UNIVERSIDADE DO VALE DO RIO DOS SINOS (UNISINOS)
UNIDADE ACADÊMICA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA
NÍVEL DOUTORADO

CLÁUDIA FONTANA

DENDROCRONOLOGIA NA FLORESTA ATLÂNTICA DE TABULEIROS:

uma abordagem sobre a floresta e o clima

SÃO LEOPOLDO
2017

CLÁUDIA FONTANA

DENDROCRONOLOGIA NA FLORESTA ATLÂNTICA DE TABULEIROS:

uma abordagem sobre a floresta e o clima

Tese apresentada como requisito parcial para obtenção do título de Doutora em Biologia, pelo Programa de Pós–Graduação em Biologia: diversidade e manejo da vida silvestre, da Universidade do Vale do Rio dos Sinos – UNISINOS.

Orientador: Dr. Juliano Morales de Oliveira
Coorientador: Dr. Paulo Cesar Botosso

SÃO LEOPOLDO
2017

FICHA CATALOGRÁFICA

F679d Fontana, Cláudia.
Dendrocronologia na Floresta Atlântica de Tabuleiros: uma abordagem sobre a floresta e o clima / Cláudia Fontana. – 2017.
xi, 123 f. : il. color. ; 30 cm.

Tese (doutorado) – Universidade do Vale do Rio dos Sinos, Programa de Pós-Graduação em Biologia: diversidade e manejo da vida silvestre, São Leopoldo, 2017.
“Orientador: Dr. Juliano Morales de Oliveira ; coorientador: Dr. Paulo Cesar Botosso.”

1. Anéis de crescimento (Botânica). 2. Climatologia. 3. Árvores – Mata Atlântica. 4. Dendrocronologia. I. Título.

CDU 630*55

Dados Internacionais de Catalogação na Publicação (CIP)
(Bibliotecária: Bruna Sant’Anna – CRB 10/2360)

CLÁUDIA FONTANA

Dendrocronologia na Floresta Atlântica de Tabuleiros: uma abordagem sobre a floresta e o clima

Tese apresentada como requisito parcial para obtenção do título de Doutora em Biologia, pelo Programa de Pós–Graduação em Biologia: diversidade e manejo da vida silvestre, da Universidade do Vale do Rio dos Sinos – UNISINOS.
Orientador: Dr. Juliano Morales de Oliveira
Coorientador: Dr. Paulo Cesar Botosso

Aprovada em 28 de novembro de 2017.

BANCA EXAMINADORA

Dra. Cátia Henriques Callado – Universidade Estadual do Rio de Janeiro (UERJ)

Dra. Karin Esemann de Quadros – Universidade da Região de Joinville (UNIVILLE)

Dra. Suzane Both Hilgert Moreira – Universidade do Vale do Rio dos Sinos (UNISINOS)

Dr. Luiz Ernesto da Costa Schmidt – Universidade do Vale do Rio dos Sinos (UNISINOS)

Dr. Juliano Morales de Oliveira – Universidade do Vale do Rio dos Sinos (UNISINOS)

Aos meus pais,

Dirceu Fontana e Lenita Dadalt Fontana

AGRADECIMENTOS

A todos os professores e funcionários do Programa de Pós-Graduação em Biologia da UNISINOS, pela atenção sempre a mim dispensada, pelo apoio e suporte durante o período em que fui aluna nessa universidade.

A todos os colegas do Laboratório de Ecologia Vegetal (LEV), pelo aprendizado, convivência e auxílio nestes últimos quatro anos. Em especial, agradeço à Gabriela Morais Olmedo pelo aprendizado, companhia em congressos e cursos, e pelas boas risadas e paciência durante os longos períodos codatando e "re-codatando" amostras.

A toda equipe que participou dos trabalhos de campo no Espírito Santo, especialmente ao Dr. Juliano Morales de Oliveira e Gabriela Reis-Ávila do LEV, pelo auxílio nas coletas; e ao Geovane Siqueira, biólogo da Reserva Natural da Vale, pelo auxílio na identificação das plantas em campo e fornecimento de dados adicionais para a tese.

Às minhas coorientadas de Iniciação Científica, Alessandra Nunes de Amorin e Victória Centeno, a Danusa Lobo, bolsista pelo projeto Biomas e Giovana De Filippo Low, pelo auxílio com minha pesquisa e pela oportunidade de aprender e crescer pessoal e profissionalmente junto a elas.

Ao Laboratório de Anatomia da Madeira da Universidade Federal do Paraná, especialmente ao Ramiro França, pela dedicação ao me repassar as técnicas de anatomia da madeira durante meu estágio nessa instituição.

Sou imensamente grata aos colegas da Universidade de São Paulo (USP) - Escola Superior de Agricultura "Luiz de Queiroz" (ESALQ) de Piracicaba, pelo carinho, entusiasmo e dedicação, e toda a disponibilidade em me ensinar durante e após meu estágio nessa universidade. À Maria Bermudez, Luiz Santini, Ricardo Ortega, e especialmente ao Dr. Mario Tomazello Filho, por fazerem parte de momentos importantes e decisivos do meu doutoramento.

Ao Dr. Cláudio Sérgio Lisi, da Universidade Federal de Sergipe, pelas preciosas dicas de dendrocronologia; elas mudaram minha forma de olhar esta ciência. Agradeço especialmente à intervenção junto a Universidade de Coimbra, o que me possibilitou realizar o sonho de fazer parte do meu doutorado sanduíche nessa renomada instituição. Não existem palavras capazes de expressar o quanto sou grata.

Ao Dr. José Luis Lousada, da Universidade de Trás-os-Montes e Alto Douro (UTAD) e toda sua equipe, pela acolhida, ensinamentos e auxílio em minha pesquisa. Em especial, agradeço ao técnico de laboratório desta instituição, o Sr. Armindo Gonçalves Teixeira, pela dedicação,

assistência e entusiasmo com que acolheu minha pesquisa, bem como sua presteza em me apresentar o belo campus dessa universidade. Os dias de estágio na UTDA serão inesquecíveis para mim.

Faço um especial agradecimento à Dra. Cristina Nabais, da Universidade de Coimbra, bem como a todos de sua equipe, pela acolhida, conhecimento compartilhado, orientação e apoio em todas as publicações às quais resultaram nesta tese. Especialmente, agradeço aos colegas Dr. Gonzalo Pérez de Lis Castro e Ana Carvalho por toda ajuda recebida.

Agradeço também ao meu orientador na UNISINOS, Dr. Juliano Morales de Oliveira e ao meu coorientador, Dr. Paulo Cesar Botosso (Embrapa Florestas), pelas oportunas contribuições ao longo do período do doutorado.

Finalmente, agradeço a toda minha família pelo apoio, suporte, paciência e compreensão a mim dedicados nesses últimos quatro anos. E à Mel, que me levou à biologia.

Meus sinceros agradecimentos!

"Só se nos detivermos a pensar nas pequenas coisas chegaremos a compreender as grandes."
José Saramago

RESUMO

Esta tese tem como objetivo contribuir para a compreensão da influência do clima sobre o crescimento das espécies arbóreas tropicais. Para isso, realizou-se uma revisão das pesquisas dendrocronológicas com abordagem climática desenvolvidas no Bioma Mata Atlântica (MA), buscando verificar os sinais climáticos evidenciados, bem como os métodos aplicados às cronologias. A anatomia da madeira de *Copaifera lucens* foi pesquisada com foco nas características anatômicas dos anéis de crescimento. Adicionalmente, também foi testada a influência do clima sobre seu crescimento. Os resultados da revisão da literatura mostraram que poucas espécies são exploradas por meio de dendrocronologia (10 spp.), e não há estudos para a região norte deste bioma. Os sinais climáticos relacionados à precipitação foram observados em 87% das cronologias e com temperatura em 50% delas, embora não haja sincronismo entre os períodos de influência dessas variáveis nas espécies. Os resultados dos estudos acerca da anatomia da madeira adicionaram características anatômicas anteriormente não descritas para *C. lucen*s, como a presença de fibras gelatinosas, fibras bifurcadas (crescimento intrusivo) e vasos agrupados. Embora as pesquisas que se referem à anatomia da madeira contribuam para a compreensão da estrutura da madeira, estudos de atividade cambial são indicados para esclarecer a formação dos anéis anuais e intranuais e, especialmente, a formação de canais secretores. Os resultados dos estudos dendrocronológicos demonstram que *C. lucens*, apesar da elevada variação de crescimento dentro e entre árvores, é promissora para reconstrução climática. Suas séries de anéis apresentaram forte correlação positiva com o índice de evapotranspiração em relação ao verão corrente. Os cenários climáticos para a região de ocorrência da espécie apontam redução na precipitação, podendo-se inferir que seu crescimento no futuro será comprometido. Como conclusão geral, observa-se que os efeitos do clima na MA ainda são pouco explorados através da dendrocronologia. É necessário intensificar estudos dendroclimáticos visando esclarecer as influências do clima nas diferentes fitofisionomias deste bioma. A anatomia do gênero *Copaifera* é complexa e os fatores que controlam a formação de anéis anuais merecem mais esforços de investigação. Dada a marcada sensibilidade das séries de largura de anéis à disponibilidade hídrica de verão e à considerável longevidade de suas árvores, *C. lucens* tem elevado potencial para reconstruções dendroclimáticas na região centro-norte do Bioma Mata Atlântica.

Palavras-chave: Anéis de crescimento. *Copaifera lucens*. Fabaceae. Sinais climáticos.

ABSTRACT

This thesis aimed to contribute to the understanding of the influence of climate on the growth of tropical tree species. For that, a review of the dendrochronological researches with a climatic approach developed in the Atlantic Forest Biome was carried out, seeking to verify the evidenced climatic signs and the methods applied to the chronologies. The wood anatomy of *Copaifera lucens* was investigated with a focus on the anatomical characteristics of the growth-rings. It has also tested the influence of climate on its radial growth. The results of the literature review showed that few species are explored through dendrochronology (10 spp.), and there are no studies for the northern part of this biome. Climatic signals related to precipitation were observed in 87% of the chronologies and to temperature in 50% of them, although there is no synchronism between the periods of the influence of these variables in the species. The results of the wood anatomy added anatomical characteristics previously not described for *C. lucens*, such as gelatinous fibers, bifurcated fibers (intrusive growth) and cluster vessels. Although the wood anatomy contributes to the understanding of the wood structure, studies of cambial activity are showed to clarify the formation of the annual and intra-annual rings, and especially the formation of secretory canals. The results of the dendrochronological studies demonstrate that *C. lucens*, despite the high growth variation within and between individuals, is promising for climate reconstruction. Their series presented a strong positive correlation with the evapotranspiration index for the current summer. The climatic scenarios for the region of occurrence of the species show a reduction in precipitation, and it can be inferred that its growth in the future will be compromised. As a general conclusion, it was observed that the effects of climate in the Atlantic Forest are still little explored through dendrochronology. It is necessary to intensify dendroclimatic studies to clarify the climatic influences in the different phytophysiognomies of this biome. The anatomy of the *Copaifera* genus is complex and the factors that control the formation of the annual ring deserve more research efforts. Given the marked sensitivity of the ring width series to the water availability of summer and the considerable longevity of its trees, *C. lucens* has a high potential for dendroclimatic reconstructions in the northern region of the Brazilian Atlantic Forest.

Key-words: Climatic signals. *Copaifera lucens*. Fabaceae. Tree-rings.

SUMÁRIO

CAPÍTULO 1

INTRODUÇÃO GERAL

O presente trabalho foi concebido no escopo do Projeto Biomas[1], especificamente ao subprojeto denominado Mata Atlântica 23 (MA23), sob coordenação da Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), com financiamento da Confederação Nacional da Agricultura (CNA) e apoio técnico da empresa Vale do Rio Doce (VRD). O sítio de estudo do projeto Biomas é a Reserva Natural da Vale (RNV), uma área de conservação privada localizada ao sul da Floresta Atlântica de Tabuleiros, no Estado do Espírito Santo.

A proposta do MA23 é estudar a estrutura etária e o crescimento retrospectivo de espécies arbóreas nativas em relação a condições edafoclimáticas. Entre as ações do projeto, consta a realização de estudos dendrocronológicos e de anatomia do lenho. Esses estudos têm por objetivo compreender a dinâmica de espécies arbóreas nativas e sua relação com condições de sítio e variações de clima (temperatura e precipitação), com vistas a subsidiar a seleção de espécies para plantios mistos.

Neste contexto, esta tese de doutoramento tem como objetivo trazer contribuições para as áreas da anatomia da madeira e dendrocronologia no âmbito das florestas tropicais. Para tanto, divide-se em cinco capítulos, utilizando a espécie *Copaifera lucens* DWYER (Fabaceae) como modelo com a finalidade de testar a influência climática sobre essa floresta. Assim, o primeiro capítulo apresenta a introdução geral ao trabalho aqui desenvolvido, abordando os principais tópicos que são explorados nos capítulos posteriores, os quais são expostos na forma de artigos científicos. No segundo capítulo, desenvolvido junto com colaboradores, objetivou-se revisar os estudos dendrocronológicos com espécies da Mata Atlântica, com vistas a conhecer as respostas climáticas evidenciadas para essa floresta, bem como avaliar os métodos empregados nas cronologias. No terceiro capítulo, o propósito foi descrever a anatomia da madeira de *C. lucens*, focando na compreensão da estrutura dos anéis de crescimento com vistas a estudos dendrocronológicos. No quarto capítulo, o foco foi testar a sensibilidade climática de *C. lucens* para aplicação em reconstrução climática. Por fim, no quinto e último capítulo, apresento as conclusões e recomendações da pesquisa desenvolvida.

---

[1] O projeto Bioma tem por objetivo "[...] apresentar aos produtores rurais modelos de uso da árvore com fins econômicos e ambientais". PROJETO BIOMAS. O que é o Projeto Biomas. Disponível em: http://www.projetobiomas.com.br/projeto/. Acesso em: 05 dez. 2016.

1.1 A FLORESTA ATLÂNTICA DE TABULEIROS

A Mata Atlântica (MA) é considerada um dos *hotspots* mundiais em virtude de sua elevada riqueza biológica e dos níveis de ameaça a que está sujeita (MYERS et al., 2000). Dentre as diversas fitofisionomias abrigadas na MA, encontra-se a Floresta Atlântica de Tabuleiros (FAT), cuja compreensão da peculiar vegetação tem despertado o interesse de muitos pesquisadores, em especial, da sua área núcleo localizada no estado do Espírito Santo. A FAT é considerada, globalmente, como a área com maior diversidade de espécies da flora por hectare: 458 plantas/ha, sendo 405 espécies arbóreas e 53 lianas (THOMAS, 2008). É um dos 14 Centros de Diversidade de Plantas do Brasil, sendo a Reserva Natural da Vale (área deste estudo) reconhecida pela UNESCO como Posto Avançado da Reserva da Biosfera na Mata Atlântica (PEIXOTO e JESUS, 2016). Além da imensa diversidade florística, essa floresta abriga importante diversidade fitofisionômica, incluindo campos nativos, caracterizados por uma vegetação predominantemente graminóide e mussunungas, tipificadas por uma vegetação arbórea-arbustiva baixa e aberta sobre solos arenosos (JESUS, 2001; GARAY et al., 2003; ROLIM; IVANAUSKA; ENGEL, 2016).

As florestas que cobrem o Espírito Santo aparecem ora associadas ao bloco florístico do Nordeste (com elementos amazônicos) ora ao bloco Sul/Sudeste (com elementos atlânticos) (SIQUEIRA, 1994; AGAREZ; GARAY; VÍNCENS, 2003). Isso sugere uma sobreposição da distribuição fitogeográfica de dois grandes blocos florísticos (SIQUEIRA, 1994). A FAT diferencia-se da Floresta Atlântica *sensu strictu* pela quase total ausência de epífitos, musgos, líquens, aráceas e polipodiáceas, entre outras; assemelhando-se à Hiléia[2] de Terra Firme Amazônica (GARAY et al., 2003). Por outro lado, contrapondo-se à Hiléia Amazônica, as árvores emergentes não superam os 40 metros de altura e aparecem entrelaçadas a abundantes lianas, elementos que indicam uma menor disponibilidade hídrica; aproximando a fisionomia às florestas africanas de baixas latitudes (PEIXOTO e GENTRY, 1990). De modo geral, há consenso entre os autores no que diz respeito à mistura florística nas Florestas de Tabuleiros do sul da Bahia e norte do Espírito Santo (RIZZINI, 1963;

---

[2] Nome proposto por Alexander von Humboldt, que utilizou a nomenclatura de Heródoto para designar a floresta equatorial sempre verde que vai das encostas orientais dos Andes, por todo o vale do Amazonas, até as Guianas. Ver mais em KOHLHEPP, G. Descobertas científicas da Expedição de Alexander von Humboldt na América Espanhola (1799-1804) sob ponto de vista geográfico. **Revista de Biologia e Ciências da Terra**, São Cristóvão, v. 6, n. 1, p. 264, 2006.

PEIXOTO e GENTRY, 1990; VELOSO, 1991; SIQUEIRA, 1994; JESUS e ROLIM, 2005). Por outro lado, para alguns pesquisadores, em razão de sua originalidade de estrutura e composição florística, a FAT merecia ser considerada uma formação singular (GARAY et al., 2003).

A classificação fitofisionômica da FAT ainda é objeto de discussão entre os pesquisadores. O Instituto Brasileiro de Geografia e Bioestatística (IBGE, 2012) classifica a fitofisionomia vegetal ao longo do litoral do Espírito Santo como Floresta Ombrófila Densa das Terras Baixas, e também a denominada “Florestas dos Tabuleiros”, apresentando-se desde a Amazônia até o Estado do Rio de Janeiro; e como Floresta Estacional Semidecidual de Terras Baixas, que se estende desde o sul de Natal (RN) até o norte do Estado do Rio de Janeiro. Contudo, a região que compreende os tabuleiros localizados no Espírito Santo e sul da Bahia tem regime de precipitação estacional bem definido (GARAY et al., 2003), o que a diferencia de outras fitofisionomias da MA. Quanto ao caráter estacional, Engel (2001), em monitoramento fenológico de dez anos na RNV, observou que aproximadamente 12,2% das espécies são caducifólias, 43,9% brevidecíduas e 43,9% são sempre-verdes. Adicionalmente, em torno de 30% das espécies e 15% das árvores apresenta queda total ou quase total de folhas, predominantemente no fim da estação seca (setembro) e início da chuvosa (outubro). Apesar disso, Engel (2001) considera que a semideciduidade na RNV é intermediária, sendo mais apropriado classificá-la como Floresta Estacional Perenifólia. Todavia, baseados em estudos mais recentes, os quais levam em conta as curvas de precipitação e as fenofases das espécies florestais na RNV, Jesus e Rolim (2005) consideram que se trata de uma Floresta Estacional Semidecidual de Terras Baixas.

Outra importante característica da FAT é o regime de precipitação anual e interanual. O período que vai de maio a setembro é caracterizado pela diminuição na precipitação, com médias mensais abaixo de 60 mm, não excedendo a 25% do total anual (VÍNCENS, AGAREZ e GARAY, 2003). Embora na FAT prevaleçam estações climáticas bem definidas, há anos em que não ocorre uma estação seca bem marcada (JESUS, 2001). Dessa forma, as médias climáticas mascaram a principal característica climática regional - que é a variação interanual das precipitações -, as quais podem chegar a reduções de 50% e desencadear secas anuais recorrentes (GARAY e SILVA, 1995). Assim, mesmo quando as precipitações anuais alcançam os valores médios, pode haver déficit hídrico no período de baixa precipitação no ano. Para Rolim, Ivanauska e Engel (2016) parece não haver dúvidas a respeito da estacionalidade climática na FAT, com um período seco de até cinco meses que se estende do final do outono ao final do inverno. Os autores acrescentam: “[...] é necessário entender como as plantas suportam períodos prolongados de seca e quais seriam as estratégias por elas utilizadas para sobreviver ao período desfavorável [...]” (ROLIM, IVANAUSKA e ENGEL, 2016, p. 52), e destacam que nenhum estudo com esses propósitos foi desenvolvido nas florestas da região.

A FAT tem sido amplamente investigada em termos de composição florística e faunística, paleoecologia, fitogeografia, diversidade funcional, restauração florestal, produtividade, solos, entre outros (GARAY et al., 2003; ROLIM, MENEZES e SRBEK-ARAUJO, 2016). Contudo, estudos dendrocronológicos são escassos para essa fitofisionomia, destacando-se o trabalho realizado por Costa et al. (2015), cuja investigação comparou a taxa de crescimento dos anéis anuais de cinco espécies de leguminosas em plantio experimental. Assim, demonstrou-se variação no crescimento de todas as espécies, mesmo sob as mesmas condições de plantio. Os autores atribuem essa diferença à influência de distúrbios endógenos no crescimento das espécies avaliadas, os quais podem desencadear crescimento não sincrônico entre as árvores.

1.2 ANATOMIA DA MADEIRA: XILEMA SECUNDÁRIO

O xilema secundário (do grego *xylon* = madeira) é um conjunto diversificado de tipos de células com propriedades específicas, que desempenham funções vitais. Ele é o principal tecido condutor de água nas plantas vasculares, também envolvido no transporte de solutos, na sustentação e no armazenamento de substâncias (FAHN, 1985; BAAS e WHEELER, 2011; EVERT, 2013). Nas angiospermas, as principais células xilemáticas são os elementos de vasos, as fibras libriformes e fibrotraquídes, e as células parenquimáticas (EVERT, 2013). O desenvolvimento, a função, a organização e as peculiaridades estruturais dessas células que constituem o lenho são objeto de estudo da anatomia da madeira (FAHN, 1985; LARSON, 1994; EVERT, 2013).

As células xilemáticas se originam da atividade do meristema lateral (câmbio vascular) por divisões periclinais e anticlinais, as quais dão origem às células iniciais fusiformes (verticalmente orientadas) e iniciais radiais (horizontalmente orientadas), respectivamente (FAHN, 1985; LARSON, 1994; EVERT, 2013). A xilogênese compreende quatro principais processos (SCHWEINGRUBER, 2007), a saber: (i) *formação* (divisão), no qual o número de células por zona de crescimento é definido; (ii) *diferenciação*, o qual determina função e forma das células; (iii) *alongamento*, no qual as células não especializadas atingem seu tamanho e forma final e (iv) *espessamento da parede* (diferenciação e lignificação da parede), em que as células especializadas atingem a estabilidade para lidar com estresse fisiológico e mecânico, e para desempenhar suas funções de condução e sustentação.

Quando o câmbio está ativo, o processo de divisão supera o de diferenciação (a zona cambial possui várias camadas de células); durante a diferenciação, há um equilíbrio entre os processos (a zona cambial e a zona diferenciada tem mais ou menos a mesma quantidade de camadas células); quando o ritmo de divisão diminui, a diferenciação é mais rápida e a zona cambial se estreita (FAHN et al., 1981). Esses processos determinam o ritmo da atividade cambial, eles são influenciados por fatores genéticos e ambientais e, em muitas espécies, ficam marcados na madeira em forma de círculos concêntricos no tronco, denominados de anéis de crescimento (FRITTS, 1976; FAHN, 1985; SCHWEINGRUBER, 2007).

Em muitas espécies, a xilogênese tem um ciclo anual o qual permite distinguir seu início e término por intermédio do reconhecimento dos limites (marcadores) dos anéis de crescimento. Nos trópicos, muitas espécies apresentam ciclo anual e os limites dos seus anéis constituem quatro principais características (WORBES, 1989); são elas: (i) Zona fibrosa com múltiplas fileiras de células, sendo as fibras com diâmetro reduzido e paredes espessadas no lenho tardio; (ii) Banda de parênquima axial marginal uni ou multiseriada, muitas vezes com células preenchidas com substâncias fenólicas ou cristais; (iii) Bandas de parênquima alternadas com faixas de fibra, as quais se tornam mais estreitas perto da borda do anel e (iv) Anéis porosos, marcados pela variação da densidade e/ou diâmetro de vasos ao longo do anel. Quando há anomalias no curso da xilogênese, pode-se formar zonas dentro do anel com características muito semelhantes aos limites dos anéis anuais (DE MICCO et al., 2016). Esses falsos anéis são referidos na literatura também como anéis duplos, múltiplas camadas de crescimento, anéis múltiplos ou bandas de crescimento intra-anual (CAMPELO et al., 2007). Para sumarizar, essas anomalias são tratadas como variações de densidade intra-anual (*intra-annual density fluctuations* – IADFs), causadas por desvios do curso esperado da xilogênese durante a estação de crescimento, e refletem anomalias nas condições ambientais no ano em que o anel está sendo formado (*e.g.*, secas ou cheias fora de época) (CHERUBINI et al., 2003; DE MICCO et al., 2016). Em anos, com extremas condições limitantes, é possível que nenhum anel seja formado, ou que anéis sejam parcialmente formados nos trechos em que nem toda extensão do cambio está ativa (LARSON, 1994).

As IADFs são muito frequentes nas espécies tropicais e constituem um dos maiores desafios para a dendrocronologia pois, se não são identificados, induzem uma sobrestimativa da idade da árvore. Por isso, muitos estudos de anatomia da madeira vêm sendo desenvolvidos a fim de auxiliar no reconhecimento de anéis verdadeiros e IADFs (WORBES, 1989; CHERUBINI et al., 2003; SCHWEINGRUBER, 2007; LISI et al., 2008; GROENENDIJK et al., 2014; LÓPEZ e VILLALBA, 2016). Dada a importância do anel de crescimento para essa ciência, a compreensão de sua anatomia é fundamental para a acurácia da datação das séries temporais de crescimento e a construção da cronologia máster de uma região.

1.3 DENDROCRONOLOGIA

A dendrocronologia foi conceitualmente desenvolvida em regiões temperadas do hemisfério norte, onde a atividade cambial tem um ritmo anual, geralmente relacionada ao comprimento do dia e à sazonalidade na temperatura, o que induz à formação de anéis de crescimento anuais nas plantas lenhosas (FRITTS, 1976; FAHN et al., 1981). Esses anéis são formados em razão de características genéticas e variações ambientais (DE MICCO et al., 2016) e refletem a dormência cambial, a qual é evidenciada pela configuração das células que formam o xilema (CHERUBINI et al, 2003). Esse padrão pode ser interrompido por período de secas no verão (FAHN et al., 1981), o que frequentemente leva a formação de IADF (SCHWEINGRUBER, 2007).

Em climas tropicais, as temperaturas tendem a ser homogêneas ao longo do ano (FAHN et al., 1981; LARSON, 1994; SCHWEINGRUBER, 2007) e, embora a precipitação seja considerada elevada, demonstrou-se que ocorrem períodos secos sazonais no ano em que são capazes de induzir a formação de anéis de crescimento anuais (BOTOSSO e VETTER, 1991). Conforme Worbes (1995), em ambientes tropicais, precipitações inferiores a 60 mm mensais e estações secas de dois a três meses podem desencadear a formação de anéis de crescimento. Por outro lado, o excesso de água também é capaz de induzir a formação de anéis anuais. Assim, estudos têm sido desenvolvidos com o objetivo de explicar as respostas das espécies tropicais quanto à disponibilidade hídrica, tais como: (i) o déficit hídrico em regiões como a Caatinga (PAGOTTO et al., 2017) e (ii) os pulsos de cheias sazonais, como na Amazônia (SCHÖNGART et al., 2005). Contudo, as reações das árvores tropicais à estação seca são mais complexas em relação às baixas temperaturas em clima temperado. Isso porque há outros mecanismos utilizados pelas plantas tropicais para evitar os efeitos da sazonalidade na precipitação, como o acesso a reservas de água no solo e outra variedade de mecanismos (BORCHERT, 1994, 1998; O'BRIEN et al. 2017). A presença de IADFs também é muito frequente nos trópicos, embora pouco investigada (DE MICCO et al., 2016).

A dendrocronologia está fundamentada em alguns princípios e conceitos (FRITTS, 1976; COOK, 1985), os quais podem ser elencados da seguinte forma (Figura 1):

Princípios da dendrocronologia

a) *Princípio da uniformidade*: os fatores que limitaram o crescimento no passado são os mesmos do presente, mas pode ter havido mudança na frequência e intensidade em que ocorreram.

b) *Princípio dos fatores limitantes*: somente se um ou mais fatores ambientais se tornarem criticamente limitantes ao crescimento, e persistirem tempo suficiente em uma ampla área geográfica, causarão variação na largura dos anéis da mesma forma e em muitas árvores.

c) *Princípio da amplitude ecológica*: quanto mais próxima a árvore estiver do seu limite de distribuição, o clima se torna o principal fator limitante ao crescimento e ela será mais sensível a estudos dendrocronológicos.

d) *Princípio da seleção de sítio*: limitar o espaço de amostragem de modo a reduzir a influência de variáveis não desejadas que possam interferir no crescimento.

e) *Princípio da sensitividade*: quanto mais a árvore for limitada por fatores ambientais, maior será a variação na largura de anel para anel (quanto mais variação, maior sensibilidade).

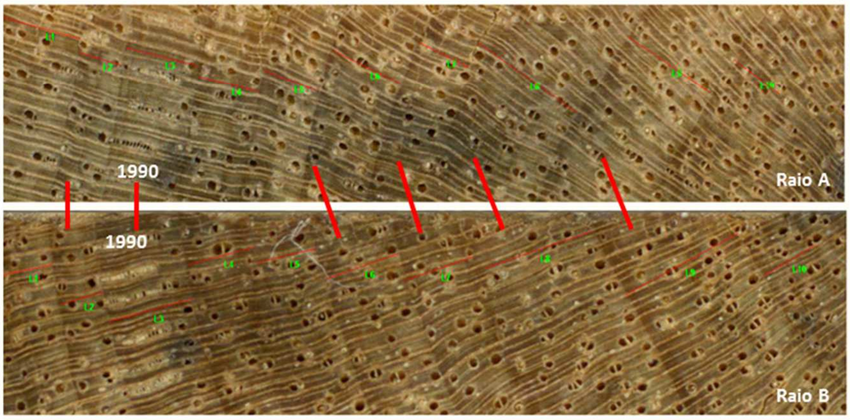
f) *Princípio da replicação*: a replicação possibilita que uma grande porção de efeitos não climáticos, os quais diferem entre indivíduos e de sítio para sítio, sejam minimizados pela média das amostras.

g) *Princípio do "Crossdating"* (codatação): é o mais importante princípio da dendrocronologia. Implica que o padrão de anéis largos e estreitos das amostras de uma árvore esteja relacionado entre si, e que as árvores de um sítio perpetuem essa relação, assim como as árvores de distintos sítios apresentem o mesmo padrão de largura de anéis em uma série temporal. Assim, o *crossdating* é possível quando condições ambientais similares limitam as larguras dos anéis em muitas árvores, produzindo um sincronismo na estrutura do anel que permita atribuir uma data exata para cada anel.

h) *Princípio do crescimento agregado* (padronização): o crescimento da planta é produto de diversos fatores. Nesse sentido, Cook (1987) desenvolveu uma equação que decompõe as interferências no crescimento das plantas em um modelo teórico com cinco variáveis principais, expressadas da seguinte forma:

$$Rt = At + Ct + \delta D1t + \delta D2t + Et$$

Onde:
- R*t* = largura observada do anel
- A*t* = tendência da largura do anel relacionada com a idade
- C*t* = sinal relacionado ao clima
- D1*t* = pulso causado por distúrbio endógeno de ação individual (ex. clareiras)
- D2*t* = pulso causado por distúrbio exógeno comum à população (ex. incêndios)
- E*t* = variabilidade não relacionada aos demais fatores ano a ano.



Fonte: FRITTS (1976) e COOK (1985, 1987).

Figura 1: Princípios e conceitos da dendrocronologia. Ilustração inferior mostra o processo de codatação, que relaciona e atribui um ano calendário para cada anel da amostra. Destaque para o ano de 1990, onde é possível visualizar um alinhamento dos vasos (variação endógena, *e.g.*, patógenos). Imagens do lenho de *Ocotea notata* (Nees & Mart.) Mez. (Lauraceae). Fonte: Elaborado pela autora.

O modelo acima proposto por Cook (1985) distingue as principais fontes de variação da largura do anel, considerando suas inter-relações e sugere algumas abordagens estatísticas para estudá-las (FRITTS e SWETNAM, 1989). Em abordagens climáticas, o objetivo é isolar o sinal da variável climática (C*t*) e minimizar os outros ruídos e erros aleatórios que também influenciam no crescimento da planta. A remoção de tendências não desejadas e a padronização das séries cronológicas são executadas em *software* desenvolvidos para aplicação em estudos dendrocronológicos (*e.g.*, HOLMES, 1986; COOK e HOLMES, 1996; RINN, 2011), os quais contribuem sobremaneira com tais pesquisas.

Em resumo, a dendroecologia investiga a relação dos anéis de crescimento com condições ambientais do passado. As informações podem ser aplicadas com o intuito de predizer o crescimento futuro (FRITTS, 1976; SCHWEINGRUBER, 1988; PAYETTE e FILION, 2010; SPEER, 2010). Quando aplicada de forma apropriada, essa ciência pode resolver uma variedade de problemas em muitos campos de pesquisa (FRITTS, 1976). Esses estudos ajudam a compreender a dinâmica do crescimento florestal e mostram-se, na atualidade, como uma importante ferramenta para gestão sustentável das florestas (SPIECKER, 2002; WORBES, 2002).

1.4 OBJETIVOS

Na presente tese de doutoramento, com o título “Dendroecologia na Floresta Atlântica de Tabuleiros: uma abordagem sobre a floresta e o clima”, objetivou-se, de forma geral, analisar os efeitos do clima sobre o crescimento de espécies arbóreas desta formação florestal tropical. Para isso, foram delineados alguns objetivos específicos, sendo eles: *i.* Investigar se as espécies estudadas até o momento na Mata Atlântica, por meio de evidencias apresentadas em cronologias robustas, têm seu crescimento radial afetado pelo clima; *ii.* Avaliar se há características anatômicas na madeira de *C. lucens* que possam ser úteis no reconhecimento dos limites dos anéis de crescimento; *iii.* Testar a influência do clima no crescimento radial de *C. lucens.*

REFERÊNCIAS

AGAREZ, F. V.; GARAY, I.; VÍNCENS, R. S. A floresta em pé: conservação da biodiversidade nos remanescentes de Floresta Atlântica de Tabuleiros. In: GARAY, I.; RIZZINI, M. C. (Ed.). **A Floresta Atlântica de Tabuleiros:** diversidade functional da cobertura arbórea. Petrópolis: Vozes, 2003. p. 27–34.

BAAS, P.; WHEELER, E. A. Wood anatomy and climate change. In: HODKINSON, T. R.; JONES, M. B.; WALDREN, S.; PARNELL, J. A. N. (Ed.). **Climate Change, Ecology and Systematics**. Cambridge: Cambridge University Press, 2011. p. 141–155.

BORCHERT, R. Water status and development of tropical trees during seasonal drought. **Trees**, v. 8, n. April, p. 115–124, 1994.

BORCHERT, R. Responses of tropical trees to rainfall seasonality. **Climatic Change**, v. 39, p. 381–393, 1998.

BOTOSSO, P. C.; VETTER, R. E. Alguns aspectos sobre a periodicidade e taxa de crescimento em 8 especies arboreas tropicais de floresta de terra firme (Amazonia). **Rev. Inst. Flor.**, Sao Paulo, v. 3, n. 2, p. 163–180, 1991.

CAMPELO, F.; NABAIS, C.; FREITAS, H.; GUTIERREZ, E. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. **Annals of Forest Science**, v. 64, n. 2006, p. 229–238, 2007.

CHERUBINI, P.; GARTNER, B. L.; TOGNETTI, R.; BRÄKER, O. U.; SCHOCH, W.; INNES, J. L. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. **Biological reviews of the Cambridge Philosophical Society**, v. 78, n. 1, p. 119–148, 2003.

COOK, E. R. **A time series analyses approach to tree ring standardization**. 1985. (Tese). University of Arizona, 1985.

COOK, E. R. The decomposition of tree-ring series for environmental studies. **Tree-Ring Bull**. v. 47, p. 37–59, 1987.

COOK, E. R.; HOLMES, R. L. Guide for computer program ARSTAN. In: GRISSINO-MAYER, H. D.; HOLMES, R. L.; FRITTS, H. C. (Ed.). **The international tree-ring data bank program library version 2.0 user'smanual.** Tuscson: Laboratory of Tree-Ring Research, University of Arizona, 1996. p. 75–87.

COSTA, M. S.; FERREIRA, K. E. B.; BOTOSSO, P. C.; CALLADO, C. H. Growth analysis of five Leguminosae native tree species from a seasonal semidecidual lowland forest in Brazil. **Dendrochronologia**, v. 36, n. November, p. 23–32, 2015.

DE MICCO, V.; CAMPELO, F.; DE LUIS, M.; BRÄUNING, A.; GRABNER, M.; BATTIPAGLIA, G.; CHERUBINI, P. Intra-annual density fluctuations in tree rings: how, when, where, and why? **IAWA Journal**, v. 37, n. 2, p. 232–259, 2016.

ENGEL, V. L. **Estudo fenológico de espécies arbóreas de uma floresta tropical em**

Linhares, ES. 2001. (Tese). Universidade de Campinas, 2001.

EVERT, R. F. **Anatomia das plantas de ESAU:** meristemas, células e tecidos do corpo da planta: sua estrutura, função e desenvolvimento. São Paulo: Blucher, 2013.

FAHN, A. **Anatomia vegetal**. 3. ed. Madrid: Ediciones Pirámides, 1985.

FAHN, Ab.; BURLEY, J.; LONGMAN, A. K.; MARIAUX, A.; TOMLINSON, B. B. Possible contributions of wood anatomy to the determination of the age of tropical trees. In: BORMANN, F. H.; BERLYN, G. (Ed.). **Age and growth rate of tropical trees:** new directions for research. New Haven: Yale University, 1981. p. 137.

FRITTS, H. C. **Tree rings and climate change**. New York: Academic Press Inc Ltd., 1976.

FRITTS, H. C.; SWETNAM, T. W. Dendroecology: a tool for evaulating variations in past and prestent forest environments. **Advances in Ecological Research**, v. 19, n. C, p. 111–188, 1989.

GARAY, I.; KINDEL, A.; LOUZADA, M. A. P.; DOS SANTOS, D. A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. In: GARAY, I; RIZZINI, C. M. (Eds.). **A Floresta Atlântica de Tabuleiros:** diversidade functional da cobertura arbórea. Petrópolis: Vozes, 2003. p. 16–26.

GARAY, I.; SILVA, B. A. O. Húmus florestais: síntese e diagnósticos das interrelações vegetação/solo. **Oecologia Brasiliensis**, v. 1, n. 1, p. 19–46, 1995.

GROENENDIJK, P.; SASS-KLAASSEN, U.; BONGERS, F.; ZUIDEMA, P. A. Potential of tree-ring analysis in a wet tropical forest: a case study on 22 commercial tree species in Central Africa. **Forest Ecology and Management**, v. 323, n. July, p. 65–68, 2014. Disponível em: <http://dx.doi.org/10.1016/j.foreco.2014.03.037>.

HOLMES, R. L. Quality control of crossdating and measuring: a user's manual for program COFECHA. In: HOLMES, R. L.; ADAMS, R. K.; FRITTS, H. C. (Ed.). **Tree-ring chronologies of western North America: California, eastern Oregon and northern Great Basin with procedures used in the chronology development work including user's manuals for computer programs COFECHA and ARSTAN**. Tucson: Laboratory of Tree-Ring Research, University of Arizona, 1986. p. 41–49.

IBGE. INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA. **Manual técnico da vegetação brasileira.** 2. ed. Rio de Janeiro: Coordenação de Recursos Naturais e Estudos Ambientais (Série manuais técnicos de geociências), 2012.

JESUS, R. M. **Manejo florestal:** impactos da exploração na estrutura da floresta e sua sustentabilidade econômica. 2001. (Tese). Universidade de Campinas., 2001.

JESUS, R. M. D.; ROLIM, S. G. Fitossociologia da Mata Atlântica de Tabuleiro. Boletim Técnico. **Sociedade de Investigações Florestais**, v. 17, p. 1–154, 2005.

KOHLHEPP, G. Descobertas científicas da Expedição de Alexander von Humboldt na América Espanhola (1799-1804) sob ponto de vista geográfico. **Revista de Biologia e Ciências da Terra**, São Cristóvão,v. 6, n. 1, p. 260-278, 2006.

LARSON, P. R. **The vascular cambium:** development and structure. New York: Springer-Verlag, 1994.

LISI, C. S.; TOMAZELLO-FO, M.; BOTOSSO, P. C.; ROIG, F. A.; MARIA, V. R. B.; FERREIRA-FEDELE, L.; VOIGT, A. R. A. Tree-ring formation, radial increment periodicity, and phenology of tree species from a Seasonal Semi-deciduous Forest in Southeast Brazil. **IAWA Journal**, v. 29, n. 2, p. 189–207, 2008.

LÓPEZ, L.; VILLALBA, R. Reliable estimates of radial growth for eight tropical species based on wood anatomical patterns. **Journal of Tropical Forest Science**, v. 28, n. 2, p. 139–152, 2016.

PROJETO BIOMAS. O que é o Projeto Biomas. Disponível em: http://www.projetobiomas.com.br/projeto/. Acesso em: 05 dez. 2016.

MYERS, N.; MITTERMEIER, R.; MITTERMEIER, C.; DAFONESCA, G.; KENT, J. Biodiversity hotspots for conservation priorities. **Conservation Biology**, v. 403, n. February, p. 853, 2000.

O'BRIEN, M. J.; REYNOLDS, G.; ONG, R.; HECTOR, A. Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. **Nature Ecology & Evolution**, v. 1, November, p. 1643-1648, 2017.

PAGOTTO, M. A.; DESOTO, L.; CARVALHO, A.; NABAIS, C.; TOMAZELLO FILHO, M.; RIBEIRO, A.; LISI, C. S. Evaluation of X-ray densitometry to identify tree-ring boundaries of two deciduous species from semi-arid forests in Brazil. **Dendrochronologia**, v. 42, n. February, p. 94–103, 2017. Disponível em: <http://dx.doi.org/10.1016/j.dendro.2017.01.007>.

PAYETTE, S.; FILION, L. **La dendroécologie:** principes, méthodes et applications. Québec: Presses de l'Université Laval, 2010.

PEIXOTO, A. L.; GENTRY, A. Diversidade e composição florística da mata de tabuleiro na Reserva Florestal de Linhares, Espírito Santo, Brasil. **Revista Brasileira de Botânica**, n. 13, p. 19–25, 1990.

PEIXOTO, A. L.; JESUS, R. M. de. Reserva Natural da Vale: memórias de 65 anos de conservação. In: ROLIM, S. G.; MENEZES, L. F. T. DE; SRBEK-ARAUJO, A. C. (Ed.). **Floresta Atlântica de Tabuleiro:** diversidade e endemismo na Reserva Natural Vale. Belo Horizonte: Rona Editora, 2016. p. 496.

RINN, F. **User reference.** Heidelberg: RINNTECH, 2011.

RIZZINI, C. T. Nota Prévia sobre a divisao fitogeográfica do Brasil. **Revista Brasileira de Geografia**, v. 1, n. January-March, p. 1–64, 1963.

ROLIM, S. G.; IVANAUSKA, N. M.; ENGEL, V. L. As florestas de tabuleiro do norte do Espírito Santo São ombrófilas ou estacionais? In: ROLIM, S. G.; MENEZES, L. F. T. DE; SRBEK-ARAUJO, A. C. (Ed.). **Floresta Atlântica de Tabuleiro:** diversidade e endemismo na Reserva Natural Vale. Belo Horizonte: Rona, 2016. p. 47–60.

ROLIM, S. G.; MENEZES, L. F. T. de; SRBEK-ARAUJO, A. C. **Floresta Atlântica de Tabuleiro:** diversidade e endemismos na Reserva natural da Vale . Belo Horizonte: Rona, 2016.

SCHÖNGART, J.; PIEDADE, M. T. F.; WITTMANN, F.; JUNK, W. J.; WORBES, M. Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. **Oecologia**, v. 145, n. 3, p. 454–461, 2005.

SCHWEINGRUBER, F. H. **Tree rings:** basics and applications of dendrochronology. Dordrecht: Kluwer Academic Publischers, 1988.

SCHWEINGRUBER, F. H. **Wood structure and environment**. Birmensdorf: Springer-Verlag Berlin Heidelberg, 2007.

SIQUEIRA, M. F. **Análise florística e ordenação de espécies arbóreas da mata atlântica através de dados binários**. 1994. (Tese). Universidade de Campinas, 1994.

SPEER, J. H. **Fundamentals of tree-ring research**. Tucson: University of Arizona Press, 2010.

SPIECKER, H. Tree rings and forest management in Europe. **Dendrochronologia**, v. 20, n. 1–2, p. 191–202, 2002.

THOMAS, W. W. **The atlantic coastal forests of northeastern Brazil**. New York: Memoirs of the New York Botanical Garden, 2008. v. 100

VELOSO, H. P. **Classificação da vegetação brasileira adaptada a um sistema universal.** Rio de Janeiro: INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA (IBGE), 1991.

VÍNCENS, R. S.; AGAREZ, F. V.; GARAY, I. A região da REBIO Sooretama e da Reserva de Linhares e seu entorno: das características físico-geográficas ao uso da terra. In: GARAY, I; RIZZINI, C. M. (Ed.). **A Floresta Atlântica de Tabuleiros:** diversidade functional da cobertura arbórea. Petrópolis: Vozes, 2003. p. 7–15.

WORBES, M. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. **IAWA Bulletin**, v. 10, n. 2, p. 109–122, 1989.

WORBES, M. How to measure growth dynamics in tropical trees. **IAWA Journal**, v. 16, n. 4, p. 337–351, 1995.

WORBES, M. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. **Dendrochronologia**, v. 20, n. 1–2, p. 217–231, 2002.

CAPÍTULO 2

OVERVIEW OF DENDROCHRONOLOGICAL RESEARCH WITH A CLIMATE APPROACH IN THE BRAZILIAN ATLANTIC FOREST[3]

---

[3] Artigo formatado conforme normas da revista Dendrochronologia (submetido)

Overview of dendrochronological research with a climate approach in the Brazilian Atlantic Forest

Cláudia Fontana[a], Gabriela Reis-Avila[b], Cristina Nabais[c], Paulo Cesar Botosso[d], Juliano Morales de Oliveira[a]

[a] University of Vale do Rio dos Sinos (UNISINOS). Av. Unisinos, 950, Cristo Rei, 93022-750, São Leopoldo, RS, Brazil. claudiafontanabio@gmail.com (corresponding author, permanent address; ORCID 0000-0003-2032-5673); julianooliveira@unisinos.br

[b] Instituto de Biociências, Universidade Federal do Rio Grande do Sul (UFRGS). Av. Bento Gonçalves 9500, Porto Alegre, RS, 91501-970, Brazil. gfravila@gmail.com

[c] Coimbra University, Department of Life Sciences, Functional Ecology Center. Calçada Martim de Freitas, 3000, nº 456, Coimbra, Portugal. crnabais@bot.uc.pt

[d] Brazilian Agricultural Research Corporation (Embrapa), Embrapa Forestry. Estrada da Ribeira - Km 111, 83411-000, Colombo, PR, Brazil. paulo.botosso@embrapa.br

ABSTRACT

To investigate effects of climatic conditions on plant species performance is a first step to predict how ecosystems will react to climate change. Dendrochronology has made important contributions to this issue, especially in temperate and boreal zones, by providing long-term growth-related series that, compared to meteorological series, reveal a species' sensitivity to climate. As dendrochronology noticeably increased in tropical regions during the last three decades, some general patterns could emerge from comprehensive analyses of case studies. Here, we investigated the state of dendrochronology's contributions to the bioclimatology of wood species in the Brazilian Atlantic Forest (AF), a major tropical forest biome in South America. More specifically, we asked: (i) Which species and sites did afford cross-datable growth-ring series used for bioclimatic inference? (ii) What were the sampling and analytical methods applied? (iii) What do these studies tell us about the plant-growth sensitivity to climate conditions? Which knowledge gaps may be identified? For this, we searched in the main scientific databases for articles addressing climate-growth relationships by means of crossdated growth-ring chronologies within the AF region. Our search resulted in 11 articles, covering 16 chronologies comprising 10 species (7 native, 3 exotic). The average number of trees in chronologies was 16 individuals, and most studies were performed by core inspection. The most commonly used numeric filter was the Cubic Spline, often combined with others, such as the exponential or linear models. 87% of chronologies evidenced some positive precipitation signal, and some positive thermal signal was identified in all chronologies that were compared to monthly or seasonal temperature series. The findings are supported by the specialized literature that points out the influence of precipitation in the tropics. However, making stronger conclusions about the evidence of climate influence in the growth of the AF species implies in intensifying the efforts on building chronologies.

Keywords: Climate-growth relationship, dendrochronological parameters, tropical forest, subtropical forest.

2.1 INTRODUCTION

Dendroclimatic studies in tropical and subtropical regions remain one of the major gaps for dendrochronology, although such studies have increased in the last three decades (Zuidema et al., 2012). The apparent absence of climatic seasonality (Fritts, 1976; Jacoby, 1989; Payette and Filion, 2010; Speer, 2010; Brienen et al., 2016) and the complexity of growth rings in tropical species (Jacoby, 1989; Stahle, 1999; Brienen et al., 2016) have left researchers pessimistic about the application of dendrochronology in these environments and hindered its development. Thus, recent studies have been concerned with describing species with dendrochronological potential (*e.g.*, Fichtler et al., 2003; Soliz-Gamboa et al., 2011; Zuidema et al., 2012; Worbes and Junk, 2014; Baker et al., 2017). These studies already form a dense theoretical body that demonstrates the feasibility of tropical dendroclimatology, but also provides information on both the natural dynamics of the climate and the relationship between climate and biological patterns. This knowledge is especially important to understand, predict and mitigate the effect of global climatic changes of anthropogenic origin, a task that is currently one of the greatest challenges for science.

Current climate change stands out for the magnitude, intensity, and speed with which they are occurring. The process has been accelerated over the last 70 years as a result of emissions of atmospheric pollutants and greenhouse gases (GHGs: carbon dioxide, methane and nitrous oxide) through the production of energy and the conversion of natural ecosystems into agriculture/pasture and urban areas (IPCC, 2014). Changes in climate include increased global average temperature (oceanic and atmospheric), changes in the hydrological cycle, acidification and rising of the sea levels, reduced ice cover and increased the occurrence of extreme events such as storms and cyclones (IPCC, 2014). Because of these changes, scientists from the most diverse areas of knowledge have mobilized to understand the impacts of these changes on the fauna and flora, and on the human health and socioeconomic development.

Vegetation is an important component of climate regulation, which involves issues related to surface roughness, evapotranspiration and albedo (Shukla et al., 1990; Anderson-Teixeira et al., 2012; Cardoso and Justino, 2014). According to Bonan (2008), "the world's forests influence climate through physical, chemical, and biological processes that affect planetary energetics, the hydrologic cycle, and atmospheric composition." In this sense, the tropical forests developed a fundamental role in the terrestrial carbon cycle since they store up to 54% of the total biomass carbon of global forests (Liu et al., 2015; Wagner et al., 2016).

The Atlantic Forest (AF) is the second largest tropical forest in South America and, because it is under high anthropogenic pressure and contains high diversity and endemism of species of flora and fauna, it was considered one of the seven priority hotspots for conservation in the continent (Myers et al., 2000; Oliveira-Filho and Fontes, 2000). In its original distribution, the forest extended from the south to the northeast of Brazil in lowlands and highlands of the Atlantic zone, spreading inland to the east of Paraguay and northwest of Argentina (Lima and Capobianco, 1997; Galindo-Leal and Câmara, 2003). However, the forest had over 93% of its coverage suppressed for economic activities and urbanization (Galindo-Leal and Câmara, 2003), with most remaining areas being small and isolated patches (<50 ha and distant more than 1000 m from other spots) (Ribeiro et al., 2009). Less than 9% of its total remaining area is currently under protection, which comprises less than 1% of the original (Ribeiro et al., 2009). In addition, future scenarios of climate change point to the rising of the mean temperature and a change in the rainfall pattern for the AF region (IPCC, 2014). As a consequence, predictive models suggest that numerous Atlantic Forest tree species will be reduced or displaced southward from their potential area of occurrence (Colombo and Joly, 2010). In this scenario, where the AF is fragmented and continuously threatened by changes in land use, and in which predicted climate changes are expected to alter the patterns of productivity, phenology, and plant distribution, it is of the utmost importance to understand the climatic factors that regulate plant growth.

Here, we investigated the state of dendrochronology's contributions to the bioclimatology of wood species in the AF. More specifically, we asked: (i) Which species and sites did afford cross-datable growth-ring series used for bioclimatic inference? (ii) What were the sampling and analytical methods applied? (iii) What do these studies tell us about the plant-growth sensitivity to climate conditions? Which knowledge gaps may be identified? In order to answer such questions and contribute to the development of tropical dendroclimatology, we have gathered information on dendroclimatic studies developed in the AF region from a bibliographic review in the main databases of scientific articles. Specifically, we evaluated: *i.* the spatial, temporal and floristic coverage of dendroclimatic studies in the AF; *ii.* the sampling effort and numerical methods used to develop the growth-ring chronologies; *iii.* the generalizations that can be made about the influence of climate on the growth of AF woody species.

2.2 MATERIAL AND METHODS

The AF is the second largest tropical forest in South America, after the Amazon forest, covering 148,194,638 ha of the Brazilian territory (Ribeiro et al. 2009). Because of its remarkable range of latitude and altitude, the AF has a high climatic variability (Oliveira-Filho and Fontes 2000) and a huge variety of vegetation types, such as mangroves, coastal plain "restingas", seasonal forests, evergreen forests (mixed ombrophilous and dense ombrophilous), subtropical grasslands and wetlands (Oliveira-Filho and Fontes, 2000; Víncens et al., 2003; Instituto Brasileiro de Geografia e Estatística - IBGE, 2012;).

The AF distribution comprises a temperature gradient that rises toward the tropics. In the south, the climate is marked by quite low winter temperatures and well-distributed rainfall throughout the year (Nimer, 1971). Northward, the intra-annual temperature variation becomes less pronounced, but dry seasons are likely to occur. Average monthly rainfall below 60 mm occurs in the central portion of the AF from May to September (Sant'Anna -Neto, 2005), while in the northern portion even drier conditions prevail from September to January (Ferreira and Mello, 2005) (Fig. 1).

Figure 1.

2.2.1 Bibliographic research

As a strategy for constructing our information base, we searched articles indexed in three electronic databases (publications until December 2016): Scopus, Scielo and Web of Science. We used the following keywords combined in different ways using Boolean operators: "dendro*", "climat*", "Atlantic Forest", tree ring, growth ring, "Brazil*". From the articles found, we considered those in which the abstract or the full text informed that the dendrochronological series used was crossdated and related to climatic series. We read these articles in full, to record the below information on climate chronologies and relationships.

2.2.2 Site, taxa, location and environmental data

We reviewed on the website Tropicos (2017) the botanical family and the scientific name of the species. For geographical coordinates of the site, if not informed, we inferred them by the given locational references (*i.e.*, name of the municipality or Conservation Unit). We did the same for site altitude, inferring it based on the estimation by Google Earth (2017) in the respective geographic location; and for the type of vegetation of the site (according to IBGE, 2012), inferring it based on the description of the vegetation and its location on the vegetation map of Brazil (IBGE, 2004).

2.2.3 Chronologies and climatic signals

We classified the information on the sampling and development of the chronologies by analyzing: the method of collecting wood samples (destructive or non-destructive), number of trees and cores extracted per tree, the total of trees and series that composed the chronology, period and extension of the mean chronology. We also analyzed the applied analytical methods and the chronology descriptions, evaluating: details of the cross-dating techniques, standardization and integration methods, series descriptions and their degree of synchronization (intercorrelation – *r*int, mean correlation between series – *r*bar, Gleichlaufigkeit – GLK, Expressed Population Signal – EPS, Mean Sensitivity Index – MSI). Finally, we verified the results related to the relationships between dendrochronological and climatic series to infer patterns of dendroclimatic signals.

2.3 RESULTS

2.3.1 Taxa and environmental characteristics of chronologies

Our search in the databases and with the selected terms resulted in 29 indexed articles. However, only 11 of these declared to be based on crossdated chronologies and related to climatic series, a condition for the inclusion in this study. These publications totaled 16 chronologies, developed with ten different species (seven native, three exotic) and under various environmental conditions (Tab. 1, Fig. 1).

The family with more taxa investigated was Fabaceae Lindl., with four species and three genera, while other families had only one species analyzed. The species with the highest number of chronologies was the conifer *Araucaria angustifolia* (Bertol.) Kunze (5), and the broadleaf trees *Cedrela fissilis* Vell. (2) and *Schizolobium parahyba* (Vell.) S.F. Blake (2). Three exotic species composed the sample, the conifers *Cryptomeria japonica* (Thunb. *ex* L. f.) D. Don and *Pinus caribaea* Morelet, and the broadleaf *Tectona grandis* L. f.. One of the studies was developed with lianas, investigating three Fabaceae species (chronologies codes 2, 3 and 4; Tab. 1).

The chronologies were concentrated in the central-southern and eastern portions of the AF, with no study in the northern and western portions. As for altitude, 11 were in elevated areas (700 - 1265 m), three in medium elevations (200 - 700 m) and two in lowlands (<100 m). This spatial distribution of chronologies comprised four types of climate and three types of vegetation. The great majority of the chronologies (14) represented temperate climate conditions, according to the classification of Köppen-Geiger (Peel et al., 2007) (*i.e.*, with average temperatures above 10º C in the hottest month, and between 0 and 18ºC in the coldest month), especially in regions with no dry season and warm summers (Cfb, 11 chronologies) or hot summers (Cfa, 2 chronologies). Only two chronologies represented sites of tropical climate (*i.e.*, with an average temperature of the hottest month above 18ºC). The chronologies included sites of mixed ombrophilous (7), dense ombrophilous (6) and seasonal (2) forests, in addition to one in a commercial plantation (Tab. 1; Fig. 1).

2.3.2 Sampling characteristic

The total number of trees collected to build the chronologies was 326, of which 248 (76%) were used in the master chronologies. The mean number of trees in each chronology was 16 individuals, ranging from five to 42 individuals (SD = 12; median = 11). The number of radii evaluated varied from two to five per tree, being more frequent the analysis of four radii per individual (Tab. 2).

The most used method for the sampling was the non-destructive (or minimal interference) method by increment borer, used in ten (63%) chronologies, while for six (37%) of the chronologies, the destructive method was used, with a section of wood discs. The destructive method allowed a better use of those wood samples collected, with an inclusion of 97% of the sampled trees. While chronologies with samples collected with increment borer resulted in an inclusion of 72% of the trees (Tab. 2).

Regarding the chronological period, trees comprised the years between 1790 and 2011, with analyzed period ranging from 6 to 218 years and mean of 68 years (SD ± 61 years, median = 39 years). It should be noted that *A. angustifolia* has the longest chronologies, with a mean of 140 years (SD ± 46, Median = 122), while the other species comprise chronologies with a mean extension of 35 years (SD ± 31, Median = 24). Among the angiosperms, the longest extension period analyzed was for *C. fissilis*, with a chronology of 110 years (Tab. 2).

Table 2.

2.3.3 Numerical methods

The cubic smoothing spline with a 50% frequency-response cutoff was the most used detrending model (applied in 63% of chronologies), often preceded by an exponential or linear model. Most chronologies (54%) that detrended the raw series did not inform if trends were filtered by ratios or residuals. Autoregressive modeling was not applied in most chronologies (63%), but serial autocorrelation levels were not given for any of these chronologies (or the others). The expected value function used to integrate the detrended series in the master chronology was informed for 50% of the chronologies, of which half used the bi-weighted robust mean and half the arithmetic mean (Tab 3).

In relation to synchronism and sensitivity, for all chronologies at least one measure of series association was informed. The most used statistic was *r*int (63%), followed by *r*bar (31%) and GLK (13%). The values of *r*int ranged between 0.28 up to 0.94, while the *r*bar were between 0.25 up to 0.69, and GLK agreement above 60% (significance level at 5%). Chronologies that informed about series' standard deviation showed mean values between 1.99 and 6.46 (mm). MSI ranged between 0.16 up to 0.57, with higher values to the north of the AF and lower to the south. However, 44% of the chronologies did not inform MSI values. EPS was only given in one study, with two chronologies, with values around 0.93 (Tab. 3).

Table 3.

2.3.4 Climatic influence on the Atlantic Forest

Despite the differences on species and environmental conditions among the AF chronologies, some dendroclimatic patterns may be drawn. All but two chronologies (87%) evidenced some positive precipitation signal, and some positive thermal signal was identified in all chronologies that were compared to monthly or seasonal temperature series (50%), *e.g.* mostly of *A. angustifolia* and *C. fissilis* in mixed ombrophilous forest under Cfb climate.

Nevertheless, precipitation and/or temperature signals occurred in quite different seasons, even among chronologies under similar climate types and/or belonging to the same species, as for *A. angustifolia* and *C. fissilis* (Fig. 2). Interestingly, climatic signals were more homogeneous in nature and schedule between pairs of chronologies reported in the same paper (chronologies: 10 and 11; 12 and 13) (Fig. 2; Table 1).

Table 1.

Figure 2.

2.4 DISCUSSION

2.4.1 Site, taxa, location and environmental data

In this study, we investigated and analyzed articles on dendrochronology with a climatic approach developed in the area covered by the Brazilian AF. According to our review, the spatial and floristic comprehensiveness of dendrochronological studies in AF is still incipient. We particularly emphasize the small number of native species applied in the investigations (7 spp.), especially considering that, among the 491 species of Brazilian flora evaluated by Alves and Angyalossy-Alfonso (2000), 48% (235 spp.) presented an anatomical growth marker. For example, among Lauraceae from the southern AF region, ten potential species were pointed out for dendrochronology (Reis-Ávila and Oliveira, 2017), as well as Fabaceae (and others) from the western AF region (Lisi et al. 2008). Furthermore, cambial activity studies confirm the annual growth rings in many species (Callado et al., 2014).

In addition, we did not find publications for the northern region of this Biome, which presents important floristic and climatic differences. An area not yet investigated contains the "Tabuleiro" Atlantic Forest, considered globally as the area with the highest diversity of flora species per hectare (Thomas et al., 2008), which adds importance to research on issues related to the temporal development of this forest. It is also noticed that there are more chronologies in the regions of high altitude, especially in regions of mixed ombrophilous forest, characterized by the floristic mixture of Australasian and Afro-Asian genera and by the low temperature in the winter (IBGE, 2012), and in mountainous regions of dense ombrophilous forest. It is possible that, during the choice of study sites, the greatest variation in the temperature presented in these areas is being considered. However, there is a strong theoretical framework demonstrating that the variation in precipitation (droughts and floods) is the main variable involved in the formation of growth rings in tropical regions (Worbes, 1989; Botosso and Vetter, 1991; Schöngart et al., 2005; Brienen et al., 2016; Pagotto et al., 2017). Thus, to contribute to the understanding of the influence of climate on AF, it is necessary to include more studies in coastal regions, as well as in the northern and inner areas of this Biome, especially because the same species may have a very different growth response depending on where it occurs, which requires independent validation (Baker et al., 2017).

This result is also inexpressive in comparison to the number of active research groups registered in the Directory of Research Groups in Brazil that includes a research line in dendrochronology (15 groups) (CNPq, 2017). Another finding in our data search is that there is a large academic production in the form of theses and dissertations, but those were not yet published in scientific journals. The publications are important to give greater visibility to the study and its validation, as well as to contribute to a better understanding of the complex relationships involved in the growth of tropical trees. In this way, considering the great floristic diversity of the country (Forzza et al., 2012) and the number of species for which the formation of annual rings has been proven to be of potential use for dendrochronology, as well as the number of existing research groups, it is necessary to unite researchers and groups and discuss mechanisms that help to expand this field in the AF.

2.4.2 Sampling characteristic

In general, the average number of trees (16 individuals) used in the chronologies is in agreement with that indicated in the literature (Briffa and Jones, 1990; Schweingruber et al., 1990; Esper and Gärtner, 2001). However, some chronologies containing few individuals consisted of sampling by the destructive method, in which wood discs were evaluated. This measure increases the use of the collections in master chronology and allows greater accuracy in the dates since it facilitates the identification of false rings, missing rings and other anomalies of the wood. The chronologies with the greatest sampling, for the most part, consisted of cores (non-destructive method), probably due to the greater agility in the collection and exemption of cut authorization. For Fichtler (2017), non-destructive sampling methods are not indicated for most tropical broad-leafed species, since the anatomical inspection of the wood and secure identification of the ring requires a larger surface than that possible by radii analysis. However, due to large deforestation in this Biome we recommend using non-destructive methods and sampling about 25% more trees in relation to the sample number desired in the study.

The number of trees in the chronologies also depends on the research objectives and cannot be generically stipulated (Mérian et al., 2013). Nevertheless, Briffa and Jones (1990) suggest at least five trees (1 radii per tree) but emphasize that the more individuals, the better. Schweingruber et al. (1990) recommend at least 10 individuals. Esper and Gärtner (2001) also indicate 10 individuals and note that 20 trees can easily emphasize site signs. Speer (2010) indicates 20 trees, two radii each. Cook (1985) mentioned between 20-40 trees and Fritts and Swetnam (1989) at least 30 or 40 trees. For Fritts (1976), a large number of trees is important, since the variation in growth is related to variation in the climate, being this common to all trees, therefore retaining the climatic variation in the means. In this way, it is possible to reduce the large proportion of non-climatic factors involved in tree growth (Fritts, 1976). The author also points out that in sites subjected to extreme climatic variations, smaller tree numbers are required; while in a site where the climate is not highly limiting, other environmental and ecological factors can influence growth, causing rings with differing marks and sizes between trees. In these cases, a large number of trees (replicates) is needed to achieve dendrochronological objectives (Fritts, 1976). As for the number of radii, Fritts (1976) points out that the reduction of errors is more dependent on the number of trees in the sample than the number of radii per tree. However, the author ponders that is possible to reduce standard errors. For example, 17 trees with one radius per tree reduce the standard error to 0.05 or less, while for 12 trees it is necessary to take four radii per tree to obtain the same result (Fritts, 1976). In a nutshell, it is preferable to have more trees than number of radii per tree, but if there are few trees in the field, it is advisable to collect more radii per tree.

This is a relevant information, considering that in the tropical forest regions most species are rare (Hubbell, 2013). This forest feature demands more financial resources and time in the field, requiring sampling efforts in a much larger and often difficult to access area when compared to the characteristics of temperate forests, for example. Thus, for dendrochronological studies in tropical forests, besides the annual ring frequency and other principles of dendrochronology (Fritts, 1976), it is necessary to consider the abundance of the species in the site while building the sample design.

As for the temporal range, most of the studies involved short periods of up to 70 years. The studies that comprise longer periods are those performed with *A. angustifolia* (218 years, Perone et al., 2016), a long-lived gymnosperm, which in Brazil occurs mainly in the subtropical region and in floristic disjunctions in refuges located in the southeastern region (IBGE, 2012). Among the angiosperms, the most extensive chronology was for *Cedrela fissilis* (110 years, Dünisch, 2005), a deciduous species classified as secondary to climax, considered locally rare, with density of 1 to 7 trees per hectare (Lorenzi, 2002; Carvalho, 2003). For dendrochronology, Briffa and Jones (1990) indicate an extension of analysis with at least 30 years, while Pilcher (1990) points to a minimum of 40 years and Stahle et al. (1999) indicate at least 50, and up to 100, years. In summary, it is desirable that the time-span period is long enough to include a few years with the climate able to limit plant growth (Fritts and Swetnam, 1989). Also, it should be taken into account that dendrochronological studies demonstrate that millenary trees are exceptions in tropical forests, and even those about 500 years old are rare, with an average age of about 200 years being the most common (Brienen et al., 2016).

In addition, there is the intense deforestation process to which tropical forests are subjected, reducing the area of primary forests, where it would be more likely to find old trees. In particular, the AF underwent several cutting cycles that greatly reduced its coverage area (Ribeiro et al., 2009). It is worth mentioning that *A. angustifolia*, a species with potential for long-term changes in tropical forest dynamics, had the culmination of its suppression process in the 20th century (Carvalho, 2012). Precisely the trees with large diameters (> 40 cm) were prioritized for cutting by the timber industry (Carvalho, 2012). Thus, it can be seen that even though some trees in this forest genetically can live for hundreds of years, the selective cutting cycles to which they were subjected reduce the possibility of finding old trees nowadays.

2.4.3 Numerical methods

The construction and interpretation of a chronology is an elaborate task since there are different statistical methods and decisions that are up to the operator to take (Esper and Gärtner, 2001). In this sense, a prerequisite for the interpretation of chronologies of tree-rings is to have access to information about the main techniques applied in the studies (Esper and Gärtner, 2001). In our review, we observed that important classical parameters in dendrochronology (Fritts, 1976) are often not mentioned. Data of trend model and correlation are the most frequently reported in the AF chronologies, while data about MSI, trend removal, and expected value function appear in approximately half of the chronologies, but EPS and autocorrelation are among the parameters with less information available (Tab. 3). In the sequence, we discuss our main result groups and approach the relevance of key parameters.

Standardization (trend model, trend removal, Tab. 3): In a dendroclimatic context, standardization involves a modeling and removal of non-climatic trends in the growth rings (Fritts, 1976; Cook, 1985). An important question involved in the choice of standardization methods is related to the characteristics of the sampling site. Cook (1985) deals with this issue in depth. For example, many of the standardization methods have been developed for the Arizona semi-arid, where the trees are spaced apart. According to Cook (1985, 1987), in such environments, simple mathematical models are enough to model tree growth, such as an exponential model, linear regression or polynomial detrending (deterministic methods). This is possible because trees growing in the open-canopy environment tend not to suffer competition, so they grow well in youth and reduce growth over the years (negative growth curve) (Cook, 1985). Considering dendroclimatic studies, such a growth trend that is not related to climatic factors should be removed from the analysis through the application of standardization methods. Keeping this in mind, in mesic environments (as in tropical forests), the forest usually has a closed-canopy, suffering competition and sporadic disturbances, which demands more elaborate mathematical models to remove noises from the chronology (Cook, 1985). In this sense, flexible empirical models (stochastics methods, such as low-pass digital filtering and cubic smoothing splines), rather than inflexible physical models (deterministic methods), appear to be better to express these complex changes (Cook, 1987, 1985; Cook and Peters, 1981; Fritts and Swetnam, 1989; Speer, 2010). The cubic spline standardization method was used in most of the studies in the AF. Nevertheless, sometimes, it was applied as a second detrending, after other deterministic methods, usually an exponential or linear model. For Speer (2010), two runs at detrending series are not necessary since the most cubic smoothing splines can remove noise such as a negative exponential curve. In this sense, this author recommends using an interactive detrending to visualize data and choose the best adjustment for each series. Another advantage of the cubic smoothing splines is that it takes into consideration the autocorrelation, i.e., "the effect of previous growth or climate on the current year's growth" (Speer, 2010).

After fitting a growth curve to the ring-width series, this is used as the expected value of growth (Cook and Peters, 1997). Thus, giving the sequence to standardization, the non-stationary ring-widths are transformed into stationary tree-ring indices, whose average is defined as 1.0, maintaining the proportions of the ring and with the variance constant (homoscedastic) (Cook, 1987). It is used to stabilize the variance and allow to compare chronologies that previously had variance differences. There are many ways to standardization series. Some of them are applied by dividing (ratio) each measured ring-width by the estimated curve, or by subtracting (residual) each measured ring-width by the expected value (Cook, 1987). The main issue in the use of ratio or residue is that in residues a previous transformation of data is necessary, *e.g.*, applying logarithms to the series. In the AF, the most used transformation method for variance stabilization was the ratio, and when residue was used, no information about transformation was given.

Many chronologies in the AF applied the autoregressive model but did not give any information about the autocorrelation. The autocorrelation is "the correlation between growth in one time interval with that in a subsequent interval calculated over all individuals of populations" (Brienen et al., 2006). Summarizing, the autocorrelation reflects how much of the growth attributed to previous years influences current growth. This accumulated growth in the year, in general, is due to non-climatic factors. If the data shows a large autocorrelation, it is recommended to apply autoregressive models that satisfactorily remove autocorrelation in most cases, which allows emphasizing the climatic signal (Brienen et al., 2006). For this reason, it is important to know what the autocorrelation in the chronology is.

Synchronism degree: The most frequent information in the studies is the value of the correlation (*r*int, *r*bar or *GLK*). The *r*int presents the correlation coefficient of each tree series compared against the master dating series (Grissino-Mayer, 2001). In the crossdating, a *t*-value above 3.5 suggests a possible match, but for conclusions higher values are desirable, *e.g.*, *t*-value > 6.0 (Grissino-Mayer, 2001). For average interseries, correlation is indicated as a value above *r*int = 0.5, although it implies considerations such as species, geographic location, and regional climate (Grissino-Mayer, 2001). Since rainforests are less susceptible to variations in climate, *e.g.*, in relation to temperate and tree-line forests, this value may be considered high for these forests. *R*bar indicates the mean correlation coefficient applied for all possible pairings of ring width series over a common time (Cook and Holmes, 1996). It is dependent on the sample depth and considered a good measure of percent common variance (Cook et al., 2000; Speer, 2010). This value is usually less than the *r*bar for the same data set. The GLK is a measurement of similarity (Speer, 2010). It calculates the sign of agreement of a sample series with a chronology or between two chronologies, presenting the sum of the equal slope intervals in percentage, generally being significant from 60% on ($p < 0.5$) (Rinn, 2011). It compares the ratio of increase and decrease in growth at the same time between two consecutive years (Esper and Gärtner, 2001; Speer, 2010). In synthesis, information about series correlation significance is fundamental to validate the chronologies, as it demonstrates how well a set of data is related.

Sensitivity statistics: The EPS is an information that is commonly lacking in the searched articles. It represents the expected correlation between the *t*-series average of a finite number of trees and a hypothetical population average, with a threshold of EPS ≥ 0.85 (Wigley et al., 1984). EPS is variable in the different parts of the chronology, being directly influenced by the number of replications, with a value that increases rapidly from one to 10 trees and gradually stabilizes from this point on (Cook and Kairiukstis, 1990). Mérian et al. (2013) agree that the increase in the number of trees increases the value of EPS but points out that increasing the number of sites is more important than increasing the number of trees per site. On the other hand, two trees per site are preferable than one, as it reduces the noise and allows estimating the signals both inside and between sites (Mérian et al., 2013). However, increase in sample size affect differently the EPS and the climate-growth relationships, so EPS should not be applied as a linear estimator of the climate-growth relationship since the common signal does not necessarily reflect this relationship (Cook and Kairiukstis, 1990; Mérian et al., 2013).

Almost half of the reviewed articles did not present mean values for MSI (the values presented were below 0.57), while the SD is a parameter that is rarely addressed in the studies. It is desirable that both parameters present high values since in this way they indicate a greater adjustment to the variability in the environmental changes (Grissino-Mayer, 2001). For MSI considerations, it is necessary to use the filtered series, and for SD one must use the unfiltered series (Grissino-Mayer, 2001). MSI is a measurement that informs about variation in tree-ring year-to-year ranging from 0 to 1 (Speer, 2010). The MSI is considered low when it is between 0.10–0.19, intermediate between 0.20–0.29, and presents the most evident climate sensitivity with values above 0.30 (Grissino-Mayer, 2001). MSI above 0.4 is so sensitive that it greatly increases the difficulty in dating because of the frequency of micro or missing rings next to very wide rings (Speer, 2010).

Autocorrelation value does not prove to be a parameter considered in the surveys in the AF since no study provided this information (data not shown). Autocorrelation indicates the correlation between growth in a given time interval with that of a subsequent interval, calculated on population individuals (Grissino-Mayer, 2001; Brienen et al., 2006;). It is strongly influenced by the relationship between size and rate of growth, *e.g.*: small trees grow more slowly than large trees; juvenile trees have higher growth rate (Brienen et al., 2006). The closer to zero, the smaller is the autocorrelation between the years, indicating that the series is random in time (Grissino-Mayer, 2001). In this way, a series with low autocorrelation tends to put more emphasis on the climatic signal. The autocorrelation can be removed from the data by standardization techniques, especially applying autoregressive models.

Expected value function: Almost half of the chronologies did not explain the expected value function. However, among the studies that presented this parameter, half applied arithmetic mean and another half used bi-weighted robust mean. The arithmetic mean is a widely used central trend measure. It represents the expected value of a variable when calculated for the population (Callegari-Jacques, 2003). It is indicated when the individuals in the sample have the same variance (Bi, 2006). Therefore, the main issue of arithmetic mean is when there are many outliers in the data. The outlier is a rare data and its discrepant value affects the mean and may cover some general phenomena expressed from the sample (Volpato and Barreto, 2016). In dendrochronology, in general, a ring can be considered an outlier if is greater than +3.0 SD or -4.5 SD of the mean of the other series for that year (Cook and Holmes, 1996; Grissino-Mayer, 2001). If there are many outliers in the series, the bi-weighted robust mean is the most appropriate choice (Bi, 2006). In weighted robust mean, low weights are attributed to observations with great variation (Bi, 2006), and this minimizes the bias caused by outliers. Bi-weight mean is strongly recommended to remove endogenous effects and to emphasize the common signal contained in the data (Cook and Holmes, 1996).

2.4.4 Climatic influence on the Atlantic Forest

In the tropics, the main factor that acts on the annual growth is the variation in precipitation that is involved in annual droughts or floods depending on the region (Worbes, 2002, 1989; Brienen et al., 2016). In subtropical regions, the temperature happens to be a regulating factor of the biological processes in the plants (Fritts, 1976; Evert, 2013;). In part, our data supports these points, but add that the precipitation in subtropical AF also affects plant growth. Observing the distribution of the sites considered in this research, one can notice that the set of sites with chronologies generated in the central part of AF (codes 2, 3, 4, 5, 8, 14, 15 and 16) show positive associations with precipitation (climatic signal), while the set of sites with chronologies generated in the south (codes 1, 6, 7, 9, 10, 11, 12 and 13), under subtropical climate, indicate positive and negative associations with temperature and precipitation, although precipitation is well distributed throughout the year in this region (Nimer, 1971) (Fig. 2). In general, both sets of data match the findings of Wagner et al. (2016), who classify the central portion of AF as “water-limited sites” and the southern one as “light-limited sites”. According to the authors, the first one is characterized by the relationship between photosynthetic capacity and precipitation, and the second one by the relationship between photosynthetic capacity and maximal temperature. However, regardless of climate limitations, wood productivity is driven by seasonal variation in precipitation (Wagner et al., 2016).

Considering *A. angustifolia*, the most studied species, one can notice that the previous growth season influences the current growth in the region of southern distribution of the species, whereas in the centermost region of the distribution there is influence only of the current season (Fig 2). One of the principles of dendrochronology is precisely about the greater climatic sensibility of the species the closer they are to the natural distribution limit (Fritts, 1976). This is possibly the case of *A. angustifolia*, when presenting climatic signs also for the previous growing season. Besides that, this species presents an opposite signal for precipitation even in the closer sites, as the case of the site located near Curitiba and two sites in Rio Grande do Sul (codes 9 and 12; 10 and 11, respectively). For the latter case, the authors suggest that the occurrence of annual anthropogenic fires (exogenous disturbance) may interfere with the growth for up to two years and, consequently, correlations with precipitation were negative (Oliveira et al., 2010). In addition to exogenous and endogenous disturbances that may affect the climatic signal in the trees, issues related to plant age and random site events should also be considered (Fritts, 1976; Cook, 1987; Speer, 2010). In this sense, a more precise characterization of the sampling, with the focus on parameters that matter for dendrochronology, may be important for future comparisons and predictions.

Finally, modeling climate scenarios indicates a change in precipitation patterns and an increase in temperature in the AF region (IPCC, 2014). In our research, it is clear that the deficiency in water supply affects negatively most of the analyzed species. It may mean that this forest will retain less carbon in the future.

2.5 FINAL REMARKS AND CONCLUSIONS

In general, there is a large number of missing information in the descriptions about numerical methods used to develop the growth-ring chronologies in the AF, especially regarding methods of trend removal. It was also noticed that many authors chose not to apply autoregressive models, but did not even inform the autocorrelation level of the series. This information is important for conclusions about chronology, because if the chronology has a moderate or strong autocorrelation level, this may affect the power of the significance test of the climatic signals. However, despite the importance of the description of statistical parameters, Holmes (1983) highlights that "determination of dating should be the responsibility of the dendrochronologist, not of the statistical parameters.".

Regarding the climatic signals in the AF, to make stronger conclusions and generalizations about the evidence of climate influence on the growth of AF species is necessary to intensify efforts on building chronologies. The increase in replication is fundamental to contribute to understand the climatic past and to infer about the future development of this forest in relation to climatic changes. This increase of replication and filling of gaps must be thinking in terms spatial, temporal and floristic.

ACKNOWLEDGEMENTS

We are grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, process nº 88881.135931/2016-01) for the scholarship granted to the first author, to Programa de Pós-Graduação em Biologia — Universidade do Vale do Rio dos Sinos (UNISINOS) and Universidade de Coimbra for the technical support.

REFERENCES

Alves, E.S., Angyalossy-Alfonso, V., 2000. Ecological trends in the wood anatomy of some Brazilian species. 1. Growth rings and vessels. IAWA J. 21, 3–30. doi:10.1163/22941932-90000233

Anderson-Teixeira, K.J., Snyder, P.K., Twine, T.E., Cuadra, S. V., Costa, M.H., DeLucia, E.H., 2012. Climate-regulation services of natural and agricultural ecoregions of the Americas. Nat. Clim. Chang. 2, 177–181. doi:10.1038/nclimate1346

Andreacci, F., Botosso, P.C., Galvão, F., 2014. Sinais climáticos em anéis de crescimento de *Cedrela fissilis* em diferentes tipologias de florestas ombrófilas do sul do Brasil. Floresta 44, 323–332.

Baker, J.C.A., Santos, G.M., Gloor, M., Brienen, R.J.W., 2017. Does *Cedrela* always form annual rings? Testing ring periodicity across South America using radiocarbon dating. Trees (topical Collect. on line), 1–11. doi:10.1007/s00468-017-1604-9

Bi, J., 2006. Sensory discrimination tests and measurements: statistical principles, procedures, and tables, 1st ed. Blackwell Pub, Virginia.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science (80-.). 320, 1444–1449. doi:10.1126/science.1155121

Botosso, P.C., Vetter, R.E., 1991. Alguns aspectos sobre a periodicidade e taxa de crescimento em 8 especies arboreas tropicais de floresta de terra firme (Amazonia). Rev. Inst. Flor., São Paulo 3, 163–180.

Brandes, A.F.N., Lisi, C.S., Barros, C.F., 2011. Dendrochronology of lianas of the Leguminosae family from the Atlantic Forest, Brazil. Trees - Struct. Funct. 25, 133–144. doi:10.1007/s00468-010-0529-3

Brienen, R.J.W., Schöngart, J., Zuidema, A., 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees, in: Tropical Tree Physiology: Adaptations and Responses in a Changing Environment. Springer, Cham, pp. 439–461. doi:10.1007/978-3-319-27422-5

Brienen, R.J.W., Zuidema, P.A., During, H.J., 2006. Autocorrelated growth of tropical forest trees: Unraveling patterns and quantifying consequences. For. Ecol. Manage. 237, 179–190. doi:10.1016/j.foreco.2006.09.042

Briffa, K., Jones, P.D., 1990. Basic chronology statistics and assesment, in: Cook, E.; Kairiukstis, L. (Ed.), Methods of dendrochronology: applications in the environmental sciences. Springer-Science, Business Media, B. V., Dordrecht, pp. 137–152. doi:10.1007/978-94-015-7879-0

Callado, C.H., de Vasconcellos, T.J., Costa, M.S., Barros, C.F., Roig, F.A., Tomazello-Filho, M., 2014. Studies on cambial activity: advances and challenges in the knowledge of growth dynamics of Brazilian woody species. An. Acad. Bras. Cienc. 86, 277–283.

doi:10.1590/0001-3765201320130033

Callado, C.H., Guimarães, C., 2010. Estudo dos anéis de crescimento de *Schizolobium parahyba* (Leguminosae: Caesalpinioideae) após episódio de mortalidade em Ilha Grande, Rio de Janeiro. Rev. Bras. Bot. 33, 85–91. doi:10.1590/S0100-84042010000100008

Callegari-Jacques, S.M., 2003. Bioestatística: princípios e aplicações. Artmed, Porto Alegre.

Cardoso, G.M., Justino, F., 2014. Simulação dos componentes da evapotranspiração sob condições climáticas atuais e de cenários climáticos futuros de aquecimento global com o uso de modelos de clima-vegetão. Rev. Bras. Meteorol. 29, 85–95. doi:10.1590/S0102-77862014000100009

Carvalho, P.E.R., 2003. Espécies arbóreas brasileiras, 21st ed. Embrapa Florestas, Colombo.

Carvalho, M.M.X. de, 2012. Os fatores do desmatamento da Floresta com Araucária: agropecuária, lenha e indústria madeireira. Esboços 18, 32–52. doi:10.5007/2175-7976.2011v18n25p32

CNPq. Conselho Nacional de Desenvolvimento Científico e Tecnológico, 2017. Diretório dos Grupos de Pesquisa no Brasil [WWW Document]. URL http://dgp.cnpq.br/dgp/faces/consulta/consulta_parametrizada.jsf (accessed 9.3.17).

Colombo, A., Joly, C., 2010. Brazilian Atlantic Forest lato sensu: the most ancient Brazilian forest, and a biodiversity hotspot, is highly threatened by climate change. Brazilian J. Biol. 70, 697–708. doi:10.1590/S1519-69842010000400002

Cook, E.R., 1987. The decomposition of tree-ring series for environmental studies. Tree-Ring Bull. 47, 37–59.

Cook, E.R., 1985. A time series analyses approach to tree ring standardization. University of Arizona.

Cook, E.R., Buckley, B.M., D’Arrigo, R.D., Peterson, M.J., 2000. Warm-season temperatures since 1600 BC reconstructed from Tasmanian tree rings and their relationship to large-scale sea surface temperature anomalies. Clim. Dyn. 16, 79–91. doi:10.1007/s003820050006

Cook, E.R., Holmes, R.L., 1996. Guide for computer program ARSTAN, in: Grissino-Mayer, H.D., Holmes, R.L., Fritts, H.C. (Eds.), The international tree-ring data bank program library version 2.0 user’smanual. Laboratory of Tree-Ring Research, University of Arizona, Tuscson, pp. 75–87.

Cook, E.R., Kairiukstis, L., 1990. Methods of dendrochronology — applications in the environmental sciences, Environment International. doi:10.2307/1551446

Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. The Holocene 7, 361–370. doi:10.1177/095968369700700314

Dobner-Jr, M., Trazzi, P.A., Higa, A.R., 2014. Dendroecologia de um povoamento de

Cryptomeria japonica (L. F.) Don. com 25 anos de idade no sul do Brasil. Ciência Florest. 24, 413–420.

Dünisch, O., 2005. Influence of the El-niño southern oscillation on cambial growth of *Cedrela fissilis* Vell. in tropical and subtropical Brazil. J. Appl. Bot. Food Qual. 79, 5–11.

Esper, J., Gärtner, H., 2001. Interpretation of tree–ring chronologies. Erdkunde 55, 277–288.

Evert, R.F., 2013. Anatomia das plantas de Esau: meristemas, células e tecidos do corpo da planta: sua estrutura, função e desenvolvimento. Blucher, São Paulo.

Ferreira, A.G., Mello, N.G. da S., 2005. Principais sistemas atmosféricos atuantes sobre a região nordeste do Brasil e a influência dos oceanos. Rev. Bras. Climatol. 1, 15–28.

Fichtler, E., 2015. Dendroclimatology using tropical broad-leaved tree species – A review. Erdkunde 71, 5–22. doi:10.3112/erdkunde.2017.01.01

Fichtler, E., Goettingen, U., Clark, D.A., 2003. Age and long-term growth of trees in an old-growth Tropical Rain Forest, based on analyses of tree rings and 14 C 1. Biotropica 35, 306–317.

Forzza, R.C., Baumgratz, J.F. a., Bicudo, C.E.M., Canhos, D. a. L., Carvalho, A. a., Coelho, M. a. N., Costa, A.F., Costa, D.P., Hopkins, M.G., Leitman, P.M., Lohmann, L.G., Lughadha, E.N., Maia, L.C., Martinelli, G., Menezes, M., Morim, M.P., Peixoto, A.L., Pirani, J.R., Prado, J., Queiroz, L.P., Souza, S., Souza, V.C., Stehmann, J.R., Sylvestre, L.S., Walter, B.M.T., Zappi, D.C., 2012. New brazilian floristic list highlights conservation challenges. Bioscience 62, 39–45. doi:10.1525/bio.2012.62.1.8

Fritts, H.C., 1976. Tree rings and climate change. Academic Press Inc Ltd., New York.

Fritts, H.C., Swetnam, T.W., 1989. Dendroecology: a tool for evaulating variations in past and prestent forest environments. Adv. Ecol. Res. v. 19 19, 111–188.

Galindo-Leal, C., Câmara, I.G., 2003. The Atlantic Forest of South America. Biodiversity satus, Threats and Outlook.

Google Earth, 2017. Google [WWW Document]. URL https://earth.google.com/web/ (accessed 1.3.17).

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program Cofecha. Tree-ring Res. 57, 205–221.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull. 43, 69–78. doi:10.1016/j.ecoleng.2008.01.004

Hubbell, S.P., 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. Ecol. Evol. 3, 3263–3274. doi:10.1002/ece3.705

IBGE. Instituto Brasileiro de Geografia e Estatística. 2012. Manual técnico da vegetação brasileira., 2nd ed. Coordenação de Recursos Naturais e Estudos Ambientais (Série manuais técnicos de geociências), Rio de Janeiro.

IBGE. Instituto Brasileiro de Geografia e Estatística, 2004. Mapa de Vegetação do Brasil [WWW Document]. URL geoftp.ibge.gov.br/informacoes_ambientais/vegetacao/mapas/brasil/vegetacao.pdf (accessed 2.1.17).

IPCC, 2014. Climate change 2014: synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPPC Panel, Geneva, Switzerland.

Jacoby, G.C., 1989. Overview of tree-ring analysis in tropical regions. Int. Assoc. Wood Anat. Bull. 10, 99–108. doi:10.1163/22941932-90000478

Latorraca, J.V. de F., Souza, Milene Teixeira de da-Silva, L.D.S.A.B., Ramos, L.M.A., 2015. Dendrocronologia de árvores de *Schizolobium parahyba* (Vell.) S. F. Blake de ocorrência na REBIO de Tinguá-RJ. Rev. Árvore 39, 385–394. doi:10.1590/0100-67622015000200018

Lima, A.R., Capobianco, P.R., 1997. Mata Atlântica: avanços legais e institucionais para sua conservação. São Paulo.

Lisi, C.S., Tomazello-Fo, M., Botosso, P.C., Roig, F.A., Maria, V.R.B., Ferreira-Fedele, L., Voigt, A.R.A., 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a Seasonal Semi-deciduous Forest in Southeast Brazil. IAWA J. 29, 189–207. doi:10.1163/22941932-90000179

Liu, Y.Y., van Dijk, A.I.J.M., de Jeu, R.A.M., Canadell, J.G., McCabe, M.F., Evans, J.P., Wang, G., 2015. Recent reversal in loss of global terrestrial biomass. Nat. Clim. Chang. 5, 470–474. doi:10.1038/nclimate2581

Lorensi, C., Prestes, A., 2016. Dendroclimatological reconstruction of spring-summer precipitation for Fazenda Rio Grande, PR, with samples of *Araucaria angustifolia* (Bertol.) Kuntze. Rev. Árvore 40, 347–354. doi:10.1590/0100-67622016000200017

Lorenzi, H., 2002. Árvores brasileiras: manual de identificaçao e cultivo de plantas arbóreas do Brasil., 4th ed. Instituto Plantarum, Nova Odessa.

Mérian, P., Pierrat, J.C., Lebourgeois, F., 2013. Effect of sampling effort on the regional chronology statistics and climate-growth relationships estimation. Dendrochronologia 31, 58–67. doi:10.1016/j.dendro.2012.07.001

Myers, N., Mittermeier, R., Mittermeier, C., DaFonesca, G., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Conserv. Biol. 403, 853. doi:10.1038/35002501

Nimer, E., 1971. Climatologia da Região Sul do Brasil, in: Instituto Brasileiro de Geografia e Estatística (Ed.), Introdução a climatologia dinâmica. IBGE, Rio de Janeiro, pp. 3–65.

Oliveira-Filho, A.A.T., Fontes, M.A.L., 2000. Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate 1. BioOne 32, 793–810.

Oliveira, J.M., Roig, F.A., Pillar, V.D., 2010. Climatic signals in tree-rings of *Araucaria angustifolia* in the southern Brazilian highlands. Austral Ecol. 35, 134–147. doi:10.1111/j.1442-9993.2009.02018.x

Pagotto, M.A., DeSoto, L., Carvalho, A., Nabais, C., Tomazello Filho, M., Ribeiro, A., Lisi, C.S., 2017. Evaluation of X-ray densitometry to identify tree-ring boundaries of two deciduous species from semi-arid forests in Brazil. Dendrochronologia 42, 94–103. doi:10.1016/j.dendro.2017.01.007

Payette, S., Filion, L., 2010. La dendroécologie : principes, méthodes et applications. Presses de l'Université Laval, Québec.

Peel, M.C., Finlayson, B.L., Mcmahon, T.A., 2007. Updated world map of the Koppen-Geiger climate classification. Hydrol. Earth Syst. Sci 11, 1633–1644.

Perone, A., Lombardi, F., Marchetti, M., Tognetti, R., Lasserre, B., 2016. Evidence of solar activity and El Nino signals in tree rings of *Araucaria araucana* and *A. angustifolia* in South America. Glob. Planet. Change 145, 1–10. doi:10.1016/j.gloplacha.2016.08.004

Pilcher, J.R., 1990. Primary data, in: Cook, E.R., Kairiūkštis, L. (Eds.), Methods of dendrochronology: applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, pp. 23–96.

Reis-Ávila, G., Oliveira, J.M., 2017. Lauraceae: a promising family for the advance of neotropical dendrochronology. Dendrochronologia 44, 103–116. doi:10.1016/j.dendro.2017.04.002

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. doi:10.1016/j.biocon.2009.02.021

Rinn, F., 2011. TSAP-Win. [WWW Document]. URL http://www.rinntech.de/index-52147.html. Access in 12-02-2017.

Sant'Anna -Neto, J.L., 2005. Decálogo da climatologia do sudeste brasieliro. Rev. Bras. Climatol. 1, 43–60.

Schöngart, J., Piedade, M.T.F., Wittmann, F., Junk, W.J., Worbes, M., 2005. Wood growth patterns of *Macrolobium acaciifolium* (Benth.) Benth. (Fabaceae) in Amazonian black-water and white-water floodplain forests. Oecologia 145, 454–461. doi:10.1007/s00442-005-0147-8

Schweingruber, F.H., Kairiukstis, L., Shiyatov, S., 1990. Sample selection, in: Cook, E.R., Kairiukstis, L. (Eds.), Methods of dendrochronology: applications in the environmental sciences. Springer-Science, Business Media, B. V., Dordrecht, pp. 23–35. doi:10.1007/978-94-015-7879-0

Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. Science (80-.). 247, 1322–1325.

Souza, B.T., Estrada, G.C.D., Soares, M.L.G., Callado, C.H., 2016. Occurrence of annual growth rings in *Rhizophora mangle* in a region with low climate seasonality. An. Acad. Bras. Cienc. 88, 517–525. doi:10.1590/0001-3765201620150009

Speer, J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.

Stahle, D.., Mushove, P.., Cleaveland, M.., Roig, F., Haynes, G.., 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. For. Ecol. Manage. 124, 217–229. doi:10.1016/S0378-1127(99)00075-4

Stahle, D.W., 1999. Usefull strategies for the development of tropical tree-ring chronologies. IAWA J. 20, 249–253. doi:10.1163/22941932-90000688

Thomas, W.W., Carvalho, A.M.V., Amorim, A.M., Hanks, J.G., Santos, T.S., 2008. Diversity of wood plants in the atlantic coastal forest of Southern Bahia, Brazil. Mem. N. Y. Bot. Gard. 100, 21–66.

Tropicos, 2017. Tropicos.org [WWW Document]. Missouri Bot. Gard. URL http://www.tropicos.org/ (accessed 7.8.17).

Venegas-González, A., Chagas, M.P., Anholetto-Júnior, C.R., Alvares, C.A., Roig, F.A., Tomazello Filho, M., 2016. Sensitivity of tree ring growth to local and large-scale climate variability in a region of Southeastern Brazil. Theor. Appl. Climatol. 123, 233–245. doi:10.1007/s00704-014-1351-4

Víncens, R.S., Agarez, F. V., Garay, I., 2003. A região da REBIO Sooretama e da Reserva de Linhares e seu entorno: das características físico-geográficas ao uso da terra, in: Garay, I; Rizzini, C.M. (Ed.), A Floresta Atlântica de Tabuleiros: diversidadefunctional da cobertura arbórea. Vozes, Petrópolis, pp. 7–15.

Volpato, G., Barreto, R., 2016. Estatística sem dor, 2nd ed. Botucatu.

Wagner, F.H., Hérault, B., Bonal, D., Stahl, C., Anderson, L.O., Baker, T.R., Becker, G.S., Beeckman, H., Souza, D.B., Botosso, P.C., David, M.J., Bowman, S., Bräuning, A., Brede, B., Brown, F.I., Camarero, J.J., Chagas, K., Chave, J., Chidumayo, E.N., Clark, D.A., Regina, F., Costa, C., Couralet, C., Henrique, P., Dalitz, H., De, V.R., Eloisa, J., Milani, D.F., Oliveira, E.C. De, Arruda, L.D.S., 2016. Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. Biogeosciences, 13, 2537–2562. doi:10.5194/bg-13-2537-2016

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Worbes, M., 2002. One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges. Dendrochronologia 20, 217–231. doi:10.1078/1125-7865-00018

Worbes, M., 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. IAWA Bull. 10, 109–122. doi:10.1163/22941932-90000479

Zuidema, P.A., Brienen, R.J.W., Schöngart, J., 2012. Tropical forest warming: looking backwards for more insights. Trends Ecol. Evol. 27, 193–194. doi:10.1016/j.tree.2011.12.007

FIGURE AND CAPTIONS

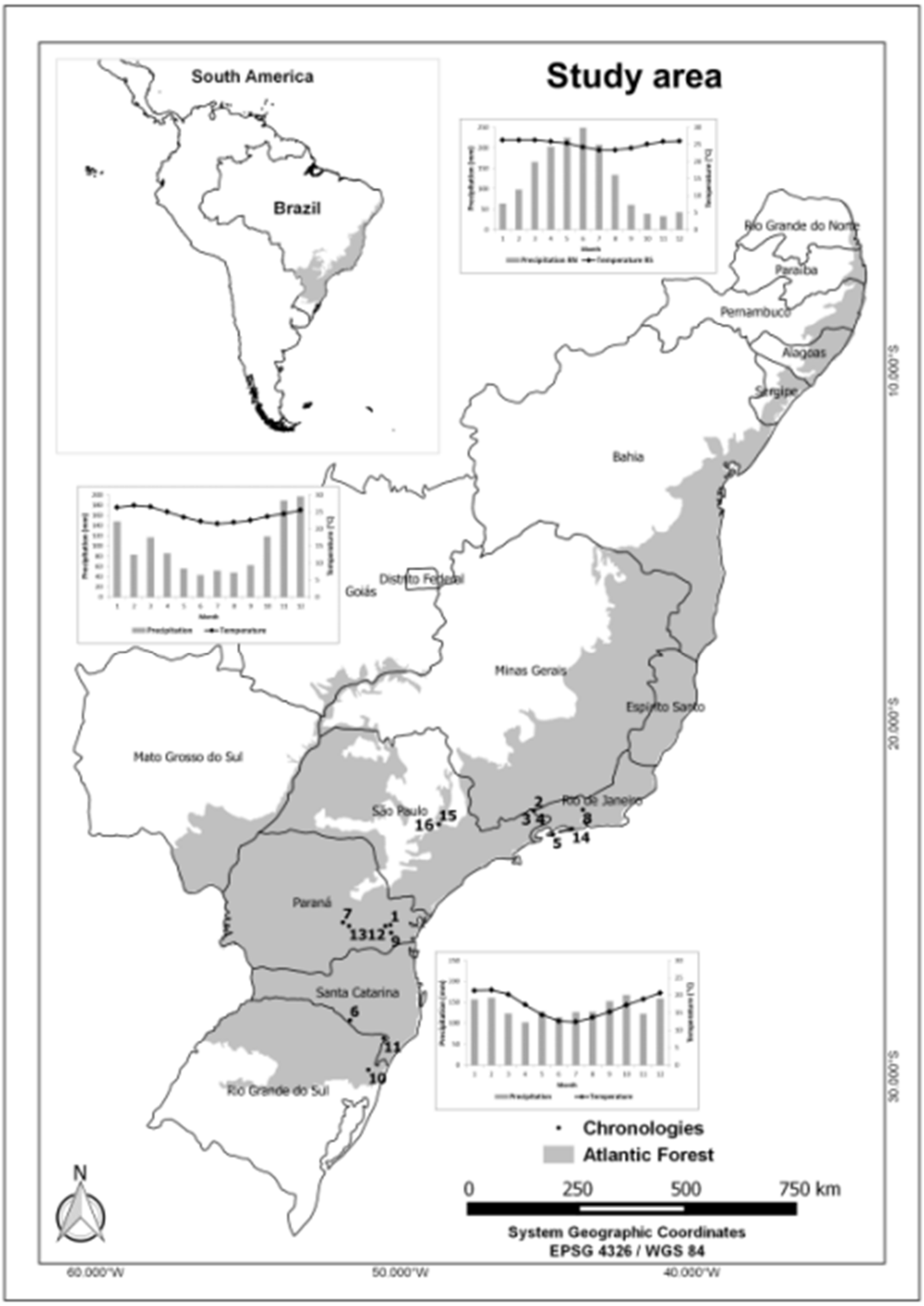
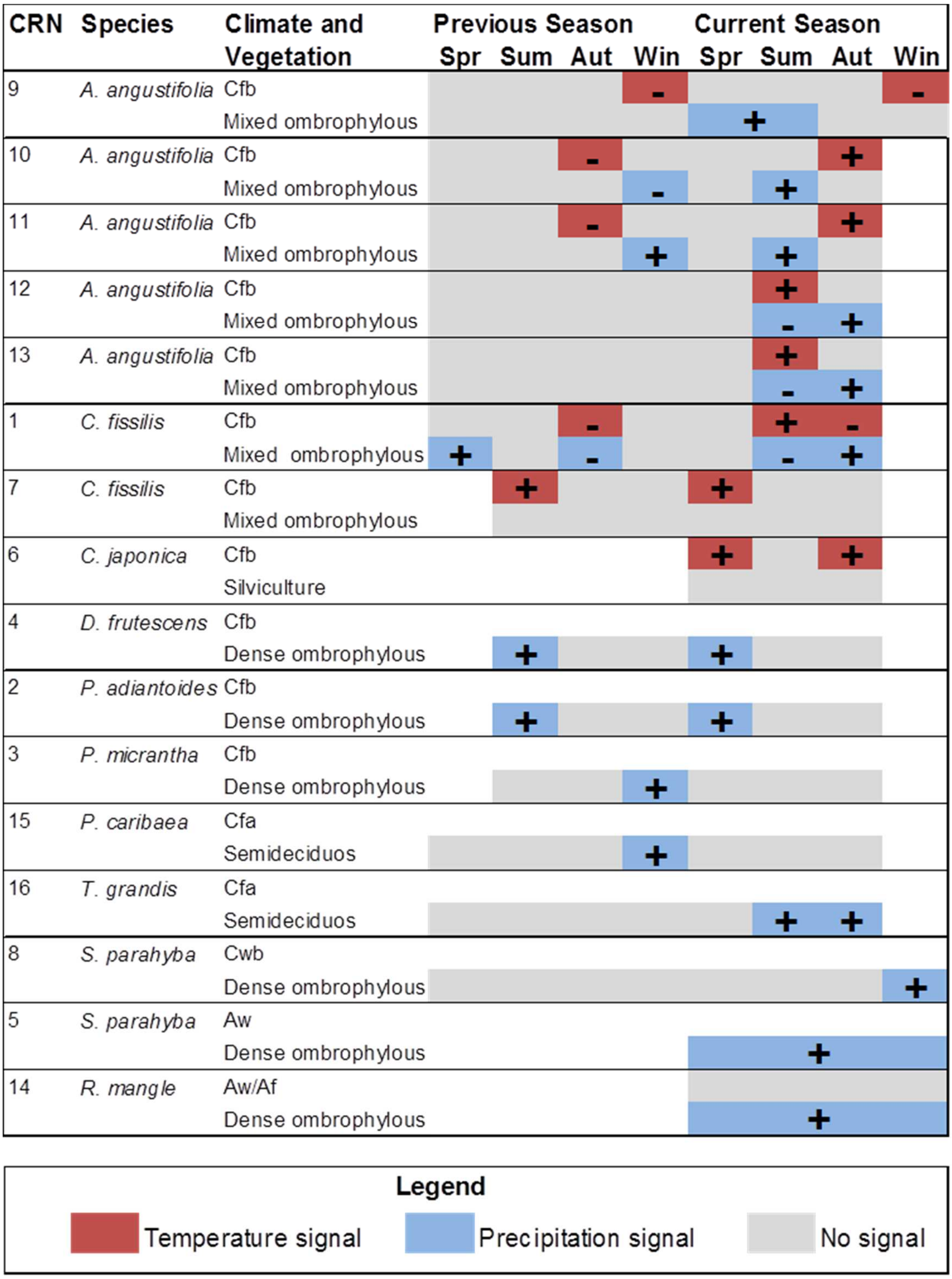


Figure 1. Location of growth-ring chronologies used in dendroclimatic studies (numbers are chronology code in this study) within the Brazilian Atlantic Forest. Climatic diagrams of the modeled historical series (1901-2014) of mean monthly temperature and mean monthly total precipitation for the southern, central and northern parts of the Atlantic Forest. Source: CRU TS3.23 (http://ckan.data.alpha.jisc.ac.uk/).



CRN	Species	Climate and Vegetation	Previous Season				Current Season			
			Spr	Sum	Aut	Win	Spr	Sum	Aut	Win
9	*A. angustifolia*	Cfb	⬜	⬜	⬜	🟥 -	⬜	⬜	⬜	🟥 -
		Mixed ombrophylous	⬜	⬜	⬜	⬜	🟦 +	🟦	⬜	⬜
10	*A. angustifolia*	Cfb	⬜	⬜	🟥 -	⬜	⬜	⬜	🟥 +	
		Mixed ombrophylous	⬜	⬜	⬜	🟦 -	⬜	🟦 +	⬜	
11	*A. angustifolia*	Cfb	⬜	⬜	🟥 -	⬜	⬜	⬜	🟥 +	
		Mixed ombrophylous	⬜	⬜	⬜	🟦 +	⬜	🟦 +	⬜	
12	*A. angustifolia*	Cfb	⬜	⬜	⬜	⬜	⬜	🟥 +	⬜	
		Mixed ombrophylous	⬜	⬜	⬜	⬜	⬜	🟦 -	🟦 +	
13	*A. angustifolia*	Cfb	⬜	⬜	⬜	⬜	⬜	🟥 +	⬜	
		Mixed ombrophylous	⬜	⬜	⬜	⬜	⬜	🟦 -	🟦 +	
1	*C. fissilis*	Cfb	⬜	⬜	🟥 -	⬜	⬜	🟥 +	🟥 -	
		Mixed ombrophylous	🟦 +	⬜	🟦 -	⬜	⬜	🟦 -	🟦 +	
7	*C. fissilis*	Cfb		🟥 +	⬜	⬜	🟥 +	⬜	⬜	
		Mixed ombrophylous		⬜	⬜	⬜	⬜	⬜	⬜	
6	*C. japonica*	Cfb					🟥 +	⬜	🟥 +	
		Silviculture					⬜	⬜	⬜	
4	*D. frutescens*	Cfb								
		Dense ombrophylous		🟦 +	⬜	⬜	🟦 +	⬜	⬜	
2	*P. adiantoides*	Cfb								
		Dense ombrophylous		🟦 +	⬜	⬜	🟦 +	⬜	⬜	
3	*P. micrantha*	Cfb								
		Dense ombrophylous		⬜	⬜	🟦 +	⬜	⬜	⬜	
15	*P. caribaea*	Cfa								
		Semideciduos	⬜	⬜	⬜	🟦 +	⬜	⬜	⬜	
16	*T. grandis*	Cfa								
		Semideciduos	⬜	⬜	⬜	⬜	⬜	🟦 +	🟦 +	
8	*S. parahyba*	Cwb								
		Dense ombrophylous	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟦 +
5	*S. parahyba*	Aw								
		Dense ombrophylous					🟦 +	🟦	🟦	🟦
14	*R. mangle*	Aw/Af					⬜	⬜	⬜	⬜
		Dense ombrophylous					🟦 +	🟦	🟦	🟦

Legend

🟥 Temperature signal 🟦 Precipitation signal ⬜ No signal

Figure 2. Seasonal dendroclimatic signals in growth-ring chronologies within the Brazilian Atlantic Forest. We considered evidence of seasonal climatic influence on plant growth if authors reported any meaningful association between the growth-ring chronology and temperature- or precipitation-related series, for any month of the season or for the entire season. Symbols identify positive or negative associations. CRN = chronology code in this study.

TABLE AND CAPTIONS

Table 1. Growth-ring chronologies used for dendroclimatic studies within the Brazilian Atlantic Forest, according to taxa, leaf phenology, environmental setting, CRN (code in this study) and reference.

Taxa	Leaf phenology	Altitude (m asl)	Climate type (Koppen)	Forest type (IBGE)	CRN	Reference
Araucariaceae						
Araucaria angustifolia (Bertol.) Kuntze	Evergreen	910	Cfb	Mixed ombrophilous	9	Lorensi and Prestes (2016)
		866	Cfb	Mixed ombrophilous	10	Oliveira et al. (2010)
		1265	Cfb	Mixed ombrophilous	11	Oliveira et al. (2010)
		940	Cfb	Mixed ombrophilous	12	Perone et al. (2016)
		800	Cfb	Mixed ombrophilous	13	Perone et al. (2016)
Cupressaceae						
Cryptomeria japonica (L.f.) D.Don	Evergreen	970	Cfb	Commercial plantation	6	Dobner-JR et al. (2014)

Fabaceae						
Dalbergia frutescens (Vell.) Britton	No data	700-1100	Cfb	Dense ombrophilous	4	Brandes et al. (2011)
Piptadenia adiantoides (Spreng.) J.F.Macbr.	No data	700-1100	Cfb	Dense ombrophilous	2	Brandes et al. (2011)
Piptadenia micracantha Benth.	No data	700-1100	Cfb	Dense ombrophilous	3	Brandes et al. (2011)
Schizolobium parahyba (Vell.) Blake	Deciduous	20-80	Aw	Dense ombrophilous	5	Callaso and Guimarães (2010)
		500	Cwb	Dense ombrophilous	8	Latorraca et al. (2015)
Meliaceae						
Cedrela fissilis Vell.	Deciduous	945	Cfb	Dense ombrophilous	1	Andreacci et al. (2014)
		890-940	Cfb	Mixed ombrophilous	7	Dünisch (2005)
Pinaceae						
Pinus caribaea var. hondurensis Morelet	Evergreen	546	Cfa	Semideciduous	15	Venegas-González et al. (2016)
Rhizophoraceae						

Rhizophora mangle L.	Evergreen	< 100	Aw	Dense ombrophilous	14	Souza et al. (2016)
Verbenaceae						
Tectona grandis Linn. F.	Deciduous	546	Cfa	Semideciduous	16	Venegas-González et al. (2016)

Table 2. Sample and crossdate efforts of growth ring chronologies used in dendroclimatic studies within the Brazilian Atlantic Forest.

Chronology code	Species	Wood sample type	Sampled individuals	Sampled radii per individual	Crossdated individuals	Crossdated period	Crossdated length (yr)
9	*A. angustifolia*	Core	10	4	8 (80%)	1907–2009	102
10	*A. angustifolia*	Core	30	2-5	17 (57%)	1882–2003	122
11	*A. angustifolia*	Core	30	2-5	18 (60%)	1861–2003	142
12	*A. angustifolia*	Core	22	2	10 (45%)	1790–2008	218
13	*A. angustifolia*	Core	44	2	39 (89%)	1891–2008	117
15	*P. caribea*	Core	10	4	10 (100%)	1971–2011	36
6	*C. japonica*	Stump	30	4	29 (97%)	1987– 2010	24
4	*D. frustescens*	Stump	15	4	15 (100%)	1970–2005	35
2	*P. adiantoides*	Stump	7	4	7 (100%)	1993–2005	12
3	*P. micracantha*	Stump	7	4	6 (86%)	1987–2005	18
5	*S. parahyba*	Stump	5	2-3	5 (100%)	1995–2001	6
8	*S. parahyba*	Core	30	4	16 (53%)	1939–2011	73
1	*C. fissilis*	Core	20	3-4	11 (55%)	1985–2009	22
7	*C. fissilis*	Core	51	2	42 (82%)	1890–2000	110
14	*R. mangle*	Stump	7	4	7 (100%)	2004–2011	7
16	*T. grandis*	Core	8	4	8 (100%)	1976–2011	41
Mean			20	4	16 (81%)		68

Chronology code	Species	Wood sample type	Sampled individuals	Sampled radii per individual	Crossdated individuals	Crossdated period	Crossdated length (yr)
Standard deviation			14	1	12 (20%)		61
Median			18	4	11 (87%)		39
Minimum			5	2	5 (45%)		6
Maximum			51	4	42 (100%)		218

Table 3. Numerical methods applied to build and describe the growth ring chronologies used in dendroclimatic studies within the Brazilian Atlantic Forest. Models applied to depict and remove ontogenetic and disturbance variations in raw growth ring series, statistics describing the synchronicity among indexed growth ring series (rint, intercorrelation; rbar, mean correlation between series; GLK agreement, Gleichlaufigkeit; EPS, expressed population signal) and their time variation degree (MSI, mean sensitivity index), and the mean function used to integrate indexed growth ring series. Interrogation indicates that no information was given. CRN = chronology code in this study.

CRN	Trend model	Trend removal	Autoregressive model	Synchronism and sensitivity statistics	Expected value function
9	Polynomial linear model (1st to 3rd order)	Ratios	No	*r*int=0.28	?
10	Cubic spline 50% cutoff (50 yr)	Ratios	Yes	*r*int=0.49 *r*bar=0.25 MSI=0.24	Bi-weighted robust mean
11	Cubic spline 50% cutoff (50 yr)	Ratios	Yes	*r*int=0.57 *r*bar=0.34 MSI=0.16	Bi-weighted robust mean
12	Exponential or linear model (slope ≤ 0) and cubic spline 50% cutoff (22 yr)	?	No	GLK > 60%	Bi-weighted robust mean
13	Exponential or linear model (slope ≤ 0) and cubic spline 50% cutoff (15 yr)	?	No	GLK > 60%	Bi-weighted robust mean
15	Exponential or linear model (slope ≤ 0), Cubic spline 50% cutoff (67%)	Ratios	Yes	*r*bar=0.69 EPS=0.95	?
6	?	Ratios	?	*r*int=0.67	?
4	Cubic spline 50% cutoff (5 yr)	?	No	*r*int=0.5	Arithmetic mean

CRN	Trend model	Trend removal	Autoregressive model	Synchronism and sensitivity statistics	Expected value function
				MSI=0.51	
2	Cubic spline 50% cutoff (5 yr)	?	No	*r*int=0.69 MSI=0.57	Arithmetic mean
3	Cubic spline 50% cutoff (5 yr)	?	No	*r*int=0.48	Arithmetic mean
5	None	None	No	MSI=0.37	?
8	?	?	No	*r*int=0.71 MSI=0.42	?
1	Exponential model (slope ≤ 0) and cubic spline 50% cutoff (67%)	?	No	*r*int=0.57 MSI=0.49	?
7	Logarithmic model	Residual	No	*r*bar=0.31	Arithmetic mean
14	?	?	?	*r*int=0.94	?
16	Exponential or linear model, cubic spline 50% cutoff (67%)	Ratios	Yes	*r*bar=0.64 EPS=0.93	?

CAPÍTULO 3

WOOD ANATOMY OF *Copaifera lucens* DWYER. (FABACEAE) FOR APPLICATION IN DENDROCHRONOLOGICAL STUDIES[4]

---

[4] Artigo formatado conforme normas da revista IAWA Journal (em processo de revisão sob o nº IAWA-1291).

Wood anatomy of *Copaifera lucens* DWYER. (Fabaceae) for application in dendrochronological studies

Cláudia Fontana[a], Luiz Santini-Junior [b], Gonzalo Pérez-de-Lis[c,d], Paulo Cesar Botosso[e], Cristina Nabais[c], Mario Tomazello-Filho[b], José Luís Penetra Cerveira Lousada[f]

[a] University of Vale do Rio dos Sinos (UNISINOS). Av. Unisinos, 950, Cristo Rei, São Leopoldo, RS, Brazil, 93022-000. ORCID 0000-0003-2032-5673. Corresponding author claudiafontanabio@gmail.com

[b] University of São Paulo (USP), Escola Superior de Agricultura "Luiz de Queiroz" (ESALQ). Av. Pádua Dias, 11, Agronomia, 13418-900 Piracicaba, SP, Brazil. luizsantini82@gmail.com; mtomazel@usp.br

[c] Coimbra University, Department of Life Sciences, Functional Ecology Center. Calçada Martim de Freitas, 3000, nº 456, Coimbra, Portugal. crnabais@bot.uc.pt

[d] INRA Grand-Est Nancy. F-54280 Champenoux, France. gonzalo.perez-de-lis-castro@inra.fr

[e] Brazilian Agricultural Research Corporation (Embrapa), Embrapa Forestry, Estrada da Ribeira - Km 111, 83411-000 Colombo, PR, Brazil. paulo.botosso@embrapa.br

[f] University Trás-os-Montes e Alto Douro/CITAB. Forestry Department, Quinta de Prados, 5001-801, Vila Real, Portugal. jlousada@utad.pt

ABSTRACT

The complex wood anatomy of numerous species in tropical and subtropical regions can sometimes restrict research in dendrochronology. The anatomical description of growth rings can help recognize potential species for dendrochronological studies. The aim of this study was to describe the wood anatomy of *Copaifera lucens* DWYER. (Fabaceae), with emphasis on growth rings. For the macroscopic analysis, wood samples from 20 trees were sanded with micro abrasive paper. For the microscopic analysis, were analyzed six individual trees applying different techniques. The macroscopic analysis of *C. lucens* revealed distinct growth layers, which are visible by naked eye and are demarcated by marginal axial parenchyma forming concentric bands and, sometimes, thick-walled fibers in the latewood. Axial parenchyma associated with the vessels are visible by naked eye, which are scanty paratracheal and vasicentric. Rays are thin, non-storied, few and irregularly spaced. Vessels are visible by naked eye, predominantly solitary and multiples of 2 to 4 (radial arrays), rarely 5 or in clusters, few and medium in size. The microscopic investigation showed solitary vessels and multiples of up to five, with diffuse distribution, circular without typical arrangement, with frequency of 1-6 mm², diameter of 33-138 µm, sometimes obstructed. The axial parenchyma is diffuse, paratracheal and scarce vasicentric. Intercellular canals are associated with axial marginal parenchyma bands, with frequency of 0-6 per mm. Crystals and tyloses present. In general, the diameter of the tangential pores of the species of *Copaifera* ranges from 90-150 µm, with a frequency of 2-6, rarely 8-10, vessels/mm^2. The ring demarcation by axial parenchyma is characteristic of the genus, and in *C. lucens* it is clear, suggesting that this species is promising for dendrochronological studies. However, there is a formation of partial and confluent rings, which may require great investment time in crossdating.

Keywords: Atlantic forest, growth layer, intra-annual rings, xylem

3.1 INTRODUCTION

Dendrochronology and wood anatomy have developed as distinct scientific areas for decades (Schweingruber 2007). Dendrochronology was mainly focused on growth patterns and in traits like tree-ring width and the ratio of earlywood/latewood to extract climatic and ecological information (Fritts 1976; Schweingruber 2007; Speer 2010), while wood anatomy was more focused on a detailed description of the tree-ring structure to be used in taxonomy (Evert 2013). However, extraction of climatic proxies at the anatomical level (*e.g.* vessel lumen area, cell wall thickness and lumen area of tracheids) has been fostered in the last decades by the development of image analysis (Schweingruber 2007). Also, the increment of dendrochronological studies involving tropical and subtropical trees has increased the interest on wood anatomical descriptions because they can aid the identification of tree-ring boundaries (Lisi *et al.* 2008).

The complex wood anatomy of numerous species in tropical and subtropical regions can sometimes restrict research in dendrochronology (Stahle *et al.* 1999; López & Villalba 2016). In this sense, wood anatomy may allow the recognition of potential new species for these purposes through the description of their growth ring structure. In addition, wood anatomy is also applied to the ecological interpretation of wood structures and may reflect the diversity and variation between habitats (Carlquist 1977; Alves & Angyalossy-Alfonso 2000; Carlquist 2001; Barros *et al.* 2006; Schweingruber 2007; Wheeler *et al.* 2007). Thus, these features can contribute to strengthening the findings and discussions of dendrochronological studies. However, given the large number of species in the tropics and subtropics, there is still a lot of work to be done into the wood anatomy and even more in dendrochronology. Although dendrochronology has been increasingly applied in these regions (Zuidema *et al.* 2012), few species have been investigated so far. Dendrochronology, among many other approaches, helped us to understand the complex effects of climate change on wood formation (Fritts 1976; Schweingruber 1988). Since tropical forests will be severely affected by climate change (Zeng *et al.* 2013; IPCC 2014), it is mandatory to generate data to subsidize dendrochronology in tropical regions.

The genus *Copaifera* (Fabaceae or Leguminosae: Caesalpinioideae) is common in Central America (4 spp.), South America (about 37 spp.) and West Africa (4 spp.) (Francisco 2005; Martins-da-Silva *et al.* 2008), with a probable species (*Copaifera palustris*) described on the island of Borneo in Malaysia (Veiga-Junior & Pinto 2002). In general, *Copaifera* species are deciduous to semi-deciduous, being classified as late secondary to climax (Carvalho 2003). In Brazil, the genus has a wide distribution comprising 24 species, 14 of which are endemic (Queiroz *et al.* 2015). The genus is characterized by the presence of axial intercellular canals (secretory canals), namely in wood (Metcalfe & Chalk 1950; Martins-da-Silva *et al.* 2008).

The oil-resin (copaiba oil) produced by *Copaifera* species has social and economic importance in the pharmaceutical, cosmetic, popular and indigenous medicine sectors, while the wood is broadly used for woodworking, carpentry, naval and charcoal production and so forth (Barbosa *et al.* 2012; Heck *et al.* 2012; Pieri *et al.* 2009). Because of these, chemical aspects of many species of the genus have been extensively studied (Veiga-Junior & Pinto 2002; Pieri *et al.* 2009). However, very few studies have concerned wood anatomy so far, with the species *C. langsdorffii, C. officinalis* and *C. multijuga* standing out as the more studied ones (Barbosa, 1982; Marcati *et al.* 2001; Marcati *et al.* 2006; Melo-Júnior *et al.* 2011; Rodríguez *et al.*2011; Barbosa *et al.*, 2012; Medeiros, 2016), being also worth to emphasize a study comparing *C. langsdorffii* with its vicarious pair *C. lucens* (Barbosa 1982).

Species of the *Copaifera* genus have a slow growth and can live about 400 years, reaching heights ranging from 25 to 40 meters (Veiga-Junior & Pinto 2002; Araújo Júnior *et al.* 2005). Long-lived species are of particular interest for dendrochronological studies, as they record important environmental information in their growth rings that have occurred during the plant's life history, containing records on century-old scales (Fritts 1976; Schweingruber 1988; Speer 2010; Rozendaal & Zuidema 2011). However, access to this information requires a greater understanding of the anatomy of the species' wood, especially the characteristics of the annual ring (Stahle *et al.* 1999; Schweingruber 2007). A more detailed understanding of the structure of the wood provides greater accuracy in dating and aids in the ecological interpretation of the results. In this context, this study aims to analyze the structure of the wood and the growth ring of *C. lucens* for dendrochronological and ecological studies.

3.2 MATERIAL AND METHODS

3.2.1 Study area

The study was carried out in the Reserva Natural da Vale (RNV), an area of 23,000 ha covered by a well-preserved tropical rainforest called "Tabuleiros" Atlantic Forest (TAF). It is located in the state of Espírito Santo, in the southeastern region of Brazil (19°S−19°14'S, 39°12'W−40°W), between 30 and 80 m a.s.l., approximately 30 km off the coast of the Atlantic Ocean (Fig. 1). The region's forest typology can be inserted into the "Lowland Dense Ombrophilous Forest" and the "Lowland Semideciduous Forest" (Veloso 1991; IBGE 2012), presenting a floristic mixture of Amazonian and Atlantic elements (Rizzini 1963; Peixoto & Gentry 1990; Veloso 1991; Siqueira 1994; Garay *et al.* 2003; Jesus & Rolim 2005).

According to the Koeppen climate classification (Koeppen 1948), the climate at RNV is of the type Aw (seasonal tropical climate with a dry season). Mean annual precipitation is 1,178 mm per year, with monthly averages for the rainy season (summer) of 130 mm to approximately 200 mm from October to April. Rainfall during the dry season (winter) does not exceed 25% of the annual total, being below 60 mm from April to September (Víncens *et al.* 2003). The mean annual temperature is 23 °C, with the mean of the warmest month (February) being 25.6 °C, and the average of the coldest month (July) 19.9 °C (Jesus 2001). Average evapotranspiration reaches 1,246 mm per year, attaining maximum values in summer, and frequently exceeding precipitation in winter (Víncens *et al.* 2003).

The predominant soil type in the region is yellow Podzolic (yellow, tertiary), being a dystrophic soil that exhibits low fertility, drastic differences in granulometry according to soil depth, and a rapid decomposition of the organic material (Garay & Silva 1995; Louzada *et al.* 1997; Garay *et al.* 2003).

Figure 1.

3.2.2 Wood collection, sample preparation and analysis

For wood anatomy description, we collected wood samples from 25 adult individuals with heights and diameters at breast height (DBH) of approximately 32 m and 50 cm, respectively. Small wood samples of 5-mm diameter were obtained at breast height (DBH ~ 1.30 m) with an increment borer (Pressler). Different protocols were used for the microscopic analysis of the three anatomical planes of wood, as recommended by Callado *et al.* (2013). Measurement and microscopic characterization of wood samples were performed according to IAWA (1989) and Coradin and Muñiz (1991).

For the microscopic description, we produced histological slides from six trees. For one individual, wood samples were softened (sapwood) for approximately 4 hours at 2 kg pressure and 90 ºC in a solution of 200 ml of 97% ethanol and 200 ml of liquid glycerin.

Micro-sections with a thickness of 17-20 µm were obtained by using a sliding microtome. In addition, cellular elements of the wood were dissolved, for which we immersed small wood chips in hydrogen peroxide 20 vol. and acetic acid (1:1) for approximately 48 hours at 75°C on a heating plate (Sybron Thermolyne). In order to verify the color of the cellular deposits, the samples were not stained (Coradin & Muñiz 1991). Digital images were captured by a camera (Marlin F-145C2) attached to a light and fluorescence microscope (Olympus BX50), using several filters and magnifications. Cellular element dimensions were evaluated by using the Image Pro Plus 4.5 software (Media Cybernetics 2001), while fibers were measured with the Lasico Auto Scaler II equipment (n = 100 fibers).

Wood samples from other two individuals were included in paraffin after being dehydrated through successive alcoholic immersions (70-100%). Histological sections with a thickness of 7-15 µm were performed on a rotating microtome (Micron HM 340E). In order to remove the paraffin, the slides were placed in the oven at 65°C for 24h and immersed in Bioclear. Absolute ethanol and a solution containing safranin and Astrablue were respectively used to dehydrate and stain the micro-sections, while Bioclear was used for subsequent clarification. Permanent slides were fixed in Eukitt. For the other three individuals, wood samples were cooked in water and glycerin for 4 hours. Transverse cuts were performed in a sliding microtome. No staining was used. Digital images were taken with a camera (Leica DFC295) attached to a light microscope (Leica DM4000B), and cell elements were measured by using the Image Pro Plus 4.5 software.

For macroscopic description, the transverse surfaces of 20 trees were analyzed throughout the wood core (from the outermost ring to the pith). For analysis, cores were sanded with micro abrasive paper and photographed by using a camera (Canon DS126311) attached to the stereomicroscope (Zeiss MZ8).

3.3 RESULTS

Anatomical characterization of the wood

Copaifera lucens DWYER

3.3.1 Macroscopic description:

Growth layers were visible to the naked eye, demarcated by axial parenchyma in marginal bands, in most cases with a reddish-brown coloration due to the accumulation of oil-resin in axial parenchyma cells. These borders were commonly associated with axial intercellular canals in tangential arrangement (Fig. 2 & 3, black arrows). Continuous axial parenchyma in marginal bands also occurred without association with axial intercellular canals (Fig. 2B, E & Fig. 3). We observed discontinuous parenchyma bands, whose cells were not usually filled with oil-resin and have a whitish appearance (Fig. 2D & 3A). In some rings, fiber wall thickness exhibited an abrupt change, resulting in tangential distinct fiber zones (Fig. 2A). Vessel density occasionally varied throughout the growth ring, with lower values in earlywood than in latewood (Fig. 2B-2E & Fig 3). Axial parenchyma arranged in confluent bands were frequent, especially in juvenile wood (Fig. 2D).

In general, growth ring sequences are easily identified in those samples showing well-defined anatomical patterns. These tree-ring boundaries can be delimited by three markers: (1) well defined marginal axial parenchyma with oil-resin accumulation imparting a reddish-brown color to the ring boundary, (2) presence of intercellular canals associated with the marginal axial parenchyma bands, and (3) a darker fiber zone exhibiting thick cell walls in latewood (Fig. 2 & 3). In addition, vessel density sporadically varied throughout the ring. All these markers did not always occur concomitantly except for the marginal parenchyma. We also noted complex growth ring patterns showing edges that were difficult to be detected both macroscopically and microscopically (Fig. 2B-2C). Distinction of the growth ring edges is even more difficult close to the pith (Fig. 2D-F). Thus, it was not possible to determine anatomically whether these characteristics indicate false rings.

Paratracheal axial parenchyma is scarce, vasicentric or rarely aliform, and arranged in marginal bands, both visible to the naked eye. ***Rays*** are visible to the naked eye, thin and few, in straight lines, irregularly spaced and non-storied. Wood is diffuse-porous, showing a few medium ***vessels*** that are visible to the naked eye, predominantly solitary and multiple radial of 2 to 4, rarely 5. ***Axial Intercellular canals*** are tangentially distributed in the marginal parenchyma, generally smaller than the vessels, but sometimes difficult to distinguish macroscopically (Fig. 2 & 3).

Figure 2.

Figure 3.

3.3.2 Microscopic description

Vessels are solitary (predominant) or in radial multiples of 2 to 4, rarely 5; while vessel clusters up to 7 are rare. Vessel frequency is very low with a mean value of 3.38 vessels per mm^2 (0-11 per mm^2, SD ± 2.03 per mm^2). Some vessels has a circular section and medium size, with a mean diameter of 108 µm (45-199 µm, SD ± 35 µm). Some vessels are partially or completely blocked by tyloses or oil resin. We noticed simple perforation plates at the extremities and lateral walls, intervessel vestured pits alternate with apertures included. Ray-vascular pits are similar to intervessel ones. ***Paratracheal axial parenchyma*** is scarce and vasicentric, 1 to 5 cells wide; also disposed in marginal bands between 2 and 8 cells wide, delimiting growth-ring edges. ***Fibers*** are libriform and non-septate, some bifurcated due to intrusive growth, predominantly short, with a mean length of 1,360 µm (650-1,969 µm, SD ± 349 µm). Fibers occasionally form bands in latewood that resemble axial parenchyma, possibly constituting tension wood, as indicated by thicker walls, a slightly more rounded cell shape, and small intercellular spaces (Fig. 4E). Gelatinous fibers also are present (Fig. 5B). There are ***heterogeneous rays*** consisting of procumbent cells with a row of square and upright cells at their margins. Ray cells are non-storied and thin, uniseriate or multiseriate up to 4 cells wide and 2 to 25 cells high, with a mean width of 34 µm (17-55 µm, SD ± 9 µm), and a mean height of 303 µm (84-619 µm, SD ± 148 µm). Ray frequency is very low, with an average of 5 rays mm^{-1} (4-8 rays mm^{-1}, SD ± 1.20 rays mm^{-1}). Parenchyma cells containing oil-resin were observed. We observed ***intercellular canals*** of exogenous origin, with epithelial cells secreting oil-resin. Their average diameter is of 57.83 µm (22-136 µm, SD ± 21 µm), with a mean of 2 canals mm^{-1} (0 to 6 canals mm^{-1}, SD ± 1.15). Prismatic calcium oxalate crystals were detected in chambers, arranged in crystalline series within the axial parenchyma cells (Fig. 4 & 5), whereas medullar macules were absent.

Figure 4.

Figure 5.

3.4 DISCUSSION

3.4.1 Macroscopic description

Wood anatomical characteristics of *C. lucens* are in agreement with those previously reported for other species of the *Copaifera* genus (Alencar 1982; Alves & Angyalossy-Alfonso 2000; Barbosa 1982; Marcati *et al.* 2001; Medeiros 2016; Melo-Júnior *et al.* 2011; Metcalfe & Chalk 1950; Wheeler & Baas 1991). After evaluating the wood anatomy of 491 Brazilian species, Alves and Angyalossy-Alfonso (2000) reported a concomitant occurrence of solitary and multiple vessels in 76% of them and 84% show diffuse porosity. According to Metcalfe and Chalk (1950), vessels in diffuse arrangement is a predominant feature of dicotyledons in the tropics and subtropics. Although the initial of earlywood could be expected to have a higher vessel density in the tropics, the increase in latewood was also observed in *Miconia cabussu* Hoehne (Melastomataceae) (Marcon & Costa 2000). Occasional variations in vessel distribution were also observed in *Daniellia ogea* (Harms) Rolfe *ex* Holl., a species that has tree-rings delimited by axial parenchyma bands (Groenendijk *et al.* 2014).

General characteristics of the axial parenchyma of *C. lucens* are in agreement with our expectations, given that paratracheal parenchyma is assumed to be the more frequent type in species from warm low-latitude regions (Wheeler & Baas 1991). Parenchymatic cells play several functions in wood, such as capacitance, through to storage and long-distance water transport, prevention and reversal of embolisms, defense against pathogens, storing crystals, and work as reservoir of many secondary products (as resins, terpenoids), among others (Glatzel & Geils 2009; Brodersen & McElrone 2013; Carlquist 2015; Morris *et al.* 2016). Marginal parenchyma bands may contain starch and can perform two physiological functions, storing photosynthesis products for rapid production of leaves and flowers, or as a reservoir of sugars that can be transferred into the vessel by hydrolysis, modifying the osmotic potential (Carlquist 2001). Additionally, parenchyma bands support the thick-walled fibers formed at the end of the growing season (Morris *et al.* 2016). Generally, these bands are wider than those in trees in temperate sites, a fact related to the greater necessity of plant defense in tropical areas (Morris *et al.* 2016). In turn, scarce axial parenchyma could be compensated by increasing production of fiber bands resembling axial parenchyma, as previously suggested (Marcon & Costa, 2000) for Melastomataceae.

Growth rings were observed in 48% of the neotropical species analyzed by Alves and Angyalossy-Alfonso (2000) and in 28% of the African species evaluated by Tarelkin *et al.* (2016). The formation of growth layers is strongly influenced by climate variation (Fritts 1976; Schweingruber 2007), as growth dynamics results from the combination of environmental conditions and internal factors such as genetics or tree age (Cherubini *et al.* 2003; Fonti *et al.* 2010). Although the tropical regions exhibit homogeneous temperatures throughout the year, variations occur in the annual precipitation regime. The TAF commonly experience a period of approximately three months of water deficit in winter (< 60 mm monthly), which may trigger cessation of cambial activity and formation of growth layers (Worbes 1995). Indeed, alternate periods of drought and flood were identified as the main factors causing the formation of the rings in the tropical regions (Worbes 1989).

Marginal parenchyma, sometimes associated with other characteristics, is the most frequent growth ring boundary in tropical species (Roig *et al.* 2005; Marcati *et al.* 2006; Groenendijk *et al.* 2014). Marginal parenchyma associated with intercellular canals was suggested to be characteristic of the genus *Copaifera* (Alencar 1982; Barbosa 1982; Marcati *et al.* 2001; Medeiros 2016; Melo-Júnior *et al.* 2011; Metcalfe & Chalk 1950). Melo-Júnior *et al.* (2011,) and Costa *et al.* (2015) observed in *C. langsdorffii* marginal bands containing normal intercellular canals along the limit of the growth layers. Albuquerque *et al.* (2016) suggested that *C. langsdorffii* has a high potential for dendrochronology because its growth rings are delimited by clear series of oil-resin ducts and marginal parenchyma. Yet, it was also reported for other species of the genus the occurrence of marginal axial parenchyma bands without association with the intercellular canals, as well as discontinuous or subdivided parenchyma bands, the latter usually close to the pith (Macedo & Langenheim 1989; Marcati *et al.* 2001; Melo-Júnior *et al.* 2011). Melo-Júnior *et al.* (2011) observed 1-7 discontinuous bands delimiting the growth ring. According to the authors, these bands may be false growth rings since they do not cover the entire circumference of the trunk. The anatomical variations that occur within the annual ring are generally treated in the literature as intra-annual density fluctuations (IADFs) or false rings (De Micco *et al.*, 2016; Groenendijk *et al.*, 2014). IADFs are better documented and studied in the Mediterranean areas (Cherubini *et al.* 2003; Campelo *et al.* 2007; Battipaglia *et al.* 2010; Vieira *et al.* 2014; De Micco *et al.* 2016), where tree-ring identification can be hindered if such fluctuations are frequent.

3.4.2 Microscopic description

Many structural features of the wood of *C. lucens* are common to other species of the genus and tropical flora, such as simple perforation plates, alternate intervessel pits, vested pits, libriform fibers and tyloses (Marcati *et al.*, 2001; Medeiros 2016; Melo-Júnior *et al.* 2011; Metcalfe & Chalk 1950; Wheeler & Baas 1991). Vessels characteristics are in agreement with those observed previously for the *Copaifera* genus, whose species have average diameters between 90 and 150 µm, solitary and radial vessels between 2 to 6, and rare of 8 to 10 per mm^2 (Barbosa 1982; Marcati *et al.* 2001; Medeiros 2016; Melo-Júnior *et al.* 2011). Rare clustered vessels have also been reported for *C. langsdorffii* (Melo-Júnior *et al.* 2011). Cluster vessels are more common in temperate and subtropical flora (Wheeler & Baas 1991) As in other species, the mean vessel frequency was below that previously reported for *Copaifera*, ranging from 4.97 to 7.2 vessels per mm^2 (Barbosa 1982; Marcati *et al.* 2001; Medeiros 2016; Melo-Júnior *et al.* 2011; Yanez-Inzunza 1992). Yanez-Inzunza (1992) found up to 37 vessels per mm^2 for *C. langsdorffii* and credited this exception to the wide distribution of the species, which may reflect high plasticity for adaptation to different environmental conditions. Previous studies also pointed out a tendency for lowland tropical forests to have larger vessels and in low frequency in the wood (Alves & Angyalossy-Alfonso 2000; Barros *et al.* 2006; Carlquist 2001). The same characteristics were related to large trees (Carlquist & Hoekman 1985). In addition, vessels with diameters similar to those of *C. lucens* and small numbers per mm^2 were associated with mesic environments (Alves & Angyalossy-Alfonso 2000). In this context, the seasonality of precipitation occurring in the TAF should not be extreme enough to trigger changes in the wood anatomy. On the other hand, the plant may have other mechanisms to face the drought periods, such as the production of gelatinous fibers and calcium oxalate crystals (Marcati & Angyalossy 2005; Marcati *et al.* 2006; Nassar *et al.* 2010).

Vessels are responsible for the hydraulic conductivity in the plant, which depends not only on the total conductive area, but also on the diameter and frequency of these elements (Poorter *et al.* 2010). Wide vessels can transport water more efficiently and are frequent in a mesic environment, while smaller vessels are considered to be safer due to the lower risk of implosion and embolism, being related to the xeric environment (Carlquist 2001; Tyree & Zimmermann 2002; Poorter *et al.* 2010). Embolism can be triggered in water deficit situations when xylem sap reaches a critical threshold, and the air is aspirated through the pit membranes forming gas bubbles that stop the sap flow (Tyree & Zimmermann 2002). In this sense, in plants that have many vessels, if some of them are embolized, many others remain to conduct the sap, while in plants with few vessels the loss of some of them is very harmful.

Few vessels of medium size can also appear in species from mesic environments (Alves & Angyalossy-Alfonso 2000), whereas other characteristics, such as gelatinous fibers and calcium oxalate crystals have been related to xeric environments (Marcati & Angyalossy 2005; Marcati *et al.* 2006; Nassar *et al.* 2010). Vessels may occasionally be obstructed by tyloses, which have also been found in *C. multijuga* (Medeiros 2016). Tyloses are associated with tree aging and embolism (De Micco *et al.* 2016) but also act in defense, reducing the spread of pathogens, and as a compartmentalization process after injury (De Micco *et al.* 2016).

Ray characteristics for *C. lucens* are similar to those reported for *C. langsdorffii*, being heterogeneous, uniseriate to multiseriate, 2-7 cell rows wide, and 2-42 cell rows high (Barbosa 1982; Marcati *et al.* 2001; Yanez-Inzunza 1992), with a frequency of 4 to 13 rays mm^{-1} (Yanez-Inzunza 1992). The only anatomical description found for *C. lucens* reported homogeneous rays in addition to the heterogeneous ones (Barbosa 1982), which could not be confirmed by our observations. In addition, Barbosa (1982) described rays of 1-4 cells wide (39-78 µm; average = 56,16) and 7-33 cells high (200-600 µm; average = 350). Such anatomical differences may reflect contrasting ecological factors because that study was carried out in a forest garden subjected to management, whereas we collected the wood samples in a native forest. Medeiros (2016) reported for the first time the presence of oil-resin in *Copaifera* ray cells, a characteristic that was also observed for *C. lucens* in the present study.

Libriform fibers also occur in *C. langsdorffii* and *C. multijuga* (Marcati *et al.* 2001; Melo-Júnior *et al.* 2011; Medeiros 2016). Barbosa (1982) reported the prevalence of fibrotracheid for *C. lucens*, which were not observed in this study. Fiber length in *Copaifera* was assumed to range from 434 to 2,315 µm, with averages of 340 to 1,328 µm (Barbosa 1982; Medeiros 2016; Yanez-Inzunza 1992), but we registered higher values for *C. lucens* (1,360 µm). We detected gelatinous fibers and fibers with intrusive growth in *C. lucens*. Although these characteristics were previously reported in *Copaifera*, they had not yet been described for the studied species (Barbosa 1982; Marcati *et al.* 2001; Medeiros 2016; Melo-Júnior *et al.* 2011). Although gelatinous fibers are commonly related to tension wood wood (Evert 2013), Nassar *et al.* (2010) found them in normal wood, suggesting that gelatinous fibers may also be involved in water retention and increased plant resistance to drought. After comparing *C. langsdorfii* in "cerrado" and mesophyll forest, Marcati *et al.* (2001) found that there is a greater proportion of individuals with gelatinous fibers in the "cerrado", attributing this characteristic to the lower water availability in this region. The TAF has a well-marked seasonal period from May to September, whose precipitation falls below 60 mm for at least three months (Víncens *et al.* 2003). According to Worbes (1995), this precipitation threshold causes stress to the plant, probably triggering the formation of gelatinous fibers in *C. lucens*.

The frequency of **intercellular canals** was similar to that reported for other species of the genus, between 1 and 12 (Yanez-Inzunza 1992; Melo-Júnior *et al.* 2011; Medeiros 2016). Secretory canals occur in few botanical families and are more common in tropical than temperate regions (Wheeler & Baas, 1991). In *Copaifera*, the canals are involved within bands of marginal parenchyma (Metcalfe & Chalk 1950; Marcati *et al.* 2001; Melo-Júnior *et al.* 2011; Medeiros 2016) and are occasionally wider than the parenchyma bands (Yanez-Inzunza 1992). Intercellular canals are difficult to detect in macroscopy, as they often resemble vessels (Guignard 1892).

Prismatic crystals were reported in other species of *Copaifera*, forming crystalline series of up to 11 crystals per series (Marcati *et al.* 2001). In *C. langsdorffii*, calcium oxalate prismatic crystals were observed in subdivided cells of the axial parenchyma, forming crystalline series of up to eight crystals, often close to the rays (Melo-Júnior *et al.* 2011). Of the nine *Copaifera* species studied by Yanez-Inzunza (1992), seven presented crystals in the axial parenchyma, mainly close to the rays. The author did not find crystals in *C. guianensis* and *C. multijuga*. The latter also did not show crystals in the studies made by Medeiros (2016). In *C. lucens*, rhombohedral crystals composed of calcium oxalate were reported in both the axial and radial parenchyma cells (Barbosa 1982). Marcati and Angyalossy (2005) found that in *Citharexylum myrianthum* (Verbenaceae) calcium oxalate crystals are produced during the dry period, when there is loss of leaves and the exchange rate is close to inactivity. According to Marcati and Angyalossy (2005), crystals probably dissolve during earlywood formation, providing calcium that is required for cell division and differentiation. Thus, the presence of crystals in *C. lucens* may indicate that the seasonal drought at the TAF is marked enough to trigger physiological responses that are imprinted in the wood structure, which is fundamental for dendroclimatic studies.

3.4.3 Does the detailed anatomical description aids in the recognition of tree-rings of *Copaifera lucens*?

The study of wood anatomy has proved to be an important tool for understanding the growth ring structure of *C. lucens*. Often, ring markers and wood features are recognized from microscopy, with subsequent search of the pattern at macroscopy and then application at dating. In this study, the recognition of the characteristics of zones with gelatinous fibers and very thick-walled fibers was possible after their comprehension at the microscopic level. In addition, the occasional variations in vessel distribution were highlighted in the meticulous macroscopic analysis. The detailed analysis allowed to identify ring markers that can be applied to complex dating portions of the sample. The importance of the association of two or more anatomical characteristics applied to the identification of ring borders in the tropics was previously highlighted (Worbes 1989; Roig *et al.* 2005; López & Villalba 2016; Tarelkin *et al.* 2016). Furthermore, we observed anatomical structures that are commonly related to environmental factors such as gelatinous fibers and prismatic crystals. These characteristics may aid in the ecological interpretation of the results obtained from dendrochronology.

The study also shed light on the recognition of intra-annual rings, which sometimes resemble the annual rings (Cherubini *et al.* 2003). Due to the high frequency of intra-annual rings in the tropics, the recognition of these structures may confer greater accuracy to dating and optimize crossdating. It should also be taken into account that the complexity and plasticity of the anatomical structure of tropical wood have prevented technical innovations for automatic dating, so the skill of experts in wood anatomy has a greater importance for the success of crossdate in the tropics (Fichtler 2015).

Concerning *C. lucens*, a full understanding of physiological processes involved in wood formation would require the monitoring of xylogenesis. Such studies may contribute to identifying particular environmental conditions triggering the formation of intra-annual rings and secretory canals (Callado *et al.* 2013; Vieira *et al.* 2014). The need for such research was also emphasized by Pumijumnong *et al.* (1995) after dendrochronological studies in *Tectona grandis* growing in the tropical forests of Thailand.

3.5 CONCLUSIONS

This work represents one of the first studies for the anatomical characterization of *C. lucens* wood that contributes to the analysis of the growth rings for this endemic species in Brazil. In general, the observed anatomical features are in accordance with the characteristics reported for the genus, with the exception that the vessel density was lower. In addition to what had already been described for *C. lucens*, we observed gelatinous fibers, fibers with intrusive growth and clustered vessels.

Regarding the ring edges, in addition to what had already been described for the genus, an occasional variation in vessel density was observed. Dendrochronological studies should draw attention to key features that contribute to the annual-ring identification, since they may occur in different combinations and frequencies, being: marginal axial parenchyma (always present) associated with intercellular canals (usually with accumulation of oil-resin in parenchyma cells), thickening of the wall of the fibers in the latewood and, more rarely, variation in vessel density.

Annual rings appear to be related to marginal parenchyma associated with intercellular canals, which would be absent in intra-annual rings. In wood cores, it is relevant to notice that bands without canals could also be a consequence of the limited available surface (≤ 5mm wide), which could be insufficient to observe intercellular canals if these are rare along a particular parenchyma band. Therefore, we recommend taking wood discs instead of wood cores when possible.

ACKNOWLEDGEMENTS

We are grateful to Embrapa Forestry for the financial support, as well to researchers from the Biomas project, who assisted with field logistics and data provision; To the Reserva Natural da Vale for the technical and financial support, in particular to the biologist Geovane Siqueira, for the support with the botanical identification to the field. We especially thank the Biomas project technician, Wagner Farias F. B. Silva, and the field assistants, Edilson da Silva and Marcos de Castro to the sampling support. We are grateful to laboratory technicians Mr. Armindo Gonçalves Teixeira from UTDA, Ana Carvalho from UC, and Maria Bermudez from ESALQ for assistance in the preparation of histological slides. We are grateful to the colleagues of the Laboratory of Plant Ecology of UNISINOS for the support in the field and laboratory, especially Gabriela Reis-Avila. This article is part of a doctoral thesis developed under the guidance of Dr. Juliano Morales de Oliveira, to whom the first author thanks for all the support received.

Funding

This work was supported by the Brazilian Agricultural Research Corporation (EMBRAPA), Confederação Nacional da Agricultura (CNA), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, process nº 88881.135931/2016-01), all related to the Brazilian government; by FCT-Portuguese Foundation for Science and Technology under the project UID/AGR/04033/2013 and POCI-01-0145-FEDER-006958 and Reserva Natural da Vale for support with hosting.

REFERENCES

Albuquerque AR, Castro VR de & Lobão MS. 2016. Comparative analysis of anatomy and micro-densitometry of the growth rings of hardwoods and conifers, with emphasis on dendrochronology. Sci For 44: 595--610. doi: dx.doi.org/10.18671/scifor.v44n111.06 595

Alencar J da C. 1982. Estudos silviculturais de uma população natural de *Copaifera multijuga* Hayne - Leguminosae, na Amazônia Central. 2 - Produção de óleo-resina. Acta Amaz 12: 75--89.

Alves ES & Angyalossy-Alfonso V. 2000. Ecological trends in the wood anatomy of some brazilian species. 1. Growth rings and vessels. IAWA J 21: 3--30. doi: 10.1163/22941932-90000233.

Araújo-Júnior FA de, Braz MN, Rocha-Neto OG da, Costa FA & Brito MVH. 2005. Efeito do óleo de copaíba nas aminotransferases de ratos submetidos à isquemia e reperfusão hepática com e sem pré-condicionamento isquêmico. Acta Cir Bras 20: 93--99. doi: 10.1590/S0102-86502005000100013.

Barbosa O. 1982. Características estruturais do lenho de *Copaifera langsdorfii* e *Copaifera lucens* Dwyer. Silvicultura 15--16: 23--36.

Barbosa PCS, Medeiros RS, Sampaio PTB, Vieira G, Wiedemanna LSM & Veiga-Junio V F. 2012. Influence of abiotic factors on the chemical composition of copaiba oil (*Copaifera multijuga* Hayne): soil composition, seasonality and diameter at breast height. J Braz Chem Soc 23: 1823--1833. doi: 10.1590/S0103-50532012005000049.

Barros CF, Marcon-Ferreira ML, Callado CH, Lima HRP, Cunha M da, Marquete O. & Costa CG. 2006. Tendências ecológicas na anatomia da madeira de espécies da comunidade arbórea na Reserva Biológica de Poço das Antas, Rio de Janeiro, Brasil. Rodriguésia 57: 443--460.

Battipaglia G, De Micco V, Brand WA, Linke P, Aronne G, Saurer M & Cherubini P. 2010. Variations of vessel diameter and δ13C in false rings of *Arbutus unedo* L. reflect different environmental conditions. New Phytol 188: 1099--1112. doi: 10.1111/j.1469-8137.2010.03443.x.

Brodersen CR & McElrone AJ. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. Front Plant Sci 4: 1--11. doi: 10.3389/fpls.2013.00108.

Callado CH, Roig FA, Tomazello-Filho M & Barros CF. 2013. Cambial growth periodicity studies of South American woody species – a review. IAWA J 34: 213--230. doi: 10.1163/22941932-00000019.

Campelo F, Nabais C, Freitas H & Gutierrez E. 2007. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. Ann For Sci 64: 229--238. doi: 10.1051/forest.

Carlquist S. 1977. Ecological factors in wood evolution: a floristic approach. Amer J Bot 64: 887--896.

Carlquist S. 2001. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood, 2nd edn. Springer-Verlag Berlin Heidelberg GmbH, Berlin.

Carlquist S. 2015. Living cells in wood. 1. Absence, scarcity and histology of axial parenchyma as keys to function. Bot J Linn Soc 177: 291--321. doi: 10.1111/boj.12247.

Carlquist S & Hoekman DA. 1985. Ecological wood anatomy of the woody southern Californian flora. IAWA Bull 6: 319--347. doi. 10.1163/22941932-90000960.

Carvalho PER. 2003. Espécies arbóreas brasileiras, 21st edn. Embrapa Florestas, Colombo.

Cherubini P, Gartner BL, Tognetti R, Bräker OU, Schoch W, Innes JL. 2003. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. Biol Rev Camb Philos Soc 78: 119--148. doi: 10.1017/S1464793102006000.

Coradin VTR & Muñiz GIB de. 1991. Normas e procedimentos em estudos de anatomia de madeira: I. Angiospermae II. Gimnospermae. IBAMA, DIRPED, LPF, Série técnica 15: 17.

Costa MS, Ferreira KEB, Botosso PC & Callado CH. 2015. Growth analysis of five Leguminosae native tree species from a seasonal semidecidual lowland forest in Brazil. Dendrochronologia 36: 23--32. doi: 10.1016/j.dendro.2015.08.004.

De Micco V, Campelo F, De Luis M, Bräuning A, Grabner M, Battipaglia G & Cherubini P. 2016. Intra-annual density fluctuations in tree rings: how, when, where, and why? IAWA J 37: 232--259. doi: 10.1163/22941932-20160132.

Evert RF. 2013. Anatomia das plantas de Esau: meristemas, células e tecidos do corpo da planta: sua estrutura, função e desenvolvimento. Blucher, São Paulo.

Fichtler E. 2015. Dendroclimatology using tropical broad-leaved tree species – a review. Erdkunde 71: 5--22. doi: 10.3112/erdkunde.2017.01.01.

Fonti P, Von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H & Eckstein D. 2010. Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol 185: 42--53. doi: 10.1111/j.1469-8137.2009.03030.x.

Francisco SG. 2005. Uso do óleo de resina de copaíba (*Copaifera officinalis* L.) em inflamação ginecológica. Femina 33: 89--93.

Fritts HC. 1976. Tree rings and climate change. Academic Press Inc Ltd., New York

Garay I, Kindel A, Louzada MAP & Dos Santos D. 2003. A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. In: Garay, I. & Rizzini CM (Orgs). A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. Vozes, Petrópolis, pp 16--26.

Garay I & Silva BAO. 1995. Húmos florestais: síntese e diagnósticos das interelações vegetação/solo. Oecologia Bras 1: 19--46.

Glatzel G & Geils BW. 2009. Mistletoe ecophysiology: host–parasite interactions: In Anais of XXII International Union of Forestry Research Organization World Congress meeting held in Brisbane, Queensland, Australia. Botany 87: 10--15. doi: 10.1139/B08-096.

Groenendijk P, Sass-Klaassen U, Bongers F & Zuidema PA. 2014. Potential of tree-ring analysis in a wet tropical forest: a case study on 22 commercial tree species in Central Africa. For Ecol Manage 323: 65--68. doi: 10.1016/j.foreco.2014.03.037.

Guignard ML. 1892. L'appareil sécréteur des *Copaifera*. Bull. la Société Bot. Fr. ISSN 233–260.

Heck MC, Ávila-Viana L, Elisa V & Vicentini P. 2012. Importância do óleo de *Copaifera* sp. (copaíba). SaBios Rev Saúde e Biol 7: 82--90.

I AWA Committee. 1989. IAWA list of microscopic features for hardwood identification. IAWA Bull. n.s. 10: 219--332.

IBGE - Instituto Brasileiro de Geografia e Estatística. 2012. Manual técnico da vegetação brasileira., 2nd edn. Coordenação de Recursos Naturais e Estudos Ambientais (Série manuais técnicos de geociências), Rio de Janeiro.

IPCC - Intergovernmental Panel on Climate Change. 2014. Climate change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPPC Panel, Geneva, Switzerland.

Jesus RMD & Rolim SG. 2005. Fitossociologia da Mata Atlântica de Tabuleiro. Boletim Técnico. Soc Investig Florestais 17: 1--154.

Koeppen W. 1948. Climatologia: con un estudio de los climas de la tierra. Fondo de Cultura Economica, Mexico, DF.

Lisi CS, Tomazello-Fo M, Botosso PC, Roig FA, Maria VRB, Ferreira-Fedele L & Voigt. 2008. Tree-ring formation, radial increment periodicity, and phenology of tree species from a seasonal semi-deciduous forest in southeast Brazil. IAWA J 29: 189--207. doi: 10.1163/22941932-90000179.

López L & Villalba R. 2016. Reliable estimates of radial growth for eight tropical species based on wood anatomical patterns. J Trop For Sci 28: 139--152.

Louzada MAP, Curvello A, Barbosa JHC & Garay I. 1997. O aporte de matéria orgânica ao solo: quantificação, fenologia e suas relações com a composição específica em área de Floresta Atlântica de Tabuleiros. Leandra 12: 27--32.

Macedo CA & Langenheim JH. 1989. Intra- and interplant leaf sesquiterpene variability in *Copaifera langsdorfii*: relation to microlepidopteran herbivory. Biochem Syst Ecol 17: 551--557. doi: 10.1016/0305-1978(89)90098-7.

Marcati CR, Angyalossy-alfonso V & Benetati L. 2001. Anatomia comparada do lenho de *Copaifera langsdorffii* Desf. (Leguminosae-Caesalpinoideae) de floresta e cerradão. Revta brasil. Bot. 24: 311--320. doi: 10.1590/S0100-84042001000300010.

Marcati CR & Angyalossy V. 2005. Seasonal presence of acicular calcium oxalate crystals in the cambial zone of *Citharexylum myrianthum* (Verbenaceae). IAWA J 26: 93--98. doi: 10.1163/22941932-90001604.

Marcati CR, Oliveira JS & Machado SR. 2006. Growth rings in cerrado woody species: occurrence and anatomical markers. Biota Neotrop 6: 1--31. doi: 10.1590/S1676-06032006000300001.

Marcon ML & Costa CG. 2000. Anatomia da madeira de quatro espécies do gênero *Miconia* Ruiz & Pavón (Melastomataceae). Rodriguésia 51: 5--10.

Martins-da-Silva RCV, Pereira JF & Lima HC De. 2008. O gênero *Copaifera* (Leguminosae - Caesalpinioidae) na Amazônia Brasileira. Rodriguésia 59: 455--476.

Medeiros R da S. 2016. Estudo da anatomia do lenho e dendrocronologia de árvores de *Copaifera multijuga* Hayne na Amazônia brasileira e sua relação com o manejo e extração de oleorresina. Escola Superior de Agricultura "Luiz de Queiroz".

Media Cybernetics. 2001. Image-Pro Plus, version 4.5 Rockville, USA.

Melo-Júnior JCF de, Ceccantini G & Bona C. 2011. Anatomia ecológica do lenho de *Copaifera langsdorffii* Desf. (Leguminosae) distribuída em diferentes condições edáficas do cerrado sul-brasileiro. Iheringia - Ser Bot 66: 189--200.

Metcalfe CR & Chalk L. 1950. Anatomy of the dicotyledons: leaves, stem, and wood in relation to taxinomy with notes on economic uses, 1st edn. Oxford University Press, Amen House, London E. C., London.

Morris H, Brodersen C, Schwarze FWMR & Jansen S. 2016. The parenchyma of secondary xylem and its critical role in tree defense against fungal decay in relation to the CODIT Model. Front Plant Sci 7: 1665. doi: 10.3389/fpls.2016.01665.

Nassar NMA, Abreu LFA & Teodoro DAP. 2010. Drought tolerant stem anatomy characteristics in *Manihot esculenta* (Euphorbiaceae) and a wild relative. GMR Genet Mol Res 9: 1023--1031. doi: 10.4238/vol9-2gmr800.

Peixoto AL & Gentry A. 1990. Diversidade e composição florística da mata de tabuleiro na Reserva Florestal de Linhares, Espírito Santo, Brasil. Rev Bras Botânica 13: 19--25.

Pieri FA, Mussi MC & Moreira MAS. 2009. Óleo de copaíba (*Copaifera* sp.): histórico, extração, aplicações industriais e propriedades medicinais. Rev. Bras. Plantas Med. 11: 465--472. doi: 10.1590/S1516-05722009000400016.

Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J, Penã-Claros M, Sterck F, Villegas Z & Sass-Klaassen U. 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. New Phytol Res 185: 481--492.

Queiroz LP, Martins-da-Silva ARCV. & Costa J. 2015. *Copaifera* in Lista de Espécies da Flora do Brasil. In: Jard. Botânico do Rio Janeiro. http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB22895.

Rizzini CT. 1963. Nota prévia sobre a divisao fitogeográfica do Brasil. Rev Bras Geogr 1: 1--

64.

Rodríguez ENP, Mateus D & Lozano I. 2011. Anatomía xilematica de Caesalpiniaceae registradas en la xiloteca de la Universidad Distrital Francisco José De Caldas. Colomb For 14: 145--171.

Roig FA, Osornio JJJ, Diaz JV, Luckman B, Tiessen H, Medina A & Noellemeyer EJ. 2005. Anatomy of growth rings at the Yucatán Peninsula. Dendrochronologia 22: 187--193. doi: 10.1016/j.dendro.2005.05.007.

Rozendaal DMA & Zuidema PA. 2011. Dendroecology in the tropics: a review. Trees - Struct. Funct. 25: 3--16. doi: 10.1007/s00468-010-0480-3.

Schweingruber FH. 2007. Wood structure and environment. Springer-Verlag Berlin Heidelberg, Birmensdorf.

Schweingruber FH. 1988. Tree Rings: basics and applications of dendrochronology. Kluwer Academic Publischers, Dordrecht.

Siqueira MF. 1994. Análise florística e ordenação de espécies arbóreas da Mata Atlântica através de dados binários. Universidade de Campinas.

Speer JH. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.

Stahle DW, Mushove PT, Cleaveland MK, Roig, F & Haynes, GA. 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. For Ecol Manage 124: 217--229. doi: 10.1016/S0378-1127(99)00075-4.

Tarelkin Y, Delvaux C, De Ridder M, El Berkani T, De Cannière C & Beeckman H. 2016. Growth-ring distinctness and boundary anatomy variability in tropical trees. IAWA J 37: 275--294. doi: 10.1163/22941932-20160134.

Tyree MT & Zimmermann MH (2002) Xylem structure and the ascent of sap, 2nd ed. Springer Berlin Heidelberg, Berlin, Heidelberg.

Veiga-Junior VF & Pinto AC. 2002. O gênero *Copaifera* L. Quim Nova 25: 273--286.

Veloso HP. 1991. Classificação da vegetação brasileira adaptada a um sistema universals. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro.

Vieira J, Rossi S, Campelo F, Freitas H & Nabais C. 2014. Xylogenesis of *Pinus pinaster* under a Mediterranean climate. Ann For Sci 71: 71--80. doi: 10.1007/s13595-013-0341-5

Víncens RS, Agarez FV & Garay I. 2003. A região da REBIO Sooretama e da Reserva de Linhares e seu entorno: das características físico-geográficas ao uso da terra. In: Garay I & Rizzini CM. (Orgs) A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. Vozes, Petrópolis, pp 7--15.

Wheeler EA, Baas P & Rodgers S. 2007. Variations in dicot wood anatomy: a global analysis based on the insidewood database. IAWA J 28: 229--258.

Wheeler EA & Baas P. 1991. A survey of the fossil record for dicotyledonous wood and its significance for evolutionary and ecological wood natomy. IAWA Bull 12: 275--332. doi: 10.1163/22941932-90001256.

Worbes M. 1995. How to measure growth dynamics in tropical trees. IAWA J 16: 337--351. doi: 10.1163/22941932-90001424.

Worbes M. 1989. Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. IAWA Bull 10: 109--122. doi: 10.1163/22941932-90000479.

Yanez-Inzunza O de LN. 1992. Anatomia da madeira de nove espécies do gênero *Copaifera* (Leguminosae - Caesalpinioideae). Universidade Federal Do Paraná.

Zeng Z, Piao S, Chen A, Lin X, Nan H, Li J & Ciais P. 2013. Committed changes in tropical tree cover under the projected 21st century climate change. Sci Rep 3: 1--6. doi: 10.1038/srep01951.

Zuidema PA, Brienen RJW & Schöngart J. 2012. Tropical forest warming: looking backwards for more insights. Trends Ecol Evol 27: 193--194. doi: 10.1016/j.tree.2011.12.007.

FIGURE AND CAPTIONS

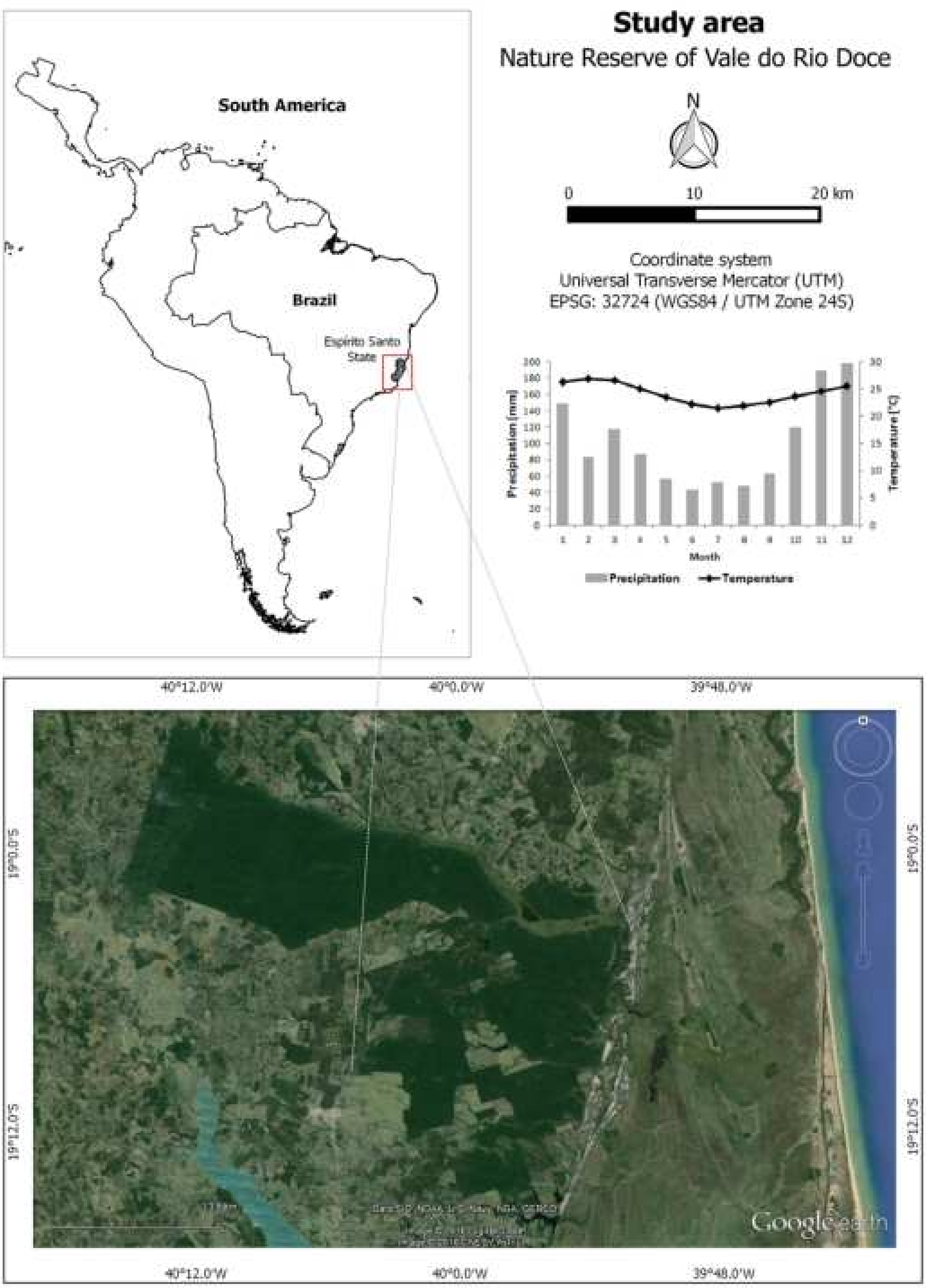


Figure 1. Location of the study area in the state of Espírito Santo, southeastern Brazil.

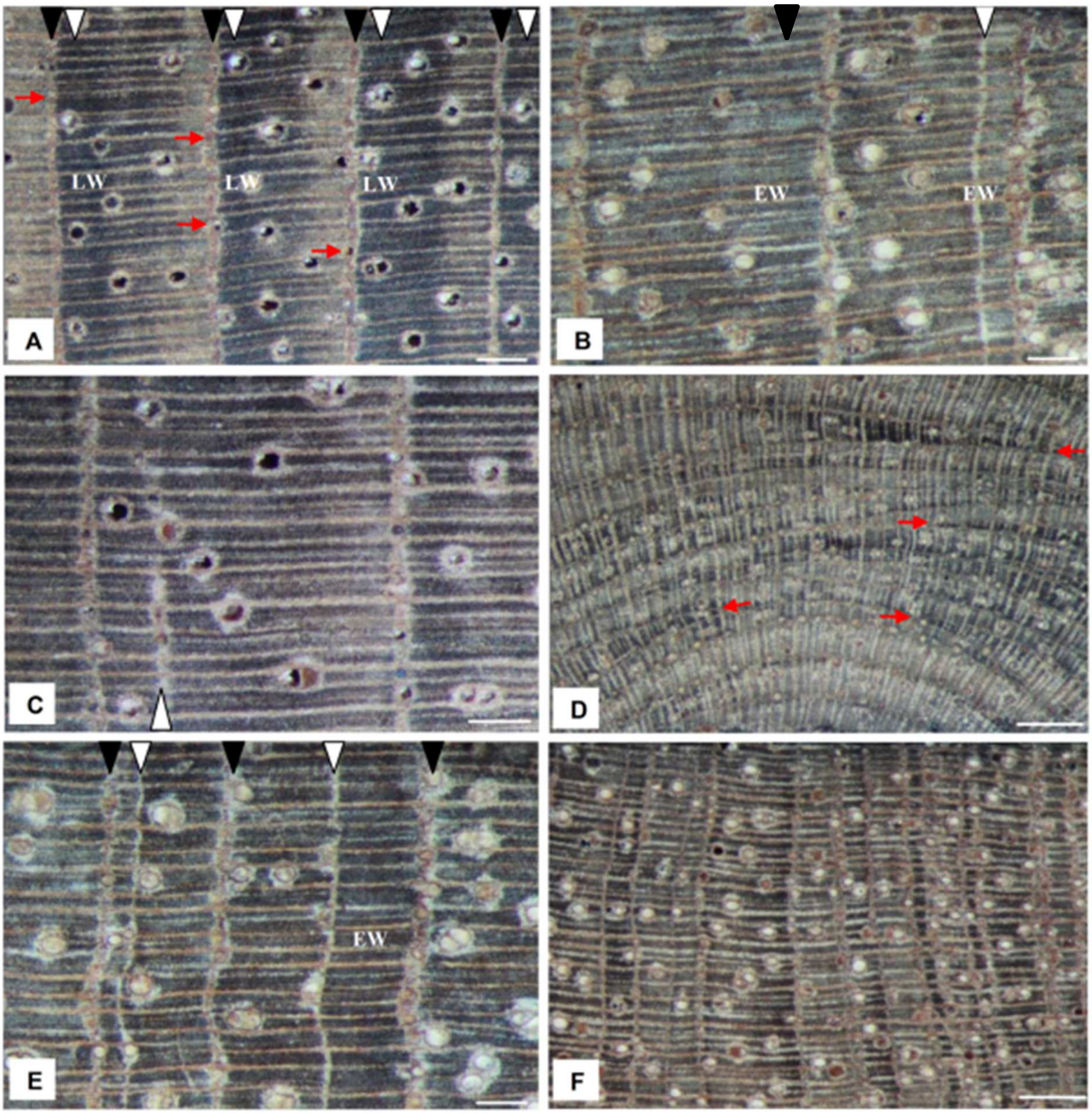


Figure 2. Growth ring characteristics in *Copaifera lucens*. -- A: Well-defined rings, axial parenchyma in marginal bands (black arrows), thick-walled latewood fibers (white arrows), and intercellular canals in long tangential lines (small red arrows); -- B: Vessel density variation, with absence of vessels at the beginning of earlywood (black arrows), distinct intra-annual rings in earlywood, clear and continuous axial parenchyma bands (white arrow); -- C: Discontinuous axial parenchyma bands (white arrow); -- D: Axial parenchyma in confluent bands near the pith (red arrows); -- E: Characteristic rings, delimited by axial parenchyma in marginal bands associated with intercellular canals (black arrows), clear lines of marginal axial parenchyma without intercellular canals (white arrows); – F: Complex rings. -- Scale bars = 1 mm. -- LW = latewood; -- EW = earlywood.

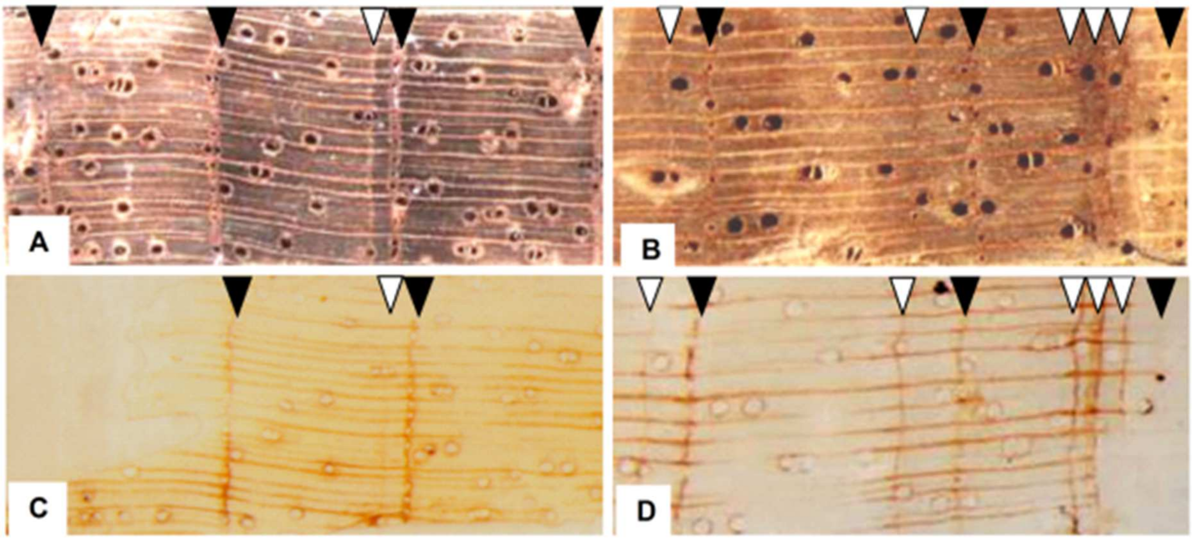


Figure 3. Macroscopic images of the transversal cross-section of *Copaifera lucens.* -- A: Diffuse porosity, marginal axial parenchyma bands showing axial intercellular canals (black arrows) or lacking them (white arrow); -- B: Poorly distinct growth layers with marginal axial parenchyma bands associated with axial intercellular canals (black arrows) or lacking them (white arrows); -- C, D: Details on histological slides of images A and B in natural color, evidencing the accumulation of oil-resin in reddish-brown color in marginal and radial parenchyma cells (black arrows); -- In (C) it is noticed that the parenchyma band evidenced in (A) does not accumulate oil-resin. -- Magnification = 0.8 ×.

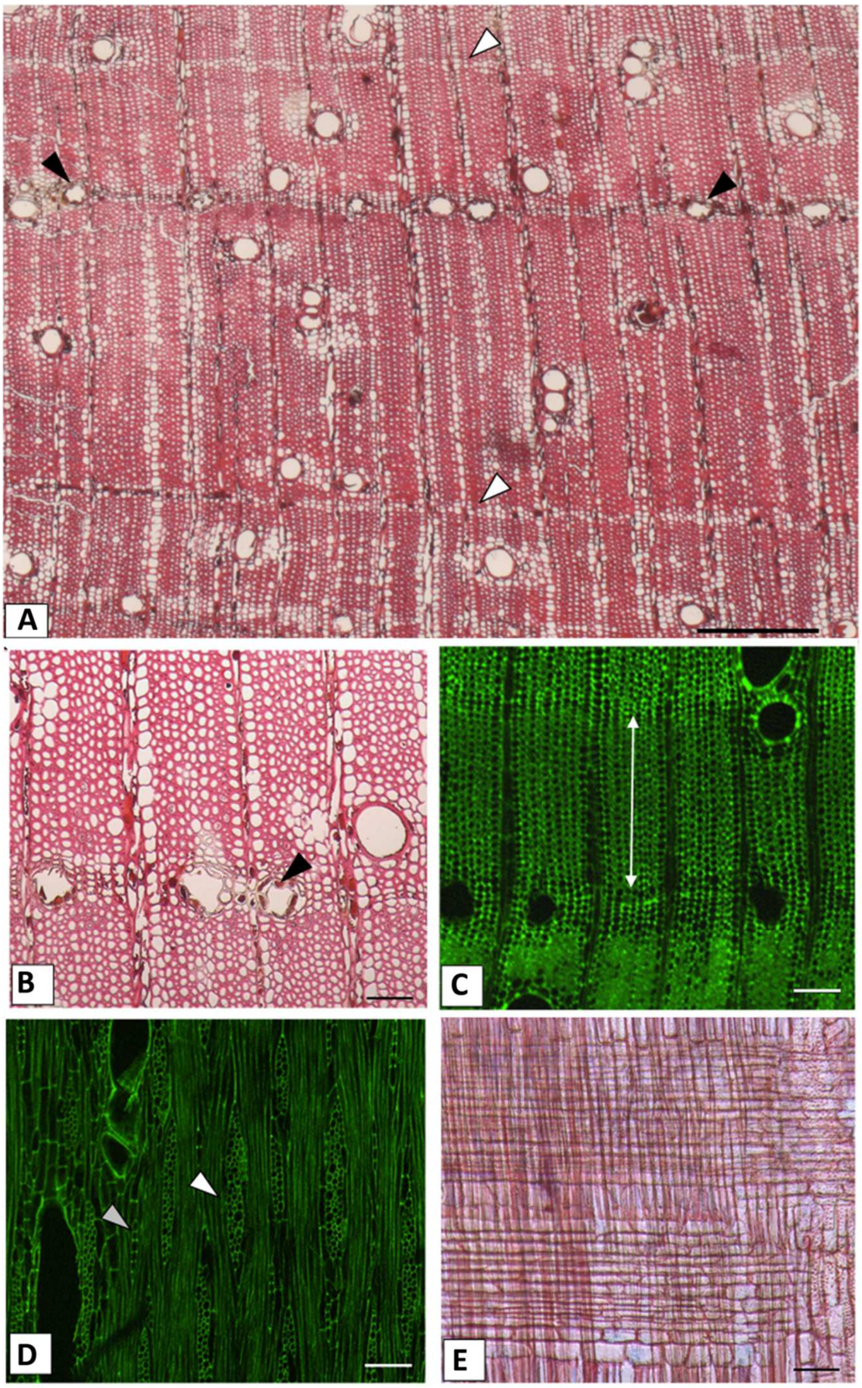


Figure 4. Microscopic images of the wood of *Copaifera lucens*. A-B-C Transverse section. -- A: diffuse vessel distribution, marginal axial parenchyma band with (black arrow) and without (white arrows) intercellular canals; -- B: details of the axial canals associated with the axial parenchyma band; -- C: detail of a band of fibers in the latewood (white arrow); -- D: tangential section showing uniseriate (gray arrow) to multiseriate rays (white arrow); -- E: radial section showing heterogeneous rays; -- Scale bars: (A) = 200µm; -- (C-D-E) = 100µm; -- (C) = 400 µm. -- (C-D) Fluorescence microscopy.

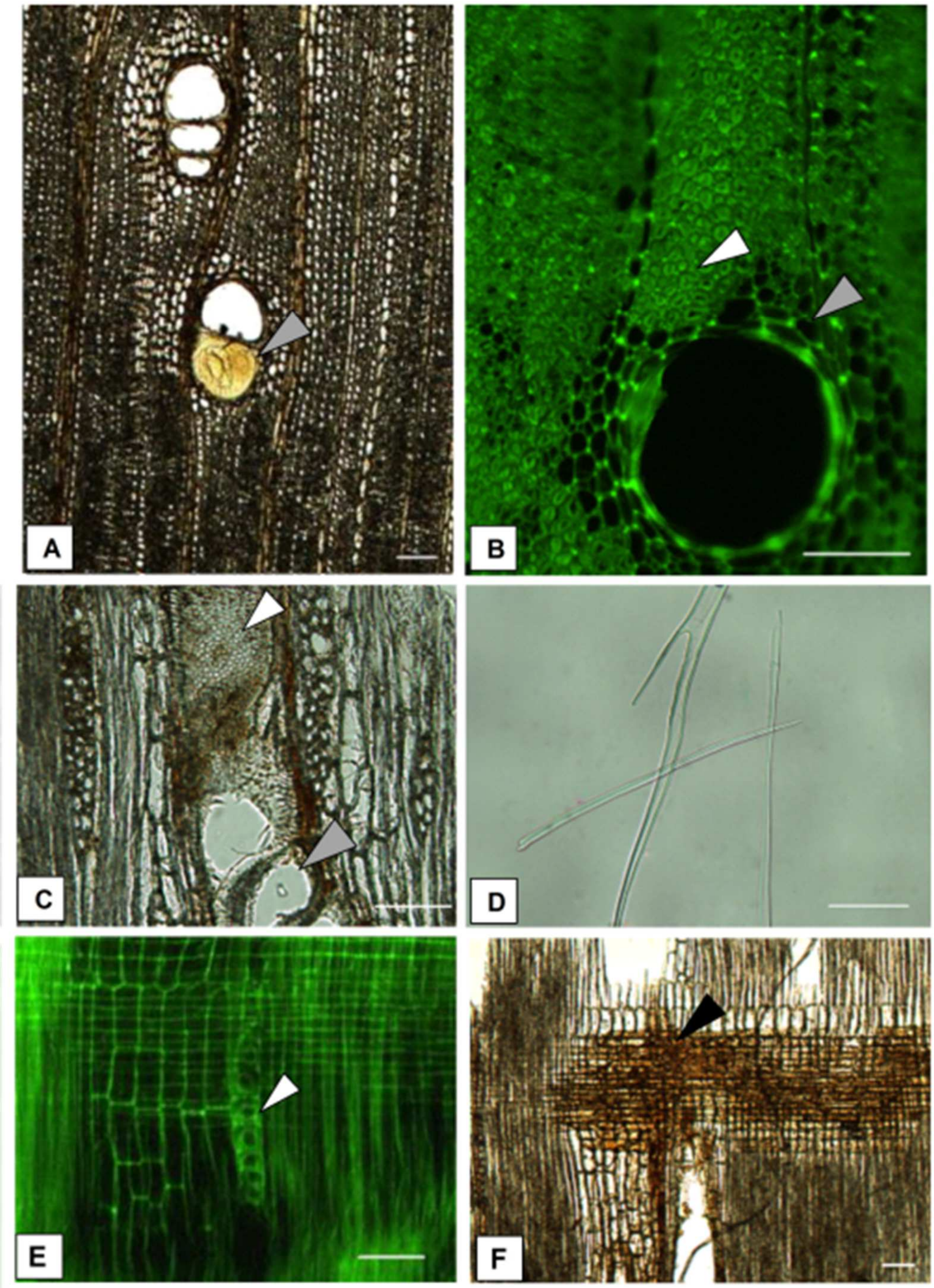


Figure 5. Microscopic images of the wood of *Copaifera lucens*. -- A: Transverse section showing a vessel completely obstructed by two tylosis vesicles and oily contents (arrow); -- B: Transverse section showing gelatinous fibers (white arrow) and vasicentric paratracheal parenchyma (gray arrow) in the transverse plane; -- C: tangential section showing simple perforation plates (gray arrow) and intervessel pits (white arrow); -- D: radial section showing dissociated fibers with ends indicating intrusive growth; – E: radial section showing Crystalline series in chambers in the axial parenchyma. – F: Rays filled with reddish-brown resin oil. -- Scale bars = 100 µm.

CAPÍTULO 4

CLIMATIC SIGNAL IN GROWTH-RINGS OF *Copaifera lucens* DWYER.: AN ENDEMIC SPECIES OF A BRAZILIAN ATLANTIC FOREST HOTSPOT[5]

---

[5] Artigo formatado conforme normas da revista Dendrochronologia (submetido).

Climatic signal in growth-rings of *Copaifera lucens* DWYER.: an endemic species of a Brazilian Atlantic Forest hotspot

Cláudia Fontana[a], Gonzalo Pérez-de-Lis[b,c], Cristina Nabais[c], José Luís Penetra Cerveira Lousada[d], Gabriela Morais Olmedo[a], Paulo César Botosso[e], Juliano Morales Oliveira[a]

[a] University of Vale do Rio dos Sinos (UNISINOS). Av. Unisinos, 950, Cristo Rei, 93022-750, São Leopoldo, RS, Brazil. claudiafontanabio@gmail.com (corresponding author, permanent address; ORCID 0000-0003-2032-5673); julianooliveira@unisinos.br; gabriela.m.olmedo@hotmail.com

[b] INRA Grand-Est Nancy. F-54280 Champenoux, France. gonzalo.perez-de-lis-castro@inra.fr

[c] Coimbra University, Department of Life Sciences, Functional Ecology Center. Calçada Martim de Freitas, 3000, nº 456, Coimbra, Portugal. crnabais@bot.uc.pt

[d] University Trás-os-Montes e Alto Douro/CITAB. Forestry Department, Quinta de Prados, 5001-801, Vila Real, Portugal. jlousada@utad.pt

[e] Brazilian Agricultural Research Corporation (Embrapa), Embrapa Forestry, Estrada da Ribeira - Km 111, 83411-000, Colombo, PR, Brazil. paulo.botosso@embrapa.br

ABSTRACT

In this study, we present the first tree-ring chronology for the tropical tree species *Copaifera lucens* and its climatic signal. Tree-ring width series were compared with local climate indices using a drought index (Standardized Precipitation Evapotranspiration Index —SPEI), in monthly, bi-monthly and four-monthly scales. We also calculated negative pointer years over the time-span of the tree-ring width. The radial growth of *C. lucens* showed a positive correlation with the SPEI of the current summer in all the three analyzed time scales, while the negative pointer years matched with the drier years. The species was highly sensitive to very low summer precipitation, which may lead to a 49% reduction in growth. We conclude that the long-living *C. lucens* has a great potential for dendrochronological studies as it shows a marked climatic signal. Our study also reinforces the importance of rainfall in regulating radial growth in tropical forests and sheds light on the local climate influence on tree growth in recent decades.

Keywords: Fabaceae, Dendrochronology, climate-growth relationship, tree-ring, tropical forest.

4.1 INTRODUCTION

Forests play multiple roles related to ecological systems, species, economy, culture, aesthetics, human health, among others (Hassan et al., 2005). In addition, forests influence global climate through physical, chemical, and biological processes that affect the hydrologic cycle and atmospheric composition (Shukla et al., 1990; Bonan, 2008; Wagner et al., 2016). On the other hand, the performance of forests is influenced by climate conditions (Fritts, 1976; Schweingruber, 1988; Speer, 2010), making up a complex feedback loop between climate and forests. Considering the evidence on current environmental and climatic changes (IPCC, 2014), as well the importance of such a feedback loop, it is relevant to investigate how plants react to changes in climate conditions (Bazzaz, 1996). In this sense, tree-ring analysis provides accurate information on the magnitude and frequency of variations in past climate patterns (Fritts, 1976; Jacoby, 1989; Cook, 1987; Esper and Gärtner, 2001). Due to this, dendrochronology has been used as a proxy to reconstruct the climatic past and to access information about the plants' responses forward over time (Cherubini et al., 2003), *e.g.*, growth rates, wood production and rotation times (Jacoby, 1989).

Many dendrochronological studies have contributed to the understanding of climate changes in various ecosystems. Brienen et al. (2010) analyzed the effect of El Niño on the rings of *Mimosa acantholoba* (Willd.) Poir, an abundant species in the dry forests of southern Mexico and Central America. The researchers concluded that their growth might decline by as much as 37% in El Niño years. Oliveira et al. (2016), in a study in the Mediterranean, found that *Quercus suber* L. also reduced its growth in dry years, with reductions of up to 42%. *Picea glauca* (Moench) Voss in the boreal forests of Alaska showed a reduction of growth under increasing concentrations of CO_2 (Barber et al., 2000). These examples highlight the importance of dendrochronology to understand the effects of climate change on forest growth and carbon stocks in several ecosystems.

The wet tropical forest stores between 25% and 54% of the terrestrial biosphere carbon and 33% of the primary terrestrial net production (Bonan, 2008; Liu et al., 2015). However, these stocks are at risk due to anthropogenic deforestation and possibility of release driven by climate change (Cramer et al., 2004). The Brazilian Atlantic Forest is a biodiversity hotspot (Myers et al., 2000) and among the most vulnerable to climate change (Bellard et al., 2014). The deforestation in the Atlantic Forest has already reached 88.27% of the original area (Ribeiro et al., 2009). Despite the great diversity of its flora (more than 19,000 plant species - Forzza et al., 2012), this forest was poorly investigated by dendroclimatology, comprising only 11 published papers with a climatic approach (Fontana et al., unpublished data).

The climatic scenarios for the Atlantic Forest region indicate an increase of temperature and changes in precipitation patterns (IPCC, 2014). A first step in predicting forest resistance and resilience to climate change is to know how it performed in relation to past climatic conditions. In this context, our goal was to analyze the influence of climate on the growth of Brazilian Atlantic Forest trees, exploring the dendrochronological potential of *Copaifera lucens* DWYER, an endemic species forming wood layers in lowland Atlantic Forest. We hypothesized that wood layers of *C. lucens* are formed on an annual basis (growth rings) due to the seasonal rainfall regime prevailing over its geographic range. Thus, we expect to find a common signal among ring-width series of trees in a site that is positively associated with inter-annual water availability.

4.2 MATERIAL AND METHODS

4.2.1 Study area and species

The study was carried out in the Reserva Natural da Vale, an area of 23,000 hectares covered by a well-preserved tropical rainforest called "Tabuleiros" Atlantic Forest (TAF). It is located in the state of Espírito Santo, in the southeastern region of Brazil (19°S − 19°14'S, 39°12'W − 40°W), between 30 and 80 m a.s.l., approximately 30 km off the coast of the Atlantic Ocean (Fig. 1).

Figure 1.

Under Koeppen's classification (Koeppen, 1948), the climate at Reserva Natural da Vale is of type Aw (seasonal tropical climate with a dry season). Mean annual precipitation is 1,178 mm per year, with monthly averages for the rainy season (summer) of 130 mm to approximately 200 mm from October to April, during which 72% of precipitation occurs (Rolim et al., 2016). Rainfall during the dry season (winter) does not exceed 25% of the annual total, being below 60 mm from April to September (Víncens et al., 2003) (Fig. 1C). It is noteworthy the strong year-to-year variation in precipitation that can vary up to 50% (Garay et al., 2003). Severe droughts are related to strong "El Niño-Southern Oscillation" (ENSO) events (Rolim et al., 2016). The mean temperature ranges between 19.9 °C in July to 25.6 °C in February through the year, the annual mean being 23 °C (Jesus, 2001). Evapotranspiration is an important climate component in this region, attaining in average 1,246 mm per year, with maximum values in summer and frequently exceeding precipitation in winter (Víncens et al., 2003).

Soils in the sampling area are predominantly yellow podzolic (yellow, tertiary argisol), dystrophic, with a drastic difference in grain size according to depth, presenting low fertility and low cation-exchange capacity (Garay and Silva, 1995; Louzada et al., 1997). Mull humus is present (~ 3.9 t / ha^{-1}), with rapid decomposition of organic inputs (~ 9 months), being the main soil nutrient reservoir (Garay and Silva, 1995; Louzada et al., 1997).

TAF presents a floristic mixture of Amazonian and Atlantic elements (Rizzini, 1963; Peixoto and Gentry, 1990; Veloso, 1991; Siqueira, 1994; Garay et al., 2003; Jesus and Rolim, 2005) and is considered to have the highest trees species density per hectare in the globe (Thomas et al., 2008). Within a broader vegetation scheme, TAF is within the Lowland Dense Ombrophilous Forest and the Lowland Semideciduous Forest (Veloso, 1991; IBGE, 2012). The contribution of organic material to the soil is another evidence of the seasonality in this forest, which shows a temporal rhythm modulated essentially by precipitation (Louzada et al., 1997). Total litterfall of many plant species shows irregularity in years with climatic anomalies, triggering changes in the community patterns (Engel, 2001).

Copaifera lucens is an endemic species that occurs in the northeastern and southeastern of Brazil (Costa, 2017). Data cataloged from the herbarium material of the Reserva Natural da Vale (unpublished data) shows that *C. lucens* is semideciduous (losing ~ 80% of the leaves in winter), flowering from February to June and fruiting in May (immature fruits) and June. Species of this genus are large and slow-growing trees, ranging from 25 to 40 meters in height, found in late secondary and climax forests (Lorenzi, 2002; Carvalho, 2003). Wood density varies from 0.60 to 0.86 g/cm^{-3} (Lorenzi, 2002; Carvalho, 2003).

The wood of *Copaifera* is characterized by intercellular canals, which are distributed in concentric bands along the marginal axial parenchyma that delimits the growth layers (Metcalfe and Chalk, 1950; Alencar, 1982; Barbosa, 1982; Martins-da-Silva et al., 2008; Grandis et al., 2010). The main marker of the annual ring in *C. lucens* is the marginal axial parenchyma associated with the axial intercellular canals (secretory canals), but canals may not be always present in wood core samples. Therefore, in many rings, the boundary may also be identified by thick-walled latewood fibers and, less often, by variation in vessel density also in the latewood (Fontana et al., unpublished data). False rings and confluent rings were reported for *Copaifera multijuga* Hayne and *Copaifera langsdorffii* Desf. (Leguminosae), being observed up to seven false rings in a year in *C. langsdorffii* (Melo-Júnior et al., 2011; Medeiros, 2016).

4.2.2 Sample collection, preparation and tree-ring analysis

For tree rings analysis, we selected 20 trees without external evidence of trunk and crown injuries distributed in a mature stand (Fig. 1). Mean trunk diameter at breast height in sampled trees was 53 cm (20-85 cm) and mean height 29 m (24-34 m). All individuals were geo-referenced. For each tree, we collected up to three transversal wood cores (radii) at breast height, using a 5-mm diameter increment borer. We treated the injuries inflicted on sampled trees with a mix of 15 grams of copper sulfate and 15 grams of whitewash dissolved in 2.5 liters of water. Wood cores were air-dried and then glued to wooden holders. After that, cross-sections were polished with sandpaper, with progressively finer grades, from 80 to 600 grits, until the anatomical characteristics of the ring boundaries were clearly identifiable.

The obtained cross-sections were visually examined under a stereomicroscope (Zeiss MZ8, ×10 magnification) and the growth-layers boundaries were identified and marked. Beside growth layers, wood anomalies were considered as possible time markers (Wils et al., 2011, 2009), such as deformed or colored filled cells (probably with oil-resin), false or indistinct rings, vessel distribution and fiber wall thickness. Wood cross-sections were then scanned with a high resolution at 1200-2400 dpi (Epson Perfection V750 PRO) with a reference scale, and the tree-ring widths (TRW) measured using the Image Pro Plus software, version 4.5.0.29 (Media Cybernetics, 2001).

4.2.3 Crossdating and chronology building

Crossdating cores proved to be very difficult, especially in the inner part of the core segments showing narrower growth layers. Thus, only the last ~50 growth rings of each tree were analyzed, taking into account that the minimum time-span indicated for crossdating is around 30 to 50 years (Briffa and Jones, 1990; Pilcher, 1990; Stahle, 1999), and because the local meteorological series available to explore climatic signals were recent (see below).

Crossdating quality was checked with help of COFECHA software (Holmes, 1986, 1983), following a stepwise process (Fig 2). After cores series were crossdated within-trees, mean TRW series per tree were obtained through a bi-weighted robust mean function, in ARSTAN software (Cook, 1985; Cook and Holmes, 1996). Crossdating among tree series was verified and a subset of five trees (2-mean and 3-radii), with higher correlation among series, was selected for the site's master chronology. The remnant mean tree series were gradually compared to the master chronology subset, and their cores reexamined accordingly to alternative dating solutions suggested in COFECHA. If changes were feasible according to the re-inspection of wood-anatomical features, dating adjustments were made and the respective tree mean series aggregated in the master chronology subset, given that its inclusion did not impair the master's overall intercorrelation. The process finished once no more inclusion of tree cores series was possible due to poor visibility of ring boundaries in some samples. Therefore, 14 trees composed the master chronology, being only two composed by mean series and 12 by one core per tree. According to Esper and Gärtner (2001), 10 to 20 trees are appropriate to detect climatic signals.

Figure 2.

After the crossdating process, ring-width series were standardized to filter non-climate-related growth variations. For each tree, we fitted a Cubic Smoothed Spline Function (50% variance cutoff in 21 years segment length) and computed ratios between observed and predicted values, obtaining indexed ring-width (RWI) series that were combined in a Standard site chronology (STD) through a bi-weighted robust mean function. Therefore, the autocorrelation of RWI series was filtered by autoregressive modeling and the resulting series combined in a Residual site chronology (RES) using a bi-weighted robust mean function (Cook, 1985). The following statistics were used to describe the resulting chronologies: average and standard deviation (SD) of tree-ring widths, mean sensitivity index (MSI), mean autocorrelation (AC), mean intercorrelation (*r*int), mean correlation between series (*r*bar) and mean expressed population signal (EPS) (Fritts, 1976; Speer, 2010; Wigley et al., 1984). These calculations were performed on ARSTAN software (except *r*int, calculated on COFECHA).

4.2.4 Detection of dendroclimatic signals

To explore radial growth responses to climatic conditions, we considered monthly total precipitation and mean temperature data recorded in a nearby meteorological station, 10 km away from the study site, carried by the Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural (INCAPER). The monthly meteorological series covers the period from 1976 to 2012, with few data gaps (12 for precipitation; 16 for temperature) that were filled with the respective month average (Fig 3).

Based on these, we estimated the Standardized Precipitation Evapotranspiration Index – SPEI (Fig. 3). This is a drought index, sensitive to global warming and based on a simple climatic water balance that takes into account the evapotranspiration. SPEI values close to zero indicate a normal monthly water balance for a given timescale (monthly or seasonal basis, for instance), while negative (or positive) values indicate drier (or wetter) than expected conditions for that timescale (Vicente-Serrano et al., 2010).

Climatic data were analyzed according to the growing season in order to determine the SPEI time scales. Precipitation below 60 mm was considered as a dry month, because this precipitation threshold may affect the growth of tropical trees (Worbes, 1995). Most years had drought events (<60 mm of precipitation) that range from one (62%) to two months (18%) during the growing season. Four consecutive months of drought in one growing season is a rare event in the analyzed series (only one year), whereas there were years with no dry months during the growing season (18% of years). In this way, we tested monthly SPEI series, calculated in monthly (SPEI1), bi-monthly (SPEI2) and four-monthly (SPEI4) scales.

Afterward, we used Correlation Function Analysis (Blasing et al. 1984) to test the existence of dendroclimatic signals in *C. lucens* by comparing the RES chronology to monthly SPEI series, calculated in monthly (SPEI1), bi-monthly (SPEI2) and four-monthly (SPEI4) scales (Fig. 3). We considered possible radial growth responses to climatic conditions through the previous and current growth year by correlating the RES chronology to SPEI series from October (spring) of the previous growth year to April (fall) of the current growth year. The statistical significance of the correlation coefficients was addressed on a 95% confidence interval obtained by bootstrap resampling (Biondi and Waikul, 2004). SPEI estimates and Correlation Function Analyses were performed on R program (RStudio Team, 2016), respectively in packages SPEI (Beguería and Vicente-Serrano, 2017) and bootRes (Zang and Biondi, 2013).

Pearson's correlations were calculated to verify the agreement between SPEI1 (most frequent event) and RWI. To verify the match between RWI and SPEI1 over time-span, negative pointer years were highlighted. Pointer years were considered to occur when RWI was at least 25% below the average of the previous four years (Oliveira et al., 2016) (Fig 6).

Figure 3.

4.3 RESULTS AND DISCUSSION

In this study, we present the first tree-ring chronology for the tropical tree species *C. lucens* (Table 1; Fig. 4) and its climatic signal (Figs. 5 and 6).

4.3.1 Crossdating and chronology building

The species has an eccentric growth that makes crossdating difficult, with many false and wedding rings. The average annual TRW ranged from 1.54 to 3.44 mm $yr.^{-1}$ with an average value of 2.25 mm yr^{-1} (Table 1). Costa et al. (2015) found in *C. langsdorffii* an annual mean TRW of 4.7 mm yr^{-1}, but they carried out the study in a young experimental plantation (30 years) under full sunlight conditions, which justifies the greater growth rate. Schongart et al. (2004) observed a mean radial increment of 1.52 and 2.66 mm $yr.^{-1}$ for *Macrolobium acaciifolium* (Benth.) growing in a nutrient-poor and nutrient-rich site, respectively; while Callado and Guimarães (2010) observed a mean radial increment of 11.1mm $yr.^{-1}$ for *Schizolobium parahyba* (Vell.) S. F. Blake, a pioneer species native from AF.

In two literature reviews covering different ecological aspects of the genus *Copaifera*, it was mentioned that the individuals could live up to an age of ~400 years (Araújo-Júnior et al., 2005; Veiga-Junior and Pinto, 2002). Based on the total number of growth-layers identified (without crossdating), we estimated that the sampled trees are between 90 and 200 years old (average = 134, DP = ±34). We carried out our study in the best-preserved area of the *C. lucens* distribution, where the oldest trees of this species are probably found. According to Brienen et al. (2016), tropical tree species rarely attain ~500 years, with a typical average age being about 200 years. Since many species of *Copaifera* are considered long-lived climax species, ~200 years old is a feasible lifespan for this species.

We crossdated the last 47 years of 20 trees and the mean correlation within trees was *r*int = 0.52 (Table 1). We have used 70% of the trees (14 out of 20) to build the chronology, with six trees being poorly correlated with the master chronology. Beside this, we could use only the internal mean of two of these trees, and for 12 of them we had sufficiently high correlations with the master chronology using only one core per tree (Fig. 4B). Brienen and Zuidema (2005) also rejected a rather high percentage of series to manage quality control in a study carried out in the Bolivian rainforest. In addition, Fritts (1976) suggested that only one core per tree would be enough for dendroclimatic analyses. We expected to enhance the chronology variance related to changes in climatic conditions by selecting the best radii correlations and sensitivity (Fritts, 1976).

Figure 4.

The mean correlation between trees was *r*int = 0.45. Grissino-Mayer (2001) suggested a threshold for inter-series correlations above *r*int = 0.50, but this implies considerations such as species, geographic location, and regional climate. In the case of lowland tropical forests, trees show less climatic sensitivity when compared with boreal and temperate forests (Schweingruber, 1988; Payette and Filion, 2010; Perone et al., 2016). Therefore, the inter-series correlation found in this study may be enough to emphasize the synchronism between trees of the same site. MSI above 0.40 also highlights the climate sensitivity (Grissino-Mayer, 2001). A MSI value of 0.47 in our study (Table 1) shows high sensitivity and high-frequency variability, which greatly increases the difficulty in dating because of the frequency of micro or missing rings next to very wide rings (Pumijumnong et al., 1995; Speer, 2010). In turn, the wide rings formed in a few years are more related to site conditions than macroclimate, promoting large variability within and between trees and sites (Fritts, 1976). The numeric parameters for the STD and RES individual series chronologies were similar, except for autocorrelation, which was removed successfully in the RES chronology (Table 1).

Table 1. Statistical characteristics of standard ring-width index chronology of *Copaifera lucens* from Tabuleiros Atlantic Forest. STD = standard chronology; RES = residual chronology.

Parameter	**Values**
Time crossdating	1966-2012 (47 years)
Mean length of series (year)	35 years (Min = 23; Max = 0.47; SD = 7)
Trees/cores dated/cores crossdated	20/50/36
Trees/cores master chronology	14/16
Individual series statistics	
Mean tree ring width (mm)	2.25 (Min = 1.54; Max= 3.44; SD = ±1.06 mm)
Mean sensitivity index (MSI)	0.47 (Min = 0.28; Max = 0.58; SD = ±0.11)
Intercorrelation within tree-series (*r*int)	0.52 (Min = 0.33; Max = 0.77; SD = ±0.19)
Intercorrelation between tree-series (*r*int)	0.45 (Min = 0.36; Max = 0.56; SD = ±0.05)
Standardized chronology statistic	
STD mean correlation between series (*r*bar)	0.35 (Min = 0.01; Max = 0.75; SD = ±0.16)
RES mean correlation between series (*r*bar)	0.31 (Min = -0.04; Max = 0.70; SD = ±0.17)
Standard error (SE) STD/RES	0.018 / 0.018
Mean expressed population signal STD/RES	0.85 / 0.83
Mean sensitivity index STD/RES	0.30 / 0.28
Second order autocorrelation STD/RES	0.08 (SD = ± 0.13) / -0.02 (SD = ± 0.05)

After standardization, the average correlation coefficient between trees and the average values for the classical parameters for the RES chronology were *r*bar = 0.31, MSI = 0.28 and EPS = 0.83 (Table 1). These values varied across the tree's time span (Fig. 4). The comparison between different periods allowed us to identify the best correlation related to growth limitation due to climatic factors as opposed to site factors (Fritts, 1976). The correlation between trees in tropical forests ranges between 0.19 and 0.38 (Pumijumnong et al., 1995 Oliveira et al., 2010); but Stahle et al. (1999) found values of 0.49 and 0.56 for *Pterocarpus angolensis* DC. growing in seasonal dry forests in Africa and Heinrich and Banks (2005) showed intercorrelation of 0.45 for *Toona ciliata* M.Roemar in Australia. These values show strong evidence that there are common factors (regional climate) acting on tree growth. By comparison, the *r*bar value we found in this study evidences a moderate growth synchronism among trees.

The mean MSI was approximated from that reported in studies carried out in tropical forests in Australia, Asia and South America (Heinrich and Banks, 2005; Chowdhury et al., 2016; Reis-Ávila and Oliveira, 2017). In general, the value we found is considered moderate. On the other hand, Taynik et al. (2016) found MSI of 0.32 at the upper treeline sites in the Russian mountains. Species in their distribution range, especially in treelines, are theoretically the most sensitive to climate (Fritts, 1976). Considering the complexity of tropical forest (*e.g.*, wood anatomy features, community diversity and competition) our results for MSI may represent a relevant sensitivity.

The EPS value for RES chronology was slightly below the threshold of 0.85 suggested by Wigley et al. (1984), which conveys the hypothetical perfect chronology for the site. Sample size affects the EPS value (Fritts, 1976; Wigley et al., 1984; Briffa and Jones, 1990; Cook and Kairiukstis, 1990; Speer, 2010; Mérian et al., 2013) and, for this reason, this parameter has been widely used as an indicator of sample adequacy (*e.g.*, Heinrich and Banks, 2005; Brienen et al., 2010; Venegas-González et al., 2016). This threshold has been the subject of new discussions among dendrochronologists (Briffa and Jones, 1990; Mérian et al., 2013; Buras, 2017). For Briffa and Jones (1990), no specific EPS value can determine whether the chronology is suitable for dendroclimatic analysis, while Buras (2017) suggested that the threshold presented by Wigley et al. (1984) actually refers to the subsample signal strength rather than the total sample size. In this regard, Campelo et al. (2007) used the subsample signal strength to establish the reliable estimate of the mean chronology, since in their study the sample depth declines in the early portions of chronology, then subsample becomes important.

4.3.2 Growth-response to climatic conditions

Our study showed a strong influence of the climatic regional conditions on the radial growth of *C. lucens* during the late rainy season, which extends from mid-summer (February) to early fall (April) (Fig. 5). The correlation coefficient between the chronology RES and the SPEI1 showed high positive values for February of the current year (r = 0.66, Fig. 5A), while SPEI2 for February (r = 0.49) and March (r = 0.58, Fig. 5B), and SPEI4 for March (r = 0.53) and April (r = 0.51, Fig. 5C). These results evidence that drought in the middle of summer (SPEI1) reduces significantly the wood production of *C. lucens*. Previous studies in tropical forests showed significant correlation coefficients for the rainy season, with values ranging from 0.28 to 0.66 (Worbes, 1999; Brienen and Zuidema, 2005; Chowdhury et al., 2016). Chowdhury et al. (2016) found a positive correlation between annual precipitation and RWI (*r* = 0.52 to 0.57) for *Heritiera fomes* Buch.-Ham growing at different sites in Bangladesh. Besides the crossdating, the strong climatic signal present in the rings of *C. lucens* also supports the hypothesis of the annual nature of the growth rings.

Figure 5.

The growing season in the TAF is presumed to extend from October to December (early growing season) and from January to April (late growing season). Most of the studies in tropical forests show the influence of rainfall in the early rainy season (Pumijumnong et al., 1995; Worbes, 1999; Brienen and Zuidema, 2005; Boninsegna et al., 2009). Worbes (1999) considers that the cambial activity in the tropics is high during the rainy season and decreases near the end of the rainy season or immediately after the beginning of the dry season. In the case of *C. lucens*, we observed that February is the drier month in the rainy season (Fig 1C). Moreover, flowering starts in February for this species (Reserva Natural da Vale, unpublished data), being this an activity that demands high energetic investment (Evert, 2014). In this sense, an explanation of the importance of rainfall in the middle of summer (late season) is because it matches with the initial period of flowering in *C. lucens*, which can express a tradeoff between flowering and radial growth under drought-stress, as it was previously observed by Borchert (1994). By evaluating primary production, Brando et al. (2008) also noted that wood production is the more sensitive aboveground component to water deficit. However, when considering a prolonged period of drought (SPEI4), we observed that rainfall throughout the late growing season period is the most important factor. In this regard, this species could be used as a proxy to investigate the duration of dry periods.

The strength of the linear correlation between tree growth and February SPEI1 can be observed over the time-span (Fig. 6). We noticed growth reductions in 1981 (34%), 1994 (49%), 1998 (34%), 2000 (36%) and 2009 (31%). These years matched with the SPEI1 calculated for the respective years, except for 1981, which was a wet year. Severe droughts episodes were registered at the study area in 1987–1989, 1996–1999 and 2007–2008, including fires in the summer-fall (1999) near the study site (Víncens et al., 2003; Gazeta-online, 2015; Rolim et al., 2016). Monthly precipitation in the first of these periods was below 100 mm, while values up to 60 mm occurred in the subsequent ones for February. In this regard, *C. lucens* seems to be very sensitive to precipitation below 60 mm (Fig. 6). It is important to note that 1994 (the negative pointer year with the greatest reduction of growth) had a very low precipitation in January and February (4.40 and 7.20 mm, respectively). Therefore, we can conclude that *C. lucens* radial growth is sensitive to drought in cases of extreme water deficit (<37 mm) during the late growing season, with growth reductions reaching up to 49%. One possible explanation for the pointer year that occurred under wet conditions in 1981 is that non-climatic exogenous factors acting in the community surpassed the climatic effect (Fritts, 1976; Cook, 1987).

Figure 6.

4.5 FINAL REMARKS AND CONCLUSIONS

This study presents the first chronology of growth rings for *C. lucens*, with which we explored, in a pioneering way, dendroclimatic signals in the region of the “Tabuleiros” Atlantic Forest. *Copaifera lucens* has annual rings and shows marked climatic responses, namely to water deficit in the drier late growing season (January to April). Our study also hints that this long-lived species could be used to investigate past drought events in tropical regions given its great potential for dendrochronological studies. Moreover, rainfall during the second half of the growing season (January-April) was found to be crucial in determining radial growth. Due to the expected decrease in precipitation in South America, we predict that there will be a reduction in the wood production of *C. lucens*. This climatic response may be similar for other wood species endemic to the Brazilian Atlantic Forest whose environmental restrictions are greater in relation to the widely distributed species. In this forest, ~ 55% of the trees are endemic (Flora do Brasil 2020, 2017), which might significantly affect the ability of this forest to sequestrate carbon.

ACKNOWLEDGEMENTS

We are grateful to Embrapa Forestry for the financial support of the project, as well as to the researchers of the Biomas project, who assisted with field logistics and data provision; To the Reserva Natural da Vale, for the technical and financial support, in particular, to the biologist Geovane Siqueira, for the support with the botanical identification in the field; To colleagues of the Laboratory of Plant Ecology of UNISINOS for the support in the fieldwork and laboratory, especially, Gabriela Reis-Ávila. We especially thank the Biomas project technician, Wagner Farias F. B. Silva, and the field assistants, Edilson A. da Silva and Marcos R. R. de Castro, for the support in the fieldwork.

Funding

This work was supported by the Brazilian Agricultural Research Corporation (EMBRAPA), Confederação Nacional da Agricultura (CNA) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, process nº 88881.135931/2016-01), all related to the Brazilian government; Reserva Natural da Vale through hosting support and by FCT-Portuguese Foundation for Science and Technology under the project UID/AGR/04033/2013 and POCI-01-0145-FEDER-006958.

REFERENCES

Alencar, J. da C., 1982. Estudos silviculturais de uma população natural de *Copaifera multijuga* Hayne - Leguminosae, na Amazônia Central. 2 - Produção de óleo-resina. Acta Amaz. 12, 75–89.

Araújo-Júnior, F.A. de, Braz, M.N., Rocha-Neto, O.G. da, Costa, F.D., Brito, M.V.H., 2005. Efeito do óleo de copaíba nas aminotransferases de ratos submetidos à isquemia e reperfusão hepática com e sem pré-condicionamento isquêmico. Acta Cir. Bras. 20, 93–99. doi:10.1590/S0102-86502005000100013

Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405, 668–673. doi:10.1038/35015049

Barbosa, O., 1982. Características estruturais do lenho de *Copaifera langsdorfii* e *Copaifera lucens* Dwyer. Silvicultura 15–16, 23–36.

Bazzaz, F.A., 1996. Plants in rapidly changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridg.

Beguería, S., Vicente-Serrano, S.M., 2017. Standardized Precipitation-Evapotranspiration Index (SPEI), Package "SPEI." CRAN, version 1.7. doi:10.1175/2009JCLI2909.1.http

Bellard, C., Leclerc, C., Leroy, B., Bakkenes, M., Veloz, S., Thuiller, W., Courchamp, F., 2014. Vulnerability of biodiversity hotspots to global change. Glob. Ecol. Biogeogr. 23, 1376–1386. doi:10.1111/geb.12228

Biondi, F., Waikul, K., 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput. Geosci. 30, 303–311. doi:10.1016/j.cageo.2003.11.004

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science (80-.). 320, 1444–1449. doi:10.1126/science.1155121

Boninsegna, J.A., Argollo, J., Aravena, J.C., Barichivich, J., Christie, D., Ferrero, M.E., Lara, A., Le Quesne, C., Luckman, B.H., Masiokas, M., Morales, M., Oliveira, J.M., Roig, F., Srur, A., Villalba, R., 2009. Dendroclimatological reconstructions in South America: a review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 281, 210–228. doi:10.1016/j.palaeo.2009.07.020

Borchert, R., 1994. Water status and development of tropical trees during seasonal drought. Trees 8, 115–124. doi:10.1007/BF00196635

Brando, P.M., Nepstad, D.C., Davidson, E.A., Trumbore, S.E., Ray, D., Camargo, P., 2008. Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: results of a throughfall reduction experiment. Philos. Trans. R. Soc. B Biol. Sci. 363, 1839–1848. doi:10.1098/rstb.2007.0031

Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martínez-Ramos, M., 2010. Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. Glob. Chang. Biol. 16, 2001–2012. doi:10.1111/j.1365-2486.2009.02059.x

Brienen, R.J.W., Schöngart, J., Zuidema, A., 2016. Tree rings in the tropics: insights into the ecology and climate sensitivity of tropical trees, in: Tropical Tree Physiology: Adaptations and responses in a changing environment. Springer, Cham, pp. 439–461. doi:10.1007/978-3-319-27422-5

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146, 1–12. doi:10.1007/s00442-005-0160-y

Briffa, K., Jones, P.D., 1990. Basic chronology statistics and assesment, in: Cook, E.; Kairiukstis, L. (Ed.), Methods of dendrochronology: applications in the environmental sciences. Springer-Science, Business Media, B. V., Dordrecht, pp. 137–152. doi:10.1007/978-94-015-7879-0

Buras, A., 2017. A comment on the expressed population signal. Dendrochronologia 44, 130–132. doi:10.1016/j.dendro.2017.03.005

Callado, C.H., Guimarães, C., 2010. Estudo dos anéis de crescimento de *Schizolobium parahyba* (Leguminosae: Caesalpinioideae) após episódio de mortalidade em Ilha Grande, Rio de Janeiro. Rev. Bras. Bot. 33, 85–91. doi:10.1590/S0100-84042010000100008

Campelo, F., Nabais, C., Freitas, H., Gutierrez, E., 2007. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. Ann. For. Sci. 64, 229–238. doi:10.1051/forest

Carvalho, P.E.R., 2003. Espécies arbóreas brasileiras, 21st ed. Embrapa Florestas, Colombo.

Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W., Innes, J.L., 2003. Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. Biol. Rev. Camb. Philos. Soc. 78, 119–148. doi:10.1017/S1464793102006000

Chowdhury, M.Q., De Ridder, M., Beeckman, H., 2016. Climatic signals in tree rings of *Heritiera fomes* Buch.-Ham. in the Sundarbans, Bangladesh. PLoS One 11, e0149788. doi:10.1371/journal.pone.0149788

Cook, E.R., 1987. The decomposition of tree-ring series for environmental studies. Tree-Ring Bull. 47, 37–59. doi:S

Cook, E.R., 1985. A time series analyses approach to tree ring standardization. University of Arizona.

Cook, E.R., Holmes, R.L., 1996. Guide for computer program ARSTAN, in: Grissino-Mayer, H.D., Holmes, R.L., Fritts, H.C. (Eds.), The International Tree-Ring Data Bank Program Library Version 2.0 User'smanual. Laboratory of Tree-Ring Research, University of Arizona, Tuscson, pp. 75–87.

Cook, E.R., Kairiukstis, L., 1990. Methods of dendrochronology: applications in the environmental sciences, Environment International. doi:10.2307/1551446

Costa, J.A.S., 2017. *Copaifera lucens* Dwyer [WWW Document]. Flora do Bras. 2020 em construção. URL http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB78656 (accessed 1.1.17).

Costa, M.S., Ferreira, K.E.B., Botosso, P.C., Callado, C.H., 2015. Growth analysis of five Leguminosae native tree species from a seasonal semidecidual lowland forest in Brazil. Dendrochronologia 36, 23–32. doi:10.1016/j.dendro.2015.08.004

Cramer, W., Bondeau, A., Schaphoff, S., Lucht, W., Smith, B., Sitch, S., 2004. Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. Philos. Trans. R. Soc. B Biol. Sci. 359, 331–343. doi:10.1098/rstb.2003.1428

Engel, V.L., 2001. Estudo fenológico de espécies arbóreas de uma floresta tropical em Linhares, ES. Universidade de Campinas.

Esper, J., Gärtner, H., 2001. Interpretation of tree–ring chronologies. Erdkunde 55, 277–288.

Evert, R.F., Eichhorn, S.E., 2014. Raven biology of plants., 8th ed. Guanabara Koogan, Rio de Janeiro.

Forzza, R.C., Baumgratz, J.F. a., Bicudo, C.E.M., Canhos, D. a. L., Carvalho, A. a., Coelho, M. a. N., Costa, A.F., Costa, D.P., Hopkins, M.G., Leitman, P.M., Lohmann, L.G., Lughadha, E.N., Maia, L.C., Martinelli, G., Menezes, M., Morim, M.P., Peixoto, A.L., Pirani, J.R., Prado, J., Queiroz, L.P., Souza, S., Souza, V.C., Stehmann, J.R., Sylvestre, L.S., Walter, B.M.T., Zappi, D.C., 2012. New brazilian floristic list highlights conservation challenges. Bioscience 62, 39–45. doi:10.1525/bio.2012.62.1.8

Fritts, H.C., 1976. Tree rings and climate change. Academic Press , New York.

Garay, I., Kindel, A., Louzada, M.A.P., Dos Santos, D., 2003. A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea., in: Garay, I., Rizzini, C.M. (Ed.), A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. Vozes, Petrópolis, pp. 16–26.

Garay, I., Silva, B.A.O., 1995. Húmus florestais: síntese e diagnósticos das interrelações vegetação/solo. Oecologia Bras. 1, 19–46.

Gazeta-online, 2015. As secas históricas do Espírito Santo: impactos econômicos e sociais marcaram esses períodos [WWW Document]. Gaz. online. URL http://www.gazetaonline.com.br/noticias/cidades/2015/12/as-secas-historicas-do-espirito-santo-1013916965.html (accessed 1.9.17).

Grandis, A., Godoi, S., Buckeridge, M.S., 2010. Respostas fisiológicas de plantas amazônicas de regiões alagadas às mudanças climáticas globais. Rev. Bras. Botânica 33, 1–12. doi:10.1590/S0100-84042010000100002

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program Cofecha. Tree-ring Res. 57, 205–221.

Heinrich, I., Banks, J.C.G., 2005. Dendroclimatological potential of the Australian red cedar. Aust. J. Bot. 53, 21–32. doi:10.1071/BT04033

Holmes, R.L., 1986. Quality control of crossdating and measuring: a user's manual for program COFECHA, in: Holmes, R.L., Adams, R.K., Fritts, H.C. (Eds.), Tree-Ring Chronologies of Western North America: California, Eastern Oregon and Northern Great Basin with Procedures Used in the Chronology Development Work Including User's Manuals for Computer Programs COFECHA and ARSTAN. Laboratory of Tree-Ring Research, University of Arizona, Tucson, pp. 41–49.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-ring Bull. 43, 69–78. doi:10.1016/j.ecoleng.2008.01.004

IBGE, R., 2012. Manual técnico da vegetação brasileira., 2nd ed. Coordenação de Recursos Naturais e Estudos Ambientais (Série manuais técnicos de geociências), Rio de Janeiro.

IPCC, 2014. Climate change 2014: synthesis report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPPC Panel, Geneva, Switzerland.

Jacoby, G.C., 1989. Overview of tree-ring analysis in tropical regions. Int. Assoc. Wood

Anat. Bull. 10, 99–108. doi:10.1163/22941932-90000478

Jesus, R.M.D., Rolim, S.G., 2005. Fitossociologia da Mata Atlântica de Tabuleiro. Boletim Técnico. Soc. Investig. Florestais 17, 1–154.

Koeppen, W., 1948. Climatologia: con un estudio de los climas de la tierra. Fondo de Cultura Economica, Mexico, DF.

Liu, Y.Y., van Dijk, A.I.J.M., de Jeu, R.A.M., Canadell, J.G., McCabe, M.F., Evans, J.P., Wang, G., 2015. Recent reversal in loss of global terrestrial biomass. Nat. Clim. Chang. 5, 470–474. doi:10.1038/nclimate2581

Lorenzi, H., 2002. Árvores brasileiras: manual de identificaçao e cultivo de plantas arbóreas do Brasil., 4th ed. Instituto Plantarum, Nova Odessa.

Louzada, M.A.P., Curvello, A., Barbosa, J.H.C., Garay, I., 1997. O aporte de matéria orgânica ao solo: quantificação, fenologia e suas relações com a composição específica em área de Floresta Atlântica de Tabuleiros. Leandra 12, 27–32.

Martins-da-Silva, R.C.V., Pereira, J.F., Lima, H.C. De, 2008. O gênero *Copaifera* (Leguminosae - Caesalpinioidae) na Amazônia Brasileira. Rodriguésia 59, 455–476.

Medeiros, R. da S., 2016. Estudo da anatomia do lenho e dendrocronologia de árvores de *Copaifera multijuga* Hayne na Amazônia brasileira e sua relação com o manejo e extração de oleorresina. Escola Superior de Agricultura "Luiz de Queiroz."

Media Cybernetics, 2001. Image-Pro Plus.

Melo-Júnior, J.C.F. de, Ceccantini, G., Bona, C., 2011. Anatomia ecológica do lenho de *Copaifera langsdorffii* Desf. (Leguminosae) distribuída em diferentes condições edáficas do cerrado sul-brasileiro. Iheringia - Ser. Bot. 66, 189–200.

Mérian, P., Pierrat, J.C., Lebourgeois, F., 2013. Effect of sampling effort on the regional chronology statistics and climate-growth relationships estimation. Dendrochronologia 31, 58–67. doi:10.1016/j.dendro.2012.07.001

Metcalfe, C.R., Chalk, L., 1950. Anatomy of the dicotyledons: leaves, stem, and wood in relation to taxinomy with notes on economic uses. Oxford University Press, Amen House, London E. C., London.

Myers, N., Mittermeier, R., Mittermeier, C., DaFonesca, G., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Conserv. Biol. 403, 853. doi:10.1038/35002501

Oliveira, J.M., Roig, F.A., Pillar, V.D., 2010. Climatic signals in tree-rings of *Araucaria angustifolia* in the southern Brazilian highlands. Austral Ecol. 35, 134–147. doi:10.1111/j.1442-9993.2009.02018.x

Oliveira, V., Lauw, A., Pereira, H., 2016. Sensitivity of cork growth to drought events: insights from a 24-year chronology. Clim. Change 137, 261–274. doi:10.1007/s10584-016-1680-7

Payette, S., Filion, L., 2010. La dendroécologie : principes, méthodes et applications. Presses de l'Université Laval, Québec.

Peixoto, A.L., Gentry, A., 1990. Diversidade e composição florística da mata de Tabuleiro na Reserva Florestal de Linhares, Espírito Santo, Brasil. Rev. Bras. Botânica 19–25.

Perone, A., Lombardi, F., Marchetti, M., Tognetti, R., Lasserre, B., 2016. Evidence of solar activity and El Nino signals in tree rings of *Araucaria araucana* and *A. angustifolia* in South America. Glob. Planet. Change 145, 1–10. doi:10.1016/j.gloplacha.2016.08.004

Pilcher, J.R., 1990. Sample preparation, cross-dating, and measurement, in: Cook, E.R., Kairiukstis, L.A. (Eds.), Methods of dendrochronology: applications in the environmental sciences. Springer-Science, Business Media, B. V., New York, pp. 40–51. doi:10.1007/978-94-015-7870-0

Pumijumnong, N., Eckstein, D., Sass, U., 1995. Tree-ring research on *Tectona grandis* in northern thailand. IAWA J. 16, 385–392.

Reis-Ávila, G., Oliveira, J.M., 2017. Lauraceae: a promising family for the advance of neotropical dendrochronology. Dendrochronologia 44, 103–116. doi:10.1016/j.dendro.2017.04.002

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. doi:10.1016/j.biocon.2009.02.021

Rizzini, C.T., 1963. Nota prévia sobre a divisao fitogeográfica do Brasil. Rev. Bras. Geogr. 1, 1–64.

Rolim, S.G., Ivanauska, N.M., Engel, V.L., 2016. As florestas de tabuleiro do norte do Espírito Santo São ombrófilas ou estacionais?, in: Rolim, S.G., Menezes, L.F.T. de, Srbek-Araujo, A.C. (Eds.), Floresta Atlântica de Tabuleiro: diversidade e endemismo na Reserva Natural Vale. Rona Editora, Belo Horizonte, pp. 47–60.

RStudio Team, 2016. R Studio.

Schöngart, J., Wolfgang, J . Junk Piedade, M.T.F., Ayres, J. M., Huttermann, A., Worbes, M., 2004. Teleconnection between tree growth in the Amazonian floodplains and the El Ninõ – Southern Oscillation effect. Glob. Chang. Biol. 10, 683–692. doi:10.1111/j.1529-

8817.2003.00754.x

Schweingruber, F.H., 1988. Tree rings: basics and applications of dendrochronology. Kluwer Academic Publischers, Dordrecht. doi:10.1007/978-94-009-1273-1

Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. Science (80-.). 247, 1322–1325.

Siqueira, M.F., 1994. Análise florística e ordenação de espécies arbóreas da mata atlântica através de dados binários. Universidade de Campinas.

Speer, J.H., 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson.

Stahle, D., Mushove, P., Cleaveland, M., Roig, F., Haynes, G., 1999. Management implications of annual growth rings in *Pterocarpus angolensis* from Zimbabwe. For. Ecol. Manage. 124, 217–229. doi:10.1016/S0378-1127(99)00075-4

Stahle, D.W., 1999. Usefull strategies for the development of tropical tree-ring chronologies. IAWA J. 20, 249–253. doi:10.1163/22941932-90000688

Taynik, A. V., Barinov, V. V., Oidupaa, O.C., Myglan, V.S., Reinig, F., Büntgen, U., 2016. Growth coherency and climate sensitivity of *Larix sibirica* at the upper treeline in the Russian Altai-Sayan Mountains. Dendrochronologia 39, 10–16. doi:10.1016/j.dendro.2015.12.003

Thomas, W.W., Carvalho, A.M.V., Amorim, A.M., Hanks, J.G., Santos, T.S., 2008. Diversity of wood plants in the atlantic coastal forest of Southern Bahia, Brazil. Mem. N. Y. Bot. Gard. 100, 21–66.

Veiga-Junior, V.F., Pinto, A.C., 2002. O gênero *Copaifera* L. Quim. Nova 25, 273–286.

Veloso, H.P., 1991. Classificação da vegetação brasileira adaptada a um sistema universal. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro.

Venegas-González, A., Chagas, M.P., Anholetto-Júnior, C.R., Alvares, C.A., Roig, F.A., Tomazello Filho, M., 2016. Sensitivity of tree ring growth to local and large-scale climate variability in a region of Southeastern Brazil. Theor. Appl. Climatol. 123, 233–245. doi:10.1007/s00704-014-1351-4

Vicente-Serrano, S.M., Beguería, S., Pez-Moreno, J.I.L.-M., 2010. A multiscalar drought index sensitive to global warming : the Standardized Precipitation Evapotranspiration Index. J. Clim. 23, 1696–1718. doi:10.1175/2009JCLI2909.1

Víncens, R.S., Agarez, F. V., Garay, I., 2003. A região da REBIO Sooretama e da Reserva de Linhares e seu entorno: das características físico-geográficas ao uso da terra, in: Garay, I., Rizzini, C.M. (Ed.), A Floresta Atlântica de Tabuleiros: diversidade functional da cobertura arbórea. Vozes, Petrópolis, pp. 7–15.

Wagner, F.H., Hérault, B., Bonal, D., Stahl, C., Anderson, L.O., Baker, T.R., Becker, G.S., Beeckman, H., Souza, D.B., Botosso, P.C., David, M.J., Bowman, S., Bräuning, A., Brede, B., Brown, F.I., Camarero, J.J., Chagas, K., Chave, J., Chidumayo, E.N., Clark, D.A., Regina, F., Costa, C., Couralet, C., Henrique, P., Dalitz, H., De, V.R., Eloisa, J., Milani, D.F., Oliveira, E.C. De, Arruda, L.D.S., 2016. Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. Biogeosciences, 13, 2537–2562. doi:10.5194/bg-13-2537-2016

Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2

Wils, T.H.G., Robertson, I., Eshetu, Z., Sass-Klaassen, U.G.W., Koprowski, M., 2009. Periodicity of growth rings in Juniperus procera from Ethiopia inferred from crossdating and radiocarbon dating. Dendrochronologia 27, 45–58. doi:10.1016/j.dendro.2008.08.002

Wils, T.H.G., Robertson, I., Eshetu, Z., Touchan, R., Sass-Klaassen, U., Koprowski, M., 2011. Crossdating *Juniperus procera* from North Gondar, Ethiopia. Trees - Struct. Funct. 25, 71–82. doi:10.1007/s00468-010-0475-0

Worbes, M., 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. J. Ecol. 87, 391–403.

Worbes, M., 1995. How to measure growth dynamics in tropical trees. IAWA J. 16, 337–351. doi:10.1163/22941932-90001424

Zang, C., Biondi, F., 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 31, 68–74. doi:10.1016/j.dendro.2012.08.001

FIGURE CAPTIONS

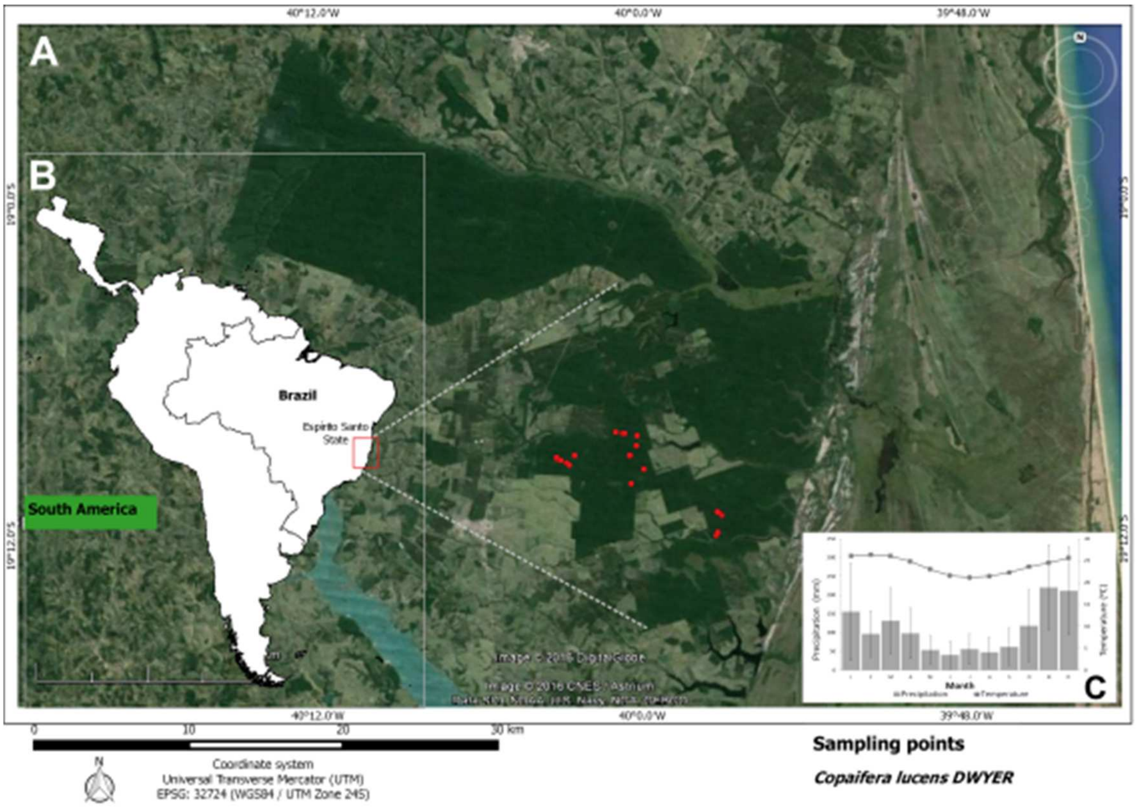


Figure 1. A – Map of the study area in the state of Espírito Santo, in southeastern Brazil. Red points indicate the georeferenced locations of the sampled trees. B – Study area location in South America and Brazil. C – Climatic diagram of the study area. Bars show standard deviation. Data provided by Instituto Capixaba de Pesquisa, Assistência Técnica e Extensão Rural (INCAPER).

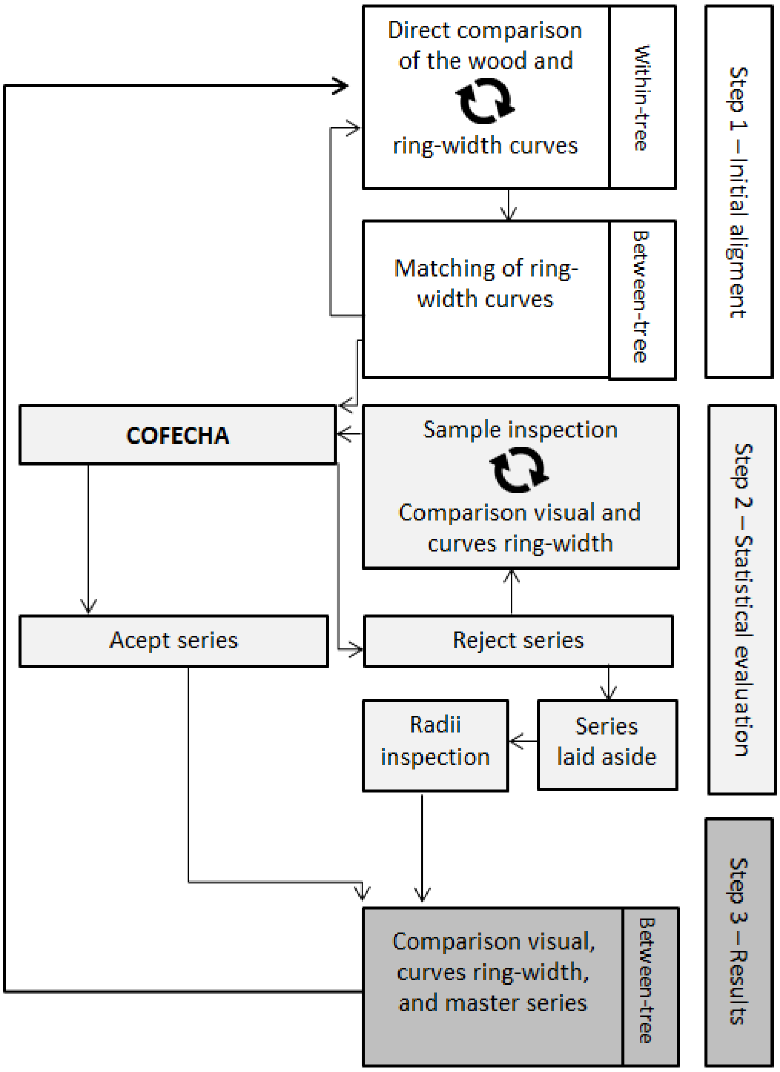


Figure 2. Scheme of the steps followed for crossdating.
Source: Adapted from Wils et al. (2011).

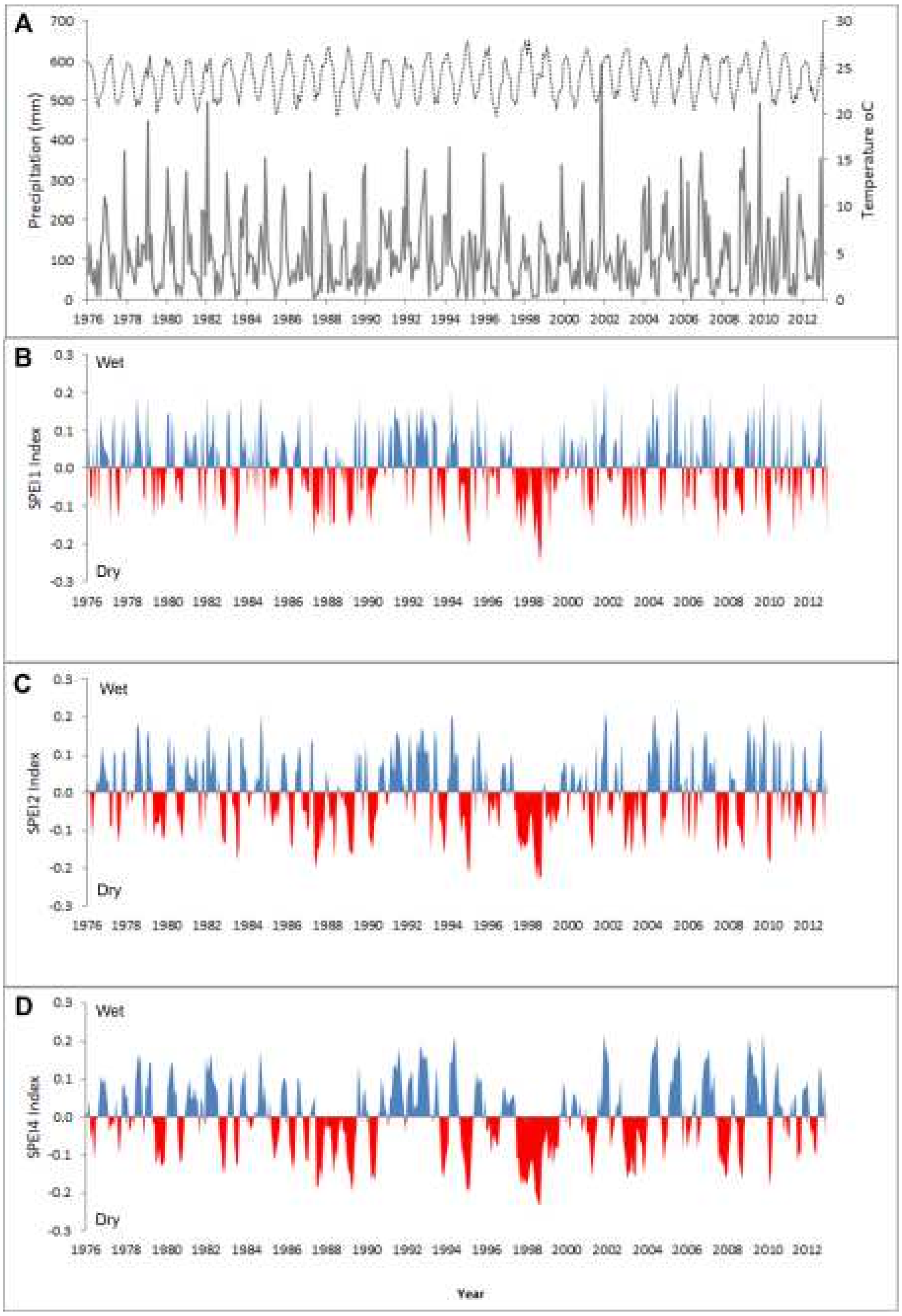


Figure 3. A – Monthly data for temperature (dashed line) and precipitation (full line) (1976-2012). B – Estimated monthly data for the Standardized Precipitation Evapotranspiration Index (SPEI) (1976-2012); C – bi-monthly SPEI and D – four-monthly SPEI.

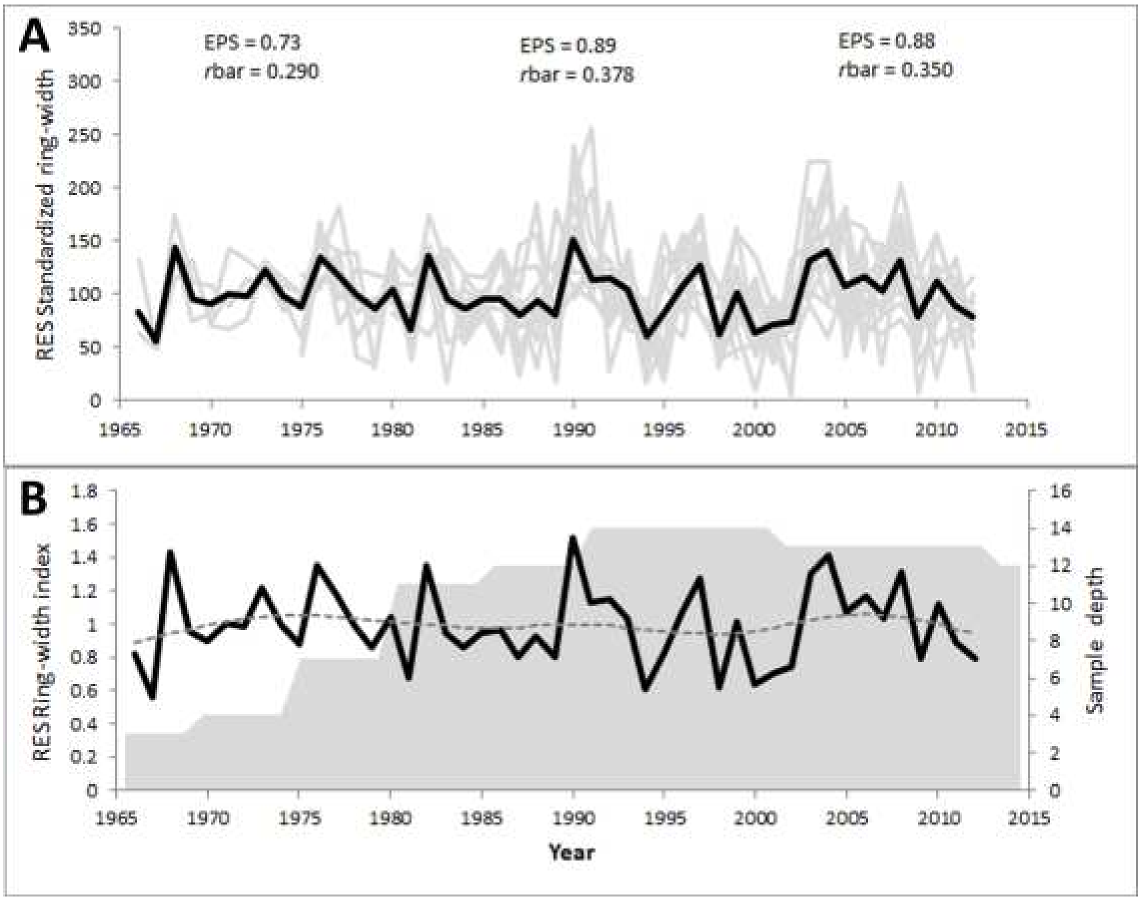


Figure 4. A - Individual ring width series of *Copaifera lucens* (gray lines) and their mean curve (black line) from "Tabuleiros" Atlantic Forest in Brazil. B - Ring width Index chronology (black line) of *Copaifera lucens* and 21 years smoothing curve (dotted line). The area in light gray shows sample depth over the analysis period.

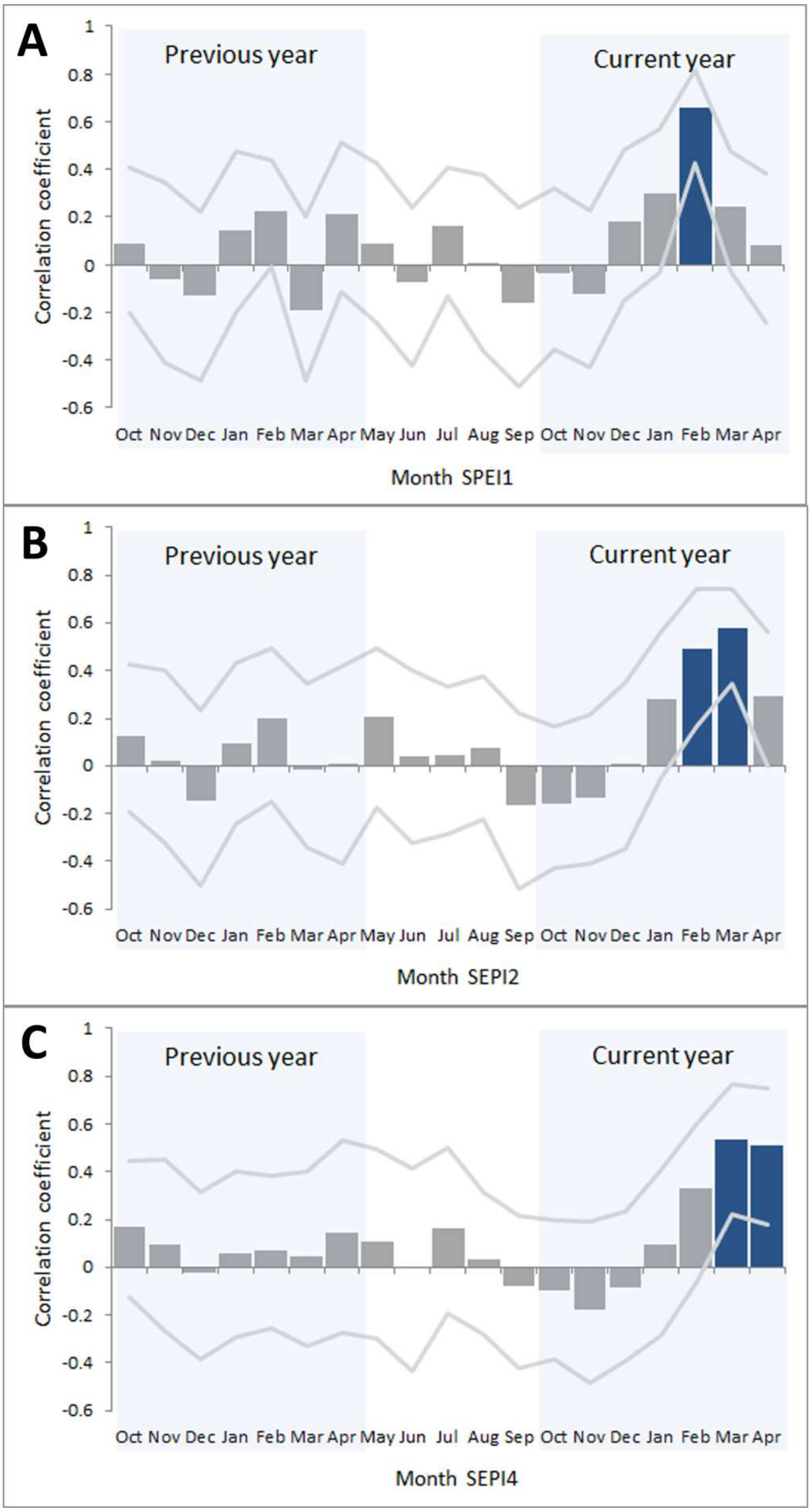


Figure 5. Correlation between ring width index and Standardized Precipitation Evapotranspiration Index (SPEI) (1976–2012). Correlation between tree-ring width index and –A– monthly, –B– bi-monthly and –C– four-monthly SPEI. Columns in dark blue indicate month with significance levels at $p < 0.05$. Grey lines delimit the 95% confidence interval. Light-blue areas show the estimated growth season period.

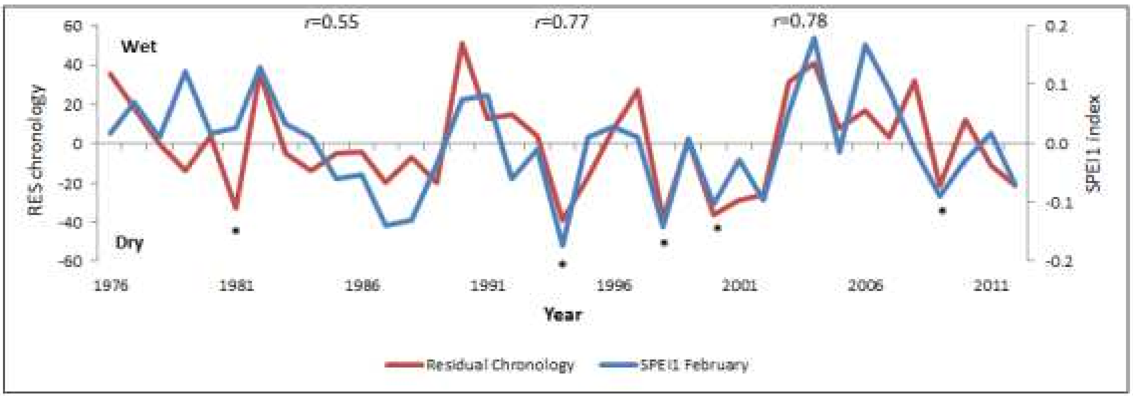


Figure 6. Residual ring width chronology superimposed on February Standardized Precipitation Evapotranspiration Index (SPEI – 1976-2012), considering growth-year. (*) Negative pointer years.

CAPÍTULO 5

CONCLUSÕES E RECOMENDAÇÕES

Esta tese atualiza e amplia as informações relativas à anatomia da madeira de *C. lucens* e apresenta a primeira cronologia de anéis de crescimento para esta espécie, e com qual se explorou, de forma pioneira, sinais dendroclimáticos na região da Floresta Atlântica de Tabuleiros. Além disso, a revisão do estado da arte traz aplicações práticas para a dendrocronologia na Mata Atlântica (MA), abordando pontos cruciais que podem contribuir para o avanço dessa ciência no Brasil.

Em relação à revisão da literatura a respeito das pesquisas dendrocronológicas na MA (Capítulo 2), observou-se que há muitas lacunas em dados que compreendem a abrangência espacial, florística e temporal dos estudos. Embora estudos dendrocronológicos venham aumentando nos trópicos nos últimos anos (ROZENDAAL e ZUIDEMA, 2011), na MA eles ainda são poucos. É preciso um grande esforço de investigação nessa floresta para que se possam realizar inferências mais robustas acerca das previsões do desempenho futuro das suas árvores. É necessário também que os autores forneçam, em seus manuscritos, informações mais detalhadas quanto aos métodos empregados na construção das cronologias. Com os dados acessados, foi possível concluir que a disponibilidade de água é o principal fator climático limitante para as árvores da MA, e a temperatura também afeta as árvores na região sul do Bioma. Tendo em vista os cenários climáticos esperados para a região, em relação à diminuição da precipitação e ao aumento da temperatura (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE - IPCC, 2014), as árvores tendem a ter um menor desempenho na produção de madeira no futuro. Em resumo, o estudo apresenta as espécies já estudadas e regiões (o que pode auxiliar na construção de redes de pesquisas); demonstra lacunas geográficas a serem preenchidas; traz insights sobre delineamento amostral e ressalta que uma explicação mais detalhada das análises aplicadas nas cronologias deve ser considerada.

No que se refere à anatomia da madeira (Capítulo 3), o estudo realça a importância da anatomia da madeira na construção de cronologias de espécies ainda não foram investigadas por dendrocronologia. Assim, o estudo foi fundamental já que possibilitou conhecer as variações na estrutura anatômica, que levaram a reconhecer padrões no lenho, os quais auxiliaram na identificação dos limites dos anéis de crescimento. Uma dúvida que ainda persiste é quanto à periodicidade da formação dos canais secretores, pois não foi possível concluir por intermédio dos estudos realizados se, de fato, eles são de periodicidade anual. A anatomia da madeira de *C. lucens* é complexa e, com o intuito de esclarecer o seu desenvolvimento, é importante que sejam realizados estudos de atividade cambial, preferivelmente de longo prazo (*e.g.*, FRANKENSTEIN, ECKSTEIN e SCHMITT, 2005; VIEIRA et al., 2014; COCOZZA et al., 2016). Tais estudos permitem identificar quais fatores ambientais desencadeiam a formação dos canais secretores, bem como de flutuações intra-anuais de densidade.

Em relação à dendrocronologia (Capítulo 4), o estudo acrescenta mais uma cronologia e mais uma espécie na lista de estudos dendrocronológicos em florestas tropicais. Apesar da complexidade anatômica da madeira e do grande investimento de tempo na datação, foi possível concluir que *C. lucens* tem um crescimento sincrônico na população estudada, regulado pela variação interanual na disponibilidade hídrica. Possivelmente, a variação sazonal da precipitação seja determinante do ritmo anual de formação dos anéis de crescimento nessa espécie. Novamente, estudos que acessem o ritmo de atividade cambial em escala intra-anual serão importantes para que se tenham respostas conclusivas acerca dessa questão. O forte sinal climático da cronologia e a longevidade estimada das árvores fazem desta uma espécie potencial para futuros estudos de reconstrução climática a partir de séries de anéis de crescimento. A redução no regime de chuvas na MA prevista para cenários futuros (IPCC, 2014) implica também em menor produtividade da madeira em *C. lucens*. Contudo, explorar como a seca influencia no crescimento, desempenho e sobrevivência de uma maior quantidade de espécies é crucial para entender o impacto das mudanças climáticas nos ecossistemas florestais (MARTIN-BENITO et al., 2017).

Por fim, as diferentes abordagens utilizadas visando compreender a influência do clima na MA por intermédio da dendrocronologia mostraram resultados promissores para o desenvolvimento dessa ciência nesse bioma. As conclusões apoiam a hipótese de a precipitação ser o principal fator climático limitante para as árvores tropicais.

REFERÊNCIAS

COCOZZA, C.; PALOMBO, C.; TOGNETTI, R.; LA PORTA, N.; ANICHINI, M.; GIOVANNELLI, A.; EMILIANI, G. Monitoring intra-annual dynamics of wood formation with microcores and dendrometers in *Picea abies* at two different altitudes. **Tree Physiology**, v. 36, n. 7, p. 832–846, 2016.

FRANKENSTEIN, C.; ECKSTEIN, D.; SCHMITT, U. The onset of cambium activity - a matter of agreement? **Dendrochronologia**, v. 23, n. 1, p. 57–62, 2005.

IPCC. **Climate Change 2014: synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change**. Geneva, Switzerland: IPPC Panel, 2014.

MARTIN-BENITO, D.; ANCHUKAITIS, K.; EVANS, M.; DEL RÍO, M.; BEECKMAN, H.; CAÑELLAS, I. Effects of drought on xylem anatomy and water-use efficiency of two co-occurring Pine species. **Forests**, v. 8, n. 9, p. 332, 2017.

ROZENDAAL, D. M. A.; ZUIDEMA, P. A. Dendroecology in the tropics: a review. **Trees - Structure and Function**, v. 25, n. 1, p. 3–16, fev. 2011.

VIEIRA, J.; ROSSI, S.; CAMPELO, F.; FREITAS, H.; NABAIS, C. Xylogenesis of *Pinus pinaster* under a Mediterranean climate. **Annals of Forest Science**, v. 71, n. 1, p. 71–80, 2014.