ARQUITETURA E FUNCIONAMENTO HIDRÁULICO DE ÁRVORES EM GRADIENTE DE RESTINGA

LETÍCIA LANES FERREIRA CUNHA

Universidade Estadual do Norte Fluminense Darcy Ribeiro

Campos dos Goytacazes, RJ

Agosto 2025

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Tese de Doutorado apresentada ao Programa de Pós-Graduação em Biociências e Biotecnologia da Universidade Estadual do Norte Fluminense Darcy Ribeiro, como parte das exigências para obtenção do título de Doutor em Biociências e Biotecnologia.

Orientadora: Dra. Maura Da Cunha

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Universidade Estadual do Norte Fluminense Darcy Ribeiro

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Sumário

Resumo

A compreensão da relação entre os mecanismos das folhas e o xilema secundário tem sido fundamental para elucidar o equilíbrio hídrico das espécies em ambientes secos, assim como suas adaptações ao longo de diferentes gradientes vegetacionais. Dentre os remanescentes da Mata Atlântica, destaca-se a restinga, uma fitofisionomia costeira caracterizada por sua instabilidade ecológica e alta vulnerabilidade às mudanças climáticas futuras. Nesse contexto, este estudo visa identificar os principais atributos funcionais das folhas e do lenho que permitem às espécies vegetais adaptarem às diferentes formações vegetacionais de restinga: mata de restinga, formação de *Clusia* e formação praial com moitas. A investigação buscou compreender os mecanismos de aclimatação em ambientes sujeitos a variações microclimáticas e restrição hídrica. Para isso, foram coletadas amostras de folhas e lenho de cinco indivíduos das espécies dominantes em cada formação de restinga localizada na RPPN Fazenda Caruara, município de São João da Barra - RJ. Foram empregados métodos convencionais de anatomia vegetal para observações em microscopia óptica, análises fisiológicas de trocas gasosas. A presente tese está estruturada em dois capítulos: Capítulo 1- Como a variação nos atributos fisiológicos e estruturais explica a ocorrência de plantas em diferentes formações de restinga? Capítulo 2- Caracterização do lenho e respostas anatofuncionais de espécies arbóreas da restinga a microambientes com restrição hídrica. Os resultados do Capítulo 1 demonstraram ampla variação nos atributos funcionais entre as três espécies estudadas. Enquanto as folhas priorizaram a eficiência no uso da água, o lenho demonstrou um comportamento mais conservador, investindo em segurança hidráulica. Essas variações foram mais acentuadas nas formações de *Clusia* e praial com moitas, caracterizadas por dosséis abertos, maior irradiância e baixa umidade do solo. Por outro lado, na mata de restinga, onde o dossel é mais fechado e a umidade do solo é elevada, foi observado um padrão voltado para eficiência fotossintética, aquisição de carbono e transporte hídrico eficiente. As adaptações aos microclimas distintos entre as formações de restinga parecem estar associadas à variação estrutural e, consequentemente, fisiológica identificada neste estudo, o que contribui para a coexistência das espécies. No Capítulo 2, foram detalhadas as características anatômicas do xilema secundário de oito espécies arbóreas representativa das diferentes formações vegetacionais da restinga, aprofundando a compreensão sobre

os mecanismos adaptativos arbóreos neste ecossistema costeiro. Os atributos anatômicos de *Scutia arenicola* (Rhamnaceae) e *Inga maritima* (Fabaceae) foram descritos pela primeira vez, com base nos critérios da IAWA. Espécies de ambientes com maior restrição hídrica apresentaram traços anatômicos compatíveis com maior segurança hidráulica, incluindo maior densidade de vasos, vasos mais estreitos e curtos, e pontuações intervasculares menores. Em *Schinus terebinthifolia* (Anacardiaceae), esses atributos diferiram das observadas em populações de áreas mais úmidas. Foram observadas diferentes relações coordenadas entre atributos anatômicos em indivíduos da mesma espécie sob distintas condições hídricas. Nas formações que apresentam maior sazonalidade de disponibilidade hídrica, os anéis de crescimento mostraram-se mais evidentes, indicando influência direta da variação hídrica sobre o ritmo cambial. Esses resultados mostram que as espécies arbóreas adotam estratégias anatômicas funcionais especificas em resposta às variações hídricas, ressaltando a relevância do conhecimento anatômico para a compreensão da ecologia funcional de ecossistemas costeiros tropicais.

Palavras-chave: Mata Atlântica, variação microclimática, variação intraespecífica, anatomia funcional da folha e do lenho, transporte hídrico.

Abstract

Understanding the relationship between leaf mechanisms and secondary xylem has been fundamental for elucidating the water balance of species in dry environments, as well as their adaptations along different vegetation gradients. Among the remnants of the Atlantic Forest, the restinga stands out, a coastal phytophysiognomy marked by ecological instability and high vulnerability to future climate change. In this context, this study aims to identify the main functional traits of leaves and wood that enable plant species to adapt to different restinga formations: the sandbanks forest formations, *Clusia* formation, and beach grass and shrub formation. This research sought to understand acclimation mechanisms in environments subjected to microclimatic variations and water restriction. For this purpose, leaf and wood samples were collected from five individuals of the dominant species in each formation, located in the RPPN Fazenda Caruara, municipality of São João da Barra, RJ. Analyses included conventional plant anatomy methods for light microscopy observations, in addition to physiological evaluations of gas exchange.This dissertation is structured into two chapters: Chapter 1- How does variation in physiological and structural traits explain the occurrence of plants in different restinga formations? Chapter 2- Characterization of secondary xylem and anato-functional responses of restinga tree species to microenvironments with water restriction. The results of Chapter 1 revealed a wide variation in functional traits among the three species studied. While leaves prioritized water-use efficiency, wood showed a more conservative behavior, investing in hydraulic safety. These variations were more pronounced in the *Clusia* formation and the beach grass and shrub formation, both characterized by open canopies, higher irradiance, and low soil moisture. In contrast, in the sandbanks forest formations, where the canopy is denser and soil moisture is higher, a pattern geared toward greater photosynthetic efficiency, carbon acquisition, and efficient water transport was observed. Thus, adaptations to the distinct microclimates of the formations appear to be associated with structural and consequently physiological variation, contributing to species coexistence. In Chapter 2, the anatomical characteristics of the secondary xylem of eight tree species representative of the different restinga vegetation formations were detailed, advancing the understanding of adaptive mechanisms in this coastal ecosystem. The anatomical traits of *Scutia arenicola* (Rhamnaceae) and *Inga maritima* (Fabaceae) were described for the first time based on IAWA criteria. Species from environments with greater water

restriction exhibited anatomical traits consistent with higher hydraulic safety, including higher vessel density, narrower and shorter vessels, and smaller intervascular pits. In *Schinus terebinthifolia* (Anacardiaceae), these traits differed from those observed in populations from wetter areas. Moreover, different coordinated relationships among anatomical traits were recorded within the same species under distinct water conditions. In formations with greater seasonality in water availability, growth rings were more evident, indicating a direct influence of water variation on cambial rhythm. These results demonstrate that restinga tree species adopt specific anatomical and functional strategies in response to water restriction, highlighting the relevance of anatomical knowledge for understanding the functional ecology of tropical coastal ecosystems.

Keywords: Atlantic Forest, microclimatic variation, intraspecific variation, functional anatomy of leaves and wood, water transport.

1. Introdução Geral

Com sua alta biodiversidade, as florestas desempenham um papel essencial no armazenamento e sequestro de carbono atmosférico, além de serem fundamentais para a oferta de serviços ecossistêmicos e a manutenção dos processos ecológicos que sustentam a vida na Terra (Bennet *et al.*, 2023; van Tiel *et al*., 2024). As mudanças climáticas, atuais e futuras, representam uma das principais ameaças aos biomas, resultando na perda da biodiversidade global, de serviços ecossistêmicos e das reservas de carbono, aumentam o risco de mortalidade de espécies em todos os biomas (Araujo *et al*., 2021). Na América do Sul, biomas como o Cerrado e a Mata Atlântica, reconhecidos como grandes *hotspots* globais (Trindade *et al*., 2020; Bonifácio-Anacleto *et al*., 2024), estão entre os mais suscetíveis à extinção de espécies devido às mudanças climáticas futuras. Dentre eles, a Mata Atlântica se destaca como o bioma mais vulnerável ao aquecimento global (Trindade *et al*., 2020).

Os fragmentos remanescentes da Mata Atlântica enfrentam riscos de savanização e perda de biodiversidade, estando sob intensa pressão antrópica (Dean, 1996; Teixeira *et al*., 2014; Oliveira, 2015; Scarano e Ceotto, 2015; Urbano, 2015). Segundo Xavier *et al*. (2023), a Mata Atlântica é uma floresta tropical altamente heterogênea, composta por diversas fitofisionomias, como florestas e restingas, cada uma com características microclimáticas e edáficas distintas, o que contribui para sua complexidade ecológica e diversidade de espécies. Entre essas fitofisionomias, destaca-se a restinga, uma formação pioneira que se estende ao longo da costa brasileira (Loureiro *et al*., 2022). Esse ecossistema forma um mosaico de diferentes fisionomias vegetais, incluindo ervas, arbustos e árvores (Assumpção e Nascimento, 2000; Cirne *et al*., 2003; Inague *et al*., 2021; Loureiro *et al*., 2022). Estabelecida em solos arenosos, a vegetação de restinga desempenha uma função na compactação e estabilização das áreas costeiras próximas à linha da maré, minimizando os efeitos da erosão provocada pelos ventos e marés.

Aproximadamente quatro por cento das espécies vegetais da Mata Atlântica são endêmicas das restingas, mas essa biodiversidade está sob constante ameaça, com várias espécies em risco de extinção (Inague *et al*., 2021). Dentre as oito espécies dominantes da restinga analisadas neste estudo encontra-se algumas espécies vegetais com ocorrência dominante em restingas que podem ser utilizadas como importantes modelos para o entendimento das estratégias adaptativas ao estresse ambiental desse ecossistema.

Entre essas espécies está *Schinus terebinthifolia* Raddi (Anacardiaceae), que é nativa da América do Sul e amplamente conhecida no Brasil pelo nome popular de aroeira-vermelha (Lorenzi e Souza, 1998). Esta espécie apresenta hábito arbustivo ou arbóreo, com copa ampla e tronco resistente, geralmente tortuoso, com diâmetro variando entre 30 e 60 cm (Lorenzi e Souza, 1998). É reconhecida por ser pioneira e invasora, devido a sua alta capacidade de adaptação e dispersão nos diferentes continentes (Cuda *et al*., 2006). Devido ao seu sucesso adaptativo tem recebido destaque em projetos de arborização urbana e restauração de ecossistemas degradados. Sua estratégia ecológica, caracterizada como pioneira ou secundária inicial, aliado a uma ampla tolerância ambiental e forte interação com a fauna local, permite à espécie colonizar desde florestas densas e abertas até ambientes litorâneos mais extremos, como manguezais e restingas (Kageyama e Gandara, 2000; Sabbi *et al*., 2010; Luz, 2011).

Outra espécie de grande importância para a restinga é *Pera glabrata* (Schott) Baill (Peraceae) (Assunção e Nascimento, 2000) a espécie nativa mais difundida do seu gênero, ocorrendo no Brasil e Venezuela, no Brasil é conhecida pelos nomes populares pau-de-sapateiro, sapateira, tamanqueira. Esta espécie pioneira possui uma ampla distribuição no Brasil, sendo particularmente frequente em formações vegetais mais secas, como restinga e cerrado (Lorenzi, 1992, Freitas *et al.*, 2011; Oliveira, 2024; Bigio e Secco, 2025). Podem apresentar hábito arbóreo ou arbustivos, podendo atingir até 35 metros de altura e 40 a 50 cm de diâmetro, ela também se destaca como espécies com potencial para enriquecimentos e restauração em áreas degradadas de restinga arbórea, utilizada também na urbanização (Lorenzi,1992; Oliveira, 2024). O fato de ser pioneira pode estar atrelado a sua alta produção e dispersão de sementes que constituem uma fonte de alimento para diversos tipos de animais (Freitas *et al*., 2011). Assunção e Nascimento (2000) ressalta a importância de *Pera glabrata* na composição florística, estrutural e fisionômica da região de restinga, destacando a possibilidade ou uma ligação com áreas impactadas.

No mesmo contexto *Scutia arenicola* (Casar.) Reissek (Rhamnaceae) é um arbusto perene nativo do Brasil, popularmente conhecido como quixabinha. Embora não seja endêmica, sua ocorrência está restrita à Mata Atlântica, sendo comumente registrada em formações de restinga e manguezal nas regiões Sul e Sudeste do país (Assumpção e Nascimento, 2000; Borri *et al*., 2017; CNCFlora, 2025; Lima *et al*., 2025). Trata-se de uma espécie de grande relevância ecológica, atualmente classificada

como “Em Perigo” na Lista Vermelha da Flora Brasileira. Estima-se que aproximadamente 80% de sua ocorrência esteja restrita às restingas, ambientes costeiros frágeis e cada vez mais ameaçados. *Scutia arenicola* possui uma área de ocupação restrita (cerca de 172 km²) e sofre degradação contínua de habitat, o que evidencia sua vulnerabilidade e a necessidade urgente de conservação (CNCFlora, 2025).

Protium heptaphyllum (Aub.) Marchand (Burseraceae) é uma espécie nativa de ampla distribuição nos biomas Amazonia, Mata Atlântica, Catinga e Cerrado, com hábito arbóreo ou arbustivo, mas não endêmica do Brasil (Reflora, 2025). No Brasil é conhecida popularmente como breu-branco ou almecéga e apreciada devido a atividades biológicas do óleo essencial e resina obtidos a partir de suas folhas. Sua resina também é utilizada na fabricação de verniz, tintas, calafetagem de embarcações, cosméticos e repelentes (de Melo *et al*., 2015; Marquina-Chidsey *et al*.,2017; Cabral *et al*., 2021). De acordo com de Melo *et al*. (2015), *Protium heptaphyllum* é uma espécie resistente a estresses ambientais, plástica e adaptável a condições adversas. Resultados de um inventário florestal, publicados por Fagg *et al*. (2004), destacam esta espécie como a de maior de importância.

Cynophalla flexuosa (L.) J. Presl (Capparaceae) é uma espécie Neotropical, sua ocorrência se estende desde os Estados Unidos até a Argentina, no Brasil, está presente nas regiões Norte, Nordeste, Centro-Oeste, Sudeste e Sul, pode ocorrer na forma de árvore ou arbusto atingindo entre três e quatro metros (Saha *et al*., 2018; Salazar *et al*., 2022; Lucena e Cruz, 2023; Soares e Luber, 2025). Popularmente conhecida como “feijão bravo” a espécie apresenta estratégias de sobrevivência favorecidas por formigas que fazem a dispersão de suas sementes (Lucena e Cruz, 2023). *Cynophalla flexuosa* possui algumas habilidades para se adaptar a ambientes secos, como a capacidade de controlar seu metabolismo em razão das condições ambientais adversas (Lucena e Cruz, 2023). Apresenta atividade biológica e é usada como combustível. Por ser palatável e se manter sempre verde durante períodos de seca é utilizada na alimentação animal em períodos de estiagem (Salazar *et al*., 2022).

Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn. (Sapotaceae) típica de regiões semiáridas ocorre na forma de arbusto ou árvore podendo atingir dezoito metros de altura. É nativa da América Central e do Sul e no Brasil já foi confirmada na Caatinga, Cerrado, Mata Atlântica e Pantanal. Utilizada na medicina popular, sua madeira é utilizada na confecção de artefatos como cabos de ferramentas, na construção

rural, civil, alimento e forragem (Pedrosa *et al*., 2015; Cruz, 2018; Alves-Araújo, 2025). Essa espécie já foi relacionada na lista vermelha de espécies ameaçadas de extinção e, segundo Cruz (2018), populações de *Sideroxylon obtusifolium* ainda são escassas, o que ressalta a necessidade de estudos direcionados à sua caracterização e conservação.

Inga Marítima Benth. (Fabaceae-Mimosoideae) é uma espécie endêmica brasileira que ocorre na região Sudeste em formações de restinga (Garcia e Bonadeu, 2025). A espécie é limitada às restingas do estado do Rio de Janeiro, atualmente classificada como "Em Perigo" (CNCFlora, 2025). Essa espécie pode ocorrer na forma de árvore ou arbusto, geralmente atingindo dois metros meio, ocupando áreas arbustivas do tipo fechado em restingas (Peixoto *et al*., 2015).

Varronia curassavica Jacq. (Cordiaceae) é um arbusto perene atingindo de meio a 4 metros de altura, nativa das Américas do Sul e Central. No Brasil ocorre em uma grande área, principalmente em regiões costeiras, incluindo domínios fitogeográficos como a Amazonia, Cerrado, Catinga, Pampas e Mata Atlântica (Brandão *et al*., 2015; El Toghlobi *et al*., 2022: Silva e Melo, 2025). Popularmente conhecida como erva-baleira *Varronia curassavica* é uma planta medicinal e aromática de grande relevância econômica que compõe a florística da restinga (El Toghlobi *et al*., 2022).

Embora desempenhem funções ecossistêmicas essenciais, a riqueza florística das áreas de restinga vêm sofrendo redução devido ao desmatamento. As principais causas incluem extração de madeira, pastoreio de bovinos e caprinos, especulação imobiliária e uma taxa de ocupação territorial cinco vezes maior do que em outros ecossistemas (Maciel, 1984; Assumpção e Nascimento, 2000; Inague *et al.*, 2021; Borges *et al*., 2024). Essas pressões agravam a vulnerabilidade da biodiversidade das restingas às mudanças climáticas (Cirne *et al*., 2003; Inague *et al*., 2021). Nesse contexto, torna-se essencial a realização de estudos detalhados sobre a vegetação e as características ambientais desses remanescentes para embasar estratégias de conservação e garantir a preservação desse ecossistema frente às incertezas futuras.

Segundo Inague *et al*. (2021), ambientes de restinga enfrenta condições mais severas em comparação com as florestas. Nesse contexto, estudos (Cicarelli e Bona, 2022; Vieira *et al*., 2022; Borges *et al*., 2024) indicam que os fatores abióticos presentes nas restingas impõem exigências específicas às plantas, levando as espécies vegetais desse ecossistema a exibirem elevada plasticidade ecológica. Isso se manifesta em adaptações como a otimização na aquisição de nutrientes e a eficiente retenção de água,

tornando a restinga um modelo para a investigação das interações entre fatores abióticos e características funcionais das plantas (Cicarelli e Bona, 2022; Vieira *et al*., 2022; Borges *et al*., 2024). Diante desse cenário, o presente estudo teve como objetivo identificar os principais atributos funcionais foliares (morfológicos e fisiológicos) e do lenho (anatômicos) que permitiram às espécies vegetais ajustarem-se às diferentes formações vegetacionais de restinga. Para tal, foram levantadas algumas questões-chave, organizadas em dois capítulos:

Capítulo 1: Como a variação nos atributos fisiológicos e estruturais explica a ocorrência de plantas em diferentes formações de restinga?

Capítulo 2: Caracterização do lenho e respostas anatofuncionais de espécies arbóreas da restinga a microambientes com restrição hídrica.

Os resultados esperados visam aprofundar a compreensão dos processos que governam a consolidação da vegetação de restinga e auxiliar na previsão de mudanças climáticas futuras. O conhecimento acumulado sobre a formação das comunidades vegetais de restinga permitirá a geração de informações científicas para a reestruturação, conservação e manejo sustentável desse ecossistema costeiro, garantindo sua resiliência frente às pressões ambientais.

2. Fundamentação Teórica

2.1 Mata Atlântica

A Mata Atlântica se estende por mais de 3.000 km ao longo da costa brasileira, desde o Rio Grande do Norte até o Rio Grande do Sul, alcançando o interior do continente e abrangendo também partes da Argentina e do Paraguai (SOS Mata Atlântica, 2021-2022; Wilson *et al*., 2021). Este bioma, que é o lar de mais de 125 milhões de brasileiros, contribui com mais de 70% do PIB do país e 2/3 da economia industrial, abrigando algumas das terras mais produtivas do Brasil e grandes centros

urbanos da América do Sul, como Rio de Janeiro e São Paulo (Rezende *et al*., 2018). A Mata Atlântica presta serviços ecossistêmicos essenciais para o bem-estar humano, como o abastecimento de água, sequestro de carbono, regulação climática, produção de alimentos, madeira e medicamentos (Rocha *et al*., 2024; Alves *et al*., 2024; Mantovani *et al*., 2024).

A mata atlântica é a segunda maior floresta tropical do mundo e um dos domínios tropicais mais ricos em biodiversidade, abrigando cerca de 8% de toda a diversidade biológica global (Ribeiro *et al*., 2009; Magnago *et al*., 2015). Este bioma possui 2.420 espécies de vertebrados e cerca de 20.000 espécies de plantas, das quais 5.044 são de porte arbóreo (Lima *et al*., 2020; Wilson *et al*., 2021). O grau de endemismo é elevado; cerca de uma em cada cinquenta espécies de plantas vasculares e dos vertebrados (exceto peixes) do planeta é endêmica deste bioma, somente entre as árvores, 1.547 espécies são endêmicas (Lima *et al*., 2020; Wilson *et al*., 2021).

Apesar de seu elevado grau de endemismo, a Mata Atlântica tem sofrido com intenso desmatamento desde o século XV, iniciado com a colonização, sendo reduzida a áreas naturais fragmentadas devido à urbanização, industrialização e expansão agrícola (Benchimol *et al*., 2017; Rezende *et al*., 2018; Vaz *et al*., 2024). A fragmentação desse bioma o transformou em um dos três hotspots de biodiversidade mais críticos e vulneráveis às mudanças climáticas, sendo considerada uma região prioritária para a conservação (Rezende *et al*., 2018; Rocha *et al*., 2024).

A Mata Atlântica perdeu entre 84% e 89% de sua vegetação original, restando apenas 11% a 16% da cobertura nativa, distribuída em um mosaico de florestas antigas, florestas secundárias, zonas urbanas e pastagens (Ribeiro *et al*., 2009; Joly *et al*., 2014; Benchimol *et al*., 2017; Mangueira *et al*., 2021; Wilson *et al*., 2021). Essa fragmentação resultou na ameaça de extinção de aproximadamente 1.544 espécies de plantas e 380 espécies de animais, o que corresponde a cerca de 60% das espécies da fauna e flora brasileiras incluídas nas listas de espécies ameaçadas (Ribeiro *et al*., 2009).

Dessa forma, as diversas fitofisionomias (Figura 1 e 2) que ainda compõem a Mata Atlântica precisam ser urgentemente protegidas contra a fragmentação, incluindo a floresta ombrófila densa, floresta ombrófila mista, floresta ombrófila aberta, floresta estacional semidecídua, floresta estacional decidual, campos de altitude e formações pioneiras, como brejos interioranos, manguezais e restingas (Brito *et al*., 2021; SOS Mata Atlântica 2021-2022).

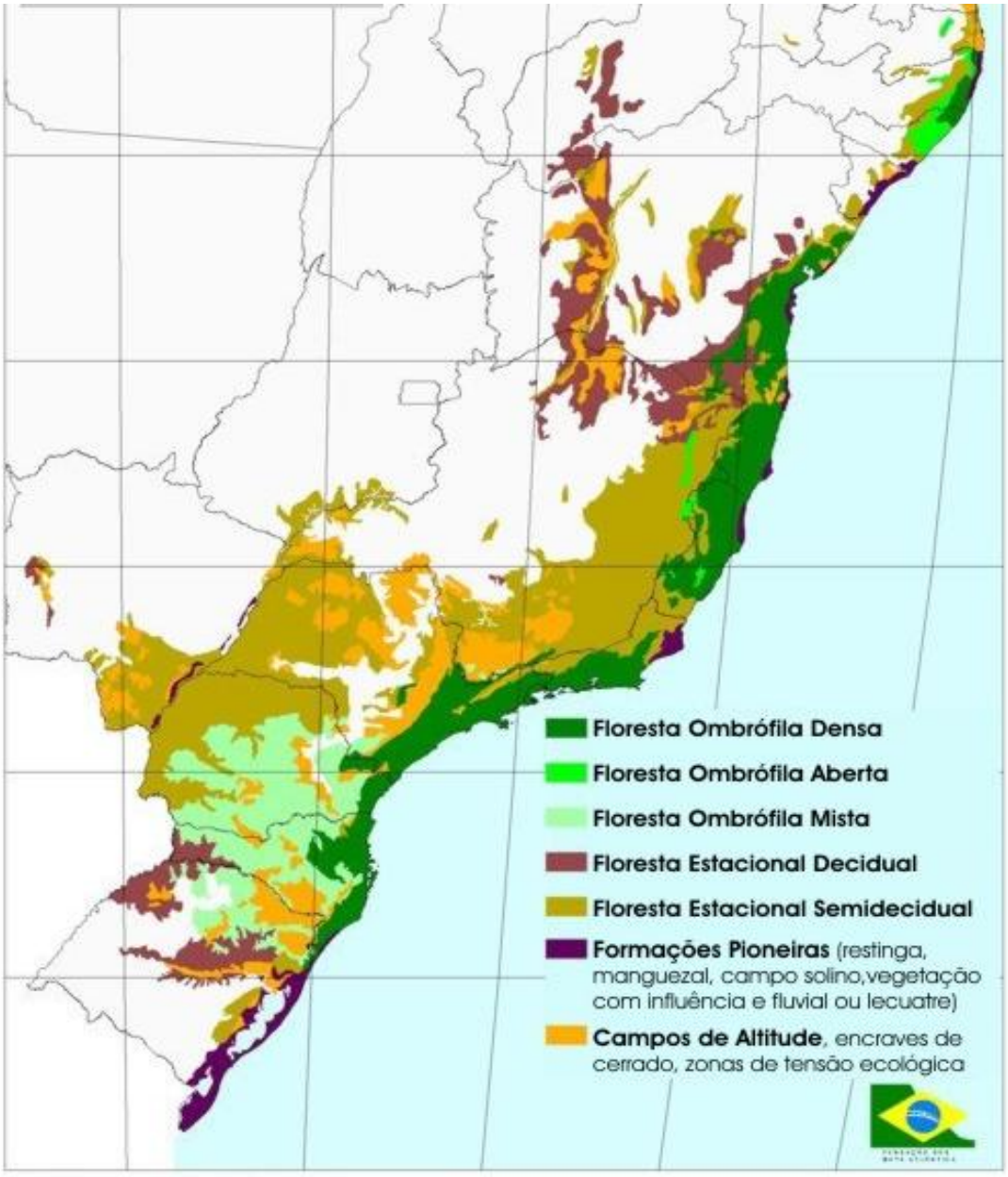

Figura 1: Mapa da distribuição das fitofisionomias da Mata Atlântica (Fonte: SOS Mata Atlântica 2021-2022).

Essa heterogeneidade vegetacional se deve à vasta extensão territorial da Mata Atlântica, que apresenta grande variação longitudinal, latitudinal e altitudinal, resultando em fitofisionomias distintas, com microclimas variados e diferenças nos índices de precipitação, irradiância e tipos de solo (Rizzini *et al*., 1990; Galindo-Leal e Câmara, 2003; Ribeiro *et al*., 2009). Toda essa diversidade de habitats explica a alta biodiversidade e endemismo do bioma (Ribeiro *et al*., 2009).

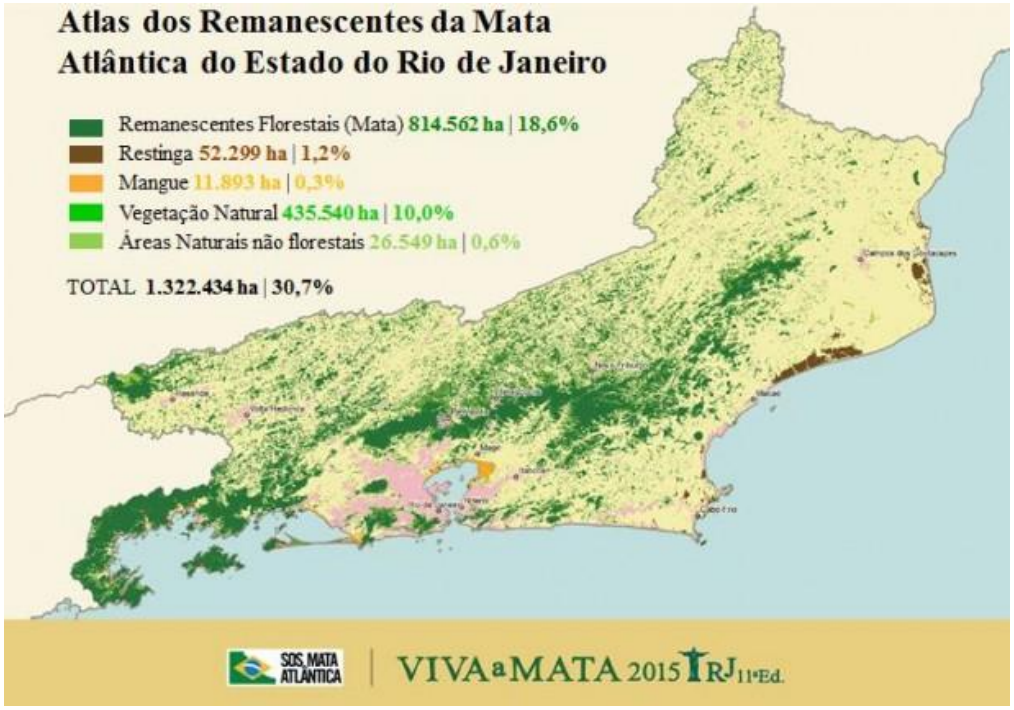

Figura 2: Distribuição de remanescentes da Mata Atlântica para o estado do Rio de Janeiro. (SOS Mata Atlântica, 2018-2019).

No entanto, o desmatamento acelerado ameaça essa riqueza biológica única e exclusiva, que resulta diretamente da diversidade das fitofisionomias associadas ao bioma, como as restingas, que também enfrentam pressões ambientais crescentes (Scarano e Ceotto, 2015).

2.2 Formações vegetacionais de restinga

Os ambientes costeiros contêm uma fauna e flora indispensáveis para o funcionamento do planeta. No Brasil, esses ambientes costeiros são extensos com uma estrutura ecológica complexa e de biodiversidade diversa (Barbier *et al*., 2008; Mendes *et al*., 2017). As restingas são formadas através de milhares de anos por deposições sedimentares fluviais e lacustres nas planícies costeiras e se estendem por mais de 7.000 km ao longo da costa brasileira (Silva, 1999; Vieira *et al*., 2022). Estas constituem um ambiente hostil formado por solos salino-arenosos, lençóis freáticos superficiais e radiação solar intensa, abrigando uma diversidade ecológica de espécies vegetais, consideradas especializada devido às características microclimáticas do ecossistema da restinga (Cerqueira, 2000; Scarano, 2002; Vieira *et al*., 2022).

Esses ambientes costeiros são formados por planícies arenosas que datam o período do Quaternário, formadas há aproximadamente 10.000 mil anos oriundos de regressões marinhas (Suguio e Tessler 1984; Cirne *et al*., 2003; Freitas *et al*., 2017; Vieira *et al*., 2022). O termo "Restinga" é definido como todo depósito arenoso, ou paralelo a linha da costa, ao longo do tempo essas faixas de areia, foram colonizadas por plantas oriundas de diferentes fitofisionomias da Mata Atlântica, como a Floresta Estacional semidecídua, Cerrado, Catinga (Freire, 1990; Assunção e Nascimento, 2000; Scarano 2002; Conama, 2012; Inague *et al*., 2021). O mosaico de formações vegetacionais que compõe esse ecossistema dinâmico, como herbáceas, árvores, arbustos, ajudam na compactação do solo estabilizando as áreas costeiras próximas a linha da maré minimizando os efeitos erosivos causados pelos ventos e pelas marés, estabilizando o substrato arenoso (Assumpção e Nascimento, 2000; Cirne *et al*., 2003; Inague *et al*., 2021; Borges *et al*., 2024). À medida que avançam para o interior do continente, as espécies vegetais aumentam em lenhosidade, estratificação e diversidade e número de espécie (Demétrio *et al*., 2023). Este ecossistema de transição possui características únicas que o diferencia das demais formações da Mata Atlântica. Destaca-se pelo alto grau de endemismo para espécies vegetais e animais, funcionando como uma área de refúgio para espécies ameaçadas de extinção (Araújo 1997; Falkenberg 1999; Carvalho e Sá, 2011; Inague *et al*., 2021). Apesar de sua riqueza esses ambientes costeiros distintos são vulneráveis aos ventos, ao spray marinho e as marés, o que torna o ambiente instável (Cirne *et al*., 2003; Ciccarelli e Bona, 2022).

As características ambientais das restingas são extremas, com baixa disponibilidade hídrica e de nutrientes, solos salinos e alta irradiância (Assumpção e Nascimento, 2000; Schwinning e Ehleringer, 2001; Pireda, 2013; Pireda *et al.*, 2019; Inague *et al*., 2021; Ciccarelli e Bona, 2022; Borges *et al*., 2024). As características de granulometria do solo nesses ecossistemas não contribuem para retenção de água. Os espaços entre as partículas são tão grandes que apenas 15% da água é retida após o solo ser completamente encharcado (Taiz e Zeiger, 2013; Borges *et al*., 2024). Os solos da região próxima a praia apresentam coloração amarelada, pouca impregnação de ácido húmico e baixa disponibilidade de matéria orgânica. Enquanto os solos próximos às formações arbóreas possuem maior teor de matéria orgânica e ácido húmico disponibilizadas pela decomposição das folhas e demais fragmentos das árvores que caem no solo (Almeida Jr. *et al*., 2009; Borges *et al*., 2024).

Segundo Araújo (2000), Freire (1990), Ciccarelli e Bona (2022) e Borges *et al*. (2024), os fatores abióticos exigem que a vegetação deste ecossistema invista em ajustes durante a colonização desse ambiente, portanto, a análise das características funcionais dessa vegetação é útil para inferir os processos de montagem em comunidades vegetais ao longo de gradientes de estresse natural. Segundo Borges *et al.* (2024), estes gradientes vegetacionais podem apresentar formações com microambientes distintos que se estendem desde a linha da maré e avançam para o interior do continente com diferentes configurações vegetais, tais como dunas frontais ou internas, planícies, baixadas com vegetação herbácea, subarbustivas e até áreas de florestas formadas por arbustos e árvores. Alguns trabalhos mostram como o ecossistema de restinga pode configurar diferentes paisagens ao longo da costa brasileira. Segundo Sá (1996), há cinco formações vegetacionais distintas na Restinga Saquarema-RJ, enquanto Assis *et al.* (2004) descreveu dez formações vegetacionais na Restinga de Sepetiba-ES, já Dau (1960) descreveu quatro formações vegetacionais na restinga de Cabo Frio-RJ, denominadas como graminóide, palmóide, parque e mata. Assunção & Nascimento (2000) encontraram quatro formações vegetacionais nas restingas do Norte do estado Rio de Janeiro denominadas de Formação de Mata de restinga, formação de *Clusia,* formação praial com moitas e formação praial graminóide (Figura 2).

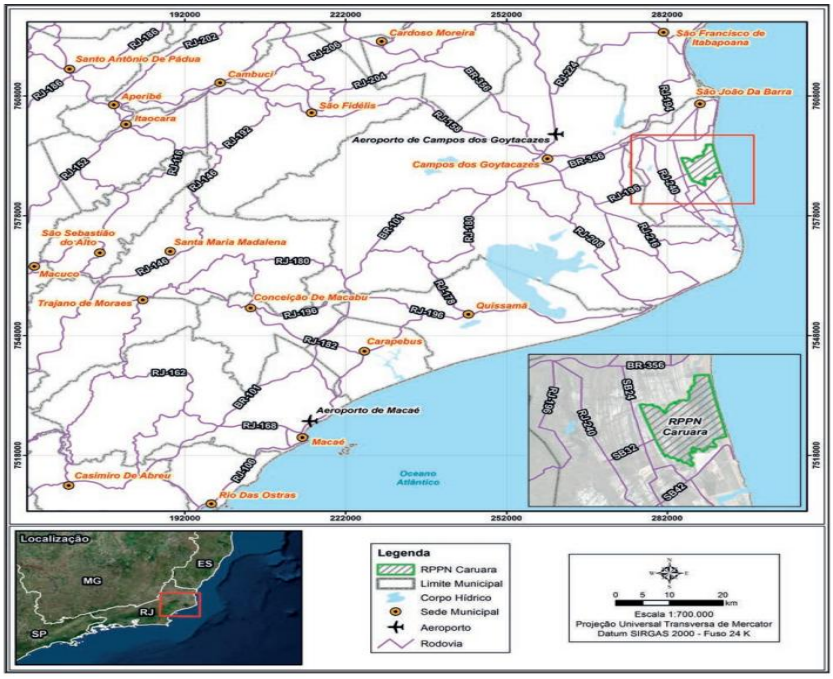

Figura 3: Delimitação territorial da Reserva Particular do Patrimônio Natural Fazenda Caruara. Zoneamento da Reserva Particular do Patrimônio Natural Fazenda Caruara, município de São João da Barra, RJ, Brasil. (Fonte: Plano de Manejo RPPN Caruara, 2018).

2.3 Restingas do Complexo Lagunar Grussaí e Iquipari

De acordo com Assunção e Nascimento (2000), as restingas do Complexo Lagunar Grussaí e Iquipari (CLGI) na região norte do estado do Rio de Janeiro exibem uma organização vegetacional distintas das outras restingas do estado (Figura 3). Possuem uma praia extensa sem a presença de dunas sendo composta por quatro formações distintas, dispostas sequencialmente do interior para a costa, que são: mata de restinga, formação de *Clusia,* formação praial com moitas e formação praial graminóide (Assunção e Nascimento, 2000). Essas formações incluem a mata de restinga, caracterizada por um ambiente com sombreamento consolidado com árvores de maior porte e solo rico em matéria orgânica (Villela *et al*., 2020). A formação de *Clusia* consiste em moitas densas, com predominância da espécie *Clusia hilariana* no centro, resultando em sombreamento intermediário (Villela *et al*., 2020). Por fim, a formação praial com moitas é composta por moitas menores com alta incidência de radiação fotossinteticamente ativa (PAR) e baixa quantidade de matéria orgânica no solo. Cada uma dessas formações vegetacionais apresenta características microclimáticas e edáficas distintas (Oliveira *et al*., 2023).

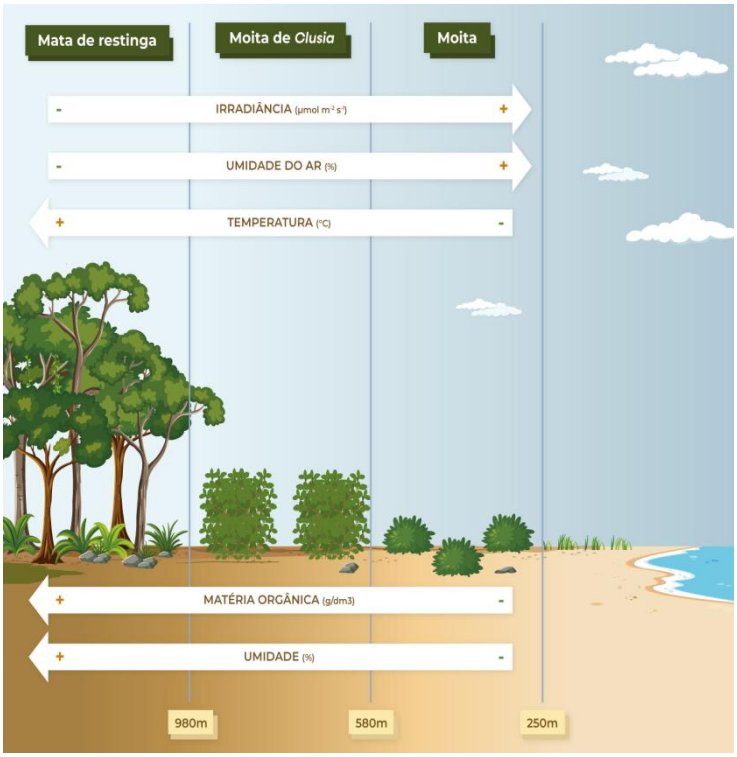

Figura 4: Representação gráfica da estrutura da vegetação e dos parâmetros edáficos microclimáticos das formações vegetacionais na restinga do Norte Fluminense. (Assumpção e Nascimento, 2000; Oliveira *et al*, 2023). Representação gráfica (Acervo pessoal).

A formação de mata de restinga tem início a partir de 980m da linha de maré, formando uma floresta continua, com poucos indivíduos atingindo acima de 6 m de altura, formando um dossel consolidado que produz maior quantidade de serapilheira, contribuindo para o aumento da taxa de ciclagem de nutrientes no solo (Assumpção e Nascimento, 2000; Pireda *et al*., 2019; Villela *et al*., 2020; Oliveira *et al.*, 2023). A presença de um dossel consolidado diminui também a quantidade de irradiância que chega ao sub-bosque (Pireda *et al*., 2019).

Quanto aos fatores climáticos, encontramos menores valores de irradiância e maiores valores de temperatura do ar e déficit de pressão de vapor (VPD), quando comparado as outras formações vegetacionais (Assumpção e Nascimento, 2000; Melo Jr. e Boeger, 2016; Oliveira *et al*., 2023). Quanto as características do solo, há maior presença de matéria orgânica, C, N, Mg, Al, maior condutividade elétrica, humidade do solo e baixo pH (Corrêa *et al*., 2020; Lourenço *et al*., 2021; Oliveira *et al*., 2023). A elevada acidez do solo leva a uma deposição e liberação de Al no solo, exercendo um papel crucial na formação do solo de restinga, transportando a matéria orgânica da superfície do solo para áreas mais profundas. Este tipo de solo está intimamente relacionado com a manutenção da umidade (Lourenço *et al*., 2021).

A formação de *Clusia* ocorre a partir de 580m e se estende até 980m da linha do mar, a espécie *Clusia hilariana* Schltdl. (Clusiaceae) se destaca nesta formação como uma espécie pioneira (Assumpção e Nascimento, 2000; Villela *et al*., 2020). A espécie fica localizada no centro da moita, em muitos casos suas folhas contribuem com até 70% da serapilheira, disponibilizando matéria orgânica, enriquecendo o solo com nutrientes através de uma lenta decomposição, contribuindo também para a redução da irradiância e temperatura do solo (Villela *et al*., 2020). A temperatura dor ar e o VPD são semelhantes à mata de restinga, com menor irradiância quando comparada a formação praial com moitas (Oliveira *et al.,* 2023). Através da análise do solo foram encontrados níveis intermediários de pH e N, além disso, valores elevados de Na, C, matéria orgânica, condutividade elétrica e umidade foram característicos do solo desta formação (Corrêa *et al*., 2020; Villela *et al*., 2020). Assim, *Clusia hilariana* nessa formação, desempenha um papel ecossistêmico chave, facilitando a colonização por outras espécies ao seu redor, resultando em moitas adensadas, fazendo a transição entre a mata de restinga e a formação praial com moitas (Assumpção e Nascimento, 2000; Melo Jr. e Boeger, 2016; Villela *et al*., 2020).

A formação praial com moitas tem início a 250 m da linha do mar chegando até 580 metros aproximadamente, as moitas são formadas por árvores e arbustos que oferecem uma cobertura menor, de apenas 25%, deixando o restante com areia exposta. bromélias e cactos formam núcleos que possibilitam o crescimento de outras espécies formando moitas menores quando comparada a formação de *Clusia* (Assumpção e Nascimento, 2000; Pireda *et al*., 2019). A temperatura do ar e o VPD são menores nessa formação, assim como a quantidade de nutrientes do solo, e maiores valores de irradiância quando comparada as outras formações (Oliveira *et al*., 2023).

A formação praial graminóide tem início na linha da maré e chegando até 250 metros aproximadamente, a vegetação é constituída por espécies herbáceas rasteiras que não apresentam caules lenhosos e recobrem apenas 24% da areia deixando 76% exposta. (Araújo e Henriques, 1984; Assumpção e Nascimento, 2000). O efeito da salinidade nessa formação é mais intenso devido à proximidade com o mar e ação das marés, a temperatura do solo também é mais elevada podendo atingir até 50 ºC (Assumpção e Nascimento, 2000). Nessa formação vegetacional a umidade do ar é maior, devido à proximidade com o mar, já a temperatura e VDP são menores (Oliveira *et al*., 2023).

As formações vegetacionais das restingas estão sujeitas a filtros ambientais severos, como alta temperatura, alta irradiância, restrição hídrica, solo arenoso e oligotrófico (Lourenço *et al*., 2021; Oliveira *et al*., 2023). Espécies que colonizam essas áreas passaram por adaptações em sua morfologia, anatomia, fisiologia, aspectos nutricionais e bioquímicos em resposta à pressão seletiva imposta pela baixa disponibilidade de água e pela alta exposição solar (Pireda *et al*., 2019; Oliveira *et al*., 2023). Estudos têm evidenciado que algumas espécies apresentam ajustes anatômicos e fisiológicos em nível e do lenho foliar (Pireda *et al*., 2019; Castelar *et al*., 2023; Xavier *et al*., 2023) em resposta aos filtros ambientais, que possibilitam o sucesso na colonização nas diferentes formações da restinga (Oliveira *et al*., 2023).

2.4 Adaptações do sistema hidráulico à seca

Em um contexto de mudanças climáticas, caracterizado por prolongados períodos de seca e fragmentação de biomas devido à ação antrópica, a compreensão dos

mecanismos de resposta das árvores de florestas tropicais a altas temperaturas, radiação solar intensa e escassez hídrica tornou-se uma prioridade (Bräuning *et al*., 2017; Polle *et al*., 2019; Waite *et al*., 2023; Xavier *et al*., 2023). Os mecanismos de resistência à seca apresentam uma complexidade notável e são objeto de estudos crescentes, visando identificar as estratégias predominantes de prevenção e tolerância à seca, bem como a adaptação a fatores de estresse, como alta radiação solar e temperaturas elevadas, que impactam o sistema hidráulico das plantas (Bräuning *et al*., 2017; Waite *et al*., 2023; Simioni *et al*., 2023; Oliveira et al., 2023; Castelar *et al*., 2023).

O sistema hidráulico das plantas arbóreas é composto por um continuum no qual o transporte de água a longas distâncias no xilema é regido pela tensão gerada pela transpiração nos estômatos e pela coesão entre as moléculas de água e as paredes dos vasos condutores (Pittermann, 2010; Schenk e Jansen, 2015; Araujo *et al*., 2024). A absorção de água é impulsionada pela taxa de transpiração nas folhas, sendo controlada pelos estômatos (Simioni *et al*., 2023; Taiz *et al.,* 2017). Durante períodos de déficit hídrico, os potenciais hídricos negativos que atuam sobre os vasos do xilema se intensificam, gerando altas tensões que podem interromper o transporte hídrico, através da formação de embolias (Araujo *et al*., 2024). Consequentemente, todos os tipos celulares estão envolvidos nesses mecanismos fisiológicos e contribuem diretamente o desempenho da planta. Pesquisas relativas à hidráulica das plantas, especialmente no *continuum* xilema-folha, têm revelado a capacidade desse sistema de se ajustar em resposta às variações ambientais (Simioni *et al*., 2023).

As plantas podem ajustar a anatomia de suas folhas de diversas maneiras para regular a perda de água ao nível foliar, como por meio da redução da área foliar e da área foliar específica (Pireda *et al*., 2019). É possível observar, em ambientes de intensa radiação e de déficit hídrico, folhas com estômatos menores e em maior densidade, com menor abertura do poro estomático, resultando em um controle mais eficiente do uso da água (Pireda *et al*., 2019; Araújo *et al*., 2021; Simione *et al*., 2023). Folhas mais espessa também são comuns nesses ambientes, atuando como barreiras físicas que evitam danos e servem como reservas de água, mantendo o fluxo de transpiração foliar (Niinemets, 2001; Pireda *et al*., 2019; Simione *et al*., 2023). Esses atributos anatômicos podem variar em conjunto com características hidráulicas, refletindo respostas específicas das espécies ao estresse hídrico, como evidenciado por Simione *et al*. (2023).

No xilema secundário, os atributos estruturais se ajustam em resposta as variações ambientais através de modificações no tamanho, número e distribuição dos vasos condutores, bem como pela organização dos mesmos (Gleason *et al*., 2016). Em ambientes secos, há uma tendência de redução do diâmetro médio dos vasos condutores, o que diminui o risco de embolia (Rodriguez-Zacaro *et al*., 2021; Dória *et al*., 2022). Vasos de menor diâmetro, em maior número e frequentemente agrupados, são observados, assim como paredes de vasos e fibras mais espessas, tornando o xilema mais seguro (Campbell *et al*., 2016; Gleason *et al*., 2016). As células de parênquima axial e radial desempenham um papel crucial na prevenção e reversão de embolias, possibilitando o transporte lateral de água por meio das pontoações nas células do parênquima vascular (Carlquist, 2018; Olson *et al*., 2020). A compreensão da coordenação entre os mecanismos foliares e o xilema secundário tem revelado um grande potencial para entender o balanço hídrico positivo das espécies em ambientes secos, auxiliando na compreensão de como as espécies se adaptam a diferentes formações vegetacionais, como o Cerrado e a Mata Atlântica (Simioni *et al*., 2023; Castelar *et al*., 2023).

3. Objetivo Geral

Investigar as estratégias de funcionamento hidráulico e descrever a anatomia do lenho das espécies arbóreas dominantes em diferentes formações de restinga (formação praial com moitas, formação de *Clusia* e mata de restinga), considerando os parâmetros fisiológicos e os filtros ambientais que influenciam essas comunidades.

3.1 Objetivos específicos

1. Caracterizar os fatores microclimáticos e edáficos de cada formação vegetacional para identificar as principais variáveis ambientais que influenciam as formações de restinga;
2. Descrever a anatomia do lenho das espécies dominantes em cada formação de restinga, destacando características estruturais relevantes para a adaptação ao gradiente ambiental;

3. Analisar os parâmetros morfológicos relacionados ao teor de matéria seca (TMS), área foliar específica (LMA) e área foliar (AF);
4. Avaliar os parâmetros fisiológicos relacionados as taxas de transpiração (E) e de condutância estomática (gs) para compreender a relevância das trocas gasosas para a sobrevivência das espécies nas formações vegetacionais.
5. Analisar os atributos estruturais do lenho, incluindo frequência e agrupamento de vasos, índice de agrupamento, diâmetro e espessura da parede dos vasos, além do diâmetro e espessura da parede das fibras;
6. Quantificar os tipos celulares do xilema secundário em porcentagens, considerando parênquima axial, parênquima radial, elementos de vaso, elementos de vaso conectados ao parênquima axial, fibras e fibras gelatinosas;
7. Investigar as diferenças na arquitetura hidráulica das espécies coocorrentes *Scutia arenicola*, *Schinus terebinthifolia* e *Pera glabrata*, avaliando como esses atributos refletem o ajuste ao gradiente de restinga.

A presente tese foi dividida em dois capítulos e serão destinados a publicação de dois artigos:

Capítulo 1: Como a variação nos atributos fisiológicos e estruturais explica a ocorrência de plantas em diferentes formações de restinga? (How does variation in physiological and structural traits explain the occurrence of plants in different restinga formations? Manustcrito publicado ao periódico *Trees*.

Capítulo 2: Caracterização do lenho e respostas anatofuncionais de espécies arbóreas da restinga a microambientes com restrição hídrica.

Este trabalho será submetido a revista IAWA.

4. How does variation in physiological and structural traits explain the occurrence of plants in different restinga formations?

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Key Message

This study reveals intraspecific variability in physiological and anatomical traits among tree species in different restinga formations, highlighting their adaptability to changing microclimatic conditions.

4.1 Abstract

Climate change, with increasingly frequent drought episodes, threatens the survival of tree species in biodiverse ecosystems like the Atlantic Forest. We investigated whether plants of the same species in different restinga formations exhibit intraspecific variability in physiological and secondary xylem traits. We evaluated five individuals of

each of three tree species (*Scutia arenicola* (Casar.) Reissek (Rhamnaceae), *Schinus terebinthifolia* Raddi (Anacardiaceae) and *Pera glabrata* (Schott) Baill. (Peraceae) all of which co-occur across three distinct formations within the restinga of northern Rio de Janeiro State: a beach grass and shrub, a *Clusia* formation and a sandbanks forest formation. We used standard methods of plant physiology and anatomy to study the traits, focusing on the structure–function relationships between leaf and secondary xylem. The evaluated species exhibited a set of variations in functional traits. While the leaves invested in water use efficiency, the wood remained conservative, prioritizing hydraulic safety. These traits vary mainly in the *Clusia* and beach grass and shrub formations, where the canopy is open and both soil moisture availability and irradiance are lower and higher, respectively. In the sandbanks forest, where the canopy is closed and soil moisture is higher, a pattern of photosynthetic efficiency, carbon acquisition, and water transport efficiency was observed. The physiological and tissue variation identified in this study may have played a role in the coexistence of the species, allowing them to adjust to variable microclimates among the different restinga formations. This variation may be essential for the persistence of these species, enabling efficient water use and safety, which is reflected in their maintenance along vegetation gradients over time and under future climate scenarios.

Keywords: Atlantic Forest, intraspecific variation, wood anatomy, water use efficiency, hydraulic safety.

4.2 Introduction

Climate change is already a reality, manifested through increases in the average global temperature, both on land and in the oceans, as well as extreme events such as prolonged droughts and heat waves (Leisner et al. 2023). These phenomena can profoundly impact several species, but particularly plants, which face increasing challenges in the face of these intensified climate variations (Leisner et al. 2023). Climate change compromises the physiological functioning to which plants are adapted, threatening the survival of some species, especially in tropical forests (Araújo et al. 2021, 2024). In this context, investigating the response mechanisms that tropical trees employ in conditions of high temperatures, intense solar radiation, and water scarcity has become essential (Bräuning et al. 2017; Polle et al. 2019; Waite et al. 2023; Araújo et al. 2024). Drought resistance mechanisms, although complex, have been the subject of studies to identify prevention and tolerance strategies, in addition to adaptation to conditions of high solar radiation and high temperatures, in tropical plant formations (Bräuning et al. 2017; Araújo et al. 2022; Waite et al. 2023; Simioni et al. 2023; Oliveira et al. 2023; Castelar et al. 2023). Such adaptations occur in response to environmental pressures, resulting in changes in the functional characteristics of plants, which manifest themselves at physiological, morphological and anatomical levels and are directly reflected in the structure of the community (Araújo et al. 2023).

The hydraulic system of woody plants functions as a continuum, in which water transport through the xylem is driven by the tension generated by transpiration in the stomata and by the cohesion between water molecules and the walls of the conducting vessels (Pittermann 2010; Schenk & Jansen 2015). Water absorption is directly influenced by the rate of leaf transpiration, controlled by stomatal regulation (Simioni et

al. 2023). Thus, structural adjustments occur in the secondary xylem that optimize water conduction, involving changes in the size, quantity, organization, and distribution of the conducting vessels (Gleason et al. 2016). Plants that occur in environments with water scarcity commonly show a reduction in average vessel element diameter, which reduces the risk of hydraulic failure by embolism (Rodriguez-Zacaro et al. 2021; Dória et al. 2022). Living cells of secondary xylem, such as axial and radial parenchyma, in direct contact with vessels, secrete solutes that create conduction gradients that promote secondary water supply (Holbrook & Zwieniecki 1999; Carlquist 2018; Olson et al. 2020). The set of xylem cells acts in synergy to avoid hydraulic failures and optimize performance in the water and solute conduction process.

The coordination between leaf mechanisms and secondary xylem acts to maintain water balance in plants in dry environments, highlighting adaptive strategies for variable environmental conditions (Simioni et al. 2023; Castelar et al. 2023). These adjustments involve reducing leaf area and increasing cuticle thickness and stomatal density, strategies that reduce transpiration and prevent water loss in environments with high luminosity and water scarcity (Zhou et al. 2013; Melo Jr. & Boeger 2016; Pireda et al. 2019; Oliveira et al. 2023). Such adaptations are evident in ecosystems such as restingas, which present strict environmental filters, such as high temperatures, high irradiance, water restriction, and sandy, nutrient-poor soils (Lourenço Jr et al. 2021; Oliveira et al. 2023). Species that colonize restinga areas have developed morphological, anatomical, physiological, and biochemical adaptations in response to the selective pressures imposed in these areas, allowing both their survival and coexistence in different phytophysiognomies, which present variation in community structure (Oliveira et al. 2023). Pireda et al. (2019) demonstrated that plants in restinga

environments make anatomical and physiological adjustments, especially in their leaves, as part of their survival strategies when compared to species from forest environments. Castelar et al. (2023) also observed intraspecific variation in secondary xylem characteristics in plants that occur in both restinga and forest areas. Thus, understanding these adjustments is relevant to unraveling the mechanisms that allow coexistence and functional diversity in different restinga formations. These findings have important implications for both the conservation and management of these ecosystems, which are sensitive to environmental changes.

This study analyzed three species — *Scutia arenicola* (Casar.) Reissek (Rhamnaceae), *Schinus terebinthifolius* Raddi (Anacardiaceae) and *Pera glabrata* (Schott) Baill (Peraceae) — co-occurring in the beach grass and shrub, the *Clusia* formation and the sandbanks forest formation in the restinga of northern Rio de Janeiro State. According to Oliveira et al. (2023), each of these formations presents distinct environmental conditions, such as variation in photosynthetically active radiation, temperature, vapor pressure deficit (VPD), humidity and level of organic matter in the soil. Therefore, we raise the following question: Do the species coexisting in the different restinga formations present intraspecific variation in characteristics linked to hydraulic architecture (i.e., physiology and anatomy of leaf and wood)?

4.3 Material and Methods

4.3.1 Study area

The research was carried out in a restinga ecosystem located in the Reserva Particular do Patrimônio Natural da Fazenda Caruara, belonging to the Complexo Lagunar de Grussaí/Iquipari (CLGI), municipality of São João da Barra, state of Rio de Janeiro, Brazil, South America. The climate is characterized as tropical sub-humid to semiarid, rainy (November to January) and dry (May to August), with average annual precipitation between 800 and 1000 mm (Cruz et al. 2021) and average annual temperature ranging from 19°C to 26°C (INEA, 2021), with a predominance of sandy soils (Cruz et al. 2021).

The Reserva Particular do Patrimônio Natural (RPPN) da Fazenda Caruara is a private natural heritage reserve and the largest private conservation area of restinga in Brazil, comprising 60% of the total RPPN area in the state of Rio de Janeiro. It has four vegetation formations of restinga: grassy beach formation, beach grass and shrub formation, *Clusia* formation and sandbanks forest formation. The present study was conducted in three of these formations, namely sandbanks forest formation, *Clusia* formation and beach grass and shrub formation (Assumpção & Nascimento 2000; Souza et al. 2010).

The sandbanks forest formation is located 980 m from the sea line and has 45 to 60% tree cover with a canopy of up to 6 m in height; thickets become denser and form a continuous forest with the presence of leaf litter (Assumpção & Nascimento 2000). This sandbanks forest formation presents low photosynthetically active radiation when compared to the other restinga formations (Oliveira et al. 2023) (Figure 1). Nonetheless,

it presents high values of temperature and vapor pressure deficit (VPD), while the soil presents low pH (5.7) and high levels of Mg, C, organic matter, N, electrical conductivity and moisture (Oliveira et al. 2023) (Figure 1).

The *Clusia* formation is located 580 m from the sea line and has an upper canopy of 1 to 3 m in height. The species *C. hilariana* enriches the soil with its leaves and allows other species to colonize around it (Villela et al. 2020). This formation has high levels of photosynthetically active radiation, temperature and VPD, similar to sandbanks forest (Oliveira et al. 2023). On the other hand, the soil has high levels of Zn, Mn, Na, C, organic matter, electrical conductivity and moisture (Oliveira et al. 2023) (Figure 1).

The beach grass and shrub formation is located 250 m from the sea line and has a canopy of no more than 1 m in height. Nucleation occurs, where cacti and bromeliads help in the emergence of other plant species (Assumpção & Nascimento 2000). According to Oliveira et al. (2023), this formation is characterized by high photosynthetically active radiation and low VPD. The soil of this formation has a more neutral pH (6.8), with low concentrations of Mg, Na, C, organic matter, Zn, Mn, N, electrical conductivity and moisture, when compared to other sandbanks forest formations and Clusia formation (Figure 1).

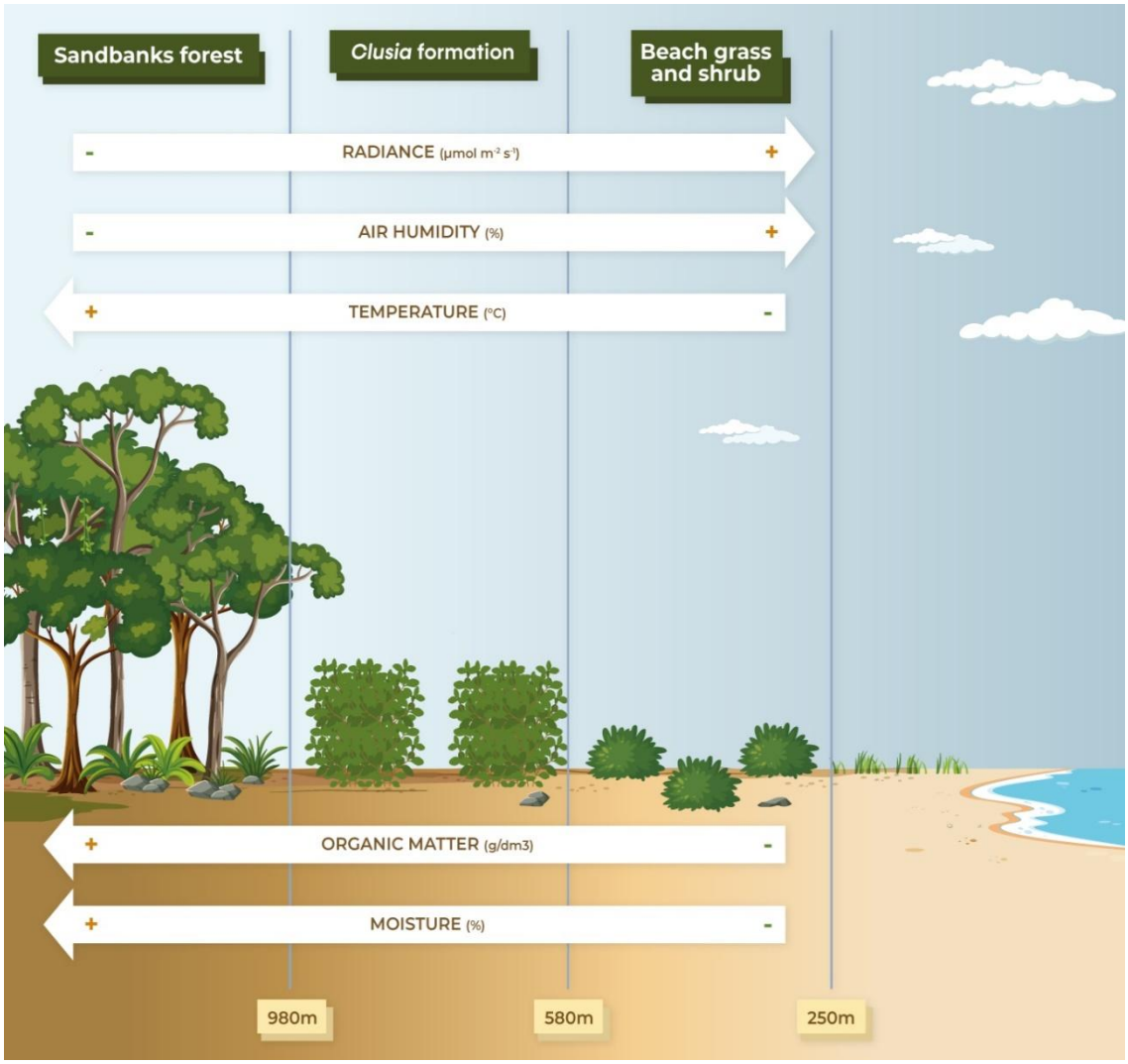

Figure 1. Graphical representation of the vegetation structure and microclimatic soil parameters of vegetation formations in the restinga of Northern Fluminense (Assumpção e Nascimento 2000; Oliveira et al. 2023).

4.3.2 Species selection and material collection

To understand the variation in leaf and wood traits, we selected the following three co-occurring dominant species (N = 5 individuals for each species) in the sandbanks forest formation, the *Clusia* formation and the beach grass and shrub formation (Table 1): *Scutia arenicola* (Casar.) Reissek (Rhamnaceae – shrub), *Schinus terebinthifolia* Raddi (Anacardiaceae - shrub/tree) and *Pera glabrata* (Schott) Baill. (Peraceae-tree).

4.3.3 Leaf traits

Leaf traits are listed in Table 2. Leaf morphological characteristics were determined by randomly selecting 25 leaves (fully expanded in full sun) of each species (five leaves per individual). Ten leaves per individual were then scanned and measured for leaf area using ImageJ software, according to Rasband (1997-2008) and Perez-Harguindeguy et al. (2013). Saturated mass was determined by hydrating leaves (10 leaves per individual) for 24 h and weighing on a digital scale (Shimadzu model AY220, Japan). The leaves were then dried in an oven at 60 °C for 72 h to obtain dry mass. Dry matter content (DMC) was calculated through the ratio between fresh weight and dry weight. Specific leaf area (SLA) was calculated through the ratio between leaf area and dry weight (Perez-Harguindeguy et al. 2013). Leaf thickness was determined using a digital pachymeter (Stainless Hardened, Switzerland).

Stomatal density and stomatal pore aperture were determined by selecting 25 leaves per species (N = 5 leaves per individual). The epidermis of the leaves was dissociated according to the Franklin method (1945), whereby samples were placed in a solution (1:1) of acetic acid and hydrogen peroxide. Semi-permanent slides were subsequently mounted and observed under a light microscope (Axioplan, ZEISS, Germany) coupled to a camera (Moticam Pro 282B, Hong Kong).

4.3.4 Gas exchange

Twenty-five leaves per species (N = 5 leaves per individual) in each restinga formation were selected for determining gas exchange. Transpiration rate (T) and stomatal conductance (Gs) were measured between 12:00 and 14:00 using a portable infrared carbon dioxide analyzer (LCpro-SD, ADC BioScientific Ltd., United

Kingdom). A chamber was subsequently used under controlled PAR conditions at 2000 μmol.m^{-2}.s^{-1}. Environmental conditions were maintained, without control of temperature and humidity. Carbon dioxide (CO_2) was captured from the environment at approximately 2 m above the leaf surface using an air collection probe.

4.3.5 Branch processing

The evaluated traits of secondary xylem are listed in Table 2. Samples from sapwood in the branches of five individuals of each species were sectioned (15–20 μm thick) in transversal and longitudinal tangential planes (Coradin & Muniz, 1992) using a sliding microtome. The sections were then washed briefly in 50% v/v aqueous sodium hypochlorite, then in distilled water and 5% v/v aqueous acetic acid and dehydrated in an ethanol series (50–100%), before double-staining in a 1:9 mixture of aqueous 1% w/v astra blue (Bukatsch, 1972) and aqueous 1% w/v safranin (Roeser, 1972). Sections were permanently mounted on glass slides in Entellan (Merck, Darmstadt, Germany) (Johansen, 1940). Quantitative analysis was performed using 12 slides per individual. The IAWA Committee standard (1989) was followed for all cell descriptions, counts and measurements. Images were processed using the Image-Pro Plus digital image processing system (Media Cybernetics, USA). Percentages of secondary xylem cell types were quantified using ten images for each individual (with a 10x objective), totaling 50 photos per species. Each image was then submitted to the Grid Mask of points in Image-Pro Plus software (Media Cybernetics, USA), being covered by 100 random points. Six classes of cell types were created, namely: axial parenchyma, radial parenchyma, vessels, axial parenchyma contacting vessels, fibers and gelatinous fibers.

The number of times that the cell types appeared under a point was quantified and used to calculate tissue percentages per image.

4.3.6 Wood density

Wood density was determined by measuring the fresh volume of wood samples by displacement in a column of water (Williamson & Wiemann 2010). Samples were initially immersed in a beaker containing water on top of a digital scale (Shimadzu model AY220, Japan). Sample volume was considered as the weight of the displaced water (e.g., 1g = 1 cm^3). The samples were then dried in an oven at 60 °C for 72 hours to obtain dry mass. Wood density was calculated as:

$$\mathbf{WD = Dm/Dv}$$

where, WD = wood density ($g.cm^3$), Dm = dry mass and Dv = displaced volume.

Table 1: Leaf and secondary xylem traits evaluated for co-occurring species in restinga formations in the Atlantic Forest. [1]Pireda et al. 2019; [2]Tecco et al. 2013; [3]Qi et al. 2014; [4]Niinemets 2001; [5]Henry et al. 2019; [6]Flexas et al. 2006; [7,8]Zhoul et al. 2013; [9, 19]Rodrigues-Zacaro et al. 2021; [10]Calquisti 2012;[12]Echeverría et al. 2022; [13]Jacobsen et al. 2005; [14]Gleason et al. 2016; [15,16,20]Janssen et al. 2020; [18] Ziemińska et al. 2013, 2015; [17,21]Słupianek et al. 2021; [22]Dória et al. 2022; [11,23]Olson 2020.

Traits	Acronym	Unit	Functional significance
Leaf area	LA	cm^2	Light capture [1].
Specific leaf area	SLA	$cm^2\ g^{-1}$	Leaf-level resource acquisition, growth rate [2].
Dry matter content	DMC	$mg\ g^{-1}$	Resource capture and/or stress tolerance [3].
Leaf thickness	LT	Mm	Resistance to physical damage and water storage [4].
Stomatal density	SD	est/mm^2	Carbon acquisition and water use efficiency [5].
Stomatal pore aperture	SPO	Mm	Carbon capture and water use efficiency [6].
Stomatal conductance	Gs	$mmol\ m^{-2}\ s^{-1}$	Percentage of leaf water loss and/or water use efficiency [7].
Transpiration rate	T	$Mol\ m^{-2}\ s^{-1}$	Water loss and maintenance of leaf temperature [8].
Vessel frequency	VF	mm^2	Hydraulic safety [9].
Vessel grouping index	VGI	mm^2	Mechanical support and safety against embolism [3, 10].
Tangential vessel diameter	VD	Mm	Efficiency and safety of water transport [11].
Vessel wall thickness	VWT	Mm	Safety of water transport [12].
Fiber diameter	FD	Mm	Flexibility and resistance [13].
Fiber lumen	FL	Mm	Water reserve, sapwood capacitance and hydraulic safety [14].
Fiber wall thickness	FWT	Mm	Mechanical support of vessels, flexibility and mechanical strength [15].
Percentage of axial parenchyma	PAP	%	Lateral transport and storage of water [16].
Percentage of radial parenchyma	PRP	%	Lateral transport, linking xylem and phloem, stores secondary metabolites, water and nutrients [17].
Percentage of fibers	PFIBER	%	Mechanical support, hydraulic safety and water storage [18].
Percentage of vessels	PVESSEL	%	Hydraulic safety[19].
Percentage of axial parenchyma contacting vessels	PAPV	%	Embolism reduction[20].
Percentage of total parenchyma	PTOTALP	%	Lateral transport and storage of substances [21].
Percentage of gelatinous fibers	PGF	%	Water storage and mechanical strength under tension [22].
Wood density	WD	$g.cm^3$	Distribution and quantity of tissues [23].

4.3.7 Statistical Analysis

Prior to analysis, data were tested for normality and homoscedasticity using the Shapiro-Wilk and Levene's tests, respectively (Levene 1960; Shapiro-Wilk 1965). Leaf and wood structural traits were compared between species and formation using split-plot ANOVAs, whereby species and the interaction between species and formation were nested within formation. The *lmer* function from the *nlme* package (Pinheiro et al. 2017) and the *lsmeans* (Lenth & Lenth 2018) and *multcomp* (Hothorn et al. 2008) packages were used for post-hoc analyses. Separate principal component analyses (PCAs) were performed for each trait group (i.e., leaves and wood) to explore variability in the data, identify patterns among functional traits and assess whether they were associated with formations and species. The coefficient of variation was calculated for each structural characteristic of leaves and wood to observe which characteristics are more variable and how they vary in terms of species and formations (Garnier et al. 2001). All analyses were performed in the R program, software version 4.2.1 (R Core Team 2022) with a significance level of 5%.

4.4 Results

4.4.1 Distribution of structural traits of leaves and wood

The principal component analysis (PCA) of leaf structural traits explained 67.5% of the total variation, with the first axis accounting for 39.6% and reflecting interspecific differences, while the second axis explained 27.9% and was primarily associated with environmental variation among restinga formations. Although the PCA was used as an exploratory tool to assess patterns of trait variation, it did not show a clear separation of individuals from the same species according to restinga formation.

Individuals tended to cluster by species rather than by environment, indicating that interspecific variation was stronger than intraspecific differences in this multivariate space. Individuals of *P. glabrata* presented the highest values of stomatal pore aperture (SPO), leaf area (LA), and specific leaf area (SLA), while individuals of *S. arenicola* showed the highest values of stomatal density (SD) and leaf thickness (LT). Meanwhile, individuals of *S. terebinthifolia* in the beach grass and shrub formation presented higher values for dry matter content (DMC), transpiration rate (T), and stomatal conductance (Gs). Stomatal conductance and transpiration rate were more strongly correlated with the first axis (Figure 2; Table S1), while stomatal density was more strongly correlated with the second axis. Although these patterns are consistent with species identity, intraspecific variation across restinga formations was statistically confirmed and is detailed in Table 2, supporting the role of environmental conditions in shaping trait expression within species.

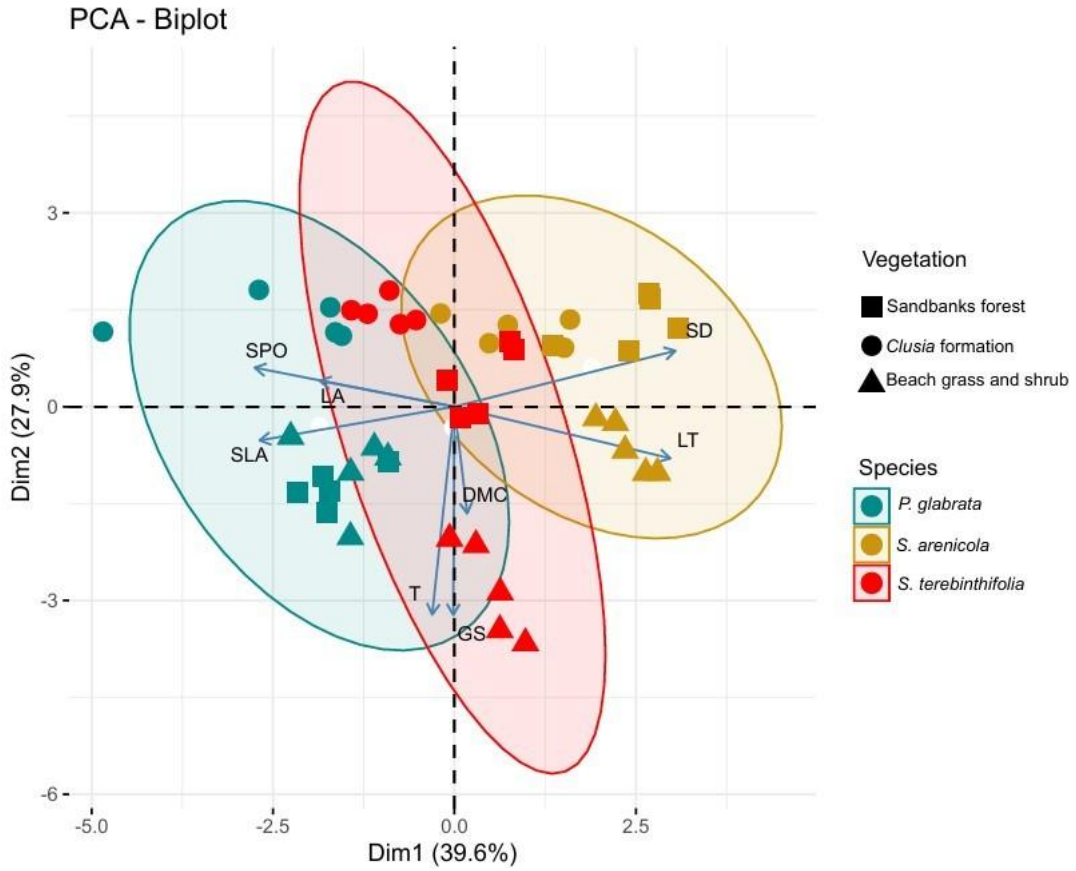

Figure 2. Principal component analysis of leaf characteristics of three co-occurring plant species in restinga formations in the Atlantic Forest. Specific leaf area (SLA); leaf area (LA); stomatal pore aperture (SPO); stomatal density (SD); leaf thickness (LT); dry matter content (DMC); stomatal conductance (Gs); and transpiration rate (T).

The principal component analysis of wood structural traits explained 60.2% of the total variation (Figure 3; Table S2). The first axis explained 37.8% of the variation and was related to differences between species, while the second axis explained 22.4% of the variation and separated the restinga formations (Figure 3; Table S2). Individuals of *Pera glabrata* had the highest values of vessel wall thickness (VWT), fiber wall thickness (FWT), vessel diameter (VD), percentage of total parenchyma (PTOTALP), fiber diameter (FD), fiber lumen (FL) and percentage of axial parenchyma (PAP) (Figure 3; Table S2). On the other hand, individuals of *Scutia arenicola* showed the

highest values of percentage of radial parenchyma (PRP) and wood density (WD). Meanwhile, individuals of *Schinus terebinthifolia* presented the highest values of fiber percentage (PFIBER), vessel grouping index (VGI), percentage of axial parenchyma contacting vessels (PVESSEL), vessel frequency (VF), and vessel percentage (PVESSEL) (Figure 3; Table S2).

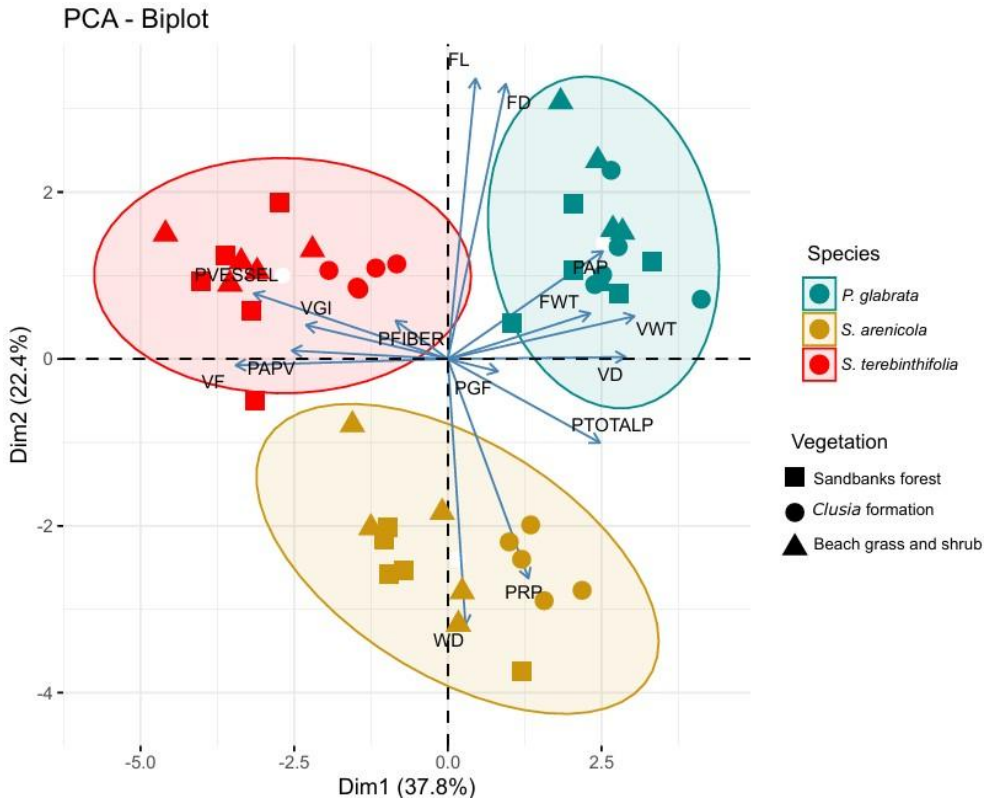

Figure 3. Principal component analysis of wood characteristics of three plant species co-occurring in restinga formations in the Atlantic Forest. Vessel diameter (VD); vessel wall thickness (VWT); fiber wall thickness (FWT); percentage of axial parenchyma (PAP); fiber diameter (FD); fiber lumen (FL); vessel grouping index (VGI); vessel frequency (VF); wood density (WD); percentage of gelatinous fiber (PGF); percentage of fiber (PFIBER); percentage of vessel (PVESSEL); percentage of axial parenchyma contacting vessels (PAPV); percentage of radial parenchyma (PRP) and percentage of total parenchyma (PTOTALP).

4.4.2 Intraspecific variation in structural traits of leaves and wood

The effect of species was significant for most functional traits, the exceptions being dry mass content (DMC) and percentage of gelatinous fiber (PGF) (Table 2; Table S3). The effect of restinga formation was significant for most functional traits, the exceptions being specific leaf area (SLA), fiber diameter (FD), fiber lumen (FL), percentage of vessel (PVESSEL) and wood density (WD). The interaction between the two effects was significant for most functional traits, the exceptions being specific leaf area (SLA), dry mass content (DMC) and wood density (WD). These effects (i.e., of species and restinga formation) will be examined successively, combining the results presented in Table S3 with the data obtained for all of the individual species (Table 2; Table S3).

Intraspecific patterns among restinga formations showed that individuals growing in the *Clusia* and beach with thicket formations generally have more conservative strategies than those growing in the sandbanks forest, regardless of species. For example, leaf thickness, a trait linked to resistance to physical damage and water storage, and stomatal density, a trait associated with carbon acquisition and water use efficiency, were higher for individuals of all three species growing in beach with thicket and *Clusia* formations (Table 2; Table S3; Figure 4).

Differences among restinga formations were less consistent among species for the other traits. For example, leaf area, a trait associated with light capture, was higher for individuals of *Scutia arenicola* and *Schinus terebinthifolia* in sandbanks forest, while individuals of *Pera glabrata* had higher leaf area values in the beach grass and shrub formation (Table 2; Table S3). On the other hand, specific leaf area, a trait

associated with resource acquisition, varied widely among individuals, being higher for individuals of *S. arenicola* in the sandbanks forest. In contrast, specific leaf area and dry matter content did not differ among individuals of *P. glabrata* nor among individuals of *S. terebinthifolia* of the different restinga formations (Table 2; Table S3).

Meanwhile, stomatal pore aperture, which represents carbon uptake and water use efficiency, was higher for individuals of all three species occurring in the sandbanks forest (Table 2; Table S3). On the other hand, stomatal conductance, a characteristic linked to the percentage of water loss by the leaf and/or water use efficiency, and transpiration rate, which demonstrates water loss and maintenance of leaf temperature, was higher for individuals growing in the Clusia and beach grass and shrub formations (Table 2; Table S3).

Vessel frequency, a characteristic associated with hydraulic safety, varied widely among individuals, being higher for *Scutia arenicola* and *Schinus terebinthifolia* in the Clusia and beach grass and shrub formations. In contrast, vessel frequency did not differ significantly among individuals of *Pera glabrata* in the *Clusia* and sandbanks forest formations (Table 2; Table S3; Figure 5). The vessel grouping index also varied widely among individuals, being higher for individuals of *S. arenicola* in the Clusia formation and higher for individuals of *S. terebinthifolia* in the beach grass and shrub formation, while not differing significantly among *P. glabrata* individuals in the evaluated formations (Table 2; Table S3; Figure 5). On the other hand, individuals of the three species presented higher vessel diameter values in the sandbanks forest (Table 2; Table S3; Figure 5). Vessel wall thickness varied widely among individuals, being greater for *P. glabrata* and *S. arenicola* in the sandbanks forest. In contrast, *S. terebinthifolia*

individuals presented greater vessel wall thickness values in the beach grass and shrub formation (Table 2; Table S3).

Fiber diameter varied widely among individuals, being greater for *P. glabrata* individuals in the beach grass and shrub formation, while it did not differ significantly among individuals of *S. arenicola* nor among individuals of *S. terebinthifolia* in the evaluated formations (Table 2; Table S3). Fiber lumen did not differ between *P. glabrata* and *S. terebinthifolia* individuals in the restinga formation. On the other hand, *S. arenicola* individuals presented a higher fiber lumen value in the Clusia formation (Table 2; Table S3). Fiber wall thickness varied widely among individuals, being greater for individuals of *P. glabrata* and individuals of *S. arenicola* in the sandbanks forest formation. In contrast, *S. terebinthifolia* individuals presented greater fiber wall thickness in the sandbanks forest and beach grass and shrub formations (Table 2; Table S3).

The percentage of axial parenchyma varied widely among individuals, being higher for individuals of *P. glabrata* and individuals of *S. arenicola* in the Clusia and beach grass and shrub formations. On the other hand, individuals of *S. terebinthifolia* presented higher percentages of axial parenchyma in the sandbanks forest and beach grass and shrub formations (Table 2; Table S3; Figure 5).

The percentage of radial parenchyma varied widely among species, being higher for individuals of *S. arenicola* and individuals of *S. terebinthifolia* in the Clusia formation, while it did not differ significantly among individuals of *P. glabrata* in the evaluated formations (Table 2; Table S3; Figure 5). The percentage of fiber was higher for *S. terebinthifolia* individuals in the Clusia and beach grass and shrub formations,

while it did not differ among individuals of *P. glabrata* nor individuals of *S. arenicola* in the evaluated formations (Table 2; Table S3). The percentage of vessels was higher for individuals of *P. glabrata* in the sandbanks forest formation, and higher for individuals of *S. arenicola* in the Clusia formation. In turn, the percentage of vessels was higher for *S. terebinthifolia* in the beach grass and shrub formation (Table 2; Table S3; Figure 5).

The percentage of axial parenchyma contacting vessels varied widely among species, being higher for individuals of the three species growing in the *Clusia* and beach grass and shrub formations (Table 2; Table 3; Figure 5). The percentage of gelatinous fibers was higher for individuals of *S. terebinthifolia* in the sandbanks forest formation, and did not differ significantly between individuals of *P. glabrata* nor among individuals of *S. arenicola* in the restinga formations (Table 2; Table S3). Wood density was higher among individuals of *P. glabrata* in the sandbanks forest formation, and did not differ significantly between individuals of *S. arenicola* and *S. terebinthifolia* in the formations evaluated (Table 2; Table S3).

Table 2: Average values (min – max) of leaf, physiological and wood traits for the species *Pera glabrata, Scutia arenicola* and *Schinus terebinthifolia* co–occurring in restinga formations int he Atlantic Forest. Significant differences were assessed using split-plot ANOVA and post-hoc tests (5% significance level).

		Pera glabrata			*Scutia arenicola*			*Schinus terebinthifolia*		
		Sandbanks forest	***Clusia***	**Beach grass and shrurb**	**Sandbanks forest**	***Clusia***	**Beach grass and shrurb**	**Sandbanks forest**	***Clusia***	**Beach grass and shrurb**
Leaf anatomy and physiology	Leaf area	10.17(5.31–15.34) a	9.61(4.96–20.12) a	13.22(8.40–21.00) b	8.56(5.02–15.82) a	6.58(4.39–11.52) b	7.31(4.57–11.67) b	7.38(4.02–12.68) a	3.53(2.45–8.63) b	3.79(1.99–6.05) b
	Specific leaf area	92.71(39.4–216.82) a	83.00(38.53–172.68) a	86.95(29.63–143.16) a	57.04(21.88–91.83) a	47.94(23.23–106.38) b	49.39(23.51–111.41) b	86.79(8.93–176.15) a	94.30(37.76–267.89) a	85.23(51.38–158.92) a
	Dry matter content	2.49(1.16–3.98) a	2.77(1.24–5.68) a	2.87(0.11–6.30) a	2.73(1.57–4.96) ab	2.48(1.27–4.41) a	3.00(1.48–5.95) b	2.83(0.27–6.81) a	2.74(1.14–5.28) a	3.66(0.54–38.91) a
	Leaf thickness	0.21(0.15–0.30) a	0.29(0.26–0.33) b	0.32(0.23–0.40) c	0.39(0.30–0.48) a	0.44(0.35–0.49) b	0.45(0.05–0.77) b	0.25(0.11–0.36) a	0.30(0.26–0.35) b	0.38(0.29–0.54) c
	Stomatal density	13.04(10.00–17.00) a	11.84(7.00–17.00) b	12.72(10.00–17.00) ab	31.38(18.00–46.00) a	41.86(32.00–53.00) b	37.08(32.00–43.00) c	25.54(18.00–36.00) ac	31.14(26.00–38.00) b	25.98(21.00–31.00) c
	Stomatal pore aperture	2.26(1.03–5.20) a	1.94(0.79–4.79) a	1.41(0.74–2.31) b	1.59(0.62–3.28) a	1.04(0.43–2.52) b	0.74(0.43–1.47) c	1.85(0.76–3.93) a	1.09(0.51–2.23) b	1.37(0.65–2.70) c
	Gs (μmol m^{-2} s^{-1})	20 (10 – 30) a	50 (30 – 50) b	40 (30 – 60) b	20 (10 – 20) a	20 (10 – 40) a	40 (30 – 50) b	10 (10 – 20) a	30 (20 – 50) b	60 (40 – 90) c
	E (mol m^{-2} s^{-1})	0.52 (0.28 – 0.78) a	1.53 (1.12 – 1.75) b	1.30 (0.88 – 1.76) c	0.58 (0.35 – 0.85) a	0.44 (0.35 – 0.62) b	1.15 (0.75 – 1.86) c	0.54 (0.32 – 0.65) a	0.71 (0.45–0.96) b	1.70 (1.12 – 2.13) c
Wood anatomy	Vessel frequency	31.00(17.00–55.00) a	33.60(13.00–74.00) a	24.00(10.00–43.00) b	94.00(53.00–147.00) a	137.00(85.00–202.00) b	120.00(73.00–198.00) c	185.74(99.00–262.00) a	230.43(165.00–346.00) b	254.40(198.00–334.00) c
	Vessel grouping index VGI)	2.00(1.00–4.00) a	1.90(0.93–4.08) a	1.90(1.00–3.22) a	1.96(1.15–2.76) a	2.35(1.60–3.36) b	2.10(1.54–2.70) c	2.37(1.29–4.84) a	2.45(1.67–3.71) a	3.02(1.82–5.39) b
	Tangential vessel diameter	61.00(19.00–118.00) a	46.39(12.17–99.00) b	40.00(13.69–96.35) b	49.33(14.86–79.55) a	30.12(6.15–64.62) b	35.68(8.54–72.35) c	39.16(4.81–73.84) a	20.36(4.51–47.76) b	23.19(6.38–49.45) b
	Vessel wall thickness	5.00(3.00–8.00) a	4.49(2.73–7.50) b	4.11(2.08–6.28) c	3.57(1.54–6.22) ac	2.89(1.19–5.29) b	3.39(1.46–6.67) c	2.26(1.08–4.07) a	2.16(1.04–3.77) a	2.81(0.85–14.19) b
	Fiber diameter	13.00(3.00–28.00) ab	11.98(3.08–31.63) a	13.90(3.94–29.23) b	7.42(1.95–16.86) a	7.45(2.56–13.85) a	6.77(2.32–13.84) a	11.40(2.84–25.08) a	10.81(2.91–25.65) a	10.41(2.14–23.06) a
	Fiber lumen	7.00(1.00–19.00) a	7.35(0.72–22.69) a	8.71(1.08–19.24) a	1.77(0.24–5.13) ac	2.24(0.51–7.39) b	1.62(0.34–5.51) c	7.13(0.54–19.95) a	6.64(0.68–20.39) a	6.06(0.68–17.51) a
	Fiber wall thickness	3.00(1.00–6.00) a	2.24(0.62–9.13) b	2.42(1.23–5.37) b	2.52(0.37–12.89) a	1.44(0.60–2.25) b	2.15(0.02–4.87) c	1.79(0.17–3.76) ab	1.72(0.85–3.15) a	1.94(0.62–3.52) b
	P. of axial parenchyma	11.44(3.00–23.00) a	(15.70(3.00–30.00) b	14.80(6.00–32.00) b	3.58(0.00–14.00) ac	7.60(1.00–18.00) b	3.54(0.00–10.00) c	3.62(0.00–20.00) ac	0.40(0.00–22.00) b	4.74(0.00–33.00) c
	P. of radial parenchyma	17.06(10.00–26.00) a	17.50(2.00–27.00) a	17.20(7.00–30.00) a	23.48(13.00–34.00) ac	28.62(3.00–60.00) b	20.52(12.00–34.00) c	10.78(2.00–20.00) ab	12.94(5.00–22.00) b	12.52(5.00–21.00) b
	P. of fibers	37.18(0.00–57.00) a	30.01(0.00–61.00) a	34.88(0.00–61.00) a	0.00(0.00–0.00) a	37.48(8.00–75.00) a	50.48(34.00–63) a	10.16(0.0–44.00) a	44.94(10.00–60.00) b	43.94(28.00–64.00) b
	P. of vessels	18.94(8.00–28.00) a	17.01(8.00–23.00) b	15.86(7.00–26.00) b	18.62(10.00–33.00) ac	21.96(11.00–39.00) b	19.06(10.00–33.00) c	26.12(19.00–39.00) a	27.76(14.00–39.00) a	30.48(21.00–45.00) b
	P. of axial parenchyma in contact with vessel	1.52(0.00–5.00) ac	5.03(0.00–14.00) b	2.28(0.00–6.00) c	2.26(0.00–9.00) a	4.36(0.00–12.00) b	6.36(1.00–17.00) c	2.88(0.00–6.00) a	7.74(1.00–16.00) b	8.7(1.00–17.00) b
	P. of gelatinous fibers	14.01(0.00–63.00) a	15.00(0.00–54.00) a	15.18(0.00–68.00) a	52.01(35.00–70.00) a	00.00(00.00–00.00) a	4.14(0.00–30.00) a	46.84(15.00–74.00) a	6.18(0.00–43.00) b	0.48(0.00–9.00) c
	P. of total parenchyma	28.48(13.00–38.00) a	33.21(21.00–44.00) b	32.00(20.00–48.00) b	27.06(17.00–36.00) ac	36.22(4.00–75.00) b	19.92(0.00–33.00) c	14.40(4.00–31.00) a	13.34(5.00–24.00) a	17.26(5.00–44.00) b
	Wood density	0.56(0.50–0.60) a	0.55(0.48–0.62) ab	0.49(0.46–0.54) b	0.76(0.72–0.78) a	0.76(0.70–0.81) a	0.75(0.48–0.89) a	0.57(0.53–0.64) a	0.56(0.49–0.79) a	0.50(0.45–0.58) a

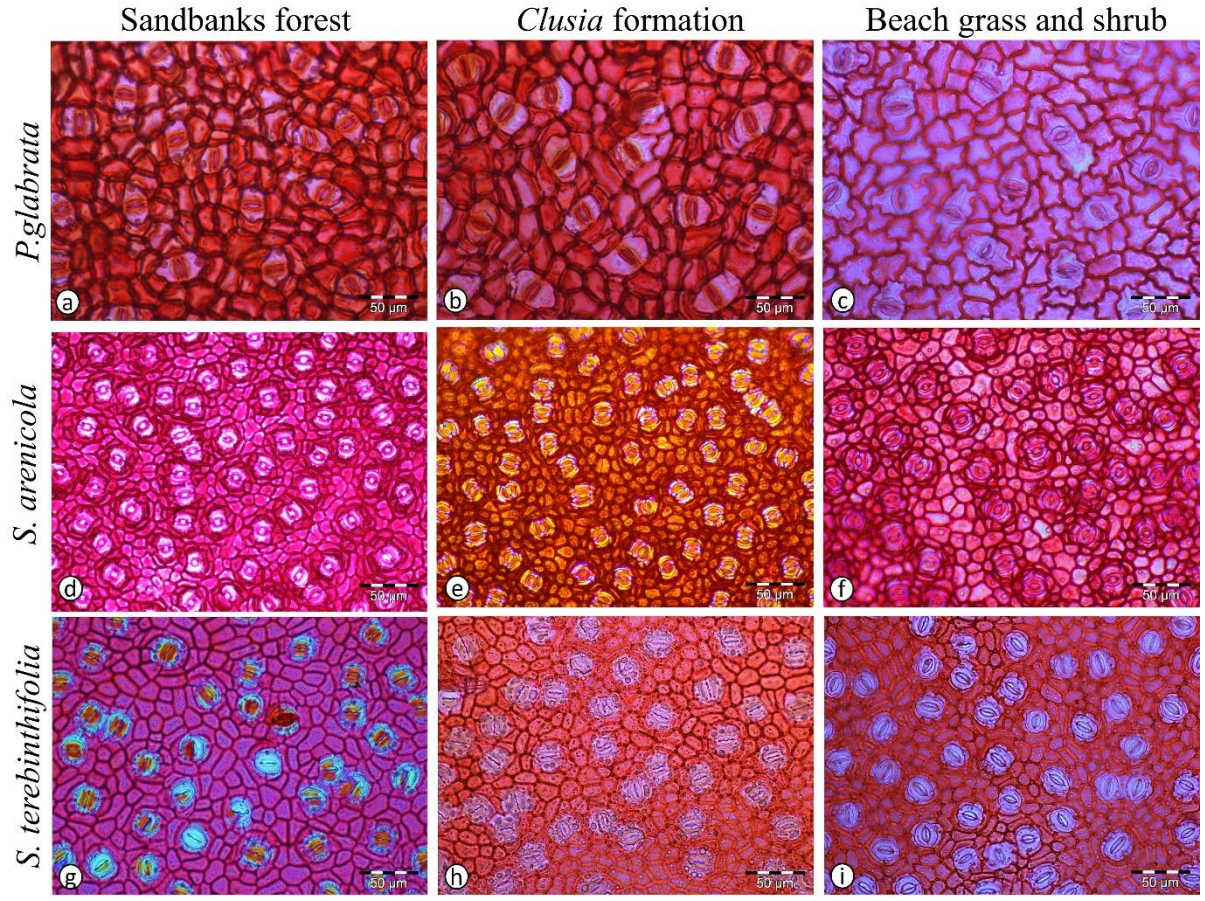

Figure 4. Epidermal dissociation of the species *Pera glabrata*, *Scutia arenicola* and *Schinus terebinthifolia* in the sandbanks forest, *Clusia* and beach grass and shrub formations. (a) Epidermal dissociation of *P. glabrata* in the sandbanks forest formation; **(b)** epidermal dissociation of *P. glabrata* in the *Clusia* formation; **(c)** epidermal dissociation of *P. glabrata* in the beach grass and shrub formation; **(d)** epidermal dissociation of *S. arenicola* in the sandbanks forest formation; **(e)** epidermal dissociation of *S. arenicola* in the *Clusia* formation; **(f)** epidermal dissociation of *S. arenicola* in the beach grass and shrub formation; **(g)** epidermal dissociation of *S. terebinthifolia* in the sandbanks forest formation; **(h)** epidermal dissociation of *S. terebinthifolia in* the *Clusia* formation; and **(i)** epidermal dissociation of *S. terebinthifolia* in the beach grass and shrub formation. Bars: 50 µm.

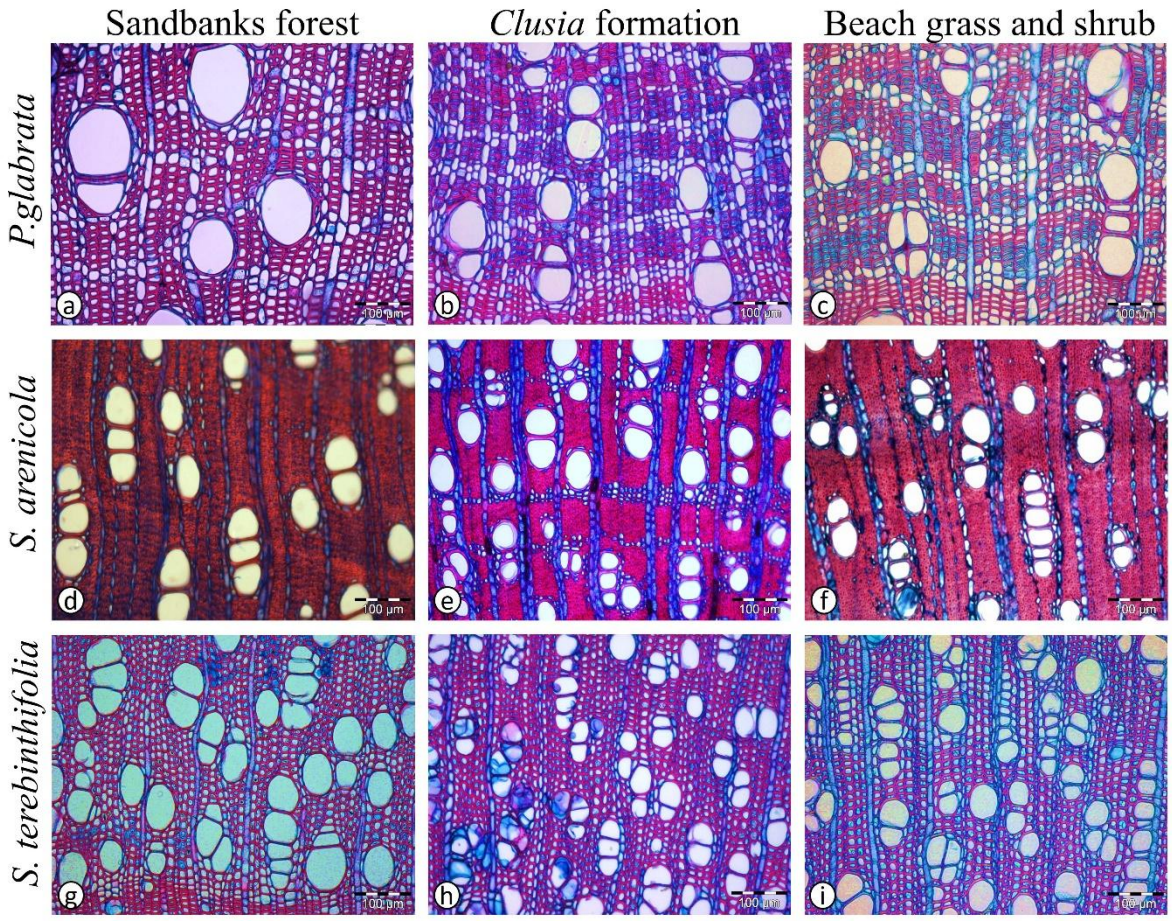

Figure 5. Transverse sections of secondary xylem of the species *Pera glabrata*, *Scutia arenicola* and *Schinus terebinthifolia* in the sandbanks forest, *Clusia* and beach grass and shrub formations. **(a)** Transverse section of *P. glabrata* in the sandbanks forest formation; **(b)** transverse section of *P. glabrata* in the *Clusia* formation; **(c)** transverse section of *P. glabrata* in the beach grass and shrub formation; **(d)** transverse section of *S. arenicola* in the sandbanks forest formation; **(e)** transverse section of *S. arenicola* in the *Clusia* formation; **(f)** transverse section of *S. arenicola* in the beach grass and shrub formation; **(g)** transverse section of *S. terebinthifolia* in the sandbanks forest formation; **(h)** transverse section of *S. terebinthifolia* in the *Clusia* formation; and **(i)** transverse section of *S. terebinthifolia* in the beach grass and shrub formation. Bars: 100 µm.

4.4.3 Coefficient of variation for morphological, anatomical and physiological traits *of leaf and wood*

In general, the coefficient of variation for the structural traits of leaves and wood differed among the three studied species (Figure 6), with higher values for *Schinus terebinthifolia* in the sandbanks forest and *Clusia* formations and higher values for *Pera glabrata* in the beach grass and shrub formation. *Scutia arenicola*, on the other hand, maintained an intermediate pattern in relation to the other species regardless of the evaluated restinga formation (Figure 6). The coefficient of variation was higher for the species in the sandbanks forest formation and decreased with the opening of the canopy (Figure 6). For all species, the most variable functional attribute in the sandbanks forest was transpiration rate, a characteristic linked to water loss and maintenance of leaf temperature, while percentage of gelatinous fibers, an attribute linked to water storage and mechanical resistance under tension, was the most variable in the *Clusia* formation (Figure 6). On the other hand, leaf area and transpiration rate were the most variable traits in the beach grass and shrub formation (Figure 6).

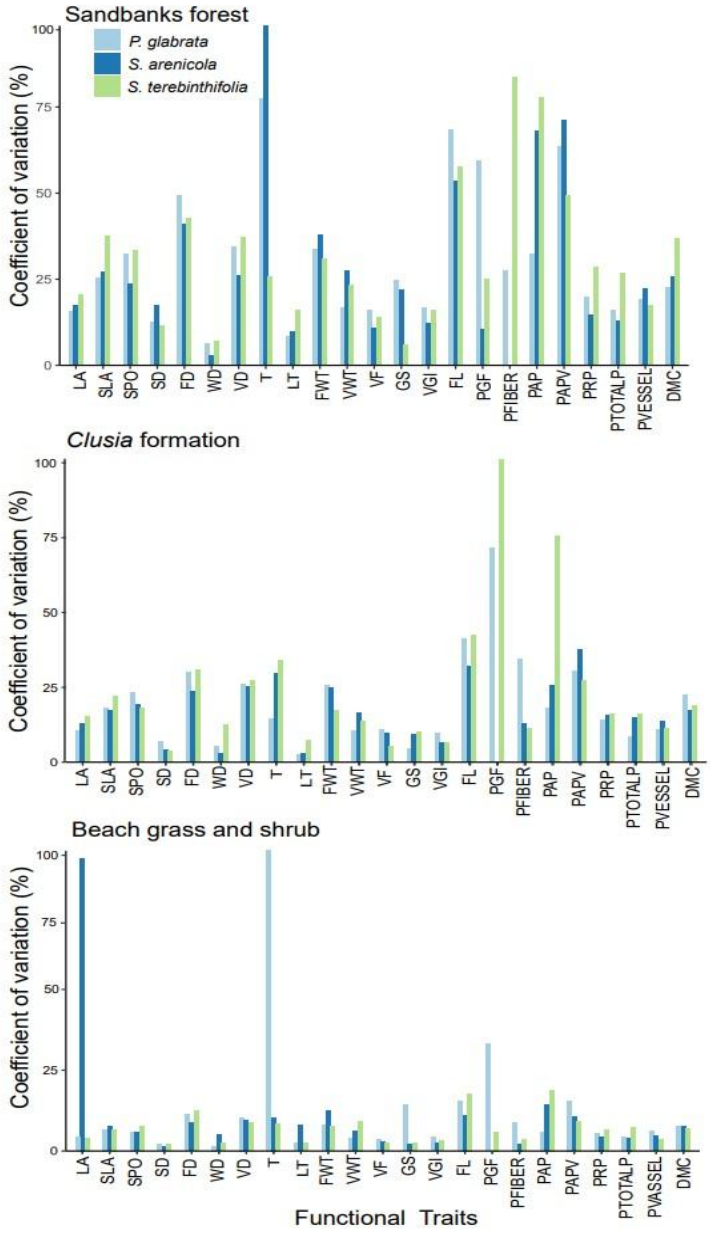

Figure 6. Coefficient of variation for morphological, anatomical and physiological traits of leaves and wood of trees in three restinga formations. Leaf area (LA); specific leaf area (SLA); stomatal pore aperture (SPO); stomatal density (SD); fiber diameter (FD); wood density (WD); vessel diameter (VD); transpiration rate (T); leaf thickness (LT); fiber wall thickness (FWT); vessel wall thickness (VWT); vessel frequency (VF); gas exchange (Gs); vessel grouping index (VGI); fiber lumen (FL); percentage of gelatinous fiber (PGF); percentage of fiber (PFIBER); percentage of axial parenchyma (PAP); percentage of axial parenchyma contacting vessels (PAPV); percentage of radial parenchyma (PRP); percentage of total parenchyma (PTOTALP); percentage of vessel (PVESSEL); and dry matter content (DMC).

4.5 Discussion

In general, the coefficient of variation for the structural traits of leaves and wood differed among the three studied species (Figure 6), with higher values for *Schinus terebinthifolia* in the sandbanks forest and *Clusia* formations and higher values for *Pera glabrata* in the beach grass and shrub formation. *Scutia arenicola*, on the other hand, maintained an intermediate pattern in relation to the other species regardless of the evaluated restinga formation (Figure 6). The coefficient of variation was higher for the species in the sandbanks forest formation and decreased with the opening of the canopy (Figure 6). For all species, the most variable functional attribute in the sandbanks forest was transpiration rate, a characteristic linked to water loss and maintenance of leaf temperature, while percentage of gelatinous fibers, an attribute linked to water storage and mechanical resistance under tension, was the most variable in the *Clusia* formation (Figure 6). On the other hand, leaf area and transpiration rate were the most variable traits in the beach grass and shrub formation (Figure 6).

The evaluated species showed wide variation in functional traits. While the leaves invested in traits related to water-use efficiency, the wood exhibited a complementary strategy, prioritizing hydraulic safety while still presenting structural adjustments that ensure a balance between safety and transport efficiency. These patterns were more evident in the *Clusia* and beach grass and shrub formations, where the canopy is open and soil moisture and irradiance are more intense. In contrast, in the sandbanks forest, where the canopy is more closed and soil moisture is higher, traits associated with photosynthetic efficiency, carbon acquisition, and efficient water transport were predominant.

The species *Pera glabrata* indicates possible acclimation for more efficient water use based on some traits such as specific leaf area, stomatal pore aperture, vessel diameter, percentage of axial parenchyma and percentage of axial parenchyma contacting vessels. According to Araújo et al. (2023), higher stomatal density may be associated with a higher rate of carbon assimilation and, consequently, higher growth rates for this species, which may explain the higher stomatal density of *P. glabrata* in the sandbanks forest formation, where the canopy is more closed. On the other hand, leaf thickness, according to Niinemets (2001), may be related to resistance against physical damage and leaf water reserve capacity, explaining the greater leaf thickness in the *Clusia* and beach grass and shrub formations. The secondary xylem of *P. glabrata* suggests optimization of water transport and storage efficiency based on variation in vessel diameter, percentage of axial parenchyma, and percentage of axial parenchyma contacting vessels. The cell types of secondary xylem with larger cells may be associated with this efficiency, despite the apparent vulnerability due to larger diameter vessels (Marcati et al. 2001; Dória et al. 2022). The species, even with larger caliber vessels in the xylem, can compensate for this characteristic with precise control over stomatal opening and the presence of storage tissue, such as parenchyma, possibly contributing to hydraulic failure avoidance (Janssen et al. 2020; Dória et al. 2022). The pattern of vessel diameter is notable, with the largest measurement in the sandbanks forest, followed by *Clusia* and beach grass and shrub, with significantly smaller diameters. This variation highlights the direct influence of microclimatic conditions on plant formations, indicating the adaptation of this species to coexist in different vegetation environments.

The *Scutia arenicola* suggests adaptive investment in hydraulic safety and water use efficiency in the studied formations based on variation in stomatal density, stomatal pore aperture, dry matter content, vessel frequency, vessel grouping index, vessel diameter, percentage of axial parenchyma contacting vessels, and percentage of radial parenchyma. According to some studies, stomata with smaller openings and greater numbers may allow more efficient control of gas exchange, minimizing water loss to the environment, as in the *Clusia* and beach grass and shrub formations (Vialet-Chabrand et al. 2017; Pireda et al. 2019; Araújo et al. 2021). This may explain the higher stomatal density and lower stomatal pore aperture in the *Clusia* and beach grass and shrub formations, influenced by the intensity of photosynthetically active radiation, temperature, and vapor pressure deficit. Among the secondary xylem traits, vessel frequency and vessel lumen varied the most in *Clusia* and beach grass and shrub formations. These traits are related to hydraulic safety and, when associated, in situations where there is water restriction (Hacke et al. 2017; Olson 2020; Rodrigues-Zacaro et al. 2021). This observation is consistent with the analysis of Wheeler et al. (2007), who studied 28 *Eucalyptus* species growing along a broad and well-defined aridity gradient across Australia. This study found a clear reduction in vessel diameter with increasing aridity, while vessel frequency increased in more arid conditions. The results indicate that water deficit, and not tree height or stem diameter, was the determining factor for mean vessel diameter and vessel frequency in *Eucalyptus* (Hacke et al. 2017). The greater number of vessels grouped together, according to Montaño-Arias et al. (2013), is also attributed to water transport safety, which may corroborate our hypothesis of investment in hydraulic safety for species in the *Clusia* and beach grass and shrub formations. In studies on the species *Tabebuia aurea* in the Caatinga and Cerrado biomes, Dória et al. (2019) highlighted the direct relationship

between parenchyma tissues and the hydraulic system, which is essential for maintaining water conductivity. Furthermore, in an extensive meta-analysis covering more than 760,000 individual trees and 475 species in several biomes, Anderegg et al. (2016) showed that tropical angiosperms under water pressure tend to have a greater amount of parenchyma in the wood. Therefore, the investment in parenchymatic tissue observed in the *Clusia* and beach grass and shrub formations may be helping the species to overcome soil water deficit and intense radiation by keeping the water column intact in the xylem vessels.

The species *Schinus terebinthifolia* showed reduced leaf area and stomatal pore aperture in the *Clusia* and beach grass and shrub formations. In addition, lower stomatal density and leaf thickness were noted in the sandbanks forest, while higher transpiration rates and stomatal conductance were exhibited in the beach grass and shrub formation. Leaf area, an attribute associated with light capture, has been previously studied in several restinga phytophysiognomies, indicating that plants in forest areas tend to have leaves with larger leaf area (Melo Júnior et al. 2019) and plants exposed to higher irradiance have smaller leaf area as a strategy to reduce water loss (Melo Jr. & Boeger 2016). Leaves with larger specific leaf area and stomata with wider stomatal pores were found in the sandbanks forest formation. Poorter et al. (2009) and Tecco et al. (2013) associated this pattern with greater photosynthetic capacity, which may explain the variation of these traits for the species in the different formations. Leaf thickness may be related to resistance against physical damage and the capacity to store water in leaves, explaining the greater leaf thickness in the *Clusia* and beach grass and shrub formations, where soil moisture is reduced and there is greater exposure to solar radiation (Niinemets 2001). The species *S. terebinthifolia*

presented a more conservative secondary xylem, characterized by an increase in the frequency of vessels per mm² and in the proportion of axial parenchyma contacting vessels, mainly in the *Clusia* and beach grass and shrub formations. Significant groupings of traits in the beach grass and shrub formation also stand out, such as the percentage of vessels and the vessel grouping index, reflecting hydraulic safety (Holbrook & Zwieniecki et al. 1999). While the leaves invested in morphological and physiological variation, investing in water use efficiency, the wood of the species remained conservative, investing in hydraulic safety. These traits varied mainly in the *Clusia* and beach grass and shrub formations. In the sandbanks forest, however, where the canopy is more closed and soil moisture is higher, a pattern of photosynthetic efficiency and carbon acquisition in the leaves and wood focused on water transport efficiency was observed.

The results of the analysis of variance show a clear distinction between the sandbanks forest formation and the other two studied formations, mainly due to the leaf and physiological traits of the studied plants. Our findings indicate that plant species that simultaneously inhabit open canopy (*Clusia* and beach grass and shrub formations) and closed canopy (sandbanks forest) environments adopt different ecological strategies to establish themselves in plant communities with divergent environmental conditions (Araújo et al. 2021b). Transpiration rate, which is directly related to water loss and leaf temperature regulation, varied more in the sandbanks forest formation, where there is higher temperature (Oliveira et al. 2023), and in the beach grass and shrub formation, possibly due to more favorable environmental conditions, such as higher air humidity and lower vapor pressure deficit (Pireda et al. 2019). The intraspecific variation observed in the species evaluated in this study may

play a crucial role in adaptation to environmental and climatic changes, in addition to contributing to the expansion of the ecological and geographic distribution of these species (Bedetti et al. 2011). Furthermore, species that exhibit high variation in their morphological and anatomical characteristics tend to occupy broader ecological niches and may occur in diverse habitats (Jung et al. 2010; Araújo et al. 2022).

4.6 Conclusion

The physiological and anatomical variation identified in this study contributes to the coexistence of species across contrasting restinga formations. *Pera glabrata* and *Scutia arenicola* showed greater intraspecific variation in functional traits, suggesting higher plasticity and potential for acclimation to microclimatic variability. In contrast, *Schinus terebinthifolia* presented more uniform xylem traits, although its known colonization ability may reflect alternative adaptive strategies. These functional differences may influence species distribution and ecosystem functioning, reinforcing the importance of trait-based approaches for ecological restoration and biodiversity conservation in restinga environments threatened by climate change.

Statements & Declarations

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Author Contribution Statement: The initial design and conception of the study were carried out by Priscila Fernanda Simioni and Igor Araújo. The identification and collection of material was carried out by Letícia Lanes Ferreira and Gabriel Amaral Ferreira. Gabriel Amaral Ferreira assisted in the morphological and anatomical analyses. The statistical analyses were conducted by Demétrius Lira-Martins and Igor Araújo. The initial version of the article was written by Letícia Lanes Ferreira. The final revision was made by Priscila Fernanda Simioni, Igor Araújo, Demétrius Lira-Martins and Maura Da Cunha. The authors are in agreement with the article.

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4.8 Appendix

Table S1. Eigenvalues of leaf structural traits in co-occurring species in restinga formations

Traits	Acronyms	PC1	PC2
Leaf area	LA	-0.307	0.079
Specific leaf area	SLA	-0.444	-0.103
Dry matter content	DMC	0.029	-0.326
Leaf thickness	LT	0.049	-0.157
Stomatal density	SD	0.504	0.170
Stomatal pore opening	SPO	-0.455	0.119
Stomatal conductance	Gs	-0.002	-0.636
Transpiration rate	T	0.002	-0.635

Table S2. Eigenvalues of wood structural traits in co-occurring species in restinga formations

Traits	Acronyms	PC1	PC2
Wood density	WD	0.033	-0.483
Vessel frequency	VF	-0.403	-0.011
Vessel grouping index	VGI	-0.269	0.061
Tangential vessel diameter	VD	0.337	0.003
Vessel wall thickness	VWT	0.354	0.077
Fiber diameter	FD	0.109	0.499
Fiber lumen	LF	0.052	0.509
Fiber wall thickness	FWT	0.270	0.082
Percentage of axial parenchyma	PAP	0.294	0.195
Percentage of radial parenchyma	PRP	0.153	-0.398
Percentage of fibers	PFIBER	-0.099	0.069
Percentage of vessels	PVESSEL	-0.368	0.119
Percentage of axial parenchyma contacting vessels	PAPV	-0.296	0.015
Percentage of total parenchyma	PTOTALP	0.288	-0.152
Percentage of gelatinous fibers	PFG	0.095	-0.022

Table S3. Split-plot ANOVA table on the influence of vegetation (VE) and species (SP). Degrees of freedom (DF), leaf area (LA), specific leaf area (SLA), dry matter content (DMC), leaf thickness (LT), stomatal density (SD), stomatal pore opening (SPO), stomatal conductance (GS), transpiration rate (T), vessel frequency (VF), vessel grouping index (VGI), tangential vessel diameter (VD), fiber lumen (FL) fiber wall thickness (FWT), percentage of axial parenchyma (PAP), percentage of radial parenchyma (PRP), percentage of fibers (PFIBER), percentage of vessels (PVESSEL), percentage of axial parenchyma contacting vessels (PAPV), percentage of total parenchyma (PPTOTALP), percentage of gelatinous fibers (PGF), wood density (WD).

Trait	Source of variation	*DF*	*F*	*P*
LA	VE	2	34.39	< 0.001
	SP	2	266.89	< 0.001
	VE*SP	4	27.33	< 0.001
	Error	41		
SLA	VE	2	1.22	0.296
	SP	2	81.14	< 0.001
	VE*SP	4	1.53	0.192
	Error	41		
DMC	VE	2	3.37	0.03
	SP	2	1.73	0.17
	VE*SP	4	0.73	0.56
	Error	41		
LT	VE	2	132.51	< 0.001
	SP	2	340.09	< 0.001
	VE*SP	4	8.39	< 0.001
	Error	41		
SD	VE	2	69.49	< 0.001
	SP	2	166.95	< 0.001
	VE*SP	4	34.98	< 0.001
	Error	41		
SPO	VE	2	56.09	< 0.001
	SP	2	54.19	< 0.001
	VE*SP	4	5.90	< 0.0001
	Error	41		
GS	VE	2	248.48	< 0.001
	SP	2	30.86	< 0.001
	VE*SP	4	44.93	< 0.001

	Error	41		
T	VE	2	346.45	< 0.001
	SP	2	79.31	< 0.001
	VE*SP	4	92.90	< 0.001
	Error	41		
VF	VE	2	163.8	< 0.001
	SP	2	237.0	< 0.001
	VE*SP	4	80.5	< 0.001
	Error	41		
VGI	VE	2	144.98	< 0.001
	SP	2	173.28	< 0 .001
	VE*SP	4	4.60	< 0.001
	Error	41		
VWT	VE	2	14.74	< 0.001
	SP	2	359.24	< 0.001
	VE*SP	4	15.78	< 0.001
	Error	41		
FD	VE	2	0.61	0.54
	SP	2	119.35	< 0.001
	VE*SP	4	3.00	0.01
	Error	41		
FL	VE	2	0.02	0.97
	SP	2	221.71	< 0.001
	VE*SP	4	3.89	0.003
	Error	41		
FWT	VE	2	38.45	< 0.001
	SP	2	53.89	< 0.001
	VE*SP	4	11.62	< 0.001
	Error	41		
PAP	VE	2	7.02	0.0009
	SP	2	278.42	< 0.001
	VE*SP	4	17.29	< 0.001
	Error	41		
PRP	VE	2	12.54	< 0.001
	SP	2	181.30	< 0.001
	VE*SP	4	8.53	< 0.001
	Error	41		
PFIBER	VE	2	205.03	< 0.001
	SP	2	5.94	0.002
	VE*SP	4	77.02	< 0.001
	Error	41		
PVESSEL	VE	2	1.41	0.24
	SP	2	184.79	< 0.001
	VE*SP	4	9.37	< 0.001
	Error	41		
PTOTALP	VE	2	15.02	< 0.001

	SP	2	232. 64	< 0.001
	VE*SP	4	17.67	< 0.001
	Error	41		
PGF	VE	2	314.58	< 0.001
	SP	2	2.51	0.08
	VE*SP	4	86.52	< 0.001
	Error	41		
WD	VE	2	2.13	0.11
	SP	2	35.71	< 0.001
	VE*SP	4	0.37	0.82
	Error	41		

5.Chap: 2 "Wood characterization and anatofunctional responses of restinga tree species to water-restricted microenvironments"

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5.1 Abstract

The vegetation formations of the restinga are characterized by pronounced environmental heterogeneity, with gradients of moisture, light, salinity, and temperature influencing the distribution of plant species. This study aimed to analyze and describe the cellular components of the secondary xylem of eight dominant woody species from three restinga plant formations, restinga forest, *Clusia* formation, and beach grass and shrub formation, located in the Fazenda Caruara Private Natural Heritage Reserve, São João da Barra, RJ, Brazil. The investigated species were *Scutia arenicola* (Rhamnaceae), *Inga maritima* (Fabaceae-Mimosoideae), *Schinus terebinthifolia* (Anacardiaceae), *Cynophalla flexuosa* (Capparaceae), *Varronia curassavica* (Cordiaceae), *Sideroxylon obtusifolium* (Sapotaceae), *Protium heptaphyllum* (Burseraceae), and *Pera glabrata* (Peraceae). Among these, the wood anatomy of *Scutia arenicola* and *Inga maritima* is described for the first time, filling an important gap in botanical knowledge. Anatomical descriptions of the species followed the standards established by the IAWA. Identification, allowing accurate comparison among species and environments. Species occurring in more water-limited environments, such as the *Clusia* and beach grass and shrub formations, exhibited xylem traits associated with increased hydraulic safety, such as higher vessel density, smaller vessel lumen diameter, and thicker fiber walls. Intervessel pits were mostly alternate and polygonal, while ray–vessel and parenchyma–vessel pits were similar in

shape and size to the intervessel pits. Fibers with simple to minutely bordered pits, mostly on radial walls, were predominant in all species. Growth ring boundaries were more distinct in formations subjected to stronger water seasonality, indicating a direct influence of water availability on cambial activity. These results demonstrate that restinga tree species adopt distinct xylem anatomical strategies to cope with water deficit, reinforcing the importance of wood anatomy for understanding the functional ecology and hydraulic adjustments of tropical coastal ecosystems.

Keywords: restinga, wood anatomy, xylem traits, hydraulic strategies, microclimatic variation.

5.2 Introduction

The restinga is an Atlantic Forest ecosystem of high scientific interest due to the complex interaction between abiotic factors and functional characteristics of plants (Cicarelli and Bona, 2022; Vieira et al., 2022; Borges et al., 2024). The plant communities of the restingas face adverse environmental conditions, such as high salinity, low water availability, and intense solar radiation, which imposes strong selective pressure, resulting in specific adjustments (Costa, 2021; Inague et al., 2021). Recent research highlights that plants in this environment exhibit high ecological plasticity, efficient nutrient acquisition strategies, and specialized water retention mechanisms, allowing their survival in adverse conditions (Cicarelli and Bona, 2022; Vieira et al., 2022; Borges et al., 2024). In addition, the restingas are home to an expressive richness of species, including about 4% of the endemic species of the Atlantic Forest. However, this biodiversity is under constant threat due to factors such as deforestation, real estate speculation, and global climate change, intensifying the vulnerability of these ecosystems (Inague et al., 2021; Lana-Costa et al., 2023). In particular, there is still a significant gap in the understanding of the morphological and anatomical aspects of plant species, especially as it relates to wood structure (Cicarelli and Bona, 2022).

Therefore, some plant species with dominant occurrence in restingas can be used as important models for understanding the adaptive strategies to the

environmental stress of this ecosystem. In this context, the analysis of the wood is important to understand the relationship between plant anatomy and the ecological functionality of the species that support the extreme conditions of the restingas. Secondary xylem cells can respond directly to severe restinga conditions, developing anatomical variations along different environmental gradients and adjusting to specific microclimates (Pireda et al., 2019; Xavier et al., 2023). In the secondary xylem, structural adaptations are evidenced by changes in the organization of the axial parenchyma and in the dimensions of the cell elements that make up the wood (Morris et al., 2018). Among the main anatomical characteristics involved, the frequency, diameter, and length of the vessel elements, the wall thickness and length of the fibers, as well as the height and width of the rays, are adaptations related to the availability of water resources, resulting in hydraulic efficiency and safety in water transport (Carlquist, 1977, 2001; Baas, 1983; Dickison, 2000; Carlquist and Schneider, 2001; Tyree and Zimmermann, 2002; Barros et al., 2006; Silva, 2018).

As for qualitative variation, in arid regions there is a tendency to decrease the diameter of the vessel elements, an adaptation that reduces the risk of embolism and ensures hydraulic functionality in conditions of water scarcity (Rodriguez-Zacaro et al., 2021; Dória et al., 2022). Vessel elements of smaller diameter, clustered and in greater number, are accompanied by thick vessel walls and fibers with thickened walls, contributing to a structurally safer xylem (Gleason et al., 2016). In addition, the presence of small-diameter intervessel pits is associated with resistance to air bubble formation (Schmitz et al., 2007). Simple perforation plates appear to be associated with environments where the transpiration rate is higher, contributing to hydraulic efficiency (Carlquist and Hoekman, 1985; Alves and Angyalossy-Alfonso, 2000). Parenchyma cells, both axial and ray parenchyma, play a key role in mitigating and reversing embolisms by facilitating lateral water transport through pits (Carlquist, 2018; Olson, 2020). Parameters such as ray height and ray width can be related to the availability of water and nutrients in the soil (Junior et al., 2016). As with the presence of prismatic crystals, the formation of tyloses is related to temperature variations (Junior et al., 2016). The functions of these xylem cell types can be identified through anatomical description, detailing their organization and relationship in response to environmental variations (Burguer and Ritcher, 1991; Botosso, 2011; Brandes et al., 2020).

The anatomical description of wood is important to understand the functional adaptations of plant species to different environments, especially in ecosystems subject to different conditions, such as restinga formations. These analyses allow the identification of characteristics related to hydraulic efficiency, safety in water transport, and resistance to environmental stresses, contributing to the understanding of the mechanisms that sustain the coexistence and distribution of species in these habitats. Thus, the objective of this work was to analyze and describe the cellular components of the secondary xylem of eight woody species (*Scutia arenicola* (Rhamnaceae), *Inga maritima* (Fabaceae-Mimosoideae), *Schinus terebinthifolia* (Anacardiaceae), *Cynophalla flexuosa* (Capparaceae), *Varronia curassavica* (Cordiaceae), *Sideroxylon obtusifolium* (Sapotaceae), *Protium heptaphyllum* (Burseraceae), and *Pera glabrata* (Peraceae) dominant in restinga plant formations, including restinga forest, *Clusia* formation, and beach grass and shrub formation, comparing their anatomical characteristics with existing descriptions in the literature.

5.3 Materials and Methods

5.3.1 Study area

The research was carried out in a restinga ecosystem located in the Reserva Particular do Patrimônio Natural da Fazenda Caruara, belonging to the Complexo Lagunar de Grussaí/Iquipari (CLGI), municipality of São João da Barra, state of Rio de Janeiro, Brazil, South America. The region has a subhumid to semi-arid tropical climate, with a rainy season concentrated between November and January and a dry season between May and August (Cruz et al., 2021). The average annual rainfall ranges from 800 to 1000 mm (Cruz et al., 2021), while the average annual temperature ranges between 19°C and 26°C (INEA, 2021), with a predominance of sandy soils (Cruz et al., 2021).

The RPPN Fazenda Caruara is recognized as the largest private restinga conservation area in Brazil, covering 60% of the total area of RPPNs in the state of Rio de Janeiro. The reserve includes four typical vegetation formations of restinga: grassoid beach formation, beach grass and shrub formation, *Clusia* formation, and restinga forest. This study was carried out in three of these formations: restinga forest,

Clusia formation, and beach grass and shrub formation (Assumpção and Nascimento, 2000; Souza et al., 2010). These formations configure an increasing vegetation gradient as they move away from the sea towards the continent (Assumpção and Nascimento, 2000). Each of these formations has distinct microclimates and edaphic characteristics, which act as severe environmental filters, directly influencing the vegetative organs of plants (Inague et al., 2021; Oliveira et al., 2023).

The restinga forest has tree cover of 45% to 60%, with canopies up to 6 m high. It is characterized by vegetation density that forms a continuous forest with the presence of leaf litter, located 980 m from the sea line (Assumpção and Nascimento, 2000). Although it presents low photosynthetically active radiation in relation to the other formations, it registers high temperature values and vapor pressure deficit (VPD). The soil has an acidic pH (5.7) and high levels of magnesium, carbon, organic matter, nitrogen, electrical conductivity, and moisture (Oliveira et al., 2023).

The *Clusia* formation, located 580 m from the sea line, is dominated by species with canopies from 1 to 3 m high, with *Clusia hilariana* being the predominant species. This formation enriches the soil with the fall of leaves, favoring the establishment of other plant species (Villela et al., 2020). It has high photosynthetically active radiation and VPD similar to the restinga forest. The soil is enriched with zinc, manganese, sodium, carbon, organic matter, electrical conductivity, and moisture (Oliveira et al., 2023).

The beach grass and shrub formation is composed of vegetation with a maximum height of 1 m, where the nucleation process occurs, facilitated by cacti and bromeliads, which promote the establishment of other plant species. Located 250 m from the sea line, this formation has high photosynthetically active radiation and low vapor pressure deficit (Oliveira et al., 2023). The soil has a pH close to neutral (6.8), with lower concentrations of magnesium, sodium, carbon, organic matter, zinc, manganese, nitrogen, electrical conductivity, and moisture compared to the restinga forest and *Clusia* formations (Oliveira et al., 2023).

5.3.2 Species selection and material collection

Based on a previous study (Oliveira et al., 2023), eight dominant woody species occurring in the three restinga formations (restinga forest, *Clusia* formation, and beach grass and shrub formation) within the study area were selected. The

selection of these species was based on their high abundance and ecological relevance within the restinga phytophysiognomy, as described by Assumpção and Nascimento (2000). For each species, branches were collected from five individuals, belonging to eight botanical families, totaling 75 individuals (Table 1).

Table 1: List of the dominant species of the restinga vegetation formations, families, popular names, dendrometric data and records.

Phytophysiognomy	Species	Family	Popular name	Nº HUENFw	Way of life	Endemism	*Conservation Status*
Restinga forest	*Protium heptaphyllum* (Aubl.) Marchand	Burseraceae	Pitch-white	640, 641, 642, 643, 644	Tree	No	DD - CNC Flora
	Cynophalla flexuosa (L.) J. Presl.	Capparaceae	Wild beans	660, 661, 662, 663, 664	Tree	No	NE-CNC Flora
	Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	Sapotaceae	Quixabeira	665, 666, 667, 668, 669	Tree	No	LC - CNC Flora
***Clusia* formation**	*Scutia arenicola* (Casar.) Reissek	Rhamnaceae	Quixabinha	680, 681, 682, 683, 684	Shrub	No	EN- CNC Flora
	Pera glabrata (Schott) Baill.	Peraceae	Shoemaker's stick	685, 686, 687, 688, 689	Shrub	No	NE-CNC Flora
	Schinus terebinthifolia Raddi	Anacardiaceae	Almecega	630, 631, 632, 633, 634	Shrub	No	NE-CNC Flora
Beach grass and shrub formation	*Inga Marítima* Benth.	Fabaceae - Mimosoideae	Inga of the sandbanks	620, 621, 622, 623, 624	Shrub	yes	VU - CNC Flora
	Varronia curassavica Jacq.	Cordiaceae	Whaling herb	635, 636, 637, 368, 639	Shrub	No	NE – CNC Flora

Legend: International Union for Conservation of Nature (IUNC) and the National Center for Flora Conservation (CNCFlora) (2025). Source: (http://floradobrasil.jbrj.gov.br/ and https://www.iucnredlist.org/).

5.3.3 Branch processing

Branch samples were sectioned with an average thickness of 15–25 μm (Muniz and Coradin, 1992) in tangential, transverse, and longitudinal planes using a sliding microtome (SM2010 R, LEICA, Germany). The sections were clarified in sodium hypochlorite (50%) and acidulated water (0.1%), dehydrated in an ascending ethanol series (50–100%) (Johansen, 1940), stained with Astra blue and hydroalcoholic safranin, and immersed in PA xylene. Permanent slides were prepared with Entellan synthetic resin (Merck).

The process of dissociation and maceration of the wood followed the method of Franklin (1945), modified by Kraus and Arduin (1997) for the measurement of cells (e.g., length of vessel elements and fibers). For each sample, small wood fragments (1 cm) were removed and placed in flasks containing a solution of glacial acetic acid and hydrogen peroxide (1:1). Subsequently, the flasks were placed in an oven at 60 °C for 48 hours or until the cells were completely dissociated.

Then, the material was washed in distilled water and stained with 1% aqueous safranin and subsequently immersed in 50% glycerin to prepare semi-permanent slides (Sass, 1951). All wood samples were deposited in the collection of the Xiloteca Dr. Cecília Gonçalves Costa at UENF (HUENFw) (Table 1).

5.3.4 Microscópico analyses

Microscopic anatomical analyses were performed using 12 slides per individual, three individuals per species. Images were captured on the histological slides in the three planes (transverse, tangential longitudinal, and radial) using a brightfield optical microscope (Axioplan, ZEISS, USA), with a camera (Moticam Pro 282B, Hong Kong) coupled to the microscope, and the images were analyzed using Image-Pro Plus software version 4.0 for Windows (Media Cybernetics, USA). All measurements of qualitative and quantitative characteristics followed the IAWA Committee (1989) standards. Subsequently, polarized light from the same microscope was used to observe the presence of crystals in the cells.

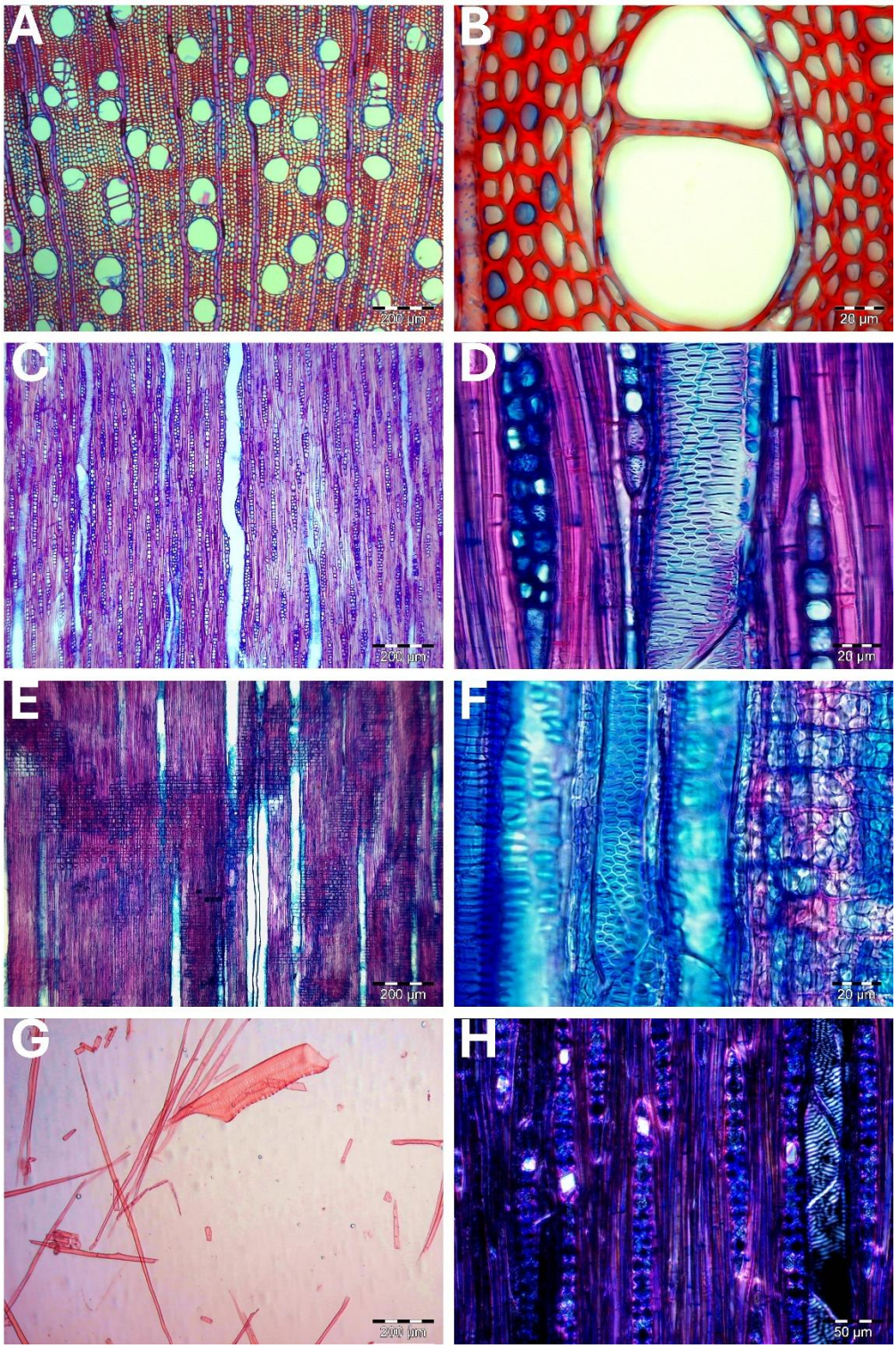
5.4 Results

Wood anatomical description

***Protium heptaphyllum* (Aubl.) Marchand (Burseraceae) (Fig. 1, Tab.2)**

Growth rings: distinct, marked by radial flattening of fibers. **Vessel elements:** diffuse-porous; mean density 68/mm²; solitary or in radial multiples of 2–12 elements, occasionally in clusters; circular to oval in transverse section; mean length 308 µm; tangential diameter 60 µm, radial diameter 63 µm; mean wall thickness 7 µm; simple perforation plates; small intervessel pits (4–7 µm), alternate, ornamented, polygonal, similar to ray–vessel and parenchyma–vessel pits; presence of tyloses and apices at both ends. **Fibers:** libriform (<3 µm), septate; mean length 570 µm; mean diameter 7 µm; lumen 4 µm; mean wall thickness 3 µm. **Axial parenchyma:** sparse to paratracheal vasicentric, 3–9 cells high. **Rays:** mean 26/mm'; uniseriate to multiseriate (1–3 cells wide), composed of procumbent and square cells in the central region, erect and/or square at the margins; mean height 205 µm. **Other characteristics:** prismatic crystals present in ray cells.

Figure 1- Wood anatomy of *Protium heptaphyllum* (Aubl.) Marchand (Burseraceae) from a restinga forest.



Legend: Optical microscopy: A–G; polarized light microscopy: H. A and B: Transverse sections showing vessel distribution and shape. C: Tangential longitudinal section showing multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Tangential longitudinal section showing crystals under polarized light. Scale bars: A, C, E, G = 200 µm; B, D, F = 20 µm; H = 50 µm.

Table 2 - Quantitative anatomical data of *Protium heptaphyllum* wood.

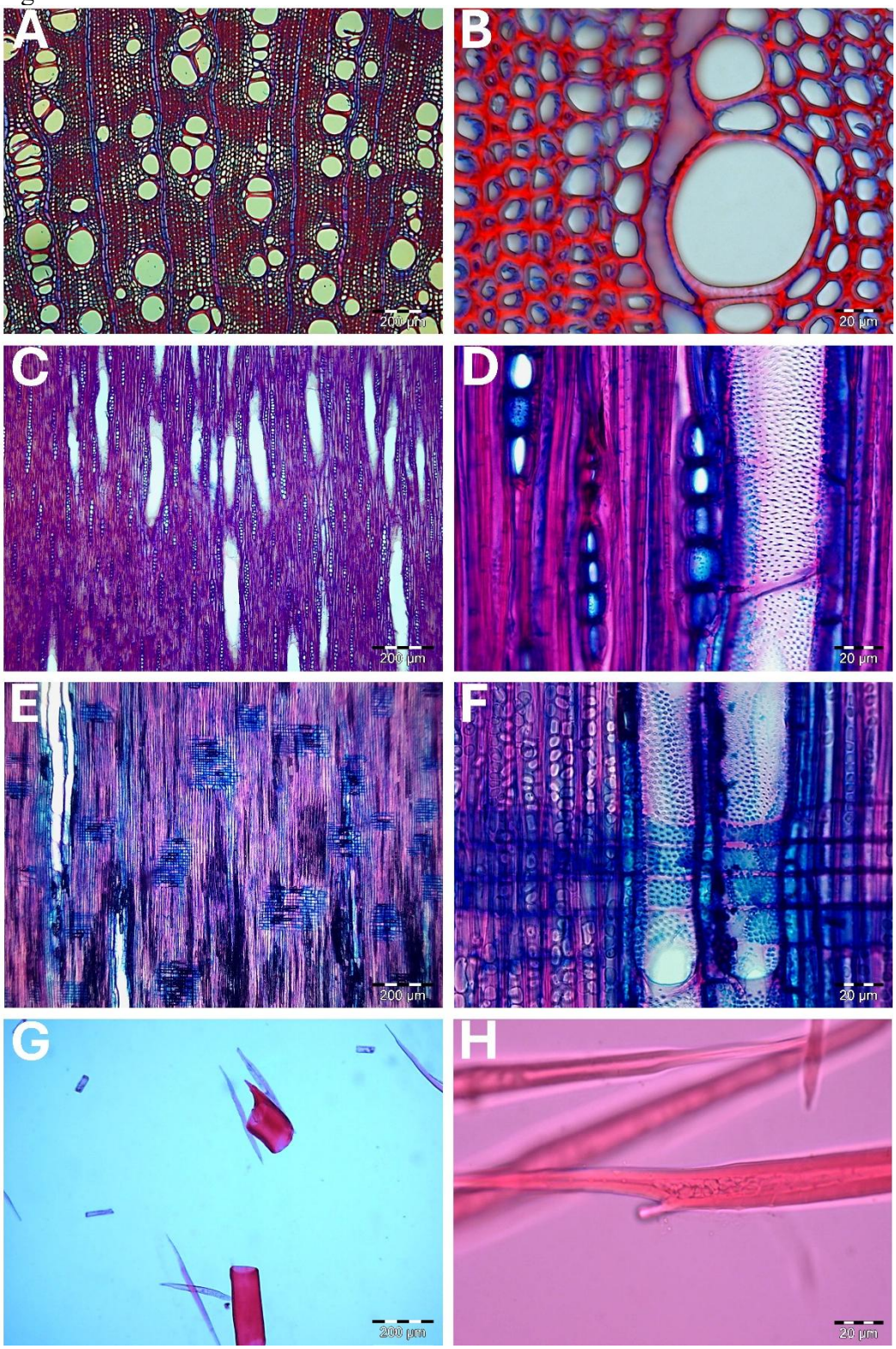
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	32,00	68,27	116,00	16,81
Length (µm)	147,07	307,78	456,43	62,67
Tangential diameter (µm)	32,02	59,88	100,92	15,35
Radial diameter (µm)	35,62	62,98	107,53	15,10
Lumen area (µm^2)	943,57	3159,57	7798,08	1538,19
Wall thickness (µm)	1,69	7,09	14,82	2,71
PITS				
Intervessel (µm)	3,30	4,64	6,33	0,59
Ray–vessel (µm)	2,61	4,29	5,85	0,66
Parenchyma-vessel (µm)	2,93	4,45	6,34	0,79
FIBERS				
Diameter (µm)	2,51	6,92	15,63	3,08
Lumen (µm)	0,6	4,17	13,44	2,90
Length (µm)	288,84	569,86	838,35	94,85
Wall thickness (µm)	0,97	2,75	6,23	1,03
Pits (µm)	1,03	1,91	2,82	0,45
AXIAL PARENCHYMA				
Length (µm)	181,62	342,07	536,23	78,15
Length (No. of Cells)	3,00	5,97	9,00	1,53
RADIAL PARENCHYMA				
Frequency / mm'	22,00	26,25	29,00	1,78
Height (µm)	104,50	25,47	340,92	59,40
Width (µm)	12,45	19,94	28,86	3,41

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

***Cynophalla flexuosa* (L.) J. Presl (Capparaceae) (Fig. 2, Tab.3)**

Growth rings: indistinct or absent. **Vessel elements:** diffuse-porous; mean density 37/mm²; solitary and in radial multiples of 2–14 elements or clusters; circular to oval in transverse section; mean length 210 µm; tangential diameter 70 µm, radial diameter 67 µm; mean wall thickness 11 µm; simple perforation plates; very small intervessel pits (<4 µm), alternate, ornamented, circular, similar to ray–vessel and parenchyma–vessel pits; vessel ends with apices present. **Fibers:** libriform (<3 µm); mean length 366 µm; mean diameter 7 µm; lumen 4 µm; mean wall thickness 3 µm. **Axial parenchyma:** paratracheal vasicentric, 2–8 cells high. **Rays:** mean 19/mm'; predominantly uniseriate to multiseriate (1–3 cells wide), composed of procumbent cells in the central portion and erect and/or square cells at the margins; mean height 192 µm.

Figure 2- Wood anatomy of *Cynophalla flexuosa* (L.) J. Presl (Capparaceae) from a restinga forest.



Legend: A-G: Optical microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G and H: Macerate showing vessels and fibers. Scale bars: A, C, E, G = 200 µm; B, D, F, H = 20 µm.

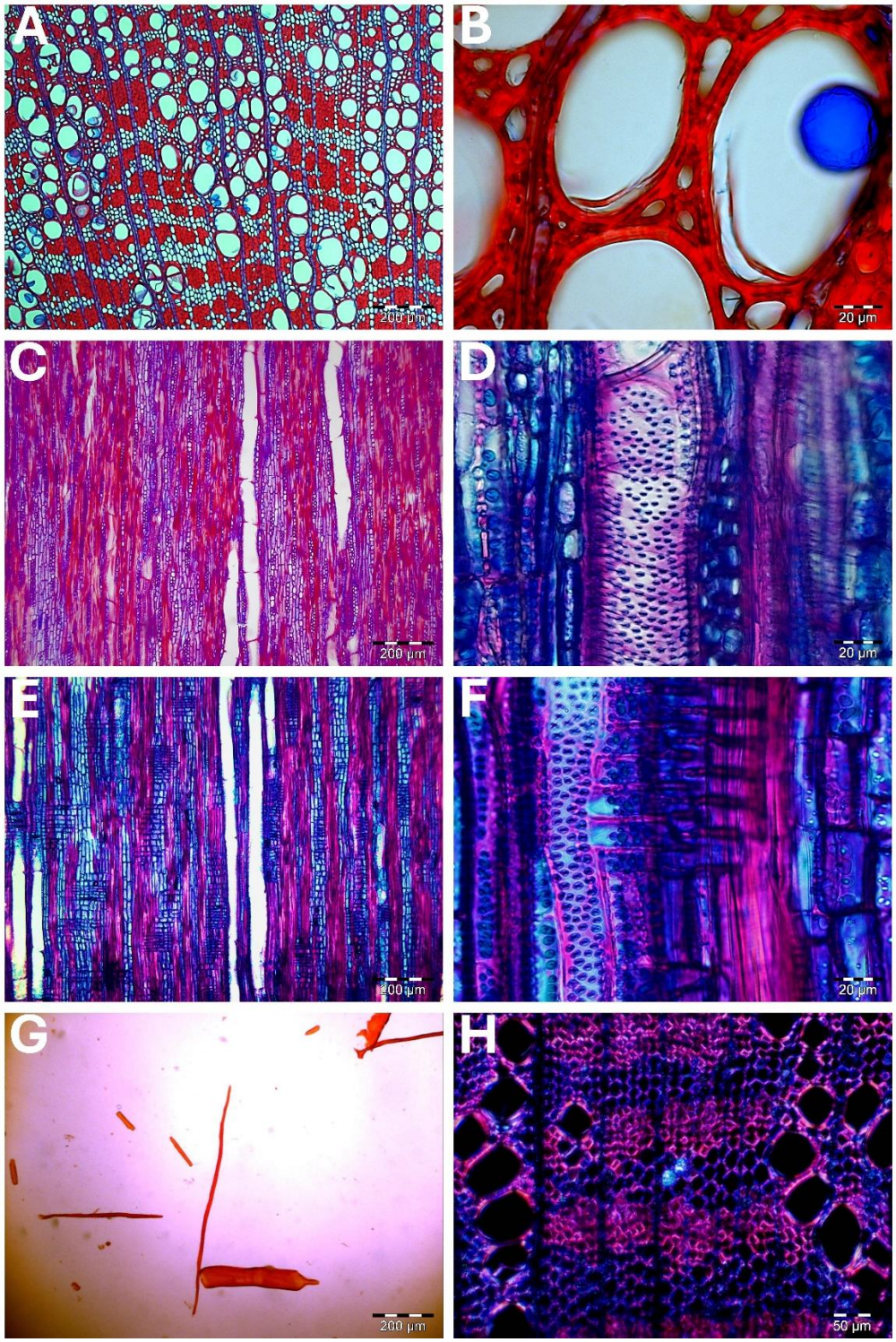
Table 3 - Quantitative anatomical data of *Cynophalla flexuosa* wood.

Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	16	37,33	76,00	11,30
Length (µm)	124,86	209,77	305,48	42,91
Tangential diameter (µm)	29,69	69,98	116,62	22,92
Radial diameter (µm)	37,01	66,69	106,91	17,74
Lumen area (µm^2)	535,36	3146,17	7687,08	1799,46
Wall thickness (µm)	4,79	10,98	18,30	3,15
PITS				
Intervessel (µm)	1,07	1,57	2,14	0,25
Ray–vessel (µm)	1,07	1,69	2,45	0,27
Parenchyma-vessel (µm)	1,03	1,57	2,33	0,30
FIBERS				
Diameter (µm)	2,56	6,65	12,82	2,57
Lumen (µm)	1,14	3,60	9,25	1,97
Length (µm)	230,76	366,25	532,42	64,44
Wall thickness (µm)	1,03	3,05	5,64	1,16
Pits (µm)	1,15	1,99	2,83	0,35
AXIAL PARENCHYMA				
Length (µm)	103,62	244,45	418,17	60,60
Length (No. of Cells)	2,00	5,05	8,00	1,50
RADIAL PARENCHYMA				
Frequency / mm'	14,00	19,72	27,00	3,48
Height (µm)	107,25	191,90	470,11	68,12
Width (µm)	11,00	16,41	24,89	3,33

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

Sideroxylon obtusifolium **(Roem. & Schult.) T.D.Penn. (Sapotaceae) (Fig. 3, Tab.4)** **Growth rings:** indistinct or absent; **Vessel elements:** diffuse-porous; mean density 74/mm²; solitary and in radial multiples or clusters of 2–14 elements; circular to oval in transverse section; mean length 337 µm; tangential diameter 72 µm, radial diameter 59 µm; mean wall thickness 12 µm; simple perforation plates; very small intervessel pits (<4 µm), alternate, ornamented, circular with elliptical apertures, similar to ray–vessel and parenchyma–vessel pits; presence of tyloses; vessel ends with apices present; **Fibers:** libriform (<3 µm); mean length 926 µm; mean diameter 7 µm; lumen 2 µm; mean wall thickness 5 µm; **Axial parenchyma:** banded, tending to form a reticulate pattern, 3–7 cells high; **Rays:** mean 19/mm'; uniseriate to multiseriate (1–3 cells wide), composed of procumbent cells in the central region and erect and/or square cells at the margins; mean height 241 µm; **Other characteristics:** prismatic crystals present in axial parenchyma cells.

Figure 3 - Wood anatomy of *Sideroxylon obtusifolium* (Roem. & Schult.) T.D. Penn. (Sapotaceae) from a restinga forest.



Legend: A–G: Optical microscopy; H: Polarized light microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Cross-section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; B, D, F = 20 µm; H = 50 µm.

Table 4 - Quantitative anatomical data of *Sideroxylon obtusifolium* wood.

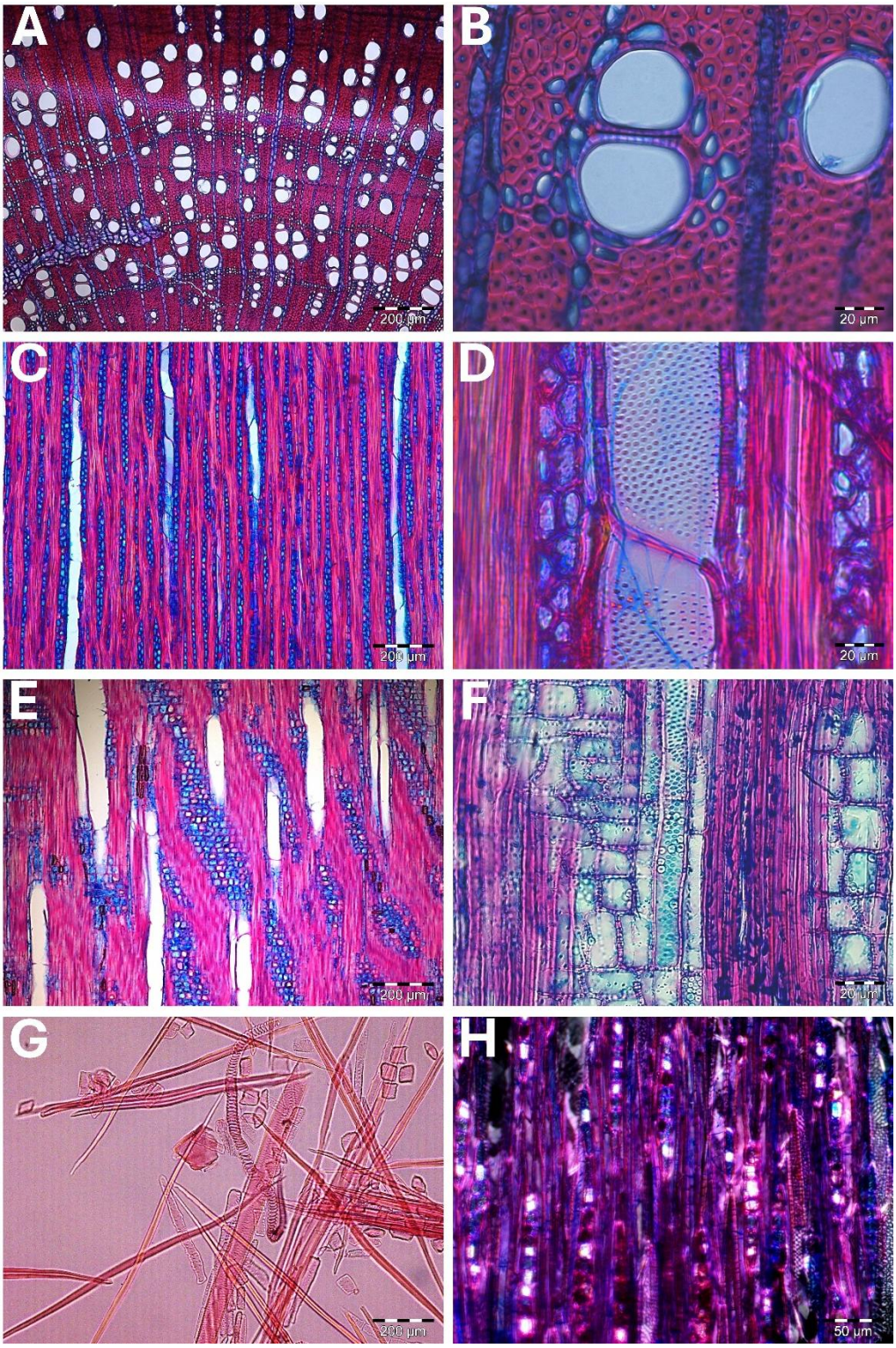
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	20,00	74,83	144,00	24,70
Length (μm)	118,60	337,34	539,60	90,64
Tangential diameter (μm)	37,38	71,89	103,64	13,99
Radial diameter (μm)	21,40	59,39	106,80	18,92
Lumen area (μm^2)	107,58	1309,77	2874,55	1243,16
Wall thickness (μm)	4,23	11,67	17,75	2,97
PITS				
Intervessel (μm)	2,23	3,25	4,64	0,49
Ray–vessel (μm)	2,23	3,62	5,48	0,64
Parenchyma-vessel (μm)	1,99	3,41	4,79	0,55
FIBERS				
Diameter (μm)	2,93	7,42	13,33	2,62
Lumen (μm)	0,54	2,15	5,74	11,53
Length (μm)	705,08	925,93	1243,16	121,04
Wall thickness (μm)	1,66	5,27	11,53	2,23
Pits (μm)	1,10	2,33	3,90	0,62
AXIAL PARENCHYMA				
Length (μm)	225,69	357,43	690,85	82,40
Length (No. of Cells)	3,00	5,16	7,00	1,24
RADIAL PARENCHYMA				
Frequency / mm'	15,00	19,33	24,00	2,8
Height (μm)	121,73	241,18	421,68	59,10
Width (μm)	12,37	19,77	35,76	4,01

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

***Scutia arenicola* (Casar.) Reissek (Rhamnaceae) (Fig. 4, Tab.5)**

Growth rings: distinct, marked by bands of marginal parenchyma; **Vessel elements:** diffuse-porous; mean density 130/mm²; solitary and in radial multiples of 2–10 elements; circular to oval in transverse section; mean length 213 μm; tangential diameter 30 μm, radial diameter 46 μm; mean wall thickness 3 μm; simple perforation plates; minute intervessel pits (<4 μm), alternate, ornamented, polygonal, with elliptical apertures, similar to ray–vessel and parenchyma–vessel pits; vessel ends with apices present; **Fibers:** libriform (<3 μm) with simple pits; mean length 505 μm; mean diameter 7 μm; lumen 2 μm; **Axial parenchyma:** sparse, arranged in marginal or apparently marginal axial bands, 3–8 cells high; **Rays:** mean 28/mm'; uniseriate to multiseriate (1–4 cells wide), heterogeneous, composed of procumbent and square cells in the central region, erect and/or square at the margins; mean height 250 μm; **Other characteristics:** prismatic crystals present in ray cells and presence of maculae.

Figure 4- Wood anatomy of *Scutia arenicola* (Casar.) Reissek (Rhamnaceae) from a *Clusia* formation.



Legend: A–G: Optical microscopy; H: Polarized light microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Cross-section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; B, D, F = 20 µm; H = 50 µm.

Table 5 - Quantitative anatomical data of *Scutia arenicola* wood.

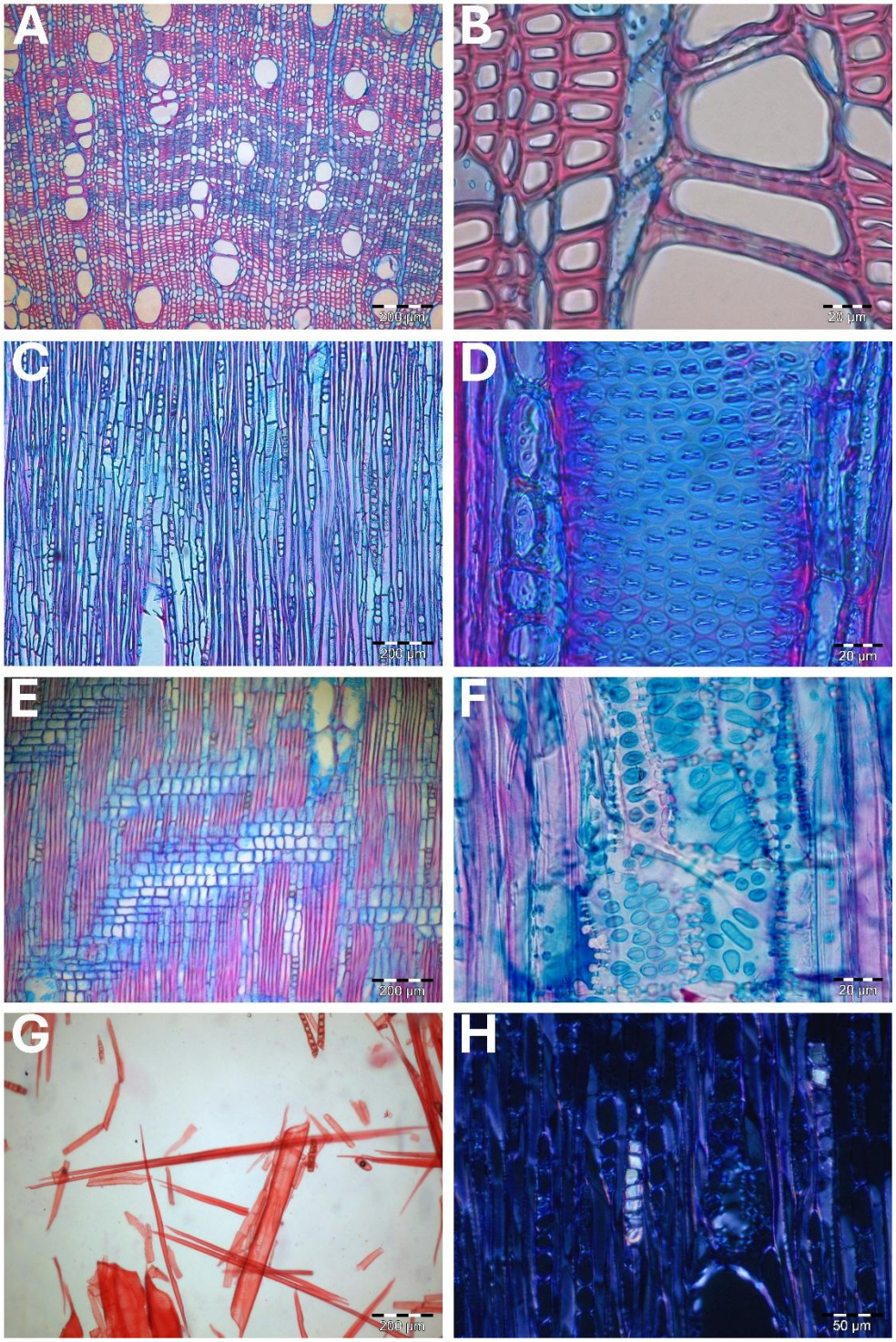
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	85	130,99	202	28,25
Length (µm)	100,37	212,81	357,97	52,10
Tangential diameter (µm)	6,15	29,91	63,42	12,57
Radial diameter (µm)	27,33	47,53	67,01	7,99
Lumen area (µm^2)	839,31	1826,62	7743,37	1225,50
Wall thickness (µm)	1,36	2,85	5,29	0,78
PITS				
Intervessel (µm)	1,29	1,96	3,02	0,42
Ray–vessel (µm)	1,03	1,70	2,41	0,27
Parenchyma-vessel (µm)	1,28	1,74	2,27	0,20
FIBERS				
Diameter (µm)	2,56	7,1	13,85	3,03
Lumen (µm)	0,51	2,18	7,39	1,47
Length (µm)	325,46	505,03	674,94	74,41
Wall thickness (µm)	0,60	1,43	3,24	0,62
Pits (µm)	1,02	1,6	2,38	0,27
AXIAL PARENCHYMA				
Length (µm)	105,87	208,53	369,20	45,27
Length (No. of Cells)	3,00	5,46	8,00	1,39
RADIAL PARENCHYMA				
Frequency / mm'	20	28,00	35	3,49
Height (µm)	127,71	250,37	434,44	75,01
Width (µm)	8,83	15,91	23,05	3,09

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

***Pera glabrata* (Schott) Baill (Peraceae) (Fig. 5, Tab.6)**

Growth rings: distinct, demarcated by bands of marginal parenchyma and by radial flattening of fibers; **Vessel elements:** diffuse-porous; mean density 28/mm²; solitary and in radial multiples of 2–9 elements or in clusters; circular to oval in transverse section; mean length 619 µm; tangential diameter 48 µm, radial diameter 97 µm; mean wall thickness 5 µm; simple perforation plates; small intervessel pits (4–7 µm), alternate, ornamented, circular with elliptical apertures, similar to ray–vessel and parenchyma–vessel pits; vessel ends with apices present; **Fibers:** libriform (<3 µm) with simple pits; presence of gelatinous fibers; **Axial parenchyma:** irregular, reticulate, 1–2 cells high; **Rays:** mean 15/mm'; uniseriate to biseriate (1–2 cells wide), heterogeneous, composed of procumbent, square, and erect cells in the central region, erect cells at the margins; mean height 312 µm; **Other characteristics:** prismatic crystals present in axial parenchyma cells.

Figure 5 –Wood anatomy of *Pera glabrata* (Schott) Baill. (Peraceae) from a *Clusia* formation.



Legend: A–G: Optical microscopy; H: Polarized light microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and biseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Tangential longitudinal section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; B, D, F = 20 µm; H = 50 µm.

Table 6 - Quantitative anatomical data of *Pera glabrata* wood.

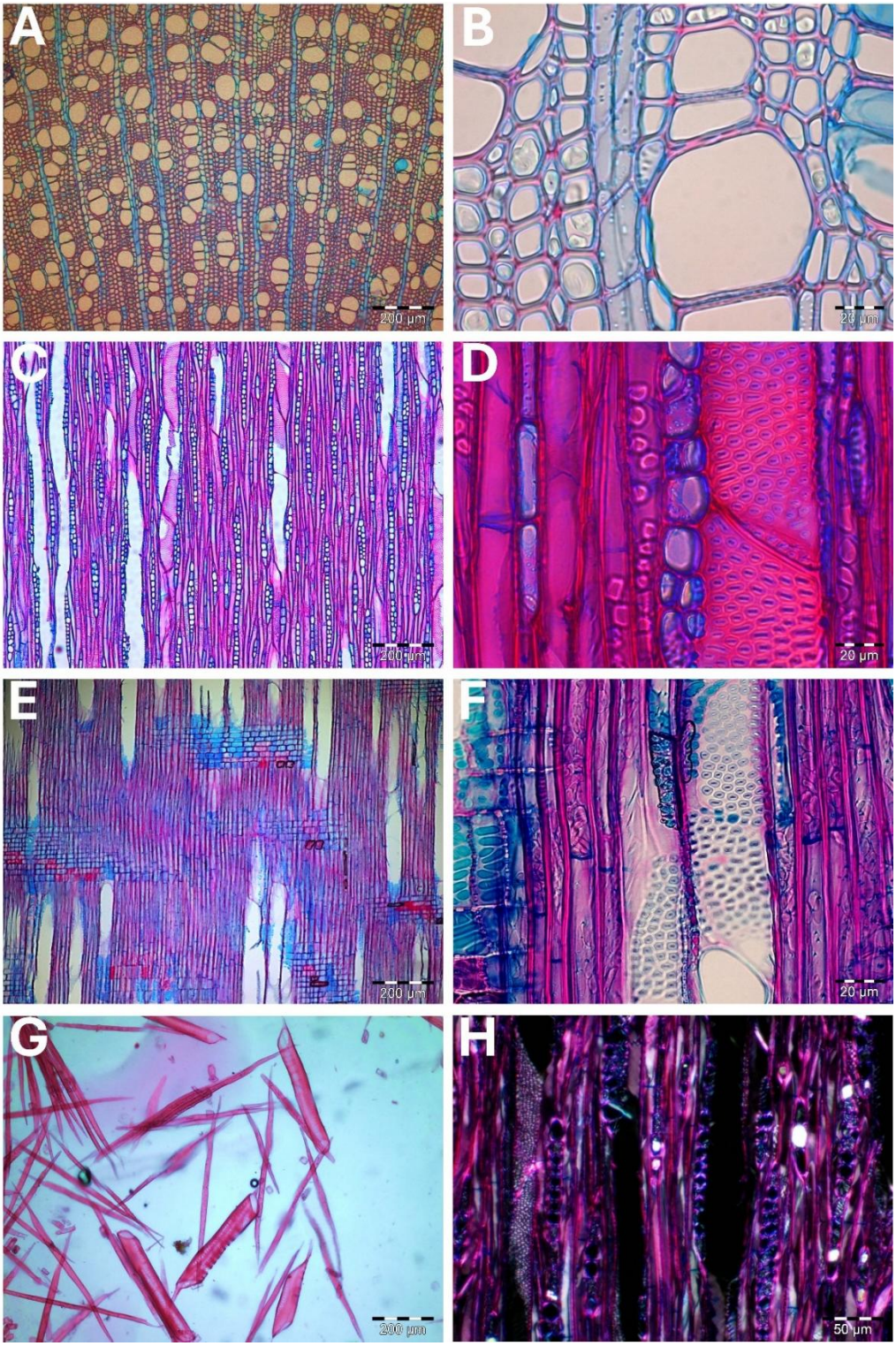
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	13,00	28,33	49,00	8,63
Length (μm)	363,96	618,90	824,46	108,58
Tangential diameter (μm)	12,17	48,42	99,51	19,65
Radial diameter (μm)	60,06	97,33	139,40	20,81
Lumen area (μm^2)	2582,10	5262,98	9368,17	161807
Wall thickness (μm)	3,07	4,68	7,51	0,87
PITS				
Intervessel (μm)	3,59	4,75	6,39	0,73
Ray–vessel (μm)	3,42	4,82	5,99	0,51
Parenchyma-vessel (μm)	3,31	4,55	5,99	0,59
FIBERS				
Diameter (μm)	3,87	12,58	31,63	6,94
Lumen (μm)	0,72	7,88	22,69	5,86
Length (μm)	660,19	924,49	1207,69	120,77
Wall thickness (μm)	1,03	2,65	9,13	1,31
Pits (μm)	1,460	2,47	3,76	0,48
AXIAL PARENCHYMA				
Length (μm)	231,18	367,55	559,19	71,64
Length (No. of Cells)	3,00	5,57	8,00	1,40
RADIAL PARENCHYMA				
Frequency / mm'	13,00	16,33	21,00	2,02
Height (μm)	187,20	311,50	446,60	60,21
Width (μm)	10,85	17,92	27,42	3,65

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

***Schinus terebinthifolia* Raddi (Anacardiaceae) (Fig. 6, Tab.7)**

Growth rings: distinct, marked by radial flattening and thickening of fiber walls; **Vessel elements:** diffuse-porous; mean density 258/mm²; solitary and in radial multiples of 2–10 elements; circular to oval in transverse section; mean length 324 µm; tangential diameter 26 µm, radial diameter 50 µm; mean wall thickness 3 µm; simple perforation plates; minute intervessel pits (<4 µm), alternate, ornamented, polygonal, with elliptical apertures, similar to ray–vessel and parenchyma–vessel pits; presence of tyloses; vessel ends with apices present; **Fibers:** libriform (<3 µm) with simple or very small pits; septate; mean length 564 µm; mean diameter 10 µm; lumen 6 µm; mean wall thickness 2 µm; presence of gelatinous fibers; **Axial parenchyma:** paratracheal, vasicentric, 3–8 cells high; **Rays:** mean 19/mm'; uniseriate to multiseriate (1–3 cells wide), heterogeneous, composed of procumbent and square cells in the central region, erect at the margins; mean height 176 µm; **Other characteristics:** prismatic crystals present in ray cells.

Figure 6 - Wood anatomy of *Schinus terebinthifolia* Raddi (Anacardiaceae) from a *Clusia* formation.



Legend: A–G: Optical microscopy; H: Polarized light microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Tangential longitudinal section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; F = 100 µm; B, D = 20 µm; H = 50 µm.

Table 7 - Quantitative anatomical data of *Schinus terebinthifolia* wood.

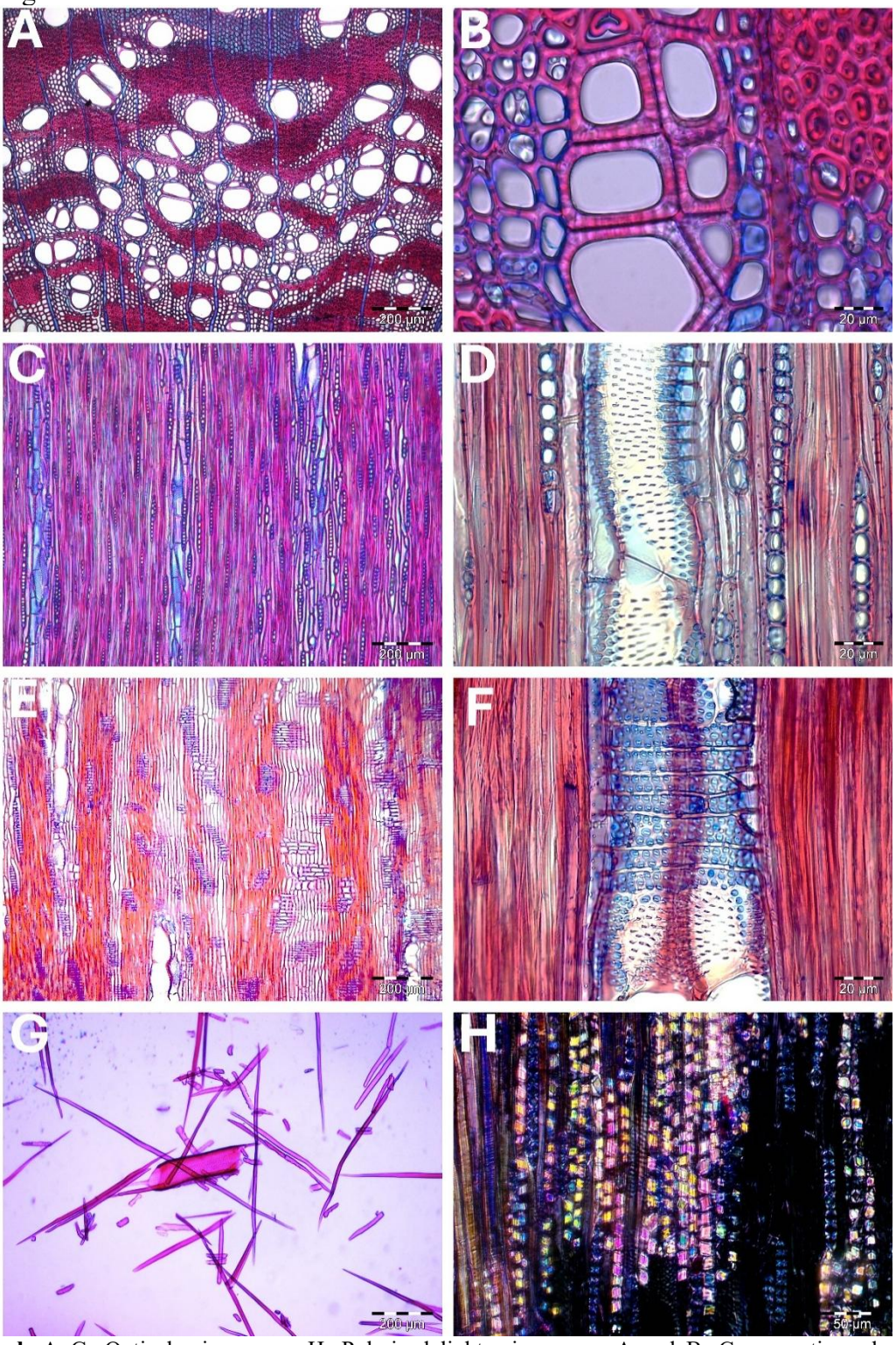
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	198	258	334	30,51
Length (μm)	202,59	323,98	465,69	60,53
Tangential diameter (μm)	6,39	26,12	49,45	10,32
Radial diameter (μm)	24,61	50,01	84,65	11,91
Lumen area (μm^2)	474,26	1655,83	3514,52	637,79
Wall thickness (μm)	0,85	3,03	14,18	2,83
PITS				
Intervessel (μm)	1,55	2,49	3,62	0,45
Ray–vessel (μm)	1,38	2,27	3,51	0,39
Parenchyma-vessel (μm)	1,47	2,02	3,43	0,35
FIBERS				
Diameter (μm)	2,57	10,45	22,76	5,11
Lumen (μm)	0,68	6,22	17,51	4,24
Length (μm)	369,65	563,98	893,59	95,62
Wall thickness (μm)	0,62	1,73	3,09	0,60
Pits (μm)	1,41	2,31	3,02	0,36
AXIAL PARENCHYMA				
Length (μm)	101,22	215,01	340,98	45,39
Length (No. of Cells)	3,00	5,53	8,00	139
RADIAL PARENCHYMA				
Frequency / mm'	14,00	19,46	24,00	2,54
Height (μm)	73,67	175,59	349,87	62,70
Width (μm)	8,14	11,82	17,67	2,17

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

***Inga maritima* Benth. (Fabaceae-Mimosoideae) (Fig. 7, Tab. 8)**

Growth rings: distinct; **Vessel elements:** diffuse-porous; mean density 57/mm²; solitary and in tangential multiples of 2–4 and radial multiples of 2–10 elements; circular to oval in transverse section; mean length 257 µm; tangential diameter 72 µm, radial diameter 67 µm; mean wall thickness 12 µm; simple perforation plates; minute intervessel pits (<4 µm), alternate, ornamented, polygonal, with elliptical apertures, similar to parenchyma–vessel pits, more rounded in ray–vessel pits; vessel ends with apices present; **Fibers:** libriform (<3 µm) with simple or very small pits; non-septate; mean length 550 µm; mean diameter 9 µm; lumen 4 µm; mean wall thickness 5 µm; **Axial parenchyma:** confluent paratracheal and aliform paratracheal, 4–8 cells high; **Rays:** mean 30/mm'; uniseriate to multiseriate (1–3 cells wide), composed predominantly of procumbent cells, heterogeneous in the central region, erect and/or square at the margins; mean height 107 µm; **Other characteristics:** prismatic crystals present in axial parenchyma cells.

Figure 7 - Wood anatomy of *Inga maritima* Benth. (Fabaceae–Mimosoideae) from the beach grass and shrub formation.



Legend: A–G: Optical microscopy. H: Polarized light microscopy. A and B: Cross-section, showing vessel distribution and shape. C: Tangential longitudinal section showing uniseriate and multiseriate rays. D: Tangential longitudinal section showing intervessel pits. E: Radial longitudinal section showing heterogeneous rays. F: Radial longitudinal section showing ray–vessel pits. G: Macerate showing vessels and fibers. H: Tangential longitudinal section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; F = 100 µm; B, D = 20 µm; H = 50 µm.

Table 8 - Quantitative anatomical data of *Inga maritima wood*. Quantitative anatomical data of *Inga maritima* wood.

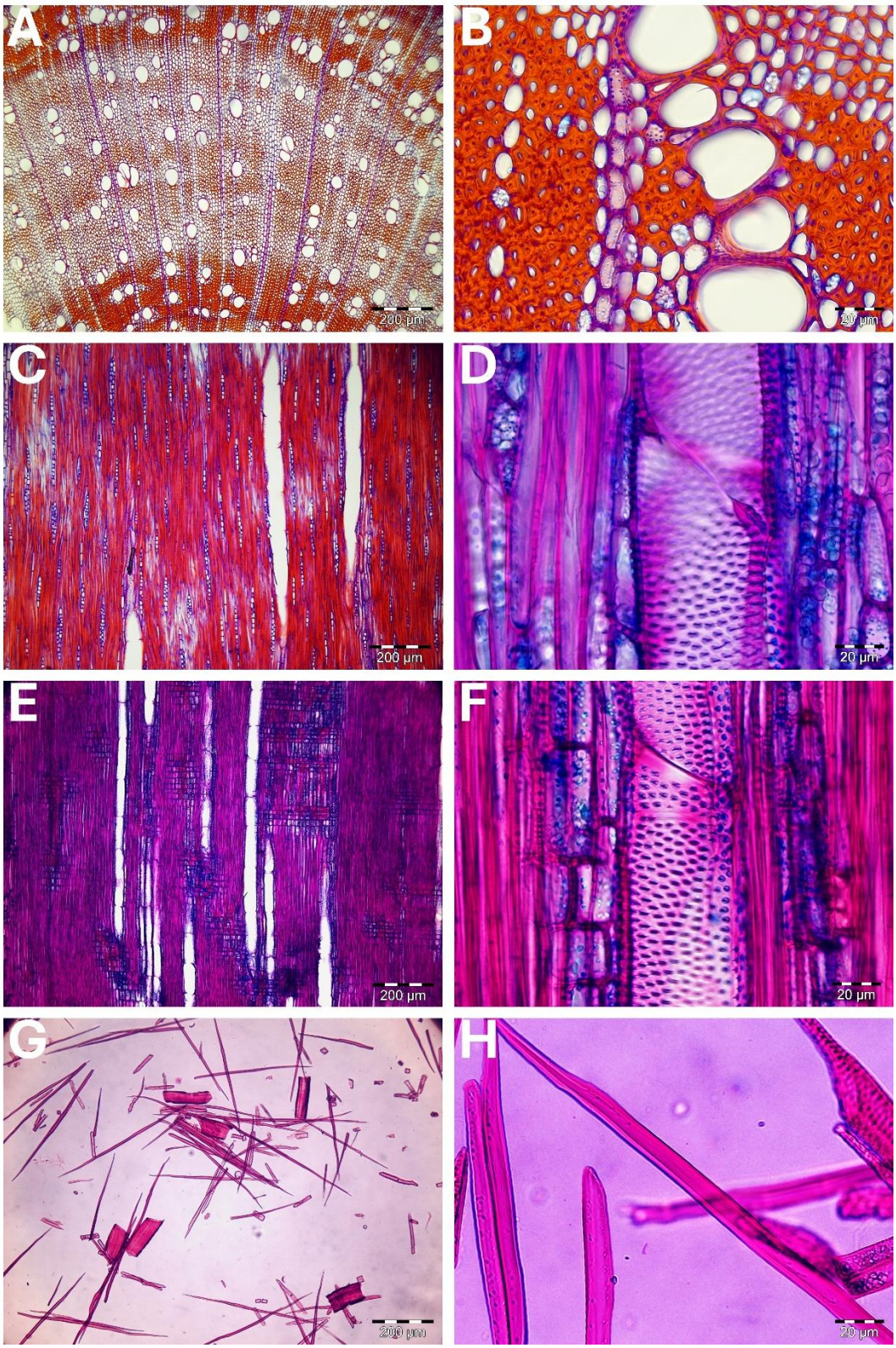
Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	24,00	56,91	144,00	20,73
Length (μm)	125,2	257,01	388,74	53
Tangential diameter (μm)	12,37	71,	123,83	20,32
Radial diameter (μm)	35,1	67,82	107,04	16,57
Lumen area (μm^2)	843,1	2828,67	6868,40	1088,99
Wall thickness (μm)	1,17	12,05	18,64	3,30
PITS				
Intervessel (μm)	1,5	2,44	3,33	0,37
Ray–vessel (μm)	1,2	2,49	3,47	0,41
Parenchyma-vessel (μm)	2,1	2,75	3,61	0,33
FIBERS				
Diameter (μm)	3,24	9,26	20,06	3,73
Lumen (μm)	0,85	3,79	13,71	2,55
Length (μm)	284,5	550,18	793,61	116,40
Wall thickness (μm)	1,85	5,47	9,82	2,00
Pits (μm)	1,14	1,87	2,76	0,40
AXIAL PARENCHYMA				
Length (μm)	143,05	321,62	494,94	71,59
Length (No. of Cells)	4,00	6,23	8,00	1,11
RADIAL PARENCHYMA				
Frequency / mm'	21,0	29,89	37,00	3,63
Height (μm)	38,0	107,34	234,83	41,39
Width (μm)	6,1	9,91	19,18	2,76

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

Varronia curassavica **Jacq**. **(Cordiaceae) (Fig. 8, Tab. 9)**

Growth rings: distinct, demarcated by differences in fiber dimensions; **Vessel elements:** diffuse-porous; mean density 99/mm²; solitary and in tangential multiples of 2–7 and radial multiples of 2–3; circular to oval in transverse section; mean length 216 µm; tangential diameter 58 µm, radial diameter 83 µm; mean wall thickness 8 µm; simple perforation plates; minute intervessel pits (<4 µm), alternate, ornamented, circular with elliptical apertures, similar to parenchyma–vessel and ray–vessel pits; vessel ends with apices present; **Fibers:** libriform (<3 µm) with simple or very small pits; non-septate; mean length 672 µm; mean diameter 7 µm; lumen 4 µm; wall thickness 3 µm; **Axial parenchyma:** sparse, paratracheal, 1–2 cells high; **Rays:** mean 14/mm'; uniseriate to multiseriate (1–3 cells wide), homogeneous, composed of square cells in the central region, heterogeneous with procumbent cells in the central region, erect and/or square at the margins; mean height 247 µm.

Figure 8 - Wood anatomy of *Varronia curassavica* Jacq. (Cordiaceae) from the beach grass and shrub formation.



Legend: Optical microscopy. A and B: Cross-section showing vessel distribution and shape. C and D: Tangential longitudinal section showing vascular rays and intervessel pits. E and F: Radial longitudinal section showing heterogeneous rays and ray–vessel pits. G and H: Macerate showing vessels and fibers; tangential longitudinal section showing presence of crystals under polarized light. Scale bars: A, C, E, G = 200 µm; F = 100 µm; B, D, F, H = 20 µm.

Table 9 - Quantitative anatomical data of *Varronia curassavica* wood.

Cell Types	Minimal	Mean	Maximum	SD
VESSEL ELEMENTS				
Vessel frequency /mm^2	64,00	98,73	162,00	16,93
Length (µm)	149,77	216,20	339,07	34,31
Tangential diameter (µm)	24,42	57,58	100,34	14,55
Radial diameter (µm)	35,59	83,09	152,20	339,07
Lumen area (µm^2)	136,17	3132,76	8951,88	1860,10
Wall thickness (µm)	3,65	7,78	16,80	2,26
PITS				
Intervessel (µm)	2,03	3,06	4,28	0,47
Ray–vessel (µm)	2,56	3,76	5,54	0,72
Parenchyma-vessel (µm)	2,45	3,99	5,48	0,60
FIBERS				
Diameter (µm)	2,70	6,72	14,15	3,01
Lumen (µm)	1,02	3,52	10,98	2,26
Length (µm)	463,32	672,45	1022,	108,85
Wall thickness (µm)	1,14	3,21	6,98	1,34
Pits (µm)	1,01	2,54	4,38	0,62
AXIAL PARENCHYMA				
Length (µm)	184,69	355,60	559,37	86,21
Length (No. of Cells)	3,00	5,09	8,00	1,32
RADIAL PARENCHYMA				
Frequency / mm'	11,00	14,15	17,00	1,38
Height (µm)	121,08	246,58	577,29	85,74
Width (µm)	13,74	24,66	35,06	6,12

Legend: Minimum, mean, maximum and standard deviation (SD) value of the number of cell characters.

5.5 Discussion

The results obtained in this study demonstrate the diversity and anatomical complexity of the secondary xylem of the dominant woody species in the different restinga plant formations. Comparative analysis with the literature allowed the identification of consistent anatomical patterns, as well as variations that may be associated with the environmental pressures characteristic of these coastal ecosystems, including high irradiance, sandy soils, water deficit, and elevated temperatures. These anatomical features, therefore, not only reflect the taxonomic identity of the species but also reveal adaptive strategies critical for survival and ecological performance in restinga environments.

The analysis of the wood of the eight species studied generally agreed with previously published anatomical descriptions, although quantitative variations were observed that may reflect adaptation to the restinga environment. The wood of *Schinus terebinthifolia* exhibits typical characteristics of Anacardiaceae (Metcalfe and Chalk, 1950), with some structural variations. *Pera glabrata*, *Protium heptaphyllum*, and *Cynophalla flexuosa* also conformed to previous reports (Barros et al., 2006; Oliveira, 2007; Sonsin-Oliveira, 2010; Sonsin et al., 2012; Oliveira and Tommasiello-Filho, 2024; Ricardo, 2019), although quantitative differences were noted in the xylem structure. *Sideroxylon obtusifolium* displayed features typical of the genus *Sideroxylon* (Costa, 2006), with measurable variations. The wood of *Scutia arenicola* corresponds to the classic anatomical descriptions of Rhamnaceae (Record and Hess, 1949; Metcalfe and Chalk, 1972), while *Inga maritima* was consistent with the anatomical pattern of Fabaceae (Stüpp et al., 2021). Finally, *Varronia curassavica* showed characteristics compatible with previous literature (Costa, 2006), in addition to quantitative variations in xylem element dimensions, including mean ray height (247 μm) and erect and/or square marginal shapes. These observations underscore the importance of anatomical characterization for understanding the functional diversity of woody species in restinga ecosystems.

In areas with limited water availability, vessel elements tend to be shorter and narrower, more numerous, with reduced diameter and length, shorter fibers, and smaller intervascular pits (Metcalfe and Chalk, 1983; Carlquist, 1977, 2001; Tyree and Zimmermann, 2002; Baas et al., 2004; Sperry, 2006; Santos et al., 2019; Castelar, 2023,

2025). The quantitative variations observed in *S. terebinthifolia* in the *Clusia* formation, compared to the data from Santos et al. (2019), may be related to differences in sampling sites. While Santos et al. (2019) studied a restinga area in Ilha Grande State Park with approximately 2000 mm of annual rainfall, the samples in this study were collected in the *Clusia* formation of Caruara RPPN, where annual precipitation ranges from 800 to 1000 mm (Cruz et al., 2021; Salgado and Vasquez, 2009).

The lower rainfall in the *Clusia* formation of Caruara RPPN indicates more limited water availability, which may explain the anatomical traits observed in *S. terebinthifolia*, including higher vessel density (258 mm²), smaller tangential diameter (26 μm), reduced vessel length (324 μm), and smaller intervascular pits (2.49 μm). These values contrast with those reported by Santos et al. (2019), suggesting that anatomical variations reflect adaptations to water stress in drier environments.

Variations in the anatomical characteristics of *P. glabrata* also appear related to the environmental conditions of the collection site, particularly water availability. Individuals from the *Clusia* formation exhibited higher vessel density (28/mm²) and lower tangential diameter (48 μm), vessel length (619 μm), and fiber length (924.49 μm) compared to values from Barros et al. (2006) in a lowland ombrophilous forest, where annual rainfall is higher (2260 mm). In this more humid environment, lower vessel density (7/mm²), longer vessels (1129.33 μm), larger tangential diameter (133.3 μm), and longer fibers (1593.93 μm) were recorded. In an intermediate condition, Sonsin-Oliveira (2010) observed a vessel density of 20/mm² for *P. glabrata* in a cerrado environment with 1306 mm of annual rainfall. These findings reinforce the influence of water availability on xylem structure and environmental adaptation.

Protium heptaphyllum from the restinga forest formation also displayed quantitative wood variation relative to the literature. In the studied formation, vessel density was lower (68.27 mm²), while vessel length (307.78 μm), diameter (59.88 μm), and fiber length (569.86 μm) were higher. Intervascular (4.64 μm) and ray–vessel pit diameters (4.29 μm) were smaller, rays were wider (19.94 μm), and radial parenchyma density was higher (26.25 mm²). Ricardo (2019), in a gallery forest area of Restinga de Jurubatiba National Park (PARNA), reported higher vessel density (99 mm²), smaller vessel diameter (29.27 μm) and length (183 μm), lower fiber length (98 μm), larger intervascular (5.57 μm) and ray–vessel pits (7.18 μm), narrower rays (9.99 μm), and lower radial parenchyma density (10 mm²). The presence of smaller pits may relate to

increased hydraulic safety, reducing embolism risk (Schmitz et al., 2007). Studies on other species also suggest that wider rays may indicate adaptation to water-limited environments (Marques et al., 2012; Lima et al., 2009).

In *P. heptaphyllum*, a functional compensation pattern was observed, combining hydraulic efficiency via larger vessels with hydraulic safety through increased parenchyma. This dual strategy of conduction and water storage was also identified in *P. glabrata* in Chapter 1, consistent with previous reports (Janssen et al., 2020; Dória et al., 2022; Rodrigues-Zacaro et al., 2021) and particularly relevant in water-limited environments such as restinga. Castelar et al. (2025) highlight that increased parenchyma in vulnerable species aids xylem water release and embolism reversal. In contrast, Ricardo (2019) reported the opposite pattern for *P. heptaphyllum* in PARNA, with denser narrow vessels and lower radial parenchyma investment, prioritizing hydraulic safety. These intraspecific variations reflect phenotypic plasticity under varying water stress levels (Simione et al., 2023; Castelar et al., 2025).

Observed vessel densities for *S. obtusifolium*, *C. flexuosa* (restinga forest), and *V. curassavica* (beach with thickets) were 65, 37, and 99 mm², respectively. Although anatomical data for these species are scarce, available literature allows preliminary comparison. Costa (2006) reported 25 mm² for *S. obtusifolium*, while Lindorf (1994) reported 42 mm² for *C. flexuosa* and 69 mm² for *V. curassavica* in a tropical forest in coastal Mamo, Venezuela, with ~558 mm annual rainfall. Values observed here, particularly for *V. curassavica*, exceed previous reports, suggesting significant variation due to local environmental conditions. For *C. flexuosa*, despite relatively low vessel density, these results support the hypothesis that species in restinga undergo xylem adjustments favoring hydraulic safety over water transport efficiency, adapting to restrictive edaphic and hydric conditions. *I. maritima* and *S. arenicola* were described here for the first time, with no prior quantitative comparison.

Growth layer analysis provides insights into tree development relative to climatic conditions, particularly water availability (Oliveira, 2007; Schweingruber, 1996). Tropical trees in the Amazon form growth layers in response to seasonal drought or flooding; 2–3 months of <60 mm precipitation are sufficient to induce layer formation (Worbes, 1985, 1995). Détienne (1989) observed that growth markers in 30 species across 16 families in Africa and French Guiana formed consistently during dry periods, but intergeneric differences were more influential than climatic factors alone.

All species from the *Clusia* and beach grass and shrub formations exhibited well-defined growth rings, whereas most restinga forest species lacked this feature. Reduced soil water availability in *Clusia* and beach formations generates pronounced dry seasons, favoring ring formation. Conversely, higher soil moisture in restinga forest, especially during winter, corresponds with less frequent growth ring formation (Oliveira et al., 2023). However, growth rings may also reflect genus-specific traits rather than solely environmental water conditions (Détienne, 1989). *P. heptaphyllum* displayed growth rings even in humid restinga forest areas, confirmed by Siosin-Oliveira (2010), with irregular growth layers in multiple Brazilian phytophysiognomies. Ricardo (2019) reported no significant variation in growth layers described as latewood with thick, radially flattened walls, indicating phylogenetic influence. These findings suggest that growth ring formation in tropical trees results from a complex interaction among phylogenetic constraints, morphological traits, and climate variability, highlighting diverse adaptive mechanisms (Souza et al., 2013; Costa, 2021).

Crystals in wood are primarily genetically controlled, with interspecific and intraspecific variation. Accumulation may relate to tree age (Vasconcelos, 1995; Ferreira, 2024). Prismatic crystals can serve as storage and defense against herbivory (Júnior et al., 2016). Water stress can also stimulate crystal formation, more frequently in dry environments (Barajas-Morales, 1985; Fahn et al., 1986; Chimelo and Mattos-Filho, 1988). In this study, crystals were observed in all species except *C. flexuosa* and *V. curassavica*.

5.6 Conclusion

The present study aimed to characterize the components of the secondary xylem of eight woody species dominant in different vegetation formations of restinga, focusing on the understanding of their anatomical strategies in the face of water variations in the environment. The detailed anatomical descriptions revealed attributes consistent with taxonomic patterns of families and genera, in addition to providing unprecedented data for *S. arenicola* and *I. maritima*, whose woods were described for the first time. Variations were observed in elements such as growth rings, vessel dimensions and frequency, parenchyma distribution, type and density of rays and crystals, reflecting

both phylogenetic inheritances and adaptations to the specific environmental pressures of the restinga.

At the community level, the data indicated that water availability directly influences the xylem structure. Species from drier formations, such as the *Clusia* formation, showed characteristics that favor hydraulic safety with more numerous, short and narrow vessels, lower scores. A trade-off in *P. heptaphyllum* was also observed between low vessel frequency and greater investment in radial parenchyma. The comparison with the literature confirmed that drier environments tend to select for more conservative vascular structures, reinforcing the hypothesis that the xylem responds functionally to the water gradient.

The presence of growth rings varied between species and reflected both climatic seasonality and phylogenetic constraints, as in *P. heptaphyllum*, which has rings even in humid environments. Crystals were detected in most species, with the exception of *C. flexuosa* and *V. curassavica*, indicating a possible relationship with water stress and defense mechanisms, although complementary histochemical studies are needed.

Thus, the results of this study offer a comprehensive anatomical-functional overview of the evaluated species, contributing not only to the taxonomy, but also to the functional ecology of the restinga vegetation. They show, above all, the role of wood anatomy as an effective tool to understand the structural adaptations of woody plants in environments with water restriction.

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6. Discussão geral

A presente tese foi dividida em dois capítulos, no primeiro capítulo analisamos os ajustes dos atributos das espécies a nível intraespecífico em três formações vegetacionais de restinga. No segundo capítulo, descrevemos o xilema secundário de oito espécies dominantes que ocorrem ao longo das três formações da restinga.

Através PCA e das análises de atributos funcionais a nível intraespecífico, foi possível observar diferenças entre as formações de mata de restinga, de *Clusia* e praial com moitas nos atributos da folha e lenho das espécies relacionados ao desempenho fisiológico. Na formação de *Clusia* e praial com moitas, onde o dossel é mais aberto e a umidade do solo é menor e a irradiância é mais intensa, observamos as seguintes características foliares nas espécies estudadas: *P. glabrata* apresentou e folhas mais espessas com maior área foliar especifica, *S. arenicola* apresentou maior densidade estomática e menor abertura do poro estomático e maior espessura foliar, a espécie *S. terebinthifolia* apresentou menor abertura dos poros estomáticos e redução da área foliar, maior espessura foliar taxas mais altas de transpiração, condutância estomática e teor de massa seca.

Os estômatos desempenham um papel fundamental na regulação do uso de água pelas plantas e no ganho de carbono. Segundo Bertolino *et al*. (2019) baixa umidade no solo, exposição a alta luminosidade, induzem ao aumento da densidade estomática e diminuição de abertura do poro, diminuindo portando e perda de água para o ambiente. Oliveira *et al*. (2023) em seu trabalho com espécies as espécies *Inga laurina* e *Schinus terebinthifolia* no ambiente de restinga encontrou atributos relacionados com a eficiência no uso da água, entre eles o espessamento da lâmina foliar. A maior espessura foliar evita a perda de água e aumenta a sua estocagem (Marschner, 2011), além de influenciar diretamente no aumento da massa foliar específica que representa quantidade de carbono gasto na construção da folha (Pireda *et al*., 2019). A menor área foliar também é uma estratégia para economia de água, pois reduz a área de contato com a luz evitando o superaquecimento e reduzindo a transpiração (Oliveira *et al*., 2023). Já uma maior densidade de estômatos, como menor abertura do poro agiliza a abertura e fechamento dos estômatos, para tentar equilibrar o fluxo de captação do CO_2 com a restrição à perda de água (Lawson e Blatt, 2014). Segundo Bertolino *et al*. (2019) a abertura do poro estomático é influenciada por muitos fatores ambientais, incluindo

mudanças na temperatura, intensidade da luz, concentração atmosférica de CO_2, umidade do ar e teor de umidade do solo, características ambientais que são encontradas na formação de *Clusia* e praial com moitas na restinga. Diferentemente dos resultados encontrados por Oliveira *et al*. (2023), aqui *S. terebinthifolia* na formação de *Clusia* e praial com moitas apresentou maior taxa de transpiração e trocas gasosas quando comparada a mata de restinga. Segundo Oliveira *et al*. (2023) em ambientes mais secos como a restinga ocorre uma menor condutância estomática e menor captação de CO_2 diminuindo a transpiração.

Essas diferenças entre os atributos foliares e fisiológicos observados nas formações de *Clusia* e praial com moitas em detrimento da mata de restinga evidência que as espécies estão investindo em eficiência no uso da água mantendo estratégias mais conservadoras nas formações com dossel mais aberto e solo com menor humidade, enquanto na mata de restinga as espécies parecem investir em maiores taxas de crescimento e assimilação de carbono.

Os resultados revelaram que as espécies estudadas apresentam estratégias hidráulicas distintas e moduladas pelas condições microclimáticas de cada formação. Observou-se uma funcionalidade distinta entre folhas e lenho: enquanto as folhas tendem a otimizar a eficiência no uso da água, especialmente nas formações mais abertas e sujeitas à maior radiação e déficit hídrico, o lenho permanece conservador, priorizando a segurança hidráulica. Esse padrão foi particularmente evidente nas formações de *Clusia* e praial com moitas, onde a alta irradiância e a baixa umidade do solo impõem um forte estresse hídrico. Em contraste, na mata de restinga, com dossel mais fechado e maior disponibilidade hídrica, as espécies apresentaram traços associados à maior eficiência fotossintética e no transporte hídrico. Essa convergência de atributos de folha e lenho ainda não está bem explicada em ambientes costeiros, não havendo um consenso (Costa *et al*., 2020). Porém, alguns trabalhos demonstram que as espécies vegetais podem exibir diferentes combinações de atributos, envolvendo anatomia, morfologia, consequentemente com variações nos tecidos, o que proporciona um ajuste fisiológico eficiente, usando de compensações e coexistindo em ambientes de restinga (Costa *et al*., 2020; Dias *et al*., 2020).

A análise integrada das espécies *Pera glabrata*, *Scutia arenicola* e *Schinus terebinthifolia* evidenciou estratégias distintas de aclimatação. *P. glabrata*, por exemplo, apresentou indícios de ajuste para uso eficiente da água, com destaque para sua alta

densidade estomática na mata de restinga e para a presença de tecidos de armazenamento, como o parênquima axial, que parecem compensar a vulnerabilidade associada aos vasos de maior calibre como observado por Morris *et al*. (2018). Esse conjunto de atributos aponta para uma estratégia de risco calculado, onde a eficiência no transporte hídrico é equilibrada por mecanismos que conferem segurança contra falhas hidráulicas. Costa *et al*. (2020) ao estudar arvores de restinga do litoral Amazônico encontrou várias estratégias de aclimatação adotado pelas árvores, algumas espécies apresentam folhas mais resistentes investindo em segurança hidráulica e lenho priorizando eficiência no uso da água com vasos mais largos.

Já *Scutia arenicola* demonstrou um claro investimento em segurança hidráulica, especialmente nas formações mais secas, por meio de vasos menores, maior frequência de vasos agrupados e elevado teor de tecido parenquimático, sugerindo uma resposta adaptativa robusta ao estresse hídrico. Segundo Donavan *et al*. (2011), em ambientes com escassez de recursos, como a restinga, é comum o desenvolvimento de estratégias mais conservativas para garantir a sobrevivência.

Os dados obtidos estão em consonância com a literatura especializada, como demonstrado por estudos (Wheeler *et al*., 2007; Anderegg *et al*., 2016; Hacke *et al*., 2017), que reforçam a relação entre o ambiente árido e a maior frequência de vasos e tecidos de reserva. A compatibilidade entre nossos achados e a literatura também confirma que o investimento em parênquima é uma estratégia recorrente em espécies submetidas a déficit hídrico, atuando como suporte ao sistema hidráulico em condições extremas (Morris *et al*., 2018). Observamos também que o xilema secundário das espécies investe em segurança hidráulica nas formações de *Clusia* e praial com moitas.

A principal contribuição desta tese está na demonstração de como espécies arbóreas de restinga articulam respostas anatômicas e fisiológicas às pressões ambientais de forma coordenada, ajustando o balanço entre eficiência e segurança hidráulica. Ao integrar dados anatômicos do xilema (elementos de vasos, fibras e parênquima) atributos foliares e trocas gasosas, este trabalho avança no entendimento do funcionamento ecológico das restingas, ecossistemas altamente dinâmicos e ainda pouco compreendidos do ponto de vista funcional.

Contudo, algumas limitações devem ser reconhecidas. O enfoque em espécies dominantes restringe a generalização dos resultados para todo o conjunto florístico da restinga. Além disso, medições sazonais mais amplas e análise do solo poderiam

aprofundar a compreensão dos mecanismos de plasticidade ao longo do ano. Futuros estudos poderiam explorar comparações interespecíficas adicionais.

A análise anatômica do xilema das espécies estudadas nas diferentes formações de restinga revelou um conjunto expressivo de adaptações estruturais relacionadas ao gradiente ambiental, especialmente à disponibilidade hídrica. Mesmo que as folhas sejam consideradas mais plásticas, os dados obtidos demonstram que a anatomia da madeira desempenha um papel fundamental na resposta funcional das espécies lenhosas frente às condições ecológicas locais, refletindo ajustes anatômicos voltados à segurança hidráulica e ao uso eficiente da água.

O objetivo principal do segundo capítulo foi descrever a anatomia do xilema das espécies dominantes em cada formação de restinga, destacando características estruturais relevantes para a adaptação ao gradiente ambiental. De forma semelhante ao que foi apresentado no primeiro capítulo, a descrição anatômica do xilema das espécies arbóreas das formações de restinga revelou uma resposta funcional ativa do xilema secundário às condições ambientais, refletindo ajustes estruturais específicos aos diferentes microclimas característicos desses ecossistemas. As espécies que ocorrem principalmente na formação de *Clusia*, apresentaram características anatômicas que favorecem a segurança no transporte de água, como vasos em maior densidade, de menor diâmetro e comprimento, e pontuações intervasculares reduzidas. Tais traços, amplamente reconhecidos na literatura como estratégias de resistência à embolia (Carlquist, 2001; Tyree e Zimmermann, 2002; Baas *et al*., 2004), foram evidentes em espécies como *S. terebinthifolia*, cujos valores obtidos no presente estudo contrastam fortemente com os de populações da mesma espécie em regiões com maior pluviosidade (Santos *et al*., 2019). A diferença nos valores de densidade de vasos, diâmetro e comprimento dos elementos vasculares entre os ambientes reforça o papel do clima local em especial da precipitação, na modulação da anatomia da madeira.

A similaridade nos padrões anatômicos observada em *P. glabrata* e *P. heptaphyllum* reforça a hipótese de que populações oriundas de formações de restinga sofrem ajustes estruturais no xilema secundário em resposta à menor disponibilidade hídrica. Em comparação com indivíduos provenientes de ambientes mais úmidos, como Florestas Ombrófilas e Matas de Galeria (Barros *et al*., 2006; Ricardo, 2019), essas espécies apresentaram aumento na densidade de vasos e redução no diâmetro e comprimento dos elementos de condução e aumento de parênquima . Tais modificações

indicam uma estratégia funcional conservadora, priorizando a segurança hidráulica frente à escassez hídrica. Resultados semelhantes foram obtidos por Ferreira (2024), ao comparar espécies de floresta ombrófila densa com espécies de restinga, demonstrando que estas últimas tendem a investir em atributos anatômicos que favorecem maior resistência à cavitação e manutenção do transporte de água em solos com baixa retenção hídrica.

Outro aspecto relevante diz respeito à formação dos anéis de crescimento. Foi possível observar que as espécies das formações de *Clusia* e praial com moitas, onde a disponibilidade hídrica varia mais ao longo do ano, tendem a apresentar anéis bem definidos, sugerindo uma relação direta com a sazonalidade climática. No entanto, o padrão observado para *P. heptaphyllum*, que apresentou anéis mesmo em áreas mais úmidas da mata de restinga, indica que fatores genéticos e filogenéticos também interferem nesse processo, como apontado por Détienne (1989). Assim, a formação de anéis parece resultar de uma combinação entre variabilidade climática e características intrínsecas das espécies (Detienne, 1989; Souza *et al*., 2013; Costa, 2021).

A ocorrência de cristais na madeira também se mostrou relevante no contexto ecológico analisado. A presença de cristais em grande parte das espécies pode estar associada a múltiplas funções, incluindo defesa contra herbivoria, armazenamento de substâncias e possíveis respostas ao estresse hídrico (Fahn *et al*., 1986; Barajas-Morales, 1985). A ausência de cristais em *C. flexuosa* e *V. curassavica* pode refletir especificidades fisiológicas ou ecológicas dessas espécies, indicando a necessidade de estudos histoquímicos mais detalhados para aprofundar essa discussão.

De maneira geral, os resultados obtidos neste trabalho indicam que as espécies de restinga não apenas refletem sua história evolutiva, mas também respondem de forma ativa às condições ambientais atuais, ajustando sua anatomia de modo a garantir funcionalidade e sobrevivência. Tais variações estruturais, relacionadas à condução de água, formação de anéis de crescimento e presença de cristais, reforçam a complexidade dos mecanismos adaptativos das espécies lenhosas em ecossistemas tropicais sob influência de gradientes ambientais marcantes.

Essas observações ampliam o conhecimento sobre a ecologia funcional da vegetação de restinga e fornecem subsídios importantes para futuras estratégias de conservação e manejo, especialmente em cenários de mudança climática e intensificação de estresses ambientais.

Em síntese, os resultados desta tese apontam para uma forte influência das condições microambientes e filogenéticas sobre os atributos estruturais e funcionais das espécies de restinga, revelando uma plasticidade ecológica significativa. Essa capacidade de ajuste confere às espécies estudadas resiliência frente a variações ambientais, sendo um elemento-chave para sua persistência em um dos ecossistemas mais heterogêneos e vulneráveis do litoral brasileiro.

7. Conclusão geral

Os resultados desta tese evidenciam que espécies arbóreas de restinga ajustam de forma coordenada atributos anatômicos, fisiológicos e morfológicos em resposta às variações microambientais ao longo de diferentes formações vegetacionais. As folhas demonstraram maior plasticidade, com alterações voltadas à eficiência no uso da água, enquanto o lenho manteve padrões conservadores, priorizando a segurança hidráulica. A análise do xilema secundário revelou adaptações estruturais consistentes com a limitação hídrica, como maior densidade de vasos, redução do diâmetro e presença de parênquima e redução nos diâmetros das pontuações intervasculares. Esses achados destacam a capacidade adaptativa das espécies lenhosas frente a estresses ambientais, reforçando o papel da anatomia vegetal na manutenção da funcionalidade ecológica. A tese contribui significativamente para o entendimento da ecologia funcional da vegetação de restinga e oferece subsídios para sua conservação em cenários de mudança climática.

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9. Anexo: Comprovante de publicação do Artigo 1

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ORIGINAL ARTICLE

How does variation in physiological and structural traits explain the occurrence of plants in different restinga formations?

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Abstract

Key message **This study reveals intraspecific variability in physiological and anatomical traits among tree species in different restinga formations, highlighting their adaptability to changing microclimatic conditions.**

Abstract Climate change, with increasingly frequent drought episodes, threatens the survival of tree species in biodiverse ecosystems like the Atlantic Forest. We investigated whether plants of the same species in different restinga formations exhibit intraspecific variability in physiological and secondary xylem traits. We evaluated five individuals of each of three tree species (*Scutia arenicola* (Casar.) Reissek (Rhamnaceae), *Schinus terebinthifolia* Raddi (Anacardiaceae), and *Pera glabrata* (Schott) Baill. (Peraceae) all of which co-occur across three distinct formations within the restinga of northern Rio de Janeiro State: a beach grass and shrub, a *Clusia* formation, and a sandbanks forest formation. We used standard methods of plant physiology and anatomy to study the traits, focusing on the structure–function relationships between leaf and secondary xylem. The evaluated species exhibited a set of variations in functional traits. While the leaves invested in water-use efficiency, the wood remained conservative, prioritizing hydraulic safety. These traits vary mainly in the *Clusia* and beach grass and shrub formations, where the canopy is open and both soil moisture availability and irradiance are lower and higher, respectively. In the sandbanks forest, where the canopy is closed and soil moisture is higher, a pattern of photosynthetic efficiency, carbon acquisition, and water transport efficiency was observed. The physiological and tissue variation identified in this study may have played a role in the coexistence of the species, allowing them to adjust to variable microclimates among the different restinga formations. This variation may be essential for the persistence of these species, enabling efficient water to use and safety, which is reflected in their maintenance along vegetation gradients over time and under future climate scenarios.

Keywords Atlantic forest · Intraspecific variation · Wood anatomy · Water-use efficiency · Hydraulic safety

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