names for analysis. Finally, we selected from that list only woody species, that is, those whose stem has consistency of wood, such as trees, shrubs, lianas subshrubs and woody creepers. Information about life-form were extracted from the Brazilian Flora Checklist (BRAZILIAN FLORA 2020) using the 'flora' package (CARVALHO, 2017).

2.2.4- Seed size data collection

We collected seed weight data for woody species from the Caatinga from two sources; i) the academic literature, and; ii) the Kew Gardens Seed Information Database (SID) (LORENZI 2008; LORENZI 2009; LORENZI 2016; SID, ROYAL BOTANIC GARDENS 2017). The SID provides seed weight expressed as the average weight in grams (g) of 1000 seeds, that is, the average of three observations for a thousand seeds, whereas LORENZI (2016) provides seed weight in kilograms (kg) of 1000 seeds.

Seed weight retrieved from SID and LORENZI (2008, 2009, 2016) were standardized to the same weight unit of the data compiled from the SID (i.e. average weight in g of 1000 seeds).

After compiling information on seed weight, we extracted records of woody species for which information of seed weight was available from the species occurrence database. Our final dataset contained 28,857 occurrences belonging to 277 woody species with information on seed weight recorded as average weight expressed in grams of 1,000 seeds (Table S2). Finally, we mapped seed weight using a rectangular grid at a spatial resolution of 5 km. The choice of a 5×5 km grid for analysis was based on the assumption that it is a reasonable area to show small variance of values of seed weight within each grid cell and still is large enough to be botanically explored. Values of seed weight for individual grid cells were calculated as the median seed weight documented for species recorded within it.

2.2.5- Accounting for uneven sampling effort

We quantified the inventory completeness of grid cells of 5 km x 5 km. To this end, we used the cumulative number of occurrences and species documented for individual grid cells to fit species accumulation curves. The slope at the last point of the species accumulation curves (SACs) of individual cells was used as a proxy for inventory completeness (HORTAL et al., 2004; LOBO et al., 2018) A flat slope (i.e. slope values close to zero) indicates saturation in the sampling and thus high inventory completeness. Thus, to control for the uneven sampling effort across the study area, we only included well-inventoried grid cells, i.e. cells with number of occurrences greater than 15 and slope smaller than 0.05; that is, collecting additional 20 records would result in 1 new species added (see HORTAL ET AL. 2004). Smoothed SACs were calculated with the method ‘exact’ of the function ‘specaccum’ in the R package vegan (OKSANEN et al., 2013).

2.2.6- Environmental data

Our choice of explanatory environmental variables was based on the reasoning that climate can exert both a direct and indirect effect on seed weight. Specifically, we defined indirect effects as those that are caused by the influence of climate on soil properties and vegetation cover. First, we extracted a wide range of variables from the WorldClim database (DEBLAUWE ET AL. 2016) that would be expected to have a direct/indirect effect on seed weight. We performed Spearman correlations to identify statistically independent variables ($r<0.7$). Based on this analysis, the final variables chosen for statistical analysis were: 1) Mean Temperature of Driest Quarter; 2) Precipitation of Warmest Quarter (seasonality); 3) Percentage of Non-Tree Cover was obtained from the MOD44B product (DIMICELI et al., 2015); 4) Aridity was retrieved from CGIAR-CSI (www.cgiar-csi.org); 5) Soil Nutrient level, and; 6) Soil bulk density (compactness) were obtained from World Soil Information Database(HENGL et al., 2017).

All layers of environmental variables were downloaded in January 2017 and re-sampled at spatial resolution of 5 km (Table S1 in Electronic supplementary material). Layers were manipulated using the R environment with the R raster package.

2.2.7-Data Analysis

We used Structural Equation Models (SEM) to test for direct and indirect effects of environmental variables on seed weight in the Caatinga biome. SEM is a statistical framework that puts together at least two linear models in the same framework to test both direct and indirect effects among a set of variables of interest. In our initial model we explored the influence of climate on soil properties and vegetation cover, and the influence of vegetation cover and soil on seed weight. We included spatial filters in our SEM to control for spatial autocorrelation (Spatial Eigenvector Mapping – (BAUMAN et al., 2018; GRIFFITH and PERES-NETO, 2006), i.e. to control for the trend that species located in close proximity tend to have seeds of similar (or dissimilar) weight due to a purely spatial effect

(LEGENDRE, 1993). Data on seed weight was log-transformed to fit a linear model. We estimated a separate variance-covariance matrix for each piecewise model to evaluate the adequacy of this initial model against the observed data (LEFCHECK, 2016). Then, we added new paths (i.e. new relationships) to the hypothesized model until it fitted the observed data (reached by a $p > 0.05$, (SHIPLEY, 2009) and excluded non-significant paths to reach a more parsimonious model (see Calatayud et al. 2016 for a similar approach). After run SEM, we inspected model residuals and they were homocedastic and normally distributed. We also checked the Variance Inflation Factors (VIF's) in the final model and all of which had values of less than 4. The SEM analysis was conducted using the packages piecewise SEM and lme4 in R environment.

2.3- Results

2.3.1-Geographical and taxonomic coverage of seed weight

As expected, sampling effort across the Caatinga was highly heterogeneous, with many areas remaining under collected (Fig.1). Moreover, information on seed weight was found for only 30 % ($N = 277$) of all woody species present in the species occurrence database. The top five families in terms of number of species with information on seed weight in our database were Fabaceae (Number of species = 91), Malvaceae ($N = 24$), Myrtaceae ($N = 18$), Apocynaceae ($N = 16$), Convolvulaceae ($N = 16$). Seed weight varied by from 0.0002 g per 1000 seeds (*Ficus enormis*, Moraceae) to 4087 g per 1000 seeds (*Anacardium occidentale*; Anacardiaceae) (Table S2).

2.3.2- Environmental effects on seed weight

After accounting for the potential confounding effect of heterogeneous sampling effort, we found that 82% of variability in soil compaction was explained by climatic predictors, % of non-tree cover, aridity and soil nutrients ($r^2 = 0.82$, $p < 0.001$). Mean temperature of the driest quarter (Standardized Path Coefficient $\beta = 0.48$, $p = 0.02$) and precipitation of the warmest quarter ($\beta = 0.15$; $p = 0.02$) had

a positive effect on bulk density. Percentage of non-tree cover also had a positive significant effect on soil compaction ($\beta = 0.20$; $p < 0.001$). Soil nutrient (CEC, $\beta = -0.32$; $p < 0.001$) and aridity ($\beta = -0.35$; $p < 0.001$) had negative effects on soil compaction. We found a positive direct effect of soil compaction (bulk density, $\beta = 0.31$; $p < 0.001$) and geographical distance ($\beta = 0.25$; $p < 0.01$) on seed weight ($r^2=0.12$, $p<0.01$) (Fig. 2).

2.4-Discussion

Most seeds from species that inhabit dry tropical forests such as the Caatinga are tiny, wind-dispersed and have very high drought tolerance (GALINDO-RODRIGUEZ; ROA-FUENTES, 2017). This is not universally true and, as we show in this study, there is abundant variation in seed size in woody plants. This variation is likely to be closely linked to the strong abiotic selective pressures in this environment that exert an influence on all aspects of a plant's life cycle, including seeds and seedlings. High temperatures, long periods of drought and infrequent, intense periods of precipitations have all shaped the physical characteristics of seeds and the general and specialized germination strategies that they adopt to survive in these harsh conditions (BARGA; DILTS; LEGER, 2017). Due to the temporal unpredictability of precipitation in the Caatinga, a common strategy is for the seed to remain dormant within the seedbank. Even though buried seeds are somewhat buffered against the biophysical conditions on the surface, the environmental characteristics within the seedbank will continue to exert an influence on influence seed traits. Indeed, previous studies indicate that about 43% of the variation in species richness and density of seeds within seedbanks in the Caatinga are attributable to depth of soil (litter and mineral soil) and precipitation in previous season (DA SILVA et al., 2012).

Seedling mortality is extremely high due to the extreme climate conditions and seedling establishment is difficult, with newly emerged seedlings often encountering high levels of mechanical soil impedance (MERINO-MARTÍN et al., 2017) which can slow or prevent penetration by seedling

roots and decrease infiltration rates (ATWELL, 1993). Consequently, rates of seedling recruitment are typically very low in semi-arid environments (JAMES ET AL. 2011; MARINO-MARTIN ET AL. 2017), greatly limiting the efficacy of restoration measures. Given the ecological importance of soil surface characteristics in semi-arid ecosystems, we hypothesized that soil compaction might be a key variable favoring larger-seeded species. This was supported by our structural equation models which show that soil compaction is positively associated with seed weight. There are two potential reasons for this: 1) larger seeds may be less likely to be removed prior to germination. In arid and semi-arid ecosystems seeds may be removed from the top surface of compacted soil by surface runoff (MAESTRE et al. 2003), and larger seeds may be more difficult to displace due to their higher mass (BOCHET, 2015). Smaller seeds may be displaced to (and germinate in) areas with lower topography, though this would be difficult to pick up at the spatial resolution used for our analysis; 2) the conditions for establishment on compacted soils may favor larger seeds post-germination. This agrees with the finding that larger seeds have greater vigor and a higher probability in seedling establishment and transition to adulthood, providing a competitive superiority over smaller seeds (VOLIS; MENDLINGER; WARD, 2002).

Compacted soils may offer particular challenges for rooting, restricting root penetration and development, and reducing infiltration of water into soils thereby limiting nutrient uptake and gas exchange by the roots (HEILMAN, 1981; UNGER; KASPAR, 1994). Correspondingly, seedlings from small seeds may be less able to penetrate into the deeper layers of soil reducing their ability to establish (SHELDON 1974). More generally, large seeds appear to be better prepared to cope with stress early in life, or loss of aerial biomass from their young seedlings due to herbivory action and/or adverse weather conditions (BONFIL, 1998). It is also possible that germination of smaller seeds was impeded in compacted soil, though this is more likely to have been a result of the lower water content (due to reduced infiltration) of compacted soils.

Overall, our results show that several factors (temperature, rainfall, soil nutrients, percentage of tree cover and aridity) have an indirect effect on seed weight, presumably mediated through their influence on soil compaction. This is not necessarily surprising: Jolly and Running (2004) noted that plants in semi-arid areas do not respond directly to precipitation events, but rather to the influence of these events on soil water potential. Our results are also concordant with those of DENG ET AL. (2016) who observed that vegetation cover had a direct effect on the moisture content of the surface soil, and that the productivity of the plant communities was mainly influenced by the soil moisture. That surface soil should play such a critical role is unsurprising given that the soil surface layer supplies up to 90% of the atmospheric water demand in the Caatinga (PINHEIRO; DE VAN LIER; BEZERRA, 2017). Our results are also broadly supportive of MUENCHOW ET AL. (2013), who revealed that soil, rather than annual mean rainfall, is the most important environmental variable structuring vegetation communities in dry tropical forest.

One of the main confounding factors in our analysis was the higher collection effort in the center and south of the Caatinga. The higher number of records in these areas probably reflects the ease of access for data collection (e.g. presence of roads, distance to research centres)(CORREIA et al., 2019) leading to a higher frequency of floristic and phytosociological inventories (MORO et al., 2015). Away from these well-sampled areas there were considerable gaps in data confirming the commonly stated observation that the Caatinga is one of the least known major biomes in South America (Silva et al. 2014). More generally, our study supports the utility of digitized species-occurrence data (available through open-access biodiversity databases) for identifying macroecological patterns when the original data is filtered, the autocorrelations corrected and the values of species richness are not obviously underestimated (GARCÍA-ROSELLÓ et al., 2015). Taking into consideration the above limitations, our data indicate that larger seeds predominate in the northern part of the Caatinga.

In conclusion, we clearly demonstrate a strong association between a key functional trait (seed weight) and soil characteristics (especially compaction) in the semi-arid Caatinga biome of northeast Brazil. These results have some interesting implications when viewed in the light of the rapid environmental change that is currently engulfing the region, especially related to the transformation of native forest to agriculture and the associated impacts on soil quality, hydraulic characteristics and erosion (LEITE et al., 2018). A recent study showed that deforested areas in the Caatinga have lower productivity in response to low levels of precipitation (ACOSTA SALVATIERRA et al., 2017). The loss of forest cover has led to the depletion of the soil through the desertification processes that result in the weakening of the hydrological cycle: precipitation, evapotranspiration, moisture convergence and runoff reduction (OYAMA; NOBRE, 2004). It is likely that these anthropogenic changes will influence the seed weight of woody species in affected areas through their effect on soil compaction. Based on our study we would predict that woody species with larger seeds are more likely to survive and thrive on compacted soil with uneven rainfall and high temperatures. Human population density and livestock density are the main factors driving changes in plant communities in the Caatinga (RIBEIRO et al., 2015). These disturbances along with changes in other environmental variables (soil fertility and precipitation) will strongly affect taxonomic composition, functional composition and the distribution of traits in plant species (SFAIR; DE BELLO; FRANÇA, 2018).

Fig. 1- Geographical coverage of records of Magnoliopsida and Liliopsida (a and b) and woody species (c and d) retrieved from GBIF and SpeciesLink in November 2016, in the Caatinga, Northeast Brazil. Map (a) depict all 510 022 records retrieved from both data portals, whereas map (b) depict 225 735 validate records, i.e. records for which geographical location, date of collection, and validity of species names were verified and duplicates were excluded (see S1 for detailed description on data filtering). Map (c) depict 81 666 records of 951 species woody species that occur in the Caatinga according to Siqueira-Filho (2012) and Moro et al. (2014). Map (d) depict 28 857 records of 277 woody species for which information on seed weight was compiled (Table S2; electronic supplementary material). Inlet in (d) highlight well-sampled grid cells, i.e. cells with number of records greater than 15 and slope smaller than 0.05. In all maps, squares indicate grid cells of 5 km x 5 km; areas within the Caatinga biome with no data are indicate in dark grey.

Fig. 1

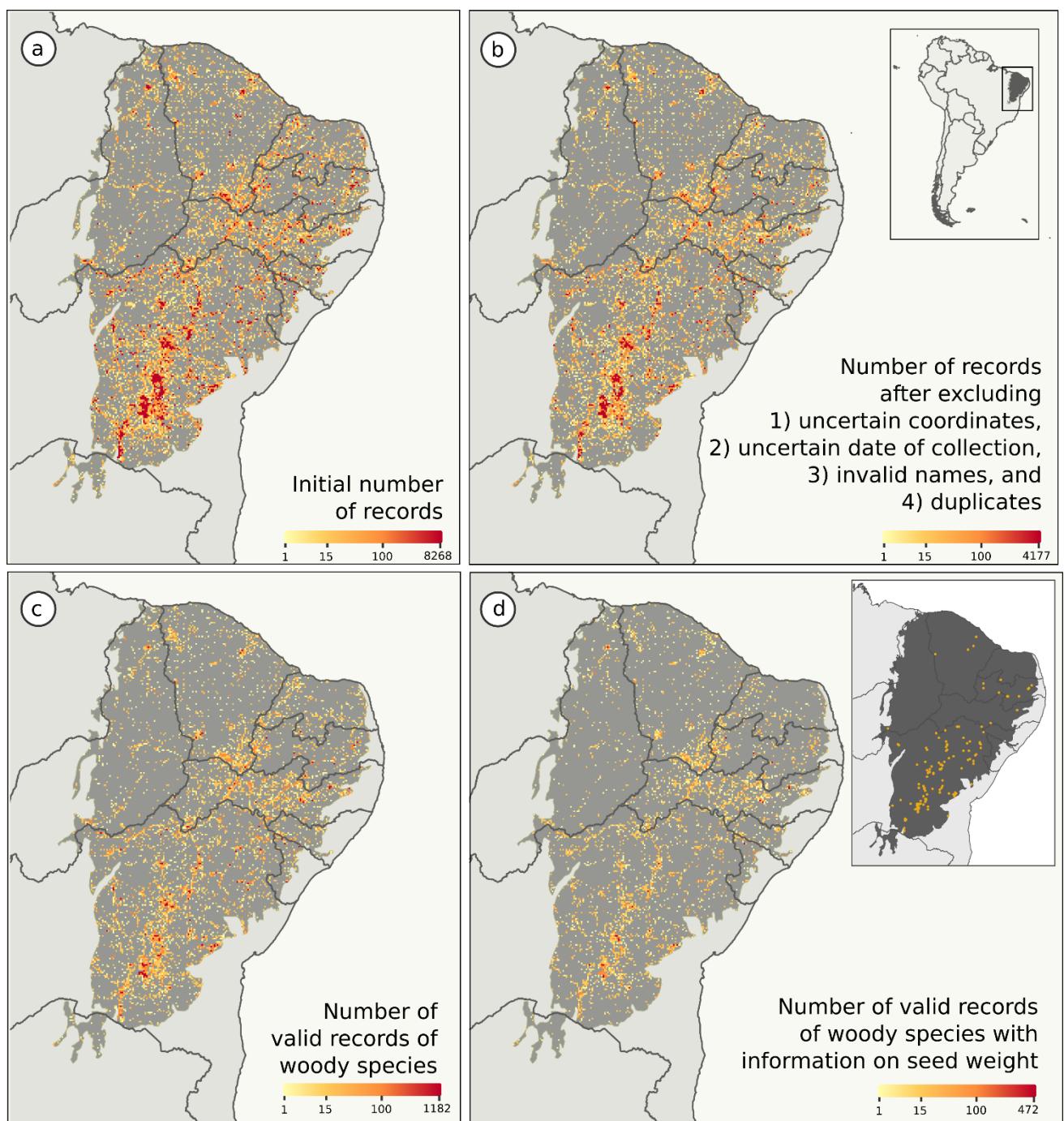
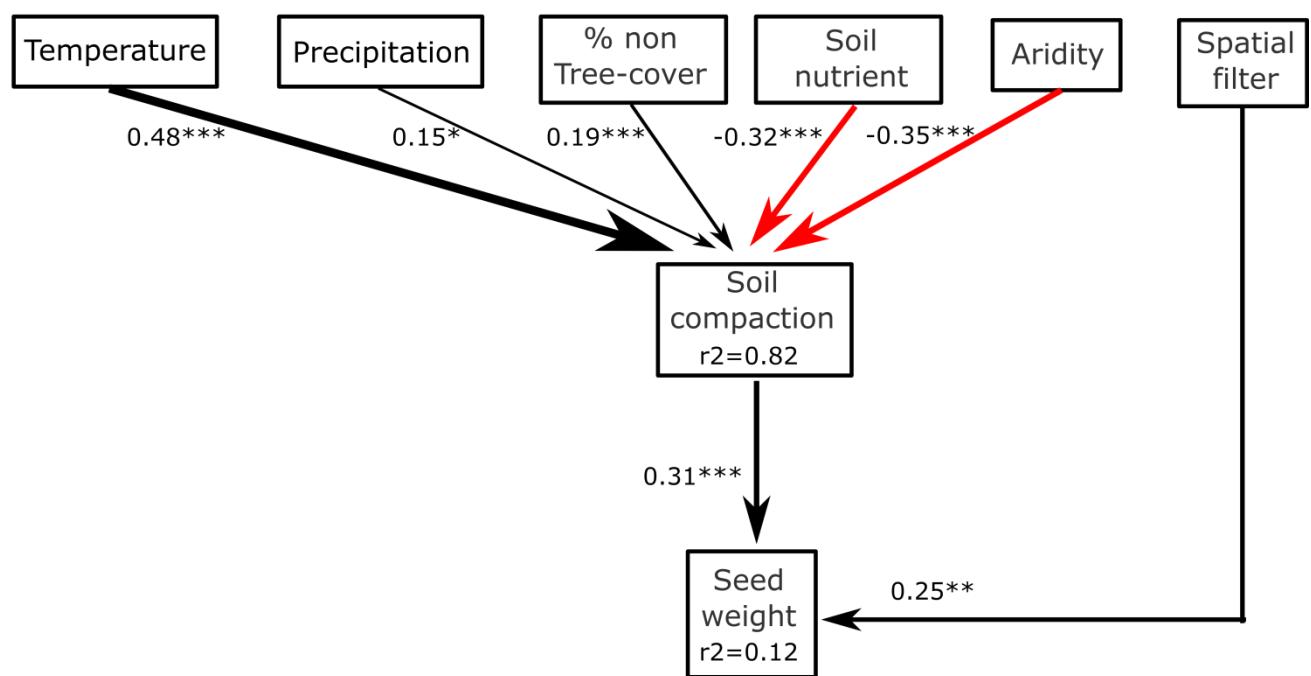


Fig. 2-Structural Equation Model describing the relationship between seed-weight and environmental, vegetation and soil predictors. The arrows indicate the significant paths with their respective standardised coefficients (numbers), the strength of interaction (arrow width) and the significance; red arrows indicate a negative effect, black arrows indicate a positive effect. r^2 values indicate the overall variability explained by the linear models and statistically significant P values: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Fig. 2



Title: *Environmental correlates of seed weight of tropical semi-arid woody species*

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Electronic Supplementary Material SI

S1.1 Description of data filtering

We retrieved from GBIF and SpeciesLink 510 022 records of species occurrence of Magnoliopsida and Liliopsida in the Caatinga. We applied to these records a data filtering that aimed to identify records with 1) implausible geographic coordinates, 2) missing and/or implausible date of collection, 3) invalid species names and 4) duplicate records, i.e. records with duplicate unique combination of species name, geographic coordinates and date of collection. This filtering led to a database containing 28,857 records collected in the Caatinga between 1818 and 2016 (Fig. S1 for an overview of workflow).

Verifying the geo-referencing

We verified the geo-referencing according to three criteria. We considered records possessing uncertain geographical coordinates all records that 1) had no decimals or only zeros as decimal places in their geographic coordinates ($N = 49\ 804$), 2) occurred outside the political borders of Brazil ($N = 40\ 408$), and 3) whose coordinates coincide with the political location of cities and villages in the Caatinga ($N= 6044$). For the later, we used the reference data for the location of cities and villages provided by the Brazilian Institute of Geography and Statistics (IBGE).

Verifying the date of collection

We considered records to be subject to a high uncertainty in the year of collection if they were collected by the same collector in a time span larger than 50 years. We consider this period as representative of the active life of a botanist (see e.g. Koek-Noorman 2004). Thus, before assessing the uncertainty in the year of collection, we standardized the spelling of

botanist names and assessed the plausibility of the names stored in the fields ‘Recordedby,’ (in GBIF) and ‘collector’ (in SpeciesLink). In our dataset, these two fields together stored 25 909 unique names of single or multiple collectors or implausible names, such as ‘unknown’ and ‘sem nome’. In order to assess the time span in which records were collected by a single collector, we created a new field in our dataset, which stores only the name of the first collector; we refer to this field as ‘first collector’. In this field, we stored the name of the first collector following the standard format adopted by Harvard Index of Botanists (HUH, 2017), in which the initials, spelled with capital letters and separated by a full stop, are followed by the surname, spelled with only the first letter capitalized.

In order to create the field ‘first collector’ we applied functions for string manipulation available in R in the packages *stringi* and *stringr*. Our automated string manipulation reduced the initial number of unique names of first collectors from 9,027 to 4 544, which we manually checked to ensure that our standards of initials followed by surname were met and that obvious spelling and errors are removed. During this manual check, we kept the original information as much as possible and only merged different collector names, when we were confident that the difference between names results from a spelling error, for instance replacing ‘Feirreira’ by ‘Ferreira’. Unfortunately, we were unable to infer whether slightly different names indeed belonged to different collectors or whether the same collector was indeed represented by different names. The latter was particularly the case for surnames such as ‘Silva’ and ‘da Silva’. In our dataset, the collectors A. G. Silva (N = 141 records) and A. G. da Silva (N = 878 records) are stored as two different collectors, although it is likely that they belong the same collector. After this manual checking, the number of unique names of the first collector decreased to 4 357.

After standardizing the name of the first collectors, we identified collectors for which the time span of collection was larger than or equal to 50 years. For these first collectors (N = 43), we retrieved from the Harvard Index of Botanists (HUH, 2017) the year of birth, year of death and/or year of first collection. This information, together with 1) number of records collected per year by the first collector, and 2) sequence of years in which the first collector was active, was used to identify years that were likely to be wrongly assigned to records. Finally, all records wrongly assigned to a specific year and first collector were considered as records possessing high uncertainty regarding the year of collection. For four out of the 43 first collectors, for which the time span of collection was larger than or equal to 50 years, we were unable to infer whether the name of the first collector referred to multiple collectors

with the same name (e.g., E. de Melo; time span 403 years; 351 records). We therefore considered all records collected by these four collectors ($N = 25\,698$ records) as uncertain.

Three additional criteria were used to assess the uncertainty in the year of collection. First, while exploring our dataset, we noticed that errors in the year of collection were more frequent for records collected before the 1900s. Therefore, we checked for these records collected whether the year of collection was plausible given the lifetime or year of first collection (HUH, 2017) of the respective first collector. If implausible years were found, we considered these records as having a high uncertainty on the year of collection.

Second, we assessed for each data provider, i.e. Herbaria providing data to GBIF and/or SpeciesLink ('dataProvider' in GBIF and 'dataprovider' in SpeciesLink), the time span of year of collection. We found that for one data provider (UFPB) nearly all records were assigned to the year 1900, although several first collectors are still active botanists. We considered all records collected in 1900 and assigned to the data provider UFPB as being highly uncertain regarding the year of collection.

Third, our approach to assess uncertainty in the year of collection is based on an attribute, i.e., name of first collector, that may be subject to errors. To account for this shortcoming, we identified records that may have the name of the first collector wrongly assigned. For this, we quantified the number of first collectors by data provider. In case a single first collector was assigned to all records of one data provider, we considered that the first collector is likely to be wrongly assigned and, therefore, the time span of year of collection cannot be properly assessed. All these records were considered as records possessing high uncertainty on the year of collection.

Standardization of taxonomic names and verification of species occurrence in the Caatinga
We assessed the validity of plant names retrieved from GBIF and SpeciesLink ($N = 15\,327$) by submitting in January 2017 all names to the Taxonomic Name Resolution Service (TNRS) version 4.0 (Boyle et al., 2013). We considered records bearing a valid species name as those for which the name of species and/or subspecies (not genus or family) matched those provided by the TNRS with an overall match score ≥ 0.9 and with a taxonomic status as 'Accepted' or 'Synonym'. In order to determine records that were identified at least at the species level, we highlighted those that had at least two strings in the field 'Accepted name' returned by the TNRS. Match scores provided by the TNRS output range from zero to one, where a score of one indicates a complete match between the string to be checked and a valid taxa name in the core database and a score of zero indicates no match. In order

to determine records that were identified at least to species level, we highlighted those that had at least two strings in the field ‘Accepted name’ returned by the TNRS.

Tabela 1-Eletronic Supplementary Material Table S2

Id	Family	Species name and author	Grams (g) of 1000 seeds*	Reference
1	Fabaceae	<i>Albizia inundata</i> (Mart.) Barneby & J.W. Grimes	54,70	SID; Royal Botanic Gardens, 2017
2	Fabaceae	<i>Albizia polyccephala</i> (Benth.) Killip ex Record	0,04	Árvores Brasileiras, 2008
3	Sapindaceae	<i>Allophylus edulis</i> (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	0,03	Árvores Brasileiras, 2008
4	Rubiaceae	<i>Alseis floribunda</i> Schott	0,0003	Árvores Brasileiras, 2009
5	Amaranthaceae	<i>Alternanthera pungens</i> Kunth	0,49	SID; Royal Botanic Gardens, 2017
6	Lamiaceae	<i>Amazonia campestris</i> (Aubl.) Moldenke	10,26	SID; Royal Botanic Gardens, 2017
7	Fabaceae	<i>Amburana cearensis</i> (Allemão) A.C. Sm.	0,61	Árvores Brasileiras, 2008
8	Bignoniaceae	<i>Amphilophium crucigerum</i> (L.) L.G. Lohmann	55,79	SID; Royal Botanic Gardens, 2017
9	Anacardiaceae	<i>Anacardium occidentale</i> L.	4087,00	SID; Royal Botanic Gardens, 2017
10	Fabaceae	<i>Anadenanthera colubrina</i> var. <i>cebil</i> (Griseb.) Altschul	82,00	SID; Royal Botanic Gardens, 2017
11	Fabaceae	<i>Andira surinamensis</i> (Bondt) Splitg. ex Amshoff	1052,00	Árvores Brasileiras, 2016
12	Convolvulaceae	<i>Aniseia martinicensis</i> var. <i>ambigua</i> Hallier f.	39,42	SID; Royal Botanic Gardens, 2017
13	Annonaceae	<i>Annona coriacea</i> Mart.	0,69	Árvores Brasileiras, 2008
14	Annonaceae	<i>Annona glabra</i> L.	213,00	SID; Royal Botanic Gardens, 2017
15	Annonaceae	<i>Annona leptopetala</i> (R.E. Fr.) H. Rainer	0,11	Árvores Brasileiras, 2016
16	Araliaceae	<i>Aralia warmingiana</i> (Marchal) J.Wen	0,01	Árvores Brasileiras, 2008
17	Apocynaceae	<i>Aspidosperma cuspa</i> (Kunth) Blake	0,05	Árvores Brasileiras, 2009
18	Apocynaceae	<i>Aspidosperma discolor</i> A. DC.	0,17	Árvores Brasileiras, 2008
19	Apocynaceae	<i>Aspidosperma parvifolium</i> A. DC.	0,20	Árvores Brasileiras, 2008
20	Apocynaceae	<i>Aspidosperma polyneuron</i> Müll. Arg.	0,07	Árvores Brasileiras, 2008
21	Apocynaceae	<i>Aspidosperma pyrifolium</i> Mart.	0,33	Árvores Brasileiras, 2009
22	Apocynaceae	<i>Aspidosperma riedelii</i> Müll. Arg.	0,04	Árvores Brasileiras, 2009
23	Apocynaceae	<i>Aspidosperma subincanum</i> Mart.	0,30	Árvores Brasileiras, 2008

24	Anacardiaceae	<i>Astronium fraxinifolium</i> Schott	31,70	SID; Royal Botanic Gardens, 2017
25	Malpighiaceae	<i>Banisteriopsis muricata</i> (Cav.) Cuatrec.	49,42	SID; Royal Botanic Gardens, 2017
26	Alstroemeriaceae	<i>Bomarea edulis</i> (Tussac) Herb.	45,94	SID; Royal Botanic Gardens, 2017
27	Fabaceae	<i>Bowdichia virgilioides</i> Kunth	26,78	SID; Royal Botanic Gardens, 2017
28	Moraceae	<i>Brosimum gaudichaudii</i> Trécul	166,67	Árvores Brasileiras, 2009
29	Moraceae	<i>Brosimum lactescens</i> (S.Moore) C.C.Berg	1000,00	SID; Royal Botanic Gardens, 2017
30	Combretaceae	<i>Buchenavia tetraphylla</i> (Aubl.) R.A. Howard	586,04	SID; Royal Botanic Gardens, 2017
31	Combretaceae	<i>Buchenavia tomentosa</i> Eichler	266,67	Árvores Brasileiras, 2009
32	Malpighiaceae	<i>Byrsinima crassifolia</i> (L.) Kunth	2,94	SID; Royal Botanic Gardens, 2017
33	Malpighiaceae	<i>Byrsinima sericea</i> DC.	0,15	Árvores Brasileiras, 2009
34	Meliaceae	<i>Cabralea canjerana</i> (Vell.) Mart.	980,00	SID; Royal Botanic Gardens, 2017
35	Vochysiaceae	<i>Callisthene fasciculata</i> Mart.	0,08	Árvores Brasileiras, 2009
36	Vochysiaceae	<i>Callisthene major</i> Mart.	0,59	Árvores Brasileiras, 2009
37	Vochysiaceae	<i>Callisthene minor</i> Mart.	0,36	Árvores Brasileiras, 2009
38	Myrtaceae	<i>Campomanesia dichotoma</i> (O. Berg) Mattos	0,03	Árvores Brasileiras, 2016
39	Myrtaceae	<i>Campomanesia eugenoides</i> (Cambess.) D.Legrand ex Landrum	0,04	Árvores Brasileiras, 2009
40	Fabaceae	<i>Canavalia brasiliensis</i> Mart. ex Benth.	485,55	SID; Royal Botanic Gardens, 2017
41	Sapindaceae	<i>Cardiospermum corindum</i> L.	36,90	SID; Royal Botanic Gardens, 2017
42	Caryocaraceae	<i>Caryocar brasiliense</i> Cambess.	689,66	Árvores Brasileiras, 2008
43	Salicaceae	<i>Casearia aculeata</i> Jacq.	23,00	SID; Royal Botanic Gardens, 2017
44	Salicaceae	<i>Casearia arborea</i> (Rich.) Urb.	1,65	SID; Royal Botanic Gardens, 2017
45	Salicaceae	<i>Casearia decandra</i> Jacq.	88,10	SID; Royal Botanic Gardens, 2017
46	Salicaceae	<i>Casearia javitensis</i> Kunth	40,00	SID; Royal Botanic Gardens, 2017
47	Salicaceae	<i>Casearia sylvestris</i> Sw.	3,00	SID; Royal Botanic Gardens, 2017
48	Lauraceae	<i>Cassytha filiformis</i> L.	40,95	SID; Royal Botanic Gardens, 2017
49	Urticaceae	<i>Cecropia pachystachya</i> Trécul	0,85	SID; Royal Botanic Gardens, 2017
50	Meliaceae	<i>Cedrela fissilis</i> Vell.	0,05	Árvores Brasileiras, 2008

51	Meliaceae	<i>Cedrela odorata</i> L.	17,00	SID; Royal Botanic Gardens, 2017
52	Malvaceae	<i>Ceiba erianthos</i> (Cav.) K. Schum.	0,06	Árvores Brasileiras, 2009
53	Malvaceae	<i>Ceiba glaziovii</i> (Kuntze) K. Schum.	0,05	Árvores Brasileiras, 2009
54	Malvaceae	<i>Ceiba pubiflora</i> (A.St.-Hil.) K. Schum.	0,20	Árvores Brasileiras, 2009
55	Malvaceae	<i>Ceiba speciosa</i> (A.St.-Hil.) Ravenna	57,67	SID; Royal Botanic Gardens, 2017
56	Cannabaceae	<i>Celtis iguanaea</i> (Jacq.) Sarg.	0,25	Árvores Brasileiras, 2009
57	Fabaceae	<i>Cenostigma macrophyllum</i> Tul.	0,50	Árvores Brasileiras, 2009
58	Fabaceae	<i>Centrolobium microchaete</i> (Mart. ex Benth.) H.C. Lima	208,33	Árvores Brasileiras, 2009
59	Fabaceae	<i>Centrolobium sclerophyllum</i> H.C. Lima	909,09	Árvores Brasileiras, 2016
60	Fabaceae	<i>Centrosema pascuorum</i> Mart. ex Benth.	10,64	SID; Royal Botanic Gardens, 2017
61	Amaranthaceae	<i>Chamissoa altissima</i> (Jacq.) Kunth	3,00	SID; Royal Botanic Gardens, 2017
62	Rubiaceae	<i>Chiococca alba</i> (L.) Hitchc.	8,90	SID; Royal Botanic Gardens, 2017
63	Fabaceae	<i>Chloroleucon mangense</i> (Jacq.) Britton & Rose	45,00	SID; Royal Botanic Gardens, 2017
64	Vitaceae	<i>Cissus erosa</i> Rich.	12,89	SID; Royal Botanic Gardens, 2017
65	Ranunculaceae	<i>Clematis dioica</i> L.	1,87	SID; Royal Botanic Gardens, 2017
66	Melastomataceae	<i>Clidemia hirta</i> (L.) D. Don	0,06	SID; Royal Botanic Gardens, 2017
67	Clusiaceae	<i>Clusia nemorosa</i> G. Mey.	0,03	Árvores Brasileiras, 2016
68	Euphorbiaceae	<i>Cnidoscolus pubescens</i> Pohl	588,24	Árvores Brasileiras, 2009
69	Euphorbiaceae	<i>Cnidoscolus urens</i> (L.) Arthur	234,45	SID; Royal Botanic Gardens, 2017
70	Polygonaceae	<i>Coccocoba mollis</i> Casar.	283,00	SID; Royal Botanic Gardens, 2017
71	Bixaceae	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	28,00	SID; Royal Botanic Gardens, 2017
72	Rhamnaceae	<i>Colubrina glandulosa</i> Perkins	0,02	Árvores Brasileiras, 2008
73	Combretaceae	<i>Combretum leprosum</i> Mart.	0,17	Árvores Brasileiras, 2009
74	Burseraceae	<i>Commiphora leptophloeos</i> (Mart.) J.B. Gillett	0,19	Árvores Brasileiras, 2009
75	Asteraceae	<i>Conyza sumatrensis</i> (Retz.) E.Walker	0,05	SID; Royal Botanic Gardens, 2017
76	Boraginaceae	<i>Cordia alliodora</i> (Ruiz & Pav.) Cham.	33,00	SID; Royal Botanic Gardens, 2017
77	Boraginaceae	<i>Cordia glazioviana</i> (Taub.) Gottschling & J.S. Mill.	0,27	Árvores Brasileiras, 2009

78	Boraginaceae	<i>Cordia oncocalyx</i> Allemão	133,33	Árvores Brasileiras, 2008
79	Boraginaceae	<i>Cordia superba</i> Cham.	0,36	Árvores Brasileiras, 2008
80	Boraginaceae	<i>Cordia trichotoma</i> (Vell.) Arráb. ex Steud.	0,03	Árvores Brasileiras, 2008
81	Rubiaceae	<i>Cordiera sessilis</i> (Vell.) Kuntze	0,04	Árvores Brasileiras, 2009
82	Rubiaceae	<i>Coutarea hexandra</i> (Jacq.) K.Schum.	4,00	SID; Royal Botanic Gardens, 2017
83	Capparaceae	<i>Crateva tapia</i> L.	230,00	SID; Royal Botanic Gardens, 2017
84	Fabaceae	<i>Crotalaria holosericea</i> Nees & Mart.	10,40	SID; Royal Botanic Gardens, 2017
85	Euphorbiaceae	<i>Croton blanchetianus</i> Baill.	6,99	SID; Royal Botanic Gardens, 2017
86	Cucurbitaceae	<i>Cucumis dipsaceus</i> Ehrenb.	5,03	SID; Royal Botanic Gardens, 2017
87	Sapindaceae	<i>Cupania racemosa</i> (Vell.) Radlk.	0,77	Árvores Brasileiras, 2016
88	Sapindaceae	<i>Cupania vernalis</i> Cambess.	0,39	Árvores Brasileiras, 2008
89	Dilleniaceae	<i>Curatella americana</i> L.	18,89	SID; Royal Botanic Gardens, 2017
90	Fabaceae	<i>Dalbergia catingicola</i> Harms	72,91	SID; Royal Botanic Gardens, 2017
91	Fabaceae	<i>Dalbergia cearensis</i> Ducke	0,38	Árvores Brasileiras, 2016
92	Fabaceae	<i>Dalbergia frutescens</i> (Vell.) Britton	162,75	SID; Royal Botanic Gardens, 2017
93	Euphorbiaceae	<i>Dalechampia scandens</i> L.	22,06	SID; Royal Botanic Gardens, 2017
94	Rubiaceae	<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	1,13	SID; Royal Botanic Gardens, 2017
95	Fabaceae	<i>Desmodium glabrum</i> (Mill.) DC.	3,40	SID; Royal Botanic Gardens, 2017
96	Fabaceae	<i>Desmodium tortuosum</i> (Sw.) DC.	2,90	SID; Royal Botanic Gardens, 2017
97	Fabaceae	<i>Dimorphandra gardneriana</i> Tul.	0,32	Árvores Brasileiras, 2016
98	Fabaceae	<i>Diptychandra aurantiaca</i> Tul.	0,59	Árvores Brasileiras, 2008
99	Sapindaceae	<i>Dodonaea viscosa</i> Jacq.	8,00	SID; Royal Botanic Gardens, 2017
100	Verbenaceae	<i>Duranta erecta</i> L.	35,40	SID; Royal Botanic Gardens, 2017
101	Fabaceae	<i>Enterolobium contortisiliquum</i> (Vell.) Morong	253,00	SID; Royal Botanic Gardens, 2017
102	Fabaceae	<i>Enterolobium timbouva</i> Mart.	200,00	SID; Royal Botanic Gardens, 2017
103	Fabaceae	<i>Erythrina velutina</i> Willd.	546,45	SID; Royal Botanic Gardens, 2017
104	Erythroxylaceae	<i>Erythroxylum deciduum</i> A.St.-Hil.	0,10	Árvores Brasileiras, 2009

105	Erythroxylaceae	<i>Erythroxylum pulchrum</i> A.St.-Hil.	0,23	Árvores Brasileiras, 2016
106	Rutaceae	<i>Esenbeckia febrifuga</i> (A.St.-Hil.) A. Juss.ex Mart.	0,04	Árvores Brasileiras, 2009
107	Myrtaceae	<i>Eugenia biflora</i> (L.) DC.	97,92	SID; Royal Botanic Gardens, 2017
108	Myrtaceae	<i>Eugenia candelleana</i> DC.	0,67	Árvores Brasileiras, 2016
109	Myrtaceae	<i>Eugenia dysenterica</i> (Mart.) DC.	0,63	Árvores Brasileiras, 2009
110	Myrtaceae	<i>Eugenia florida</i> DC.	0,83	Árvores Brasileiras, 2009
111	Myrtaceae	<i>Eugenia luschnathiana</i> (O. Berg) Klotzsch ex B.D. Jacks.	11,00	SID; Royal Botanic Gardens, 2017
112	Myrtaceae	<i>Eugenia pyriformis</i> Cambess.	0,85	Árvores Brasileiras, 2008
113	Myrtaceae	<i>Eugenia uniflora</i> L.	258,29	SID; Royal Botanic Gardens, 2017
114	Moraceae	<i>Ficus enormis</i> Mart.ex Miq.	0,00	Árvores Brasileiras, 2009
115	Celastraceae	<i>Fraunhofera multiflora</i> Mart.	0,03	Árvores Brasileiras, 2016
116	Fabaceae	<i>Galactia striata</i> (Jacq.) Urb.	23,59	SID; Royal Botanic Gardens, 2017
117	Rubiaceae	<i>Genipa americana</i> L.	103,00	SID; Royal Botanic Gardens, 2017
118	Bignoniaceae	<i>Godmania dardanoi</i> (J.C. Gomes) A.H. Gentry	0,04	Árvores Brasileiras, 2016
119	Amaranthaceae	<i>Gomphrena celosioides</i> Mart.	2,90	SID; Royal Botanic Gardens, 2017
120	Fabaceae	<i>Goniorrhachis marginata</i> Taub.	0,91	Árvores Brasileiras, 2009
121	Nyctaginaceae	<i>Guapira graciliflora</i> (Mart. ex Schmidt) Lundell	0,14	Árvores Brasileiras, 2009
122	Nyctaginaceae	<i>Guapira opposita</i> (Vell.) Reitz	0,14	Árvores Brasileiras, 2009
123	Malvaceae	<i>Guazuma ulmifolia</i> Lam.	47,00	SID; Royal Botanic Gardens, 2017
124	Rubiaceae	<i>Guettarda viburnoides</i> Cham. & Schltl.	0,42	Árvores Brasileiras, 2009
125	Bignoniaceae	<i>Handroanthus chrysotrichus</i> (Mart. ex DC.) Mattos	0,01	Árvores Brasileiras, 2008
126	Bignoniaceae	<i>Handroanthus heptaphyllus</i> (Vell.) Mattos	0,03	Árvores Brasileiras, 2008
127	Bignoniaceae	<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	0,11	Árvores Brasileiras, 2008
128	Bignoniaceae	<i>Handroanthus ochraceus</i> (Cham.) Mattos	0,01	Árvores Brasileiras, 2008
129	Bignoniaceae	<i>Handroanthus serratifolius</i> (Vahl) S.O. Grose	0,04	Árvores Brasileiras, 2008
130	Malvaceae	<i>Helicteres guazumifolia</i> Kunth	1,66	SID; Royal Botanic Gardens, 2017
131	Chrysobalanaceae	<i>Hirtella ciliata</i> Mart. & Zucc.	0,12	Árvores Brasileiras, 2009

132	Fabaceae	<i>Hymenaea courbaril</i> L.	3678,00	SID; Royal Botanic Gardens, 2017
133	Fabaceae	<i>Hymenaea martiana</i> Hayne	384,62	Árvores Brasileiras, 2016
134	Fabaceae	<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	2725,00	SID; Royal Botanic Gardens, 2017
135	Fabaceae	<i>Indigofera suffruticosa</i> Mill.	3,10	SID; Royal Botanic Gardens, 2017
136	Fabaceae	<i>Inga capitata</i> Desv.	227,27	Árvores Brasileiras, 2016
137	Fabaceae	<i>Inga laurina</i> (Sw.) Willd.	188,68	Árvores Brasileiras, 2009
138	Convolvulaceae	<i>Ipomoea alba</i> L.	99,98	SID; Royal Botanic Gardens, 2017
139	Convolvulaceae	<i>Ipomoea carnea</i> Jacq.	79,20	SID; Royal Botanic Gardens, 2017
140	Convolvulaceae	<i>Ipomoea hederifolia</i> L.	12,76	SID; Royal Botanic Gardens, 2017
141	Convolvulaceae	<i>Ipomoea purpurea</i> (L.) Roth	27,50	SID; Royal Botanic Gardens, 2017
142	Convolvulaceae	<i>Ipomoea sericophylla</i> Meisn.	13,68	SID; Royal Botanic Gardens, 2017
143	Bignoniaceae	<i>Jacaranda brasiliiana</i> (Lam.) Pers.	0,03	Árvores Brasileiras, 2009
144	Convolvulaceae	<i>Jacquemontia tamnifolia</i> (L.) Griseb.	4,30	SID; Royal Botanic Gardens, 2017
145	Lythraceae	<i>Lafoensia glyptocarpa</i> Koehne	0,02	Árvores Brasileiras, 2008
146	Chrysobalanaceae	<i>Licania rigida</i> Benth.	0,77	Árvores Brasileiras, 2016
147	Fabaceae	<i>Lonchocarpus sericeus</i> (Poir.) Kunth ex DC.	180,00	SID; Royal Botanic Gardens, 2017
148	Malvaceae	<i>Luehea candidans</i> Mart. & Zucc.	0,01	Árvores Brasileiras, 2008
149	Malvaceae	<i>Luehea divaricata</i> Mart. & Zucc.	0,00	Árvores Brasileiras, 2008
150	Malvaceae	<i>Luehea grandiflora</i> Mart. & Zucc.	0,01	Árvores Brasileiras, 2008
151	Malvaceae	<i>Luehea paniculata</i> Mart. & Zucc.	0,00	Árvores Brasileiras, 2009
152	Fabaceae	<i>Luetzelburgia auriculata</i> (Allemão) Ducke	490,54	SID; Royal Botanic Gardens, 2017
153	Fabaceae	<i>Machaerium brasiliense</i> Vogel	0,14	Árvores Brasileiras, 2009
154	Fabaceae	<i>Machaerium opacum</i> Vogel	0,40	Árvores Brasileiras, 2009
155	Fabaceae	<i>Machaerium scleroxylon</i> Tul.	0,22	Árvores Brasileiras, 2008
156	Fabaceae	<i>Machaerium stipitatum</i> Vogel	0,16	Árvores Brasileiras, 2008
157	Fabaceae	<i>Machaerium villosum</i> Vogel	0,48	Árvores Brasileiras, 2008
158	Moraceae	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	0,00	Árvores Brasileiras, 2008

159	Fabaceae	<i>Macroptilium gracile</i> (Poepp.ex Benth.) Urb.	4,45	SID; Royal Botanic Gardens, 2017
160	Sapindaceae	<i>Magonia pubescens</i> A.St.-Hil.	223,71	Árvores Brasileiras, 2008
161	Malvaceae	<i>Malvastrum americanum</i> (L.) Torr.	1,49	SID; Royal Botanic Gardens, 2017
162	Euphorbiaceae	<i>Manihot carthagenensis</i> (Jacq.) Müll. Arg.	261,98	SID; Royal Botanic Gardens, 2017
163	Euphorbiaceae	<i>Manihot carthagenensis</i> subsp. <i>glaziovii</i> (Müll. Arg.) Allem	372,03	SID; Royal Botanic Gardens, 2017
164	Sapotaceae	<i>Manilkara salzmannii</i> (A. DC.) H.J. Lam	0,26	Árvores Brasileiras, 2009
165	Euphorbiaceae	<i>Maprounea guianensis</i> Aubl.	11,00	SID; Royal Botanic Gardens, 2017
166	Apocynaceae	<i>Marsdenia altissima</i> (Jacq.) Dugand	55,04	SID; Royal Botanic Gardens, 2017
167	Sapindaceae	<i>Matayba guianensis</i> Aubl.	0,21	Árvores Brasileiras, 2016
168	Apocynaceae	<i>Matelea maritima</i> (Vell.) Fontella	0,81	SID; Royal Botanic Gardens, 2017
169	Celastraceae	<i>Maytenus rigida</i> Mart.	0,05	Árvores Brasileiras, 2016
170	Malvaceae	<i>Melochia tomentosa</i> L.	1,47	SID; Royal Botanic Gardens, 2017
171	Convolvulaceae	<i>Merremia aegyptia</i> (L.) Urb.	54,20	SID; Royal Botanic Gardens, 2017
172	Convolvulaceae	<i>Merremia cissoides</i> (Lam.) Hallier f.	19,97	SID; Royal Botanic Gardens, 2017
173	Convolvulaceae	<i>Merremia dissecta</i> (Jacq.) Hallier f.	129,60	SID; Royal Botanic Gardens, 2017
174	Convolvulaceae	<i>Merremia macrocalyx</i> (Ruiz & Pav.) O'Donell	25,21	SID; Royal Botanic Gardens, 2017
175	Convolvulaceae	<i>Merremia umbellata</i> (L.) Hallier f.	44,00	SID; Royal Botanic Gardens, 2017
176	Fabaceae	<i>Mimosa caesalpiniifolia</i> Benth.	0,05	Árvores Brasileiras, 2008
177	Fabaceae	<i>Mimosa ophthalmocentra</i> Mart.ex Benth.	9,99	SID; Royal Botanic Gardens, 2017
178	Fabaceae	<i>Mimosa tenuiflora</i> (Willd.) Poir.	12,32	SID; Royal Botanic Gardens, 2017
179	Melastomataceae	<i>Mouriri pusa</i> Gardner	0,21	Árvores Brasileiras, 2016
180	Anacardiaceae	<i>Myracrodrodon urundeava</i> Allemão	0,02	Árvores Brasileiras, 2008
181	Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	0,06	Árvores Brasileiras, 2008
182	Myrtaceae	<i>Myrcia multiflora</i> (Lam.) DC.	0,02	Árvores Brasileiras, 2008
183	Myrtaceae	<i>Myrcia splendens</i> (Sw.) DC.	173,00	SID; Royal Botanic Gardens, 2017
184	Myrtaceae	<i>Myrcia tomentosa</i> (Aubl.) DC.	0,27	Árvores Brasileiras, 2009
185	Fabaceae	<i>Myroxylon peruferum</i> L.f.	284,98	SID; Royal Botanic Gardens, 2017

186	Lauraceae	<i>Nectandra membranacea</i> (Sw.) Griseb.	0,77	Árvores Brasileiras, 2009
187	Lauraceae	<i>Nectandra nitidula</i> Nees	0,21	Árvores Brasileiras, 2009
188	Convolvulaceae	<i>Operculina macrocarpa</i> (L.) Urb.	485,94	SID; Royal Botanic Gardens, 2017
189	Fabaceae	<i>Parkia platycephala</i> Benth.	0,48	Árvores Brasileiras, 2009
190	Sapindaceae	<i>Paullinia elegans</i> Cambess.	110,00	SID; Royal Botanic Gardens, 2017
191	Malpighiaceae	<i>Peixotoa jussieuana</i> Mart.ex A. Juss.	72,15	SID; Royal Botanic Gardens, 2017
192	Fabaceae	<i>Peltogyne confertiflora</i> (Mart.ex Hayne) Benth.	0,83	Árvores Brasileiras, 2009
193	Fabaceae	<i>Peltophorum dubium</i> (Spreng.) Taub.	197,35	SID; Royal Botanic Gardens, 2017
194	Fabaceae	<i>Periandra coccinea</i> (Schrad.) Benth.	34,97	SID; Royal Botanic Gardens, 2017
195	Fabaceae	<i>Piptadenia gonoacantha</i> (Mart.) J.F. Macbr.	42,28	SID; Royal Botanic Gardens, 2017
196	Fabaceae	<i>Piptadenia stipulacea</i> (Benth.) Ducke	39,21	SID; Royal Botanic Gardens, 2017
197	Fabaceae	<i>Piptadenia viridiflora</i> (Kunth) Benth.	33,43	SID; Royal Botanic Gardens, 2017
198	Fabaceae	<i>Pithecellobium diversifolium</i> Benth.	0,23	Árvores Brasileiras, 2016
199	Fabaceae	<i>Plathymenia reticulata</i> Benth.	0,03	Árvores Brasileiras, 2008
200	Myrtaceae	<i>Plinia cauliflora</i> (Mart.) Kausel	0,30	Árvores Brasileiras, 2016
201	Fabaceae	<i>Poecilanthe ulei</i> (Harms) Arroyo & Rudd	254,06	SID; Royal Botanic Gardens, 2017
202	Fabaceae	<i>Poiretia punctata</i> (Willd.) Desv.	3,71	SID; Royal Botanic Gardens, 2017
203	Sapotaceae	<i>Pouteria gardneriana</i> (A. DC.) Radlk.	0,30	Árvores Brasileiras, 2016
204	Salicaceae	<i>Prockia crucis</i> P. Browne ex L.	0,00	Árvores Brasileiras, 2016
205	Malvaceae	<i>Pseudobombax grandiflorum</i> (Cav.) A.Robyns	54,21	SID; Royal Botanic Gardens, 2017
206	Malvaceae	<i>Pseudobombax marginatum</i> (A.St.-Hil.) A. Robyns	0,26	Árvores Brasileiras, 2009
207	Malvaceae	<i>Pseudobombax simplicifolium</i> A. Robyns	0,04	Árvores Brasileiras, 2009
208	Myrtaceae	<i>Psidium acutangulum</i> DC.	75,00	SID; Royal Botanic Gardens, 2017
209	Myrtaceae	<i>Psidium guineense</i> Sw.	8,73	SID; Royal Botanic Gardens, 2017
210	Myrtaceae	<i>Psidium myrtoides</i> O. Berg	136,99	Árvores Brasileiras, 2009
211	Myrtaceae	<i>Psidium sartorianum</i> (O. Berg) Nied.	0,36	Árvores Brasileiras, 2009
212	Fabaceae	<i>Pterocarpus rohrii</i> Vahl	178,00	SID; Royal Botanic Gardens, 2017

213	Vochysiaceae	<i>Qualea grandiflora</i> Mart.	0,19	Árvores Brasileiras, 2008
214	Vochysiaceae	<i>Qualea parviflora</i> Mart.	0,03	Árvores Brasileiras, 2008
215	Rhamnaceae	<i>Rhamnidium elaeocarpum</i> Reissek	0,05	Árvores Brasileiras, 2008
216	Fabaceae	<i>Rhynchosia minima</i> (L.) DC.	13,10	SID; Royal Botanic Gardens, 2017
217	Acanthaceae	<i>Ruellia geminiflora</i> Kunth	5,68	SID; Royal Botanic Gardens, 2017
218	Polygonaceae	<i>Ruprechtia laxiflora</i> Meisn.	0,04	Árvores Brasileiras, 2009
219	Vochysiaceae	<i>Salvertia convallariodora</i> A.St.-Hil.	0,13	Árvores Brasileiras, 2008
220	Sapindaceae	<i>Sapindus saponaria</i> L.	767,00	SID; Royal Botanic Gardens, 2017
221	Euphorbiaceae	<i>Sapium glandulosum</i> (L.) Morong	34,00	SID; Royal Botanic Gardens, 2017
222	Euphorbiaceae	<i>Sapium haematospermum</i> Müll. Arg.	40,00	SID; Royal Botanic Gardens, 2017
223	Anacardiaceae	<i>Schinopsis brasiliensis</i> Engl.	167,50	SID; Royal Botanic Gardens, 2017
224	Euphorbiaceae	<i>Sebastiania brasiliensis</i> Spreng.	0,02	Árvores Brasileiras, 2009
225	Fabaceae	<i>Senegalia polyphylla</i> (DC.) Britton & Rose	0,10	Árvores Brasileiras, 2008
226	Fabaceae	<i>Senna alata</i> (L.) Roxb.	38,50	SID; Royal Botanic Gardens, 2017
227	Fabaceae	<i>Senna macranthera</i> (DC.ex Collad.) H.S. Irwin & Barneby	0,04	Árvores Brasileiras, 2008
228	Fabaceae	<i>Senna multijuga</i> (Rich.) H.S. Irwin & Barneby	7,10	SID; Royal Botanic Gardens, 2017
229	Fabaceae	<i>Senna obtusifolia</i> (L.) H.S. Irwin & Barneby	23,00	SID; Royal Botanic Gardens, 2017
230	Fabaceae	<i>Senna occidentalis</i> (L.) Link	17,00	SID; Royal Botanic Gardens, 2017
231	Fabaceae	<i>Senna spectabilis</i> (DC.) H.S. Irwin & Barneby	21,30	SID; Royal Botanic Gardens, 2017
232	Fabaceae	<i>Senna spectabilis</i> var. <i>excelsa</i> (Schrad.) H.S. Irwin & Barneby	36,16	SID; Royal Botanic Gardens, 2017
233	Fabaceae	<i>Senna trachypus</i> (Benth.) H.S. Irwin & Barneby	5,89	SID; Royal Botanic Gardens, 2017
234	Malvaceae	<i>Sida acuta</i> Burm. f.	2,50	SID; Royal Botanic Gardens, 2017
235	Malvaceae	<i>Sida glomerata</i> Cav.	0,81	SID; Royal Botanic Gardens, 2017
236	Malvaceae	<i>Sida spinosa</i> L.	2,40	SID; Royal Botanic Gardens, 2017
237	Malvaceae	<i>Sidastrum micranthum</i> (A.St.-Hil.) Fryxell	1,23	SID; Royal Botanic Gardens, 2017
238	Malvaceae	<i>Sidastrum paniculatum</i> (L.) Fryxell	1,76	SID; Royal Botanic Gardens, 2017
239	Sapotaceae	<i>Sideroxylon obtusifolium</i> (Humb.ex Roem. & Schult.) T.D. Penn.	0,50	Árvores Brasileiras, 2009

240	Simaroubaceae	<i>Simaba floribunda</i> A.St.-Hil.	363,64	Árvores Brasileiras, 2016
241	Simaroubaceae	<i>Simarouba amara</i> Aubl.	0,27	Árvores Brasileiras, 2008
242	Simaroubaceae	<i>Simarouba versicolor</i> A.St.-Hil.	151,52	Árvores Brasileiras, 2009
243	Solanaceae	<i>Solanum capsicoides</i> All.	2,30	SID; Royal Botanic Gardens, 2017
244	Solanaceae	<i>Solanum crinitum</i> Lam.	5,51	SID; Royal Botanic Gardens, 2017
245	Anacardiaceae	<i>Spondias tuberosa</i> Arruda	204,08	Árvores Brasileiras, 2008
246	Malvaceae	<i>Sterculia apetala</i> (Jacq.) H.Karst.	1899,00	SID; Royal Botanic Gardens, 2017
247	Malvaceae	<i>Sterculia striata</i> A.St.-Hil. & Naudin	250,00	Árvores Brasileiras, 2008
248	Bignoniaceae	<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	0,15	Árvores Brasileiras, 2008
249	Bignoniaceae	<i>Tabebuia roseoalba</i> (Ridl.) Sandwith	0,01	Árvores Brasileiras, 2008
250	Apocynaceae	<i>Tabernaemontana catharinensis</i> A.DC.	0,15	Árvores Brasileiras, 2016
251	Apocynaceae	<i>Tabernaemontana hystrix</i> Steud.	0,07	Árvores Brasileiras, 2008
252	Sapindaceae	<i>Talisia esculenta</i> (Cambess.) Radlk.	714,29	Árvores Brasileiras, 2008
253	Combretaceae	<i>Terminalia fagifolia</i> Mart.	0,04	Árvores Brasileiras, 2009
254	Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schltl.) K.Schum.	23,37	SID; Royal Botanic Gardens, 2017
255	Cannabaceae	<i>Trema micrantha</i> (L.) Blume	7,00	SID; Royal Botanic Gardens, 2017
256	Meliaceae	<i>Trichilia hirta</i> L.	51,45	SID; Royal Botanic Gardens, 2017
257	Polygonaceae	<i>Triplaris gardneriana</i> Wedd.	0,06	Árvores Brasileiras, 2009
258	Polygonaceae	<i>Triplaris weigeltiana</i> (Rchb.) Kuntze	0,05	Árvores Brasileiras, 2008
259	Malvaceae	<i>Triumfetta semitriloba</i> Jacq.	21,27	SID; Royal Botanic Gardens, 2017
260	Sapindaceae	<i>Urvillea ulmacea</i> Kunth	8,16	SID; Royal Botanic Gardens, 2017
261	Fabaceae	<i>Vatairea macrocarpa</i> (Benth.) Ducke	142,86	Árvores Brasileiras, 2009
262	Asteraceae	<i>Verbesina macrophylla</i> (Cass.) S.F. Blake	0,50	SID; Royal Botanic Gardens, 2017
263	Lamiaceae	<i>Vitex cymosa</i> Bertero ex Spreng.	0,54	Árvores Brasileiras, 2009
264	Lamiaceae	<i>Vitex gardneriana</i> Schauer	0,26	Árvores Brasileiras, 2016
265	Lamiaceae	<i>Vitex polygama</i> Cham.	0,45	Árvores Brasileiras, 2008
266	Malvaceae	<i>Waltheria rotundifolia</i> Schrank	1,40	SID; Royal Botanic Gardens, 2017

267	Malvaceae	<i>Wissadula amplissima</i> (L.) R.E. Fr.	3,31	SID; Royal Botanic Gardens, 2017
268	Annonaceae	<i>Xylopia aromatica</i> (Lam.) Mart.	0,09	Árvores Brasileiras, 2008
269	Annonaceae	<i>Xylopia sericea</i> A.St.-Hil.	0,06	Árvores Brasileiras, 2008
270	Salicaceae	<i>Xylosma ciliatifolia</i> (Clos) Eichler	0,01	Árvores Brasileiras, 2016
271	Rutaceae	<i>Zanthoxylum fagara</i> (L.) Sarg.	10,18	SID; Royal Botanic Gardens, 2017
272	Rutaceae	<i>Zanthoxylum monogynum</i> A.St.-Hil.	0,06	Árvores Brasileiras, 2009
273	Rutaceae	<i>Zanthoxylum rhoifolium</i> Lam.	0,01	Árvores Brasileiras, 2008
274	Rutaceae	<i>Zanthoxylum riedelianum</i> Engl.	0,02	Árvores Brasileiras, 2008
275	Bignoniaceae	<i>Zeyheria tuberculosa</i> (Vell.) Bureau ex Verl.	0,07	Árvores Brasileiras, 2008
276	Rhamnaceae	<i>Ziziphus joazeiro</i> Mart.	0,58	Árvores Brasileiras, 2008
277	Fabaceae	<i>Zornia latifolia</i> Sm.	1,31	SID; Royal Botanic Gardens, 2017

Tabela 2-Description of environmental variables used in this study Table S2

Variables	Author	Short description	Resolutions used (?)	Original spatial resolution	Temporal coverage
Aridity values	(Zomer et al.,2007, 2008)	The aridity values for the study region were calculated using the Global Potential EvapoTranspiration (Global-PET) set of rasters layers, which is the measure of the atmosphere's ability to remove water through Evapotranspiration (ET) and Global Aridity Index (Global-Aridity), used to quantify precipitation availability in relation to the demand of atmospheric water		at 30 arc seconds (~ 1km at equator)	Anual (?)
Soil properties	("SoilGrids" (www.SoilGrids.org),	Bulk density (fine earth) in kg, cation exchange capacity in cmolc / kg, Soil PH x	1km	250 m	2000 to 2016

		10 in H ₂ O, coarse fragments volumetric in percentage values (%).The depth standard was 0.05m for all variables			
Bio_9	Deblauwe et al. (2016).	Mean temperature of driest quarter		3 arc-minutes and 6 arcminutes	2000-2014
Bio_18	Deblauwe et al. (2016)	Precipitation of warmest quarter		3 arc-minutes and 6 arcminutes	2000-2014

Tabela 3-Descriptive statistics of environmental variables used in this study

	Soil bulk density	BIO09	% non-tree-cover	CEC	BIO18	Median	Seed Weight
Min 1st	1254	18,67	48,34	7,45	8,33	0,11	
Quartil	1356	21,73	62,97	12,47	118,83	0,62	
Median	1405	23,79	67,58	13,80	184,21	2,29	
Mean 3rd	1403	24,12	67,52	13,64	176,25	12,71	
Quartil	1446	26,23	70,35	15,00	223,95	12,12	
Max	1524	33,4	126,16	20,26	378,45	234,45	
SD	60,07	3,13	8,38	2,26	82,81	32,22	

Capítulo II

3- Title: Macroecological analysis of physiological activity of Neotropical semi-arid woody species

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Abstract

Aims: Macroscale studies are of fundamental importance to understand the distribution of leaf traits and their relationship with environmental conditions. Here, we evaluate the influence of aridity and soil physico-chemical properties on the mean size of woody plant leaves in the Caatinga.

Methods

We use a model of structural equations (SEM) to evaluate the direct and indirect effect of aridity and soil properties on the average leaf size.

Results: Our results indicate that aridity influences soil pH, that together with cation exchange affect leaf size.

Conclusions: The environmental variables linked to the physical and chemical properties of the soil most affect leaf area of woody plant species of the Caatinga

Keywords: Leaf size, Arid and Semi-arid, Dry forest, Vegetation, Caatinga, Databases

3.1-Introduction

Leaves are among the most important organs of the a plant. They first form as rod-like structures protruding from the shoot's apical meristema (RODRIGUEZ et al., 2014) and

develop diverse morphologies that reflect a wide variety of functions (TORRE, 2004; WALDHOFF; PAROLIN, 2010). They show considerable intraspecific and interspecific trait variability in, for example, area, thickness, shape, capacity for gas exchange and drought tolerance (LAUTERBACH et al., 2016; SACK et al., 2003). Leaves are by far the most studied plant organ due to their importance in photosynthesis (OGUCHI et al., 2005; SMITH et al., 1997). Chloroplasts are distributed across the leaf surface and are responsible for light absorption by the leaf (TERASHIMA et al., 2011) and leaves are the main route for the diffusion of CO₂ through the mesophyll (PEGUERO-PINA et al.; 2017 ; PIERUSCHKA et al.; 2005). Leaves are also responsible for a substantial part ($\geq 30\%$) of the water flow through plants due to transpiration (SACK et al., 2003).

As in other biomes, in dry tropical forests the leaf characteristics of woody species, such as leaf area, weight, specific leaf area (SLA) and chlorophyll content, reflect the variability of local conditions (PANDEY et al., 2009). Due to frequent droughts in such environments, there is strong selection for woody species with small leaves that minimize water loss resulting on a correlation between leaf area and water availability (XU et al., 2008, 2009). This is because stomatal conductivity is strongly correlated with a leaf area, so plants that can reduce the conductance under water stress have better physical conditioning (NICOTRA; DAVIDSON, 2010). Similarly, at high altitudes where environmental conditions can be very severe, leaf area correlates positively with average annual rainfall (SUN et al., 2016).

Ecotones from hosting (humid to semi-arid environments) are often characterized by woody species that are able to adapt to arid conditions by decreasing leaf area, thus reducing water loss (BORGES et al., 2016; QIN et al., 2019). Some woody species from arid and semi-arid environments also have greater rooting depth, allowing them to acquire water from deeper soil layers during water stress(LIU et al., 2010; LOPEZ-IGLESIAS et al.,

Consequently, species originating from arid and semi-arid environments under high water deficit conditions often use more water when compared to temperate species under the same conditions (GOEDHART; PATAKI, 2012). Responses to saline stress in these environments also result in a range of morphological, physiological and biochemical responses, including reduction of leaf area (BACHA et al., 2017; TOSCANO et al., 2019).

The Caatinga semiarid ecosystem of northeast Brazil is characterized by a mosaic of scrubs and patches and is the largest seasonally dry ecosystems of South America (SANTOS et al., 2011). In this ecosystem, plant species are strongly influenced by the interaction of their functional traits with rainfall gradients and soil conditions (PINHO et al., 2019). Macroclimatic factors (e.g. aridity) and geomorphological factors (e.g. soil chemistry) can affect the availability of nutrients and modify the pH of the soil. Some of these nutrients, such as potassium (K^+), can act on the leaves of plant, regulating the opening and closing of stomata, thus influencing the exchange of gases and rate of photosynthesis. This type of regulation is very important in arid and semi-arid environments where there is a trade-offs between the controlling of water loss and maximization of growth under different climatic and edaphic conditions. To explore this relationship in more depth, we evaluated the influence of aridity and soil physic-chemical properties on the mean size of woody plant leaves in the Caatinga.

3.2-Methods

3.2.1-Study area

The Caatinga biome is characterized by a seasonal climate marked by irregular and often prolonged periods of drought, high evaporation rates, high average temperatures (around 27° C), normally low relative humidity, and rainfall levels of 250mm to 750mm per year (EMBRAPA-1986,1988) crystalline origin, being shallow, stony and fertile. A smaller portion of Caatinga is covered by sedimentary soils, which are deep, sandy and oligotrophic (GIONGO et al., 2011; SILVA et al., 2017). The flora of Caatinga is extremely diverse, formed by a mosaic of vegetation types, typically deciduous, xerophious and thorny, which are usually associated with soil characteristic and climate (NOGUEIRA FERRAZ et al., 2003; PEREIRA et al., 2003; SANTOS et al., 2012; SIQUEIRA-FILHO et al., 2012)

3.2.2-Selection of woody species

The list of woody plant species of the Caatinga was generated from the lists of Moro et al. (2014) and (SIQUEIRA-FILHO et al., 2012).Woody species include trees, shrubs, lianas subshrubs and woody climbers (Brazilian Flora 2020,CARVALHO 2017). We checked the spelling and synonyms with the Taxonomic Name Resolution Service software (TNRS) version 4.0 (BOYLE et al., 2013) and retained only accepted names (i.e., illegitimate, invalid, misapplied, rejected names and synonyms were excluded from the analysis). Our final list of woody species of the Caatinga contained 1,147 species, 434 genera and 83 families.

3.3-Database Construction

3.3.1-Digital Imagens of dry herbarium specimens

In May 2017 we retrieved a total of 999,322 occurrence records of Angiosperms from the (GBIF; SpeciesLink 2017). First, we identified 33,569 occurrence records (6,725 species) with digital images available through these platforms. We then checked these 6,725 names using the TNRS. After removing the duplicate records and only considering valid names we identified 6,134 species with digital images. This species list with digital imagens was cross-checked against the list of woody species to generate a final list of 716 species with digital images for Caatinga. Occurrence records from GBIF were retrieved using the package rgbif (CHAMBERLAIN, 2016) for the software (TEAM, 2017).

We download 4,715 hyperlinks of digital images of dried herbarium specimens through three international virtual herbaria Kew Royal Botanic Gardens (n= 3311/site: <http://specimes. kew.org. herbarium>), Muséu National D' Histoire Naturalle of France (n= 787 /site: <http://coldb.mnhn.fr/catalognumber/mnhn>) and the Smithsonian National Museum of Natural History (n=617/ site <https://collections.nmmh.si.edu/search/>). A total of 192 species had digital images that the met our inclusion criteria, i.e. images with minimum 600 dpi resolution and height of 2000 pixels. Images that did not provide geographical coordinates indicating where the specimen had been collected, a date of collection, damaged or overlapping leaves, and without a complete description of the local collection were excluded from the analysis.

3.3.2-Metrics of leaves

The digital images of the exsiccatae were processed using the free software Adobe® Photoshop® CS3 (Adobe Systems In.). We removed all additional information from digital exsiccatae and the files were converted to black and white images. Digital exsiccatae with damaged, overlapping leaves or with doubtful collection data were excluded. Digital images

of leaves were processed using Leaf Area package (KATABUCHI, 2015) on ImageJ ([imagej.nih.gov/ ij/download](http://imagej.nih.gov/ij/download)). Leaf area estimates were processed using the run.ij()function. To calibrate the function parameters we used the distance.pixel=47 know argument.distance=1. Initial description of the qualitative shape characterisctics was achieved by use by the Illustrated morphology dictionary (GONÇALVES; LORENZI, 2011) and size classes followed (RAUNKIAER, 1934).

3.3.3- Environmental variables and data analysis

To maximize occurrence data two data sources were used: Costa et al. (2019) and our own database (Table S1 supplementary material) with the area measures leaf. The environmental variables used were aridity and soil properties, both with a spatial resolution of 30°. The environmental variables were resized to a spatial resolution of 0.5 decimal degree (from the calculation of the average of the values). Subsequently, the average (and variance) of the leaf area of the Caatinga woody plants was calculated for cells of 0.5 decimal degree.

To evaluate the direct and indirect effects of aridity and soil properties on average leaf size, we used a structural equation model, based on three equations, to quantify:

- the influence of the size of the soil fragment on the cation exchange capacity:

(Eq. 1) cation_exchange ~ coarse_fragments

- the influence of aridity and cation exchange capacity on soil pH

(Eq. 2) soil_pH ~ aridity + cation_exchange

- the influence of pH and cation exchange capacity on the average leaf size

(Eq. 3) mean_leaf_log ~ cation_exchange + soil

3.4-Results

3.4.1- Characterization of leaves

Among the 192 woody species from the Caatinga in our digital image database, 57.81% (N=111) had simple leaves and 42.19% (N=81) had compound leaves (Fig.3). Within the *Fabaceae* family 20.59% of the compound leaves are trifoliolate. The shape of the leaves varied considerably (Table S1 supplementary material) among species studied: 32.81% are ovate, 9.89 % obovate and oblong either and 6.77% lanceolate. The families with the greatest variety of shape of leaves were the Fabaceae and the Apocynaceae.

3.4.2- Leaf Metrics

We measured 2,400 leaves belonging to 24 botanical families and 192 woody species from the Caatinga. Caatinga species have a great diversity in the leaf size and shape: the species with the largest leaf areas were *Ipomoea megapotamica* ($60.987 \text{ cm}^2 \pm 0.216$) and *Tabebuia aurea* ($47.474 \text{ cm}^2 \pm 6.233$), while *Aeschynomene martii* (0.747 ± 0.032) and *Enterolobium timbouva* (0.727 ± 0.020) had the smallest leaf areas (Table S1 supplementary material). The dominant leaf size class in the Caatinga (Fig.4) was Nanophyll ($0.25\text{-}2.2\text{.25 cm}^2$), which is widely distributed across botanical families (Fig.5) and ecoregions (Fig.6).

3.4.3-Leaf size and environmental variables

The availability of cations in the soil is positively related to the availability of coarse fragments- “coarse fragments” ($r^2 = 0.28$). In addition, 67% of the Caatinga pH variation is explained by aridity, which prevents nutrient leaching by rain, and by the availability of cations (“cation exchange”) in the soil ($r^2 = 0.67$). We found a positive relationship between the leaf area mean (Table 1, Fig.1) with the availability of cationic minerals (i.e “cation exchange”) and a negative relationship between average leaf size and the soil pH ($r^2 = 0.6$). Despite the low predictive power, $r^2 = 6\%$, the relationship with leaf size, the availability of

cationic minerals in the soil, and pH values, may reflect the relationship between these minerals and the stomata (see discussion). We also calculate the distribution of mean temperature distribution and aridity index for the region (Fig.2)

3.5- Discussion

Our results indicate that leaf area in woody plant species of in the Caatinga is directly influenced by soil pH through the action of “coarse fragments” and “Cation Exchange”. Soil pH has been recognized as an important factor effecting the distribution of plants in tropical dry seasonal forests and savannahs (VIANI et al., 2014). In these environments, the variation in nutrients in new and evergreen leaves is closely aligned with general measures of soil fertility (MIATTO et al., 2016). In the present study, the *Fabaceae* have the greatest variety in leaf area and are also the most abundant (in terms of species) family in the Caatinga. Due to its high number of taxa and the distribution patterns of its species, *Fabaceae* thus represent a model group for the analysis of biogeographic hypotheses related to Caatinga (DE QUEIROZ, 2006). The *Fabaceae* has a high frequency of species with compound leaves (almost 50% in the study area) and tend to be found in areas such as the Caatinga with high temperatures and low rainfall (STOWE; BROWN, 1981). Though the adaptive significance of compound leaves is complex and reflects a number of selective pressures (GIVNISH, 1978; MALHADO et al., 2010), they seem to confer some advantage in dry environments such as improved light capture, reduced overheating and loss of water (AARSSEN, 2012). In the *Fabaceae*, this might be reflected in functional differences between simple and compound-leaved species resulting in higher relative growth rates of leaves in arid conditions (WU et al., 2019). Hydraulic efficiency and carbon assimilation capacity are also higher in compound leaves when taking into account the size of the leaf area (SONG et al., 2018).

The variation in leaf area was lower among the *Fabaceae* when compared to other families. This may be a consequence of the leaflet structure, and thus small size of compound leaves (SINHA, 1997). However, it is by no means clear whether leaflets of compound leaves should be treated as analogous to simple leaves or whether all the leaflets within a leaf unit are functionally equivalent to a single simple leaf (CHAMPAGNE; SINHA, 2004). If the latter is true they may be gaining some of the advantages of larger leaves (e.g. expanded area of light capture) without some of the associated costs (e.g. increased water loss). In any case, leaves and leaflets are smaller in species from arid and semi-arid environments when compared to species that occur in humid environments (GIBSON, 1998). The effect of water stress on leaf area reported on the whole leaf scale is the same as that reported for the different leaflets that make up a compound leaf (KOCH et al., 2018). Many of the Caatinga species in our study possessed trifoliate (20.59%) compound leaves, probably as an adaptation to the xeric environment: narrow leaves reduce evaporation by reducing the size of the boundary layer (XU et al., 2009). The *Fabaceae* of the Caatinga possess compound pinnate, alternative, petiolate, leaves that are evergreen and with trichomes (CARDOSO; QUEIROZ, 2008; GOMES et al., 2018; TERRA; GARCIA, 2016).

The shape of the dominant leaf blade in the Caatinga was ovate (32.81%) with the widest blade shape close to the base, differing only in the length versus width ratio (GONÇALVES; LORENZI, 2011). SHUDE et al., (2004) demonstrated that species with ovate and lanceolate forms were more tolerant to drought because they have well-developed xeromorphic structures (*i.e* thickened epidermal layer, hypodermis, stoma with substomatal chamber and mucilage cells). The lanceolate leaves in the present study are narrow when compared to ovate leaves. This is expected given that arid conditions seem to favor the selection of small, narrow leaves divided into parts (LEIGH et al., 2017). This explains the close relationship between leaf size and shape in soils with low nutrient content

in humid tropical forests (MALHADO et al., 2009b). Leaf size and shape will also be moulded by the necessity for leaf auto-thermoregulation, especially influencing leaf thickness (NICOTRA; DAVIDSON, 2010). The wide variety in blade shape of the Fabaceae in our analysis is largely due to the division of the leaf limbus. Generally, dissected leaves are found in more xerophytic phylogenetic clades and are thought to represent an evolutionary response to extreme abiotic factors (JONES et al., 2009).

Among the ecoregions within our study area, four have the largest number of species in our data: Caatinga (120 sp), Atlantic Dry Forest (32 sp.), Campos Rupestres Montane Savanna (15sp); Pernambuco Coastal Forests (8sp.) and three families, Fabaceae, Solanaceae, Pernambuco Coastal Forests (8 sp) and three families, Fabaceae, Solanaceae and Erythroxylaceae. There are many subtypes of plant communities in the Caatinga ecoregion. Moro et al. 2014 classified as a semi-arid region of the South American in nine ecoregions on the type of plants existing (MORO et al., 2014). A recent classification (SILVA et al., 2017) of Caatinga differs from previous studies, but based on a initial classification by (IBGE, 2004), this edition was done with exclusion, renaming and adding new regions.

Aridity indices associated with current productivity are associated with floristic variability in the nine biogeographic regions of the Caatinga (SILVA; SOUZA, 2018). In certain ecoregions of the Caatinga, the dominance of the *Fabaceae* is a clear consequence of their preference for climatic components such as temperature and precipitation over geographical proximity (LIMA et al., 2012). The four regions of the Caatinga with more representative assemblies of woody species have a higher proportion of Microphyll leaves (followed by Nanophyll). Small leaves are considered adaptations to the stress caused by the lack of water in tropical forests (MEDINA, 1983). The Caatinga ecoregion in particular is characterized by: i) a considerable number of endemic species and genera; ii) a large

number of new occurrence records for the region, and; iii) a high frequency of threatened species (SILVA et al, 2018). Ecoregions such as the rocky grasslands (campos rupestres) also have a high number of exclusive taxa for the northeast semi-arid Caatinga (VALENTE; PÔRTO; BASTOS, 2013).

In summary, we observed considerable variation in the leaf area among taxonomic families, with the *Fabaceae* contributing significantly to the richness and diversity of leaf forms of woody species in the Caatinga. The families with the largest variation in leaf size are *Solanaceae*, *Convolvulaceae*, *Apocynaceae*, *Vochysiaceae* and *Asteraceae*. Recent biogeographic studies have shown considerable heterogeneity between the main plant communities of the region with the presence of distinct vegetation nuclei (MORO et al., 2016). It appears that different environmental filters operate in coastal and mixed forests in comparison to the other ecoregions of the Caatinga (which contain more xeromorphic vegetation), such as Caatinga, Bahia interior forests, Pernambuco interior forests, rocky grasslands (campos rupestres) and montane savannah. Although the inventoried species are widely occurring in the semi-arid region, our results produced so far have not yet been able to understand which environmental variable affect the leaf area of the Caatinga woody species.

Tabela 1-Direct and indirect effects of environmental variables and physical-chemical properties of the soil on the leaf size of woody plants in the Caatinga.

Response	Predictor	Estimate	Std.Error	DF	Crit.Value	P.Value	Std.Estimate
cation_exchange	coarse_fragments	0.5248	0.0544	245	96.499	0.0000	0.5248
soil_pH	aridity	-0.0005	0.0000	244	-165.369	0.0000	-0.6097
soil_pH	cation_exchange	0.4986	0.0369	244	135.234	0.0000	0.4986
mean_leaf_log	cation_exchange	0.1569	0.0538	244	29.160	0.0039	0.2176
mean_leaf_log	soil_pH	-0.1824	0.0538	244	-33.894	0.0008	-0.2529

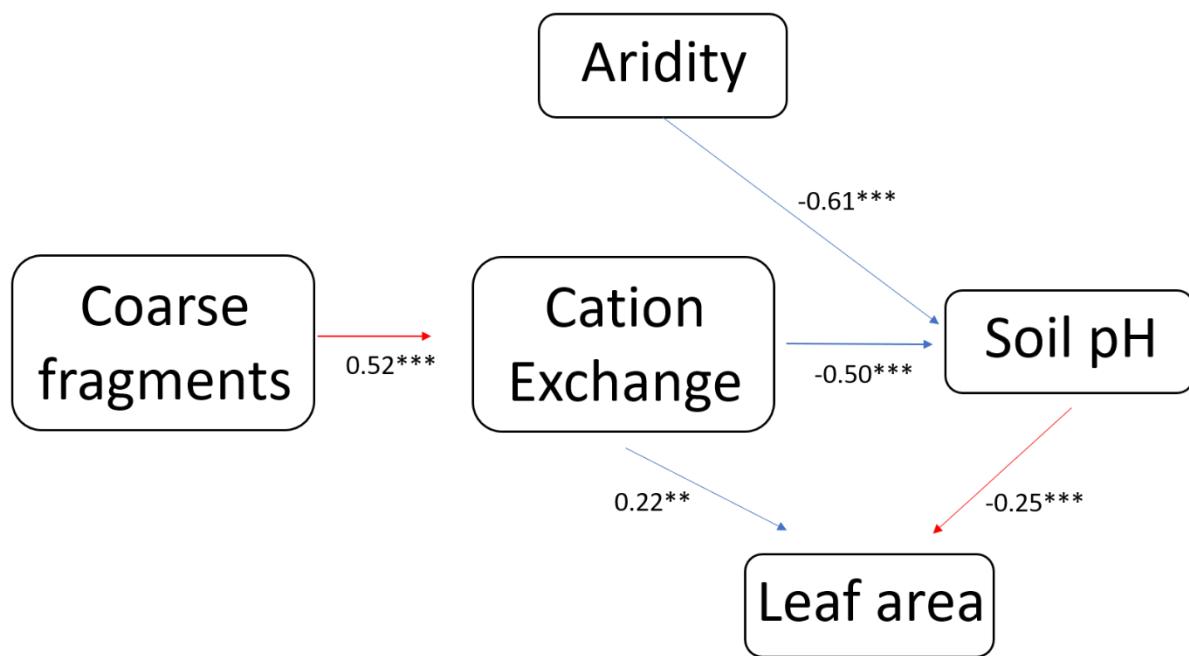


Fig.1-Structural Equation Model (SEM)- relationship between the effect of aridity and physicochemical properties of the soil in leaf size. In our model, aridity influences soil pH, and cation exchange affect leaf size.

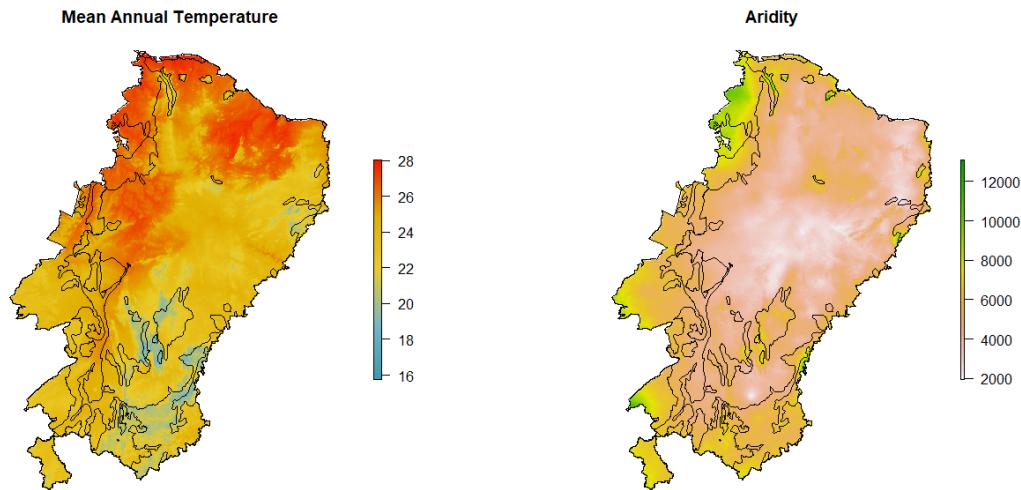


Fig.2 –Spatial distribution of mean annual temperature and aridity in the Caatinga.

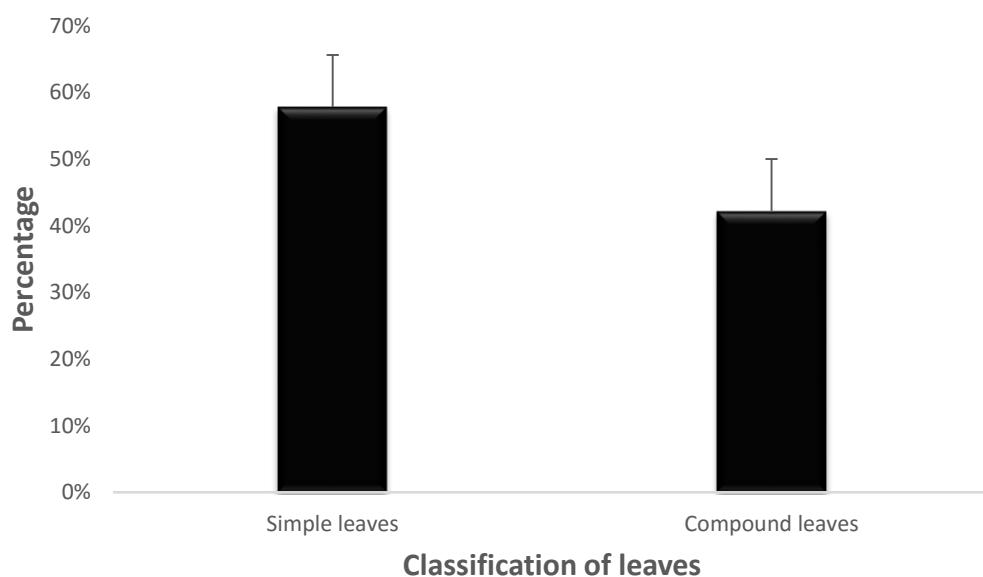


Fig.3-Percentage of simple and compound leaves occurring in the Caatinga.

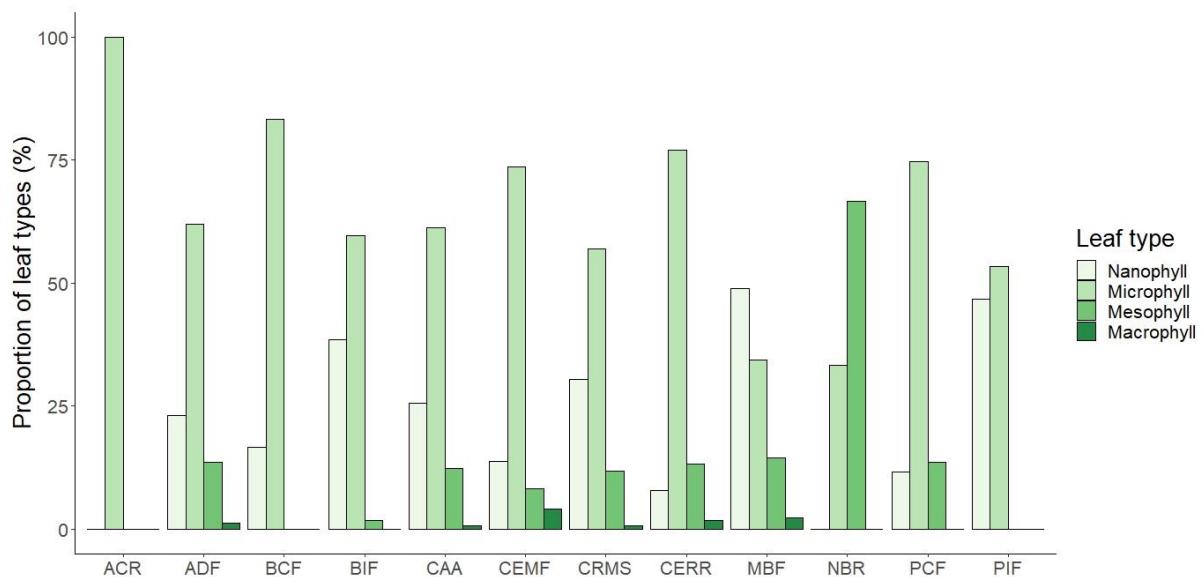


Fig.4-Life size categories (Raunkier 1931) in the different Caatinga ecoregions.

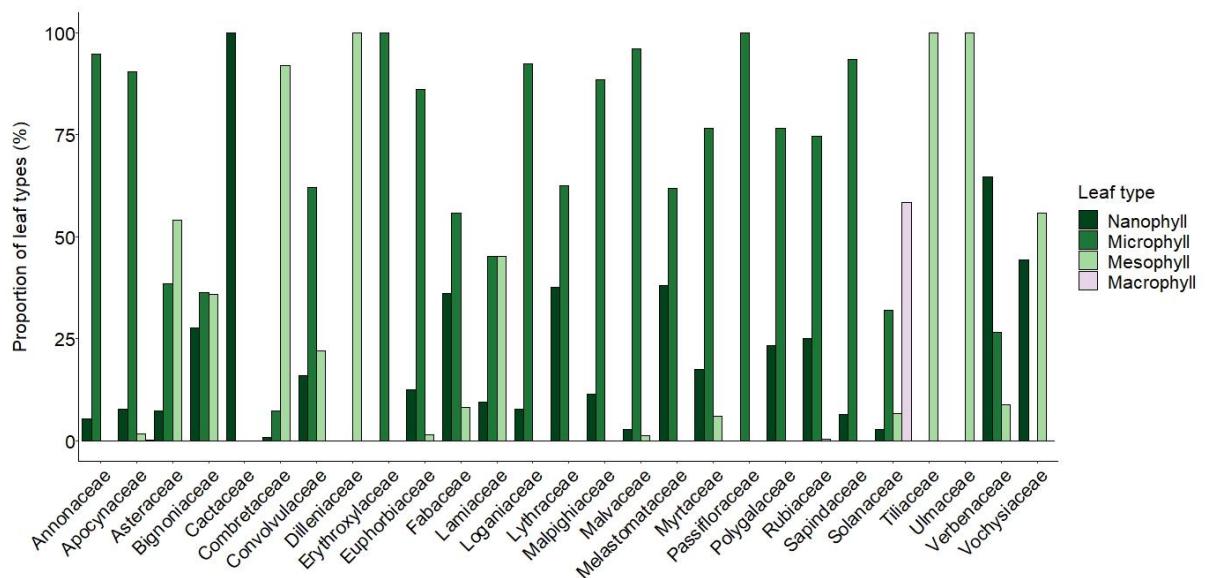


Fig.5-Proportion of leaf types across the taxonomic families of the Caatinga woody plant.

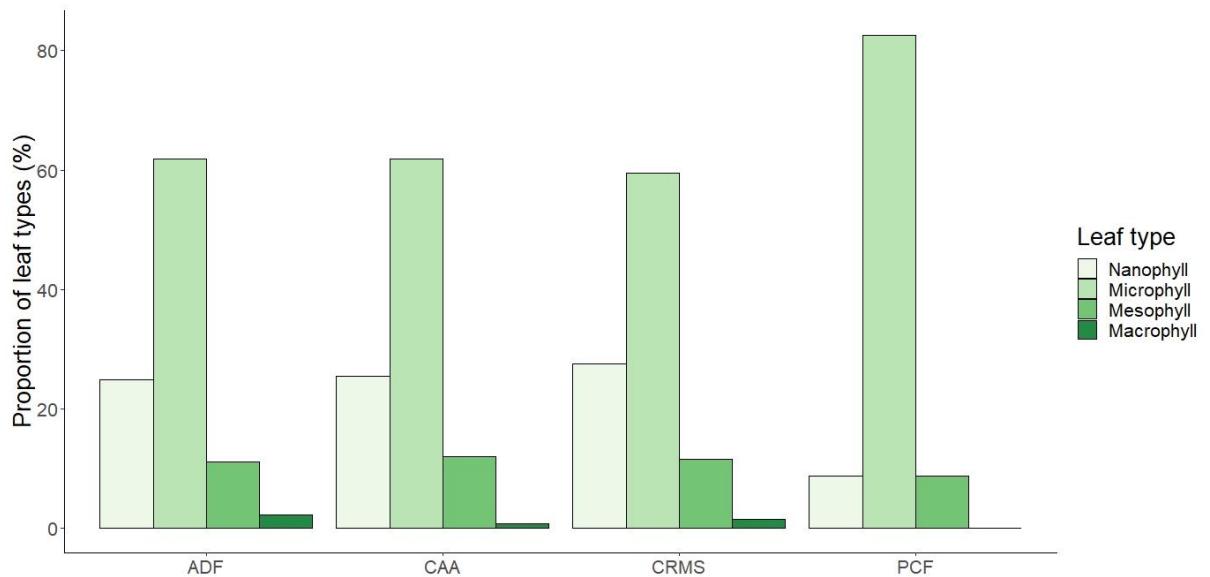


Fig.6 -Proportion of leaf types in four Ecorregions – ADF: Atlantic Dry Forest, CAA: Caatinga, CRMS: Campos rupestres montane savanna, PCF: Pernambuco Costal Forests.

Tabela 2-Eletronic Supplementary Material Table S1

Herbaria				Mean Leaf area (cm ²)	Std.Error	Sample unit	Long	Lat	Date	Classification of leaves	Shape leaf
ID	vouchers	Family	Species								
1	184648	Malpighiaceae	<i>Janusia schwannioides</i> W.R. Anderson	1,872	1,358	11	41 16 W	10 27 S	07/03/1976	Simple leaves	Elliptic Obovate (Bifoliolate)
2	405182	Fabaceae	<i>Hymenaea martiana</i> Hayne	20,838	3,179	5	42 0 W	9 0 S	25/03/1983	Compound leaves	Ovate-oblong Obovate (Bifoliolate)
3	405873	Fabaceae	<i>Hymenaea courbaril</i> L.	11,141	2,260	14	42 32 W	14 10 S	27/10/1993	Compound leaves	Ovate (Pinnate, imparipinnate)
4	407114	Fabaceae	<i>Hymenaea maranhensis</i> Y.T. Lee & Langenh.	19,696	6,311	5	41 15 W	7 7 S	01/01/1907	Compound leaves	Ovate (Bifoliolate)
5	407961	Fabaceae	<i>Hymenaea eriogyne</i> Benth.	5,256	1,208	18	43 36 4 W	9 22 12 S	17/06/2007	Compound leaves	Ovate (Bifoliolate)
6	407977	Fabaceae	<i>Hymenaea velutina</i> Ducke.	12,353	4,162	13	41 22 20 W	9 28 44 S	05/10/2003	Compound leaves	Ovate (Bifoliolate)
7	459609	Fabaceae	<i>Luetzelburgia auriculata</i> (Allemão) Ducke	4,236	1,321	16	42 0 W	9 0 S	19/01/1982	Compound leaves	Ovate (Pinnate, imparipinnate)
8	472042	Fabaceae	<i>Macroptilium martii</i> (Benth.) Maréchal & Baudet	6,986	2,771	9	41 50 W	13 43 S	03/04/1991	Compound leaves	Ovate
9	485116	Asteraceae	<i>Isocarpha megacephala</i> Mattf.	4,180	0,797	4	40 7 15 W	6 36 1 S	01/07/2004	Simple leaves	Lanceolate (Trifoliolate)
10	488491	Convolvulaceae	<i>Ipomoea rosea</i> Choisy	1,668	0,520	7	40 8 W	6 37 S	25/04/1996	Compound leaves	Ovate
11	490293	Convolvulaceae	<i>Ipomoea nil</i> (L.) Roth	148,767	-	1	35 52 W	7 46 S	30/06/1990	Simple leaves	Ovate
12	490579	Convolvulaceae	<i>Jacquemontia glaucescens</i> Choisy	5,620	3,108	7	41 49 W	13 18 S	31/01/1992	Simple leaves	Ovate
13	496765	Verbenaceae	<i>Lippia grata</i> Schauer	0,845	0,100	9	37 10 W	8 37 S	05/05/1995	Simple leaves	Ovate
14	496780	Verbenaceae	<i>Lippia magentea</i> T. Silva	40,101	18,584	4	41 20 W	10 22 S	08/03/1974	Simple leaves	Ovate
15	496914	Verbenaceae	<i>Lantana caatingensis</i> Moldenke	1,032	0,343	7	35 49 W	8 12 S	08/02/1996	Simple leaves	Ovate Oblong (Pinnate, imparipinnate)
16	497085	Fabaceae	<i>Indigofera</i> Benth.	1,147	0,254	20	40 15 W	9 55 S	24/02/1974	Compound leaves	Ovate
17	497456	Convolvulaceae	<i>Ipomoea incarnata</i> (Vahl) Choisy	21,816	3,939	4	41 22 W	12 30 S	23/05/1980	Simple leaves	Ovate
18	497498	Convolvulaceae	<i>Ipomoea subincana</i> (Choisy) Meisn.	43,978	24,350	6	41 47 W	13 33 S	18/01/1972	Simple leaves	Ovate
19	497511	Convolvulaceae	<i>Ipomoea marcellia</i> Meisn.	17,353	5,959	2	35 52 W	7 46 S	27/07/1990	Simple leaves	Ovate (Pinnate, imparipinnate)
20	501743	Fabaceae	<i>Machaerium brasiliense</i> Vogel	5,797	5,793	26	41 0 W	11 20 S	17/01/1997	Compound leaves	Ovate
21	513899	Verbenaceae	<i>Lantana canescens</i> Kunth	2,326	0,886	6	41 43 W	13 36 S	15/11/1988	Simple leaves	Ovate
22	514052	Verbenaceae	<i>Lantana fucata</i> Lindl.	1,494	0,705	5	40 27 W	13 26 S	00/09/1906	Simple leaves	Ovate

23	549428	Bignoniaceae	<i>Fridericia limae</i> (A.H. Gentry) L.G. Lohmann	3,55	1,205	7	37 10 W	8 37 S	20/05/1995	Compound leaves	Oblong (Trifoliolate)
24	550876	Apocynaceae	<i>Mandevilla funiformis</i> (Vell.) K. Schum.	2,971	0,655	7	41 20 32 W	12 58 30 S	01/02/1994	Simple leaves	Obovate
25	567037	Bignoniaceae	<i>Godmania dardanoi</i> (J.C. Gomes) A.H. Gentry	1,339	0,487	8	40 25 W	7 14 S	15/02/1985	Compound leaves	Elliptic (hand) Elliptic (Bipinnate/ Pinnate)
26	585190	Bignoniaceae	<i>Jacaranda jasminoides</i> (Thunb.) Sandwith	1,178	0,649	16	40 7 15 W	6 36 1 S	26/01/2005	Compound leaves	Compound leaves
27	588711	Apocynaceae	<i>Mandevilla leptophylla</i> (A. DC.) K. Schum.	2,710	1,477	12	40 7 15 W	6 36 1 S	25/01/2005	Simple leaves	Narrow-Elliptic
28	593351	Fabaceae	<i>Machaerium opacum</i> Vogel	6,509	1,784	8	45 36 3 W	11 53 41 S	04/02/2000	Compound leaves	Ovate (Bipinnate)
29	604845	Myrtaceae	<i>Eugenia stictopetala</i> DC.	6,750	4,081	14	41 16 W	10 27 S	05/03/1974	Simple leaves	Ovate
30	610922	Convolvulaceae	<i>Ipomoea brasiliiana</i> Meisn.	8,211	4,510	6	38 29 W	9 20 S	06/06/2004	Simple leaves	Ovate
31	610940	Convolvulaceae	<i>Ipomoea megapotamica</i> Choisy	60,987	0,153	2	35 52 W	7 46 S	27/07/1990	Simple leaves	Ovate
32	612954	Malpighiaceae	<i>Galphimia brasiliensis</i> (L.) A. Juss.	1,326	0,589	26	40 15 W	10 23 S	27/02/1974	Simple leaves	Ovate
33	620697	Myrtaceae	<i>Eugenia uniflora</i> L.	2,449	1,199	38	41 53 W	13 16 S	29/02/1992	Simple leaves	Elliptic
34	629142	Myrtaceae	<i>Eugenia candelleana</i> DC.	19,739	5,306	7	40 28 31 W	11 11 47 S	02/04/1996	Simple leaves	Elliptic
35	634486	Myrtaceae	<i>Eugenia florida</i> DC.	10,126	2,647	9	41 48 W	13 18 S	27/12/1992	Simple leaves	Elliptic
36	635935	Myrtaceae	<i>Eugenia dysenterica</i> DC.	19,217	2,652	3	42 54 W	12 19 S	12/10/1981	Simple leaves	Elliptic
37	637705	Myrtaceae	<i>Eugenia punicifolia</i> (Kunth) DC.	3,184	1,050	41	44 2 W	12 7 S	07/07/1983	Simple leaves	Elliptic Obovate
38	684419	Bignoniaceae	<i>Fridericia caudigera</i> (S. Moore) L.G. Lohmann	31,988	11,424	6	39 50 W	7 15 S	15/02/1985	Compound leaves	(Trifoliolate)
39	754738	Rubiaceae	<i>Guettarda angelica</i> Mart. ex Müll. Arg.	3,499	1,273	18	39 52 W	12 54 S	06/03/1977	Simple leaves	Elliptic
40	755413	Rubiaceae	<i>Machaonia acuminata</i> Bonpl.	8,502	4,335	9	42 50 W	10 48 S	25/02/1997	Simple leaves	Elliptic
41	55828	Myrtaceae	<i>Myrcia guianensis</i> (Aubl.) DC.	3,509	1,373	37	39 12 W	6 53 S	1839	Simple leaves	Elliptic
42	55834	Myrtaceae	<i>Myrcia multiflora</i> (Lam.) DC. <i>Chamaecrista cytisoides</i> (DC. ex Collad.) H.S. Irwin & Barneby	4,383	1,674	28	44 28 W	10 13 S	1841	Simple leaves	Elliptic Oblanceolate
43	126835	Fabaceae	<i>Alvimiantha tricamerata</i> Grey-Wilson <i>Chamaecrista barbata</i> (Nees & Mart.) H.S. Irwin & Barneby	5,121	3,468	16	41 23 W	10 16 S	07/03/1974	Compound leaves	(Pinnate,paripinnate)
44	214741	Myrtaceae	<i>Alvimiantha tricamerata</i> Grey-Wilson <i>Chamaecrista barbata</i> (Nees & Mart.) H.S. Irwin & Barneby	4,905	3,897	19	41 1 W	11 39 S	04/03/1977	Simple leaves	Ovate
45	412883	Fabaceae	<i>Chamaecrista repens</i> (Vogel) H.S. Irwin & Barneby	0,907	0,276	33	41 28 5 W	12 27 17 S	26/09/1994	Compound leaves	Ovate (Paripinnate) Oblong (Paripinnate)
46	415625	Fabaceae	<i>Albizia inundata</i> (Mart.) Barneby & J.W. Grimes	2,144	0,596	38	41 5 W	12 6 S	1838	Compound leaves	Linear-falcate
47	441050	Rubiaceae	<i>Chiococca alba</i> (L.) Hitchc.	3,220	2,216	20	41 9 32 W	11 37 30 S	10/03/2002	Simple leaves	Ovate Ovate
48	446420	Rubiaceae	<i>Amburana cearensis</i> (Allemão) A.C. Sm.	6,534	1,306	14	43 13 W	13 10 S	22/07/1981	Compound leaves	(Imparipinnate)

50	469415	Fabaceae	<i>Chaetocalyx scandens</i> (L.) Urb.	1,189	0,230	19	39 52 W	12 5 S	03/05/1980	Compound leaves	Obovate (Trifoliolate)
51	470925	Fabaceae	<i>Centrolobium sclerophyllum</i> H.C. Lima	26,103	7,847	8	43 0 W	13 35 S	02/07/1983	Compound leaves	Ovate (imparipinnate)
52	501720	Fabaceae	<i>Canavalia dictyota</i> Piper	25,972	1,907	3	42 30 W	11 24 S	22/02/1977	Compound leaves	Ovate (Trifoliolate)
53	501734	Fabaceae	<i>Canavalia brasiliensis</i> Mart. ex Benth.	13,820	1,822	6	39 47 W	12 47 S	02/06/1993	Compound leaves	Ovate (Trifoliolate) Lanceolate
54	506532	Fabaceae	<i>Centrosema pascuorum</i> Mart.ex Benth	2,175	0,972	31	41 51 W	13 38 S	28/03/1991	Compound leaves	Ovate (Trifoliolate)
55	544387	Apocynaceae	<i>Allamanda blanchetii</i> A. DC.	5,612	3,289	13	38 5 W	10 16 S	21/10/1981	Simple leaves	Obovate
56	545340	Apocynaceae	<i>Aspidosperma discolor</i> A. DC.	5,146	2,154	9	41 46 W	13 18 S	27/02/1992	Simple leaves	Ovate
57	547121	Fabaceae	<i>Aeschynomene martii</i> Benth.	0,747	0,026	3	41 52 W	13 18 S	20/01/1994	Compound leaves	Oblong (Pinnate)
58	548855	Apocynaceae*	<i>Allamanda puberola</i> A.DC	3,130	1,336	8	41 49 W	13 18 S	31/01/1992	Simple leaves	Lanceolate
59	550232	Apocynaceae	<i>Aspidosperma pyrifolium</i> Mart. & Zucc.	4,150	1,041	9	37 9 15 W	8 37 30 S	10/10/1995	Simple leaves	Elliptic
60	565384	Bignoniaceae	<i>Anemopaegma laeve</i> DC.	4,391	1,845	15	41 48 W	13 18 S	27/12/1992	Compound leaves	Ovate (Bifoliate) Oblong (Unifoliolate)
61	571835	Fabaceae	<i>Bionia pedicellata</i> (Benth.) L.P. Queiroz	18,580	9,393	9	41 28 15 W	12 27 20 S	26/10/1994	Compound leaves	Ovate (Trifoliolate)
62	575497	Bignoniaceae	<i>Anemopaegma velutinum</i> Mart.ex DC.	19,666	6,380	6	41 57 W	13 33 S	20/03/1977	Compound leaves	Ovate (Bifoliate)
63	578200	Apocynaceae	<i>Blepharodon ampliflorum</i> E. Fourn.	5,716	2,602	9	41 55 W	13 32 S	23/01/1974	Simple leaves	Linear- lanceolate
64	578225	Apocynaceae	<i>Blepharodon manicatum</i> (Decne.) Fontella	2,007	0,903	26	41 45 44 W	13 37 19 S	06/02/2004	Simple leaves	Ovate
65	593563	Asteraceae	<i>Chresta martii</i> (DC.) H. Rob.	15,944	4,011	4	40 13 46 W	10 6 10 S	13/04/2006	Simple leaves	Ovate- rhomboid
66	594012	Annonaceae	<i>Annona sylvatica</i> A. St.-Hil.	8,451	5,126	19	40 10 W	10 23 S	27/02/1974	Simple leaves	Obovate
67	601651	Apocynaceae	<i>Calotropis procera</i> (Aiton) W.T.Aiton <i>Blanchetiodendron blanchetii</i> (Benth.) Barneby & J.W. Grimes	156,252	56,132	3	43 1 W	6 46 S	12/07/1962	Simple leaves	Obovate
68	645956	Fabaceae	<i>Alseis floribunda</i> Schott	0,834	0,161	42	41 52 W	13 17 S	28/12/1988	Compound leaves	Oblong (Bipinnate)
69	676271	Vochysiaceae	<i>Callisthene minor</i> Mart.	0,832	0,138	5	41 52 W	13 19 S	03/03/1994	Simple leaves	Oblong
70	688989	Solanaceae	<i>Brunfelsia uniflora</i> (Pohl) D.Don	7,794	4,633	12	40 34 29 W	15 15 53 S	25/03/1996	Simple leaves	Ovate
71	745290	Polygalaceae	<i>Bredemeyera brevifolia</i> (Benth.) A.W. Benn.	2,633	1,686	26	41 20 W	10 20 S	06/03/1974	Compound leaves	Elliptic
72	745604	Rubiaceae	<i>Alseis floribunda</i> Schott	7,426	1,947	8	39 20 W	10 27 S	20/02/1974	Simple leaves	Ovate-oblong
73	748895	Rubiaceae	<i>Alibertia edulis</i> (Rich.) A. Rich.	14,364	10,244	7	41 50 W	13 28 S	19/01/1974	Simple leaves	Lanceolate-oblong
74	786079	Lamiaceae	<i>Amazonia campestris</i> (Aubl.) Moldenke	27,104	6,774	5	41 47 W	12 13 S	23/02/1971	Simple leaves	Oblanceolate
75	787569	Lamiaceae	<i>Aegiphila pernambucensis</i> Moldenke	7,987	6,790	7	41 50 W	13 39 S	13/12/1984	Simple leaves	Ovate
76	827750	Myrtaceae	<i>Campomanesia eugeniooides</i> (Cambess.) D. Legrand	1,074	0,232	30	40 58 W	13 33 S	27/04/1978	Simple leaves	Elliptic
77	271770	Erythroxylaceae	<i>Erythroxylum simonis</i> Plowman	8,121	3,639	15	35 42 15 W	6 58 12 S	28/11/1980	Simple leaves	Elliptic

78	297987	Asteraceae	<i>Dissothrix imbricata</i> (Gardner) B.L. Rob	3,155	1,361	5	42 8 W	7 1 S	05/1839	Simple leaves	Ovate- lanceolate
79	425678	Fabaceae	<i>Diptychandra aurantiaca</i> Tul.	1,766	0,553	17	42 19 W	13 52 S	28/10/1993	Compound leaves	Ovate (Paripinnate)
80	427207	Fabaceae	<i>Dimorphandra gardneriana</i> Tul.	2,609	0,233	39	41 40 W	6 30 S	09/01/1985	Compound leaves	Ovate (Bipinnate) Falcate-oblong (Bipinnate)
81	451231	Fabaceae	<i>Enterolobium timbouva</i> Benth.	0,727	0,016	3	35 42 W	6 58 S	01/12/1980	Compound leaves	(Bipinnate)
82	452779	Euphorbiaceae	<i>Croton campestris</i> A. St.-Hil.	8,399	2,765	12	41 27 W	12 27 S	22/05/1980	Simple leaves	Lanceolate-liner Lanceolate
83	463636	Fabaceae	<i>Crotalaria holosericea</i> Nees & C. Mart.	1,412	0,432	9	41 49 W	13 35 S	15/01/1974	Compound leaves	(Trifoliolate) Lanceolate
84	465230	Fabaceae	<i>Crotalaria vitellina</i> Ker Gawl	5,964	1,874	11	35 42 W	6 58 S	08/06/1979	Compound leaves	(Trifoliolate) Ovate (Bipinnate, imparipinnate)
85	473283	Fabaceae	<i>Dalbergia cearensis</i> Ducke	1,931	0,660	33	41 20 W	7 25 S	08/01/1985	Compound leaves	Oblong-elliptic (Imparipinnate) Oblong (Bipinnate,
86	473519	Fabaceae	<i>Dalbergia catingicola</i> Harms	12,053	8,332	13	40 33 27 W	8 6 42 S	14/10/1995	Compound leaves	Orbicular
87	497036	Fabaceae*	<i>Chloroleucon dumosum</i> (Benth.) G.P. Lewis	1,030	0,343	14	38 13 W	6 8 S	14/05/1984	Compound leaves	Obovate
88	497101	Fabaceae	<i>Dioclea violacea</i> Mart.ex Benth.	31,526	9,480	3	41 17 W	10 36 S	13/04/1999	Compound leaves	(Trifoliolate)
89	501357	Fabaceae	<i>Dioclea sclerocarpa</i> Ducke	22,026	22,026	3	42 48 W	5 5 S	25/08/1995	Compound leaves	(Trifoliolate)
90	501663	Fabaceae	<i>Desmodium glabrum</i> (Mill.) DC.	6,410	3,299	7	13 38 W	41 51 S	16/04/1991	Compound leaves	Ovate (Trifoliolate)
91	505946	Fabaceae	<i>Cratylia mollis</i> Mart. ex Benth.	9,068	6,150	10	42 0 W	9 0 S	23/01/1982	Compound leaves	Ovate (Trifoliate)
92	505978	Fabaceae	<i>Dioclea grandiflora</i> Mart.ex Benth. <i>Eplingiella fruticosa</i> (Salzm.ex Benth.) Harley &	37,842	4,926	3	42 0 W	9 0 S	24/01/1982	Compound leaves	Ovate (Trifoliate)
93	523587	Lamiaceae	J.F.B. Pastore	0,860	0,086	10	37 10 W	8 37 S	16/09/1994	Simple leaves	Ovate
94	540923	Euphorbiaceae	<i>Ditaxis malpighiacea</i> (Ule) Pax & K. Hoffm.	2,763	1,164	24	41 48 53 W	13 36 56 S	02/02/2004	Simple leaves	Oblong
95	546534	Bignoniaceae	<i>Cuspidaria argentea</i> (Wawra) Sandwith	6,073	2,247	5	39 34 W	10 47 S	22/02/1974	Compound leaves	Ovate (Trifoliolate) Lanceolate
96	556426	Euphorbiaceae	<i>Dalechampia scandens</i> L.	16,418	7,276	2	40 10 W	10 23 S	27/02/1974	Simple leaves	(Trilobate) Orbicular
97	562788	Bignoniaceae	<i>Dolichandra quadrivalvis</i> (Jacq.) L.G. Lohmann	20,058	1,533	3	45 1 W	11 31 S	13/10/1994	Compound leaves	(Bifoliolate) Deltoid
98	572429	Fabaceae	<i>Erythrina velutina</i> Willd.	26,701	5,176	3	43 36 59 W	16 33 50 S	06/07/2001	Compound leaves	(Trifoliolate)
99	576971	Euphorbiaceae	<i>Dalechampia pernambucensis</i> Baill.	13,132	1,595	2	40 7 15 W	6 36 1 S	29/04/2004	Simple leaves	Trilobate
100	579096	Apocynaceae	<i>Ditassa oxyphylla</i> Turcz.	1,134	0,317	6	39 52 W	12 54 S	06/03/1977	Simple leaves	Lanceolate
101	581019	Euphorbiaceae	<i>Dalechampia brasiliensis</i> Lam.	4,694	1,624	4	39 51 9 W	12 52 17 S	13/03/2005	Simple leaves	Trilobate
102	606321	Asteraceae	<i>Cyrtocymura harleyi</i> (H. Rob.) H. Rob.	9,068	6,150	10	41 0 4 W	11 37 41 S	03/02/2008	Simple leaves	Ovate
103	606427	Apocynaceae	<i>Cynanchum roulinioides</i> (E. Fourn.) Rapini	4,703	1,028	5	41 52 W	13 18 S	04/06/1994	Simple leaves	Cordate,cordiform

104	638999	Combretaceae	Combretum mellifluum Eichler	25,346	7,496	3	42 29 W	14 9 S	11/04/1980	Simple leaves	Sublanceolate
105	639056	Combretaceae	Combretum monetaria Mart.	3,080	0,849	10	41 23 W	10 16 S	07/03/1974	Simple leaves	Sublanceolate
106	644397	Lythraceae	Cuphea circaeoides Sm. ex Sims	6,745	1,671	6	41 45 54 W	13 37 13 S	07/02/2004	Simple leaves	Ovate
107	644419	Lythraceae	Cuphea campestres Koehne	1,020	0,367	4	43 10 W	9 15 S	15/02/1972	Simple leaves	Oblong-lanceolate
108	663994	Lythraceae*	Cuphea impatientifolia A.St.-Hil.	3,885	2,522	6	38 8 9 W	7 53 57 S	02/04/2001	Simple leaves	Ovate
109	736767	Asteraceae	Dasyphyllum sprengelianum (Gardner) Cabrera Declieuxia fruticosa (Willd. ex Roem. & Schult.)	1,745	0,520	9	41 49 W	13 19 S	04/07/1994	Simple leaves	Elliptic
110	765275	Rubiaceae	Kuntze	1,149	0,410	30	41 46 W	13 23 S	24/01/1994	Simple leaves	Elliptic
111	766387	Rubiaceae	Emmeorhiza umbellata (Spreng.) K. Schum.	4,826	1,426	8	35 49 W	8 12 S	05/10/1995	Simple leaves	Lanceolate
112	440452	Fabaceae	Calliandra leptopoda Benth.	1,811	0,717	19	41 47 W	13 48 S	26/03/1991	Compound leaves	Obovate (Pinnate)
113	506535	Fabaceae	Centrosema arenarium Benth.	19,312	1,806	3	35 42 W	6 58 S	06/11/1980	Compound leaves	Ovate (Trifoliolate)
114	540856	Euphorbiaceae	Cnidoscolus urnigerus (Pax) Pax	29,395	-	1	41 57 W	13 32 S	02/01/2000	Simple leaves	5-Palmatilobate
115	560034	Apocynaceae	Aspidosperma multiflorum A. DC.	5,589	1,814	3	40 7 15 W	6 36 1 S	25/01/2005	Simple leaves	Elliptic
116	576983	Euphorbiaceae	Dalechampia fernandesii G.L. Webster	12,114	1,359	3	40 7 15 W	6 36 1 S	09/09/2004	Simple leaves	Trilobate Obovate-suborbicular
117	635369	Vochysiaceae	Callisthene fasciculata Mart. Martiodendron mediterraneum (Mart. ex Benth.)	36,258	8,877	3	43 13 W	13 9 S	17/04/1980	Simple leaves	Elliptic
118	126794	Fabaceae	R.C. Koeppen	7,886	3,287	10	42 8 W	7 1 S	03/1839	Compound leaves	Oblong (Pinnate) Elliptic
119	406228	Fabaceae	Copaifera coriacea Mart.	2,956	1,128	63	43 32 14 W	9 14 42 S	17/06/2007	Compound leaves	(Paripinnate)
120	226896	Melastomataceae	Tibouchina lithophila Wurdack	2,576	1,100	21	39 52 W	12 54 S	06/03/1977	Simple leaves	Oblong lanceolate
121	407105	Fabaceae	Peltogyne pauciflora Benth	11,868	5,706	5	40 12 W	12 42 S	17/12/1981	Compound leaves	Elliptic (Bifoliate)
122	409954	Fabaceae	Pterogyne nitens Tul.	7,433	1,105	23	41 45 W	13 35 S	06/01/1994	Compound leaves	Oblong (Bipinnate) Rhombose
123	412638	Fabaceae	Rhynchosia minima (L.) DC. Senna macranthera (DC. ex Collad.) H.S. Irwin & Barneby	2,384	0,844	14	36 0 W	8 30 S	01/12/1994	Compound leaves	(Trifoliolate) Elliptic
124	417411	Fabaceae	Barneby	3,545	1,3901	11	38 58 W	11 25 S	19/07/1962	Compound leaves	(Paripinnate) Oblong
125	418409	Fabaceae	Poeppigia procera C. Presl	0,834	0,105	20	41 40 W	13 14 S	28/12/1991	Compound leaves	(Paripinnate) Elliptic
126	418977	Fabaceae	Senna rizzinii H.S. Irwin & Barneby	1,865	4,473	29	41 16 W	10 27 S	05/03/1974	Compound leaves	(Tetrafoliate) Lanceolate
127	420376	Fabaceae	Senna splendida (Vogel) H.S. Irwin & Barneby	6,328	3,809	19	37 10 W	8 37 S	18/05/1995	Compound leaves	(Paripinnate)
128	420950	Fabaceae	Senna georgica H.S. Irwin & Barneby	37,281	-	1	35 42 W	6 58 S	02/10/1980	Compound leaves	Ovate (Tetrafoliate) Obovate
129	422152	Fabaceae	Senna lechriosperma H.S. Irwin & Barneby	7,485	4,088	8	44 17 W	9 0 S	20/06/1983	Compound leaves	(Paripinnate)

130	422383	Fabaceae	<i>Senna occidentalis</i> (L.) Link	4,940	2,823	15	35 42 W	6 58 S	07/01/1981	Compound leaves	Lanceolate (Paripinnate) Oblong- obovate (Paripinnate, bipinnate) Oblong
131	422591	Fabaceae	<i>Senna rugosa</i> (G. Don) H.S. Irwin & Barneby	8,611	2,832	20	39 29 W	7 14 S	30/07/1997	Compound leaves	
132	423452	Fabaceae	<i>Senna martiana</i> (Benth.) H.S. Irwin & Barneby	2,410	1,049	16	42 30 W	9 14 S	22/06/1983	Compound leaves	Elliptic (Paripinnate)
133	424387	Fabaceae	<i>Senna acuruensis</i> (Benth.) H.S. Irwin & Barneby <i>Senna trachypus</i> (Mart. ex Benth.) H.S. Irwin &	2,016	0,509	22	41 40 W	13 16 S	22/09/1992	Compound leaves	Obovate (Paripinnate)
134	425112	Fabaceae	Barneby	0,995	0,203	102	41 33 W	5 19 S	13/06/1995	Compound leaves	(Paripinnate) Obovate
135	425290	Fabaceae	<i>Senna aversiflora</i> (Herb.) H.S.Irwin & Barneby	0,947	0,122	6	35 49 W	8 12 S	11/10/1995	Compound leaves	(Paripinnate) Oblong
136	425291	Fabaceae	<i>Senna spectabilis</i> (DC.) H.S.Irwin & Barneby	3,844	1,730	24	42 54 50 W	9 35 38 S	02/03/2000	Compound leaves	(Paripinnate)
137	426516	Fabaceae	<i>Peltophorum dubium</i> (Spreng.) Taub. <i>Parapiptadenia zehntneri</i> (Harms) M.P.Lima &	0,909	0,140	2	41 47 W	13 48 S	21/03/1991	Compound leaves	Oblong (Bipinnate) Oblong (
138	430959	Fabaceae	H.C.Lima	0,956	0,119	25	38 34 15 W	8 36 0 S	17/09/1995	Compound leaves	Bifoliolate)
139	452953	Fabaceae	<i>Trischidium molle</i> (Benth.) H.E. Ireland	5,280	1,727	20	38 42 W	10 55 S	16/06/1994	Compound leaves	Elliptic
140	457436	Fabaceae	<i>Pterodon abruptus</i> (Moric.) Benth.	1,043	0,222	60	41 20 W	7 25 S	08/01/1985	Compound leaves	Widely ovate Obovate
141	467346	Fabaceae	<i>Zornia brasiliensis</i> Vogel	0,975	0,211	13	42 13 W	13 33 S	30/11/1988	Compound leaves	(Tetrafoliolate)
142	467938	Fabaceae	<i>Zornia latifolia</i> Sm.	1,029	0,178	12	41 21 W	12 59 S	25/01/1980	Compound leaves	Oblong
143	485185	Verbenaceae	<i>Stachytarpheta coccinea</i> Schauer	4,651	0,187	4	40 23 W	13 25 S	24/01/1965	Simple leaves	Ovate
144	499405	Cactaceae	<i>Pereskia bahiensis</i> Gürke	0,867	0,091	6	41 49 W	13 45 S	23/11/1988	Simple leaves	Elliptic Narrow-oblong
145	501633	Fabaceae	<i>Sesbania exasperata</i> Kunth	0,880	0,134	12	39 5 W	12 32 S	ago/80	Compound leaves	(paripinnate)
146	502530	Ulmaceae	<i>Trema micrantha</i> (L.) Blume	25,422	2,654	8	41 9 58 W	12 46 17 S	02/03/2003	Simple leaves	Lanceolate
147	506267	Asteraceae	<i>Praxelis clematidea</i> (Griseb.) R.M.King & H.Rob.	5,759	1,284	4	39 52 W	12 54 S	06/03/1977	Simple leaves	Ovate Obovate
148	514219	Fabaceae	<i>Tephrosia purpurea</i> (L.) Pers.	1,053	0,238	41	38 19 W	10 23 S	18/12/1993	Compoud leaves	(Imparipinnate)
149	525403	Euphorbiaceae	<i>Romanoa tamnooides</i> (A.Juss.) Radcl.-Sm.	14,367	3,905	4	42 44 W	11 7 S	25/02/1977	Simple leaves	Cordate,cordiform
150	526356	Euphorbiaceae	<i>Sapium obovatum</i> Klotzsch ex Müll.Arg.	12,169	2,585	5	41 57 W	13 33 S	20/03/1977	Simple leaves	Obovate
151	531566	Apocynaceae	<i>Temnadenia violacea</i> (Vell.) Miers <i>Muellera obtusa</i> Benth.) M.J. Silva & A.M.G.	12,909	5,358	7	41 47 W	13 36 S	25/12/1988	Simple leaves	Elliptic Ovate
152	535656	Fabaceae	<i>Azevedo</i>	2,804	1,072	54	41 45 25 W	13 37 38 S	03/02/2004	Compound leaves	(Imparipinnate)
153	536577	Apocynaceae	<i>Skytanthus hancorniifolius</i> (A.DC.) Miers	3,144	1,034	26	39 2 46 W	12 15 16 S	07/12/1992	Simple leaves	Oblong Rhomboid
154	542033	Euphorbiaceae	<i>Stillingia trapezoidea</i> Ule	2,797	0,872	5	41 20 35 W	10 29 31 S	08/03/1997	Simple leaves	(Trifoliolate)

155	542045	Euphorbiaceae	<i>Stillingia uleana</i> Pax ex K.Hoffm.	4,952	1,520	7	41 55 W	13 15 N	24/02/1992	Simple leaves	Oblanceolate
156	545839	Malvaceae	<i>Sidastrum micranthum</i> (A.St.-Hil.) Fryxell	11,116	11,290	6	41 26 W	12 28 S	27/05/1980	Simple leaves	Cordate, cordiform
157	555099	Asteraceae	<i>Wedelia villosa</i> Gardner <i>Neojobertia candolleana</i> (Mart. ex DC.) Bureau &	22,417	7,318	3	39 23 W	7 14 S	09/1838	Simple leaves	Ovate
158	555820	Bignoniaceae	<i>K. Schum.</i>	3,569	1,504	37	41 45 W	13 37 S	25/12/1988	Simple leaves	Ovate (Imparipinnate)
159	559787	Bignoniaceae	<i>Pyrostegia venusta</i> (Ker Gawl.) Miers <i>Tanaecium cyrtanthum</i> (Mart. ex DC.) Bureau &	13,604	0,088	2	41 28 20 W	12 27 0 S	30/08/1994	Compound leaves	Ovate (Trifoliolate)
160	569001	Bignoniaceae	<i>K. Schum.</i>	12,988	5,764	3	40 7 15 W	6 36 1 S	05/11/2003	Compound leaves	Subovate
161	571362	Fabaceae	<i>Periandra coccinea</i> (Schrad.) Benth	12,413	5,612	12	41 22 57 W	12 35 10 S	13/09/1992	Compound leaves	Ovate (Trifoliolate)
162	574671	Apocynaceae	<i>Secondatia floribunda</i> A.DC <i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex	3,065	0,910	6	41 45 26 W	13 14 46 S	09/11/1996	Simple leaves	Widely elliptic
163	575626	Bignoniaceae	<i>S. Moore</i>	47,474	5,089	3	42 26 W	13 48 S	07/08/1993	Compound leaves	Oblong (Hand)
164	577683	Apocynaceae	<i>Rauvolfia ligustrina</i> Willd.	5,87	2,26	13	35 W	7 57 S	12/07/1990	Simple leaves	Ovate
165	585319	Solanaceae	<i>Solanum rhytidandrum</i> Sendtn.	8,504	2,961	3	35 42 15 W	6 58 12 S	20/12/1980	Simple leaves	Elliptic
166	589419	Apocynaceae	<i>Petalostelma dardanoi</i> Fontella	6,039	3,701	8	35 52 W	7 46 S	27/07/1990	Simple leaves	Elliptic
167	592860	Apocynaceae	<i>Prestonia bahiensis</i> Müll.Arg.	19,062	3,153	6	41 47 W	13 23 S	12/05/1994	Simple leaves	Ovate
168	601677	Apocynaceae	<i>Schubertia multiflora</i> Mart.	50,400	6,093	4	41 49 W	13 16 S	24/02/1992	Simple leaves	Obovate
169	613702	Loganiaceae	<i>Strychnos rubiginosa</i> A.DC.	4,709	1,334	13	41 21 10 W	9 32 10 S	29/11/2003	Simple leaves	Widely-elliptic
170	618645	Solanaceae	<i>Nicotiana glauca</i> Graham	3,484	1,238	6	35 52 W	7 46 S	30/06/1990	Simple leaves	Elliptic
171	728099	Asteraceae	<i>Trixis vauthieri</i> DC.	7,482	0,231	2	41 24 W	12 57 S	15/07/1996	Simple leaves	Elliptic-oblanceolate
172	733166	Asteraceae	<i>Verbesina macrophylla</i> (Cass.) S.F.Blake	136,466	-	1	41 16 W	12 30 S	11/09/1992	Simple leaves	Elliptic
173	735367	Asteraceae	<i>Tilezia baccata</i> (L.f.) Pruski	25,763	11,874	4	42 33 W	12 39 S	04/02/1999	Simple leaves	Ovate
174	735560	Asteraceae	<i>Wedelia hookeriana</i> Gardner	6,067	2,082	7	41 0 W	11 21 S	01/07/1996	Simple leaves	Ovate
175	735999	Asteraceae	<i>Simsia dombeyana</i> DC.	12,704	5,873	5	44 25 W	13 40 S	24/04/1980	Simple leaves	Deltoid
176	740616	Asteraceae	<i>Trichogonia salvifolia</i> Gardner	14,208	2,573	5	41 1 W	11 39 S	04/03/1977	Simple leaves	Narrow-triangulated
177	745342	Polygalaceae	<i>Securidaca diversifolia</i> (L.) S.F.Blake	15,703	3,240	7	39 28 W	12 51 S	12/03/1993	Simple leaves	widely ovate
178	751595	Rubiaceae	<i>Tocoyena formosa</i> (Cham. & Schldl.) K.Schum	14,166	4,003	6	41 48 W	13 18 S	30/12/1991	Simple leaves	Elliptic
179	787701	Lamiaceae	<i>Vitex polygama</i> Cham.	22,837	6,254	6	35 49 W	8 12 S	08/02/1996	Simple leaves	Elliptic
180	805982	Passifloraceae	<i>Passiflora foetida</i> L.	3,841	0,412	6	39 41 W	9 40 S	12/08/1983	Simple leaves	Ovate (Trilobed) Palmatipartite
181	816187	Passifloraceae	<i>Passiflora cincinnata</i> Mast.	9,919	1,608	2	41 47 W	13 33 S	18/01/1972	Simple leaves	(Oblong)
182	816193	Passifloraceae	<i>Passiflora luetzelburgui</i> Harms	3,678	0,602	6	41 5 W	11 25 S	18/11/1986	Simple leaves	Ovate

183	818978	Myrtaceae	<i>Psidium guineense</i> Sw.	34,435	7,728	5	41 36 W	12 50 S	07/09/1981	Simple leaves	Elliptic
184	826643	Myrtaceae	<i>Psidium appendiculatum</i> Kiaersk	7,654	3,439	11	41 48 W	13 18 S	30/03/1992	Simple leaves	Oblancolate
185	826675	Myrtaceae	<i>Psidium schenckianum</i> Kiaersk	4,996	2,429	5	40 25 w	13 25 S	07/03/1983	Simple leaves	Large-eliptical
186	903022	Solanaceae	<i>Solanum asperum</i> Vahl	29,584	11,906	5	35 42 0 E	6 58 0 S	1980	Simple leaves	Lanceolate
187	903532	Solanaceae	<i>Solanum crinitum</i> Lam.	192,247	-	1	41 22 0 W	12 33 0 S	21/05/1980	Simple leaves	Ovate
188	904411	Solanaceae	<i>Solanum paludosum</i> Moric.	11,995	5,153	8	35 42 15 E	6 58 0 S	1981	Simple leaves	Ovate
189	904424	Solanaceae	<i>Solanum paniculatum</i> L.	70,156	1,88	2	39 40 0 W	7 8 0 S	27/02/1972	Simple leaves	Ovate
190	907129	Solanaceae	<i>Solanum thomasiifolium</i> Sendtn.	28,873	22,436	2	41 51 W	13 38 S	28/03/1991	Simple leaves	Ovate
191	907279	Solanaceae	<i>Solanum stipulaceum</i> oem. & Schult.	10,384	4,292	6	41 45 0 W	13 35 0 S	25/03/1977	Simple leaves	Elliptic
192	423014	Fabaceae	<i>Apuleia leiocarpa</i> (Vogel) J.F. Macbr.	3,592	1,733	22	42 19 W	13 52 S	28/10/1993	Compound leaves	Ovate

Conclusão

Este trabalho utiliza aspectos da biogeografia espacial e funcional para descrever e explicar a distribuição de características funcionais de sementes e folhas das espécies lenhosas da Caatinga. Nós exploramos a relação das condições climáticas e edáficas na distribuição do peso das sementes na Caatinga através da combinação de um conjunto de dados abertos e inéditos aliados a uma análise estatística robusta. Assim, verificamos que característica funcional (peso das sementes) está diretamente relacionada a compactação do solo. Em nossas análises a temperatura, mais que a precipitação, exerce forte influência sobre a compactação do solo e indiretamente sobre o peso das sementes na Caatinga. Os padrões investigados no presente estudo indicam que a distribuição espacial do peso das sementes ocorrem nas sub-regiões sertão e agreste da Caatinga devido a maior frequência das coletas botânicas. Entretanto, esses resultados nos permitem identificar o padrão de uma maior proporção de sementes maiores em ambientes ensolarados, mais secos e quentes.

Nós consideramos que a relevante conclusão alcançada nessa pesquisa é que a compactação do solo é a principal causa das diferenças no peso das sementes e que os fatores ambientais afetam indiretamente o peso das sementes através da compactação do solo. Nossa principal contribuição é auxiliar na compreensão dos fatores que determinam as pressões seletivas sobre os principais traços funcionais, principalmente sobre o tamanho das sementes que permanecem sobre a superfície do solo; e melhorar significativamente o entendimento sobre os mecanismos que envolvem as interações planta-solo. Compreendemos também que ampla abordagem biogeográfica e sem precedentes sobre peso de sementes das espécies lenhosas da Caatinga poderá ter utilidades práticas nas ações de conservação na região. Sementes e mudas das espécies da Caatinga tornam-se mais vulneráveis aos estresses abióticos causados pela redução da precipitação e aumento da temperatura provocados pelas mudanças climáticas globais e as informações geradas na presente pesquisa podem facilitar o desenvolvimento de modelos climáticos de vegetação que auxiliam na recuperação das áreas degradadas e nos serviços ambientais.

Nós investigamos os efeitos diretos e indiretos das propriedades físico-químicas do solo e do pH sobre a área foliar das espécies lenhosas da Caatinga. Em nosso modelo, a aridez influencia o pH do solo e a troca de cátions afeta o tamanho das folhas. Verificamos que as propriedades edáficas exercem influência direta sobre o padrão de distribuição do tamanho das sementes. Por outro lado, diferente do esperado inicialmente não encontramos

fortes relações entre as variáveis ambientais, isto é; temperatura e precipitação sobre o tamanho das folhas, o que pode ser explicado pela irregularidade da distribuição desses fenômenos na região. Nossa abordagem macrogeográfica permitiu identificar alguns padrões nas ecorregiões da Caatinga, como as classes de tamanho de folhas amplamente distribuída nas quatro ecorregiões. Nossos resultados nos leva a concluir que apesar do recorte no número das espécies, que está mais ligada à limitação prática de obtenção de dados do que a falha, mas que ainda assim nos fornece indícios de um padrão ecológico para as espécies lenhosas da Caatinga como a evidência do efeito direto e indireto da aridez e das propriedades do solo no tamanho das folhas. Entendemos que o nosso conjunto de dados pode ser o principal indicador do estado atual do conhecimento da distribuição do tamanho de folhas no nível macroecológico para a Caatinga juntamente com um conjunto de dados topográficos. Por fim, essa abordagem pode ajudar a entender como as plantas da Caatinga respondem a ameaças como a desertificação e o desmatamento que inviabiliza a agricultura e põem em risco a biodiversidade.

Finalmente, o presente trabalho pode ser considerado o marco inicial com enfoque biogeográfico envolvendo a biota Caatinga, até então intensamente investigados nas florestas tropicais úmidas, apesar da nossa pesquisa não concluir ou esgotar o tema, mas esperamos que os resultados obtidos na primeira etapa da pesquisa (capítulo 2) e complementado na segunda etapa (capítulo 3) abram caminhos para novas pesquisa e conservação da Caatinga.

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