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ANÉIS DE CRESCIMENTO EM ESPÉCIES DA FAMÍLIA LAURACEAE: CARACTERÍSTICAS ANATÔMICAS E SINAIS DENDROCLIMÁTICOS

SÃO LEOPOLDO, JUNHO DE 2015

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ANÉIS DE CRESCIMENTO EM ESPÉCIES DA FAMÍLIA LAURACEAE: CARACTERÍSTICAS ANATÔMICAS E SINAIS DENDROCLIMÁTICOS

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ANÉIS DE CRESCIMENTO EM ESPÉCIES DA FAMÍLIA LAURACEAE: CARACTERÍSTICAS ANATÔMICAS E SINAIS DENDROCLIMÁTICOS

RESUMO

Anéis de crescimento são estruturas anatômicas, formadas no xilema secundário de plantas, que demarcam ciclos de crescimento e dormência em resposta a regimes climáticos sazonais. Visto que cada anel corresponde a um ciclo anual de crescimento e que variam suas características em função das condições do meio físico e biótico, essas estruturas são registros históricos únicos, com alta resolução e extensão temporal sobre mudanças ambientais. A dendrocronologia – ciência que investiga anéis de crescimento em plantas – é ainda incipiente em ecossistemas tropicais, dado seu avanço em regiões temperadas, e deve ser desenvolvida, uma vez que provém informações sobre autoecologia, ecologia florestal e climatologia, bases para o manejo da biodiversidade tropical. Reconhecer espécies com anéis de crescimento anatomicamente visíveis no xilema e sensíveis a flutuações climáticas é o passo primordial para o desenvolvimento da dendrocronologia. Nessa dissertação eu reviso e desenvolvo estudos dendrocronológicos com espécies neotropicais da família Lauraceae, principalmente em remanescentes florestais do sul da Mata Atlântica, um dos hotspots mundiais de biodiversidade. Foco meus esforços em Lauraceae devido à importância ecológica e fisionômica das espécies para as florestas úmidas neotropicais. Informação sobre anéis de crescimento está amplamente disponível na literatura, principalmente em estudos de anatomia da madeira. É notável que grande parte das lauráceas forma anéis de crescimento, em diversos ecossistemas (139 das 156 espécies levantadas em revisão bibliográfica). Com o intuito de facilitar estudos futuros e o reconhecimento dos anéis, apresento uma lista de 156 espécies descritas pela aparência dos anéis e realizo descrições anatômicas de outras 14 frequentes no sul da Mata Atlântica. Estudando séries temporais de largura de anéis de crescimento, verifiquei que *Ocotea puclhella*, *Cinnamomum glaziovii* e *Ocotea elegans*, espécies que ocorrem em regiões montanas subtropicais do Brasil possuem tendências comuns de crescimento entre os indivíduos (sincronismo) e são sensíveis a variações climáticas relacionadas tanto à temperatura quanto à precipitação. Esses resultados contribuem para o avanço da dendrocronologia neotropical, contribuindo para o melhor entendimento sobre as características dos anéis de crescimento de uma das mais importantes famílias botânicas em regiões tropicais.

TREE-RINGS IN LAURACEAE SPECIES: ANATOMICAL FEATURES AND DENDROCLIMATIC SIGNAL

ABSTRACT

Tree-rings are anatomical structures formed in the secondary xylem of wood plants. These structures delimit the growth cycles and dormancy as response to seasonal climate regimes. Since each ring correspond to one annual growth cycle varying their features as result of physical and biotic conditions, these structures are unique historical records with high resolution and temporal depth reflecting environmental changes. The dendrochronology – science that investigates tree-rings in wood plants – is incipient in tropical ecosystems, taking into account its advancement in temperate zones, and should be developed in tropical zones to provide clearer information about autoecology, forest ecology and climatology, base to tropical biodiversity management. To recognize species forming visible tree-rings in their xylems and that are sensible to climatic fluctuations is the first and prime step to development of dendrochronology. In this Master Dissertation I revise and perform dendrochronological analysis in the neotropical Lauraceae family, mainly in remaining forests of Southern rain forest of Brazil, a hotspot of biodiversity. I focus my efforts in Lauraceae family due to ecological and physiognomic importance of their species to neotropical rain forests. Information about tree-rings are widely available in the scientific literature, especially in the anatomical wood researches. Most species of Lauraceae family form tree-rings in different ecosystems (139 of 156 revised species). In order to facilitate future studies and the recognition of tree-rings I present 156 species described by tree-ring appearance plus 14 other frequent species in Southern rain forest. With temporal series of tree-ring width I verify that *Ocotea pulchella*, *Cinnamomum glaziovii* and *Ocotea elegans*, species from subtropical montane regions of Brazil, have the same growth tendency between individuals (synchronism). Moreover, are sensible to climate variations mainly related to temperature and precipitation. The findings of this dissertation are essential to contribute to development of neotropical dendrochronology, providing a better understanding about tree-rings features of one of the most important families in the tropical regions**.**

INTRODUÇÃO GERAL

Anéis de crescimento são estruturas anatômicas do xilema secundário de plantas lenhosas que vistas em corte transversal formam círculos concêntricos ao redor da medula (Fritts 1976). São definidos basicamente por três tipos de estruturas anatômicas: (1) variação no número e diâmetro dos vasos; (2) diferenças na espessura da parede e achatamento radial das fibras; e (3) presença de uma faixa de parênquima marginal delimitando os anéis (Roig 2000). Tais características diagnósticas são normalmente constantes em uma espécie, embora sua distinção possa variar de acordo com o ambiente ou até mesmo com a idade da planta (Schweingruber 1996, 2007).

Anéis de crescimento resultam da atividade periódica do câmbio vascular, meristema responsável pelo crescimento lateral em plantas (Fritts 1976; Schweingruber 1988). A periodicidade cambial é resultante da interação entre fatores genéticos que determinam os recursos necessários ao crescimento e fatores exógenos, principalmente climáticos, que controlam a disponibilidade desses recursos no ambiente (Van Schaik et al. 1993). Assim, quando árvores estão sujeitas a um período do ano com condições climáticas desfavoráveis ao crescimento, anéis de crescimento anuais são formados (Jacoby 1989).

As plantas registram na estrutura de suas células, tecidos e órgãos mudanças ambientais e fisiológicas ocorridas ao longo de suas vidas (Wimmer 2002). Por essa razão, anéis de crescimento são considerados registros ecológicos históricos, pois suas características (em geral largura, densidade, quantidade de vasos, composição química) variam em função das condições do ambiente físico e biótico. Sendo que cada anel corresponde a um ciclo anual de crescimento e que árvores são organismos longevos, séries dendrocronológicas tem resolução calendária anual e podem alcançar extensões seculares ou milenares, dependendo da longevidade das plantas e das condições de durabilidade e conservação da madeira após morte do indivíduo (Fritts 1976; Schweingruber 1988).

Historicamente, o primeiro reconhecimento de anéis de crescimento em árvores foi de Theophrastus, pupilo de Aristóteles (372-287 AC) que viveu na Grécia antiga e que também é considerado o pai da Botânica. Leonardo da Vinci (séc. XVI) observou que em árvores de Pinus da Itália os "anéis nos troncos das árvores serradas mostram a idade e, de acordo com sua largura, anos que foram mais ou menos secos. Assim, eles refletem os mundos individuais aos quais pertencem, no norte [da Itália] são muito mais largos do que no sul". No entanto, a dendrocronologia teve progresso acentuado a partir do início do século 20, com Andrew Ellicott Douglass, astrônomo norte-americano. Andrew Douglass buscava compreender fenômenos astronômicos e reconstruir ciclos solares a partir de cronologias de anéis de crescimento em sequoias-gigante. É considerado o pai da dendrocronologia pela contribuição na implementação da datação-cruzada, princípio e técnica básica para estudos de anéis de crescimento.

Dendrocronologia é o estudo de anéis de crescimento em árvores. Em seu sentido mais amplo, preocupa-se em datar indivíduos, reconstruir condições e eventos ambientais pretéritos e obter informações ecológicas nos níveis de indivíduo a ecossistemas. Essa ciência é amplamente difundida em regiões temperadas, onde a marcada sazonalidade térmica induz a formação de anéis de crescimento em grande parte das espécies lenhosas. Nessas condições, anéis de crescimento tem sido utilizados para estudar a dinâmica do clima (*e.g.* Esper et al. 2002; Wilson et al. 2005), de distúrbios ecológicos (*e.g.* Lorimer & Frelich 1989; Veblen et al. 1999), de populações de espécies arbóreas (*e.g.* Villalba and Veblen 1997), entre outras aplicações (Schweingruber 1996). Segundo alguns autores, ecossistemas tropicais e subtropicais apresentariam uma menor proporção de espécies arbóreas com anéis de crescimento bem definidos (Jacoby 1989; Stahle 1999; Roig 2000; Rozendaal and Zuidema 2011) devido às condições climáticas menos pronunciadas e mais heterogêneas do que aquelas das regiões temperadas.

Estudos dendroecológicos em regiões de menor latitude tem se intensificado, notavelmente a partir da década de 1980 (Worbes 2002). Contudo, considerando a diversidade florística dos trópicos e subtrópicos, uma menor proporção de espécies foi investigada em relação a biomas temperados. Uma razão para tal fato é o ainda insuficiente conhecimento da diversidade florística, da autoecologia das espécies e de processos em ecossistemas tropicais e subtropicais, limitando a realização de estudos dendroecológicos.

Ainda, nos trópicos, as espécies possuem maior complexidade anatômica da madeira e maior ocorrência de irregularidades que dificultam a datação acurada dos anéis de crescimento, como falsos anéis, anéis parciais ou anéis indistintos (Détienne 1989; Priya & Bhat 1998; Lorimer et al. 1999; Stahle 1999; Worbes 2002; Brienen et al. 2009). Ao mesmo tempo, a prospecção de espécies com potencial dendrocronológico tem dado lugar a estudos avançados com espécies que conhecidamente formam anéis de crescimento, como os aplicados à reconstrução do clima (*e.g.* Roig et al. 2001; Roig & Villalba 2008), de distúrbios (*e.g.* Veblen et al. 1999) e de dinâmica florestal (*e.g.* Villalba & Veblen 1997).

Neste contexto, a família Lauraceae Jussieu é uma família pantropical que tem substancial importância em ecossistemas tropicais e subtropicais (Stern 1954; Richter 1981; Rohwer 1993a, b). É um dos *taxa* mais basal em Angiospermas, pertencendo à divisão Magnoliophyta, ordem Laurales (APG III 2009). Existem aproximadamente 55 gêneros e entre 2500 e 3500 espécies atuais, na sua maioria arbórea, com exceção do gênero *Cassytha* que apresenta-se como ervas parasitas (Chanderbali et al. 2001). A família tem na América tropical e sudeste da Ásia seus mais importantes centros de diversidade de espécies, ocorrendo também com alta representatividade e importância em ecossistemas da Austrália e de Madagascar (Werff & Richter 1996).

No Neotrópico, correspondem a um grupo de espécies arbóreas ecológica e funcionalmente importantes. Com aproximadamente 30 gêneros e 800 espécies, tem ampla distribuição geográfica e ecológica, ocorrendo na grande maioria dos ecossistemas, desde o equador aos subtrópicos, do nível do mar às grandes altitudes dos Andes, em florestas úmidas e estacionais, savanas e restingas (Werff & Richter 1996). Nestes ambientes, é um componente importante do estrato superior da vegetação ou frequentemente domina o dossel, sobretudo em florestas úmidas montanas (Gentry 1988). Em remanescentes florestais da Mata Atlântica, estudos fitossociológicos apontam que Lauraceae é uma das mais comuns em número de indivíduos e de espécies (Souza & Lorenzi 2005). O dossel e subdossel de florestas montanas subtropicais no sul da Mata Atlântica são compostos por diversidade alta de espécies da família (Klein 1984; Canalez 2006; Longhi et al. 2006; Gomes et al. 2008).

Lauraceae é considerada uma família de difícil distinção entre espécies e até mesmo gêneros. Estudos filogenéticos evidenciam ainda a natureza polifilética de muitos gêneros não bem circunscritos, como *Ocotea*, o gênero que abriga o maior número de espécies entre os gêneros da família (Chanderbali et al. 2001; Werff 1991). Além disso, Lauraceae tem valor econômico importante e os mais antigos registros de utilização de espécies da família datam de 2800 anos A.C, originários na Grécia antiga. Algumas espécies são historicamente usadas na culinária ou para fins medicinais, porém seus usos mais comuns estão na indústria de extração de óleos essenciais e madeireira. Neste último fim, destaca-se o gênero *Ocotea* que apresenta espécies para utilização nos mais diversos fins e que foram intensamente exploradas (Marques 2008). Ainda, muitas Lauraceae estão atualmente nas listas vermelhas devido à superexploração e desmatamento.

A estrutura anatômica da madeira de espécies de Lauraceae é bastante uniforme, porém possui clara diferenciação em relação a outras famílias arbóreas. As características anatômicas do lenho que se destacam em Lauraceae são a porosidade difusa, presença de vasos solitários ou radial-múltiplos de poucos elementos, parênquima paratraqueal, raios estreitos e mudança na densidade das fibras (Stern 1954; Richter 1981). Estudos dendroecológicos são raros, destacando-se os de Spathelf et al. (2000, 2010) que investigaram os padrões de crescimento e a influência do clima em duas espécies sul-americanas, *Ocotea pulchella* e *Nectandra megapotamica*. Considerando a elevada diversidade, a ampla distribuição geográfica e ecológica e a facilidade em encontrar indivíduos nas formações florestais, as lauráceas são pouco estudadas, principalmente com relação a taxas de crescimento e autoecologia. Atualizar o estado da arte em relação aos estudos de Lauraceae no Neotrópico pode contribuir para esclarecer as demandas existentes e as lacunas do conhecimento em dendrocronologia de lauráceas.

Com o objetivo de contribuir para o desenvolvimento da dendrocronologia neotropical e para o entendimento da autoecologia de lauráceas do sul da Mata Atlântica, nesta dissertação eu reviso e desenvolvo estudos dendrocronológicos com espécies neotropicais da família Lauraceae, principalmente em remanescentes florestais do sul da Mata Atlântica, um dos hotspots mundiais de biodiversidade. O capítulo 1 "Lauraceae: a promising family for advance of neotropical dendrochronology" traz uma revisão sobre alguns aspectos da dendroecologia e da identificação de anéis de crescimento em lauráceas na região Neotropical. Ao fim, o capítulo compila uma lista de espécies de lauráceas neotropicais que formam anéis de crescimento passíveis de datação de que podem ser empregados em estudos dendrocronológicos. O capítulo 2 “Tree-ring appearance and climate-growth relationship in *Ocotea elegans* Mez (Lauraceae) growing in subtropical montane rainforest” analisa com maior profundidade a formação de anéis de crescimento e a existência de sinais dendroclimáticos em *Ocotea elegans*, laurácea comum em regiões montanas no sul da Mata Atlântica.

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CAPÍTULO 1

LAURACEAE: A PROMISING FAMILY FOR ADVANCE OF NEOTROPICAL DENDROCHRONOLOGY†

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ABSTRACT

Dendrochronological knowledge in tropical and subtropical zones is poorly understood despite their higher biodiversity. Dendrochronology in Neotropics could provide strong and valuable information improving knowledge of autecology, vegetation ecology, and climatology and supporting management of neotropical biodiversity. Recognizing potential species to dendrochronology is primordial to develop this science. Lauraceae is one of the most frequent family inhabiting the neotropical forests. In this paper, we reviewed some aspects of neotropical dendrochronology and compiled an extensive list of lauraceous species' tree-ring features, distributed throughout several types of biomes and climates of Neotropics. In addition, we brought to light our first studies of Lauraceae tree-rings in southern Atlantic forest. Our results contribute to dendrochronological science advance at Neotropics providing better understanding on tree-ring features of one of the most important families in tropical zones.

Keywords: tree-rings, annual rings, growth dynamics, cambial periodicity, climate-growth relationship, dendroecology.

INTRODUCTION

Neotropics comprises subtropical and tropical ecosystems from the southern North America to South America, presenting a great variation in rainfall, temperature, geomorphology and topography (Burnham & Graham 1999). Ecosystems as diverse as deserts, savannas, grasslands, seasonal forests or humid rainforests occur in the region that includes seven biodiversity hotspots with high number of endemism and rarities (Myers *et al.* 2000). Major tropical forests extension is present at this domain becoming Neotropics relevant to biodiversity conservation at global scale.

Long-term data about age and growth rates of trees and interactions with ecological factors, as climate and disturbances, are needed to support correct management and conservation of forests. However, such data are scarce in Neotropics because continuous forest inventories are still very few and do not encompass the long lifespan of trees. Meanwhile, dendrochronological evidences, the most temporal and geographical extended record to provide precise and high-resolution information on tree and forest ecology (Schweingruber 1988), is scarce.

Dendrochronology applies tree-rings to date trees, to reconstruct past environmental events and conditions and to obtain ecological information from individuals to ecosystems. Dendrochronology has been used in forestry, botany, climatology, Earth sciences (Worbes 1995) and in anthropology and archaeology (Stokes & Smiley 1968). The science of dendrochronology is well-developed in temperate regions due to longer science advance as a whole than in the complex biodiverse tropical areas. In Neotropics, since promising results at the end of last century, much progress has been achieved concerning dendrochronological methods (*e.g.* Worbes & Junk 1989, 1999; Worbes 1995), useful species (*e.g.* Worbes 2002), tree growth dynamics (*e.g.* Dünisch 2005), forest dynamics (*e.g.* Brienen *et al.* 2006, 2009) and climate reconstruction (see reviews in Boninsegna *et al.* 2009; Villalba *et al.* 2009).

Basic investigations aiming to assess the appearance and timing of wood layers in neotropical species are the main body of research and should be further encouraged, since the dendrochronological relevance of the huge neotropical tree diversity was accessed only to few species and ecological conditions. The improvement of such studies in tropics and subtropics should be encouraged since they provide valuable information on tree autecology, forest ecology and climatology, for example.

Here, we aim to contribute to the advance of neotropical dendrochronology by reviewing some aspects concerning tree-ring studies in species of Lauraceae Jussieu, providing a list of useful species to dendrochronological purposes. We focused our effort in studying Lauraceae species because of its functional and structural importance in entire scope of neotropical ecosystems (Moraes 2005). Lauraceae also has significant economic value, offering high quality timber and non-timber resources as spices and essential oils (Marques 2008). Therefore, several lauraceous species are currently in red lists due to overexploitation and deforestation. Updating the state of art regarding studies of Lauraceae in Neotropics can contribute clarifying demands to further studies and filling the gaps in dendrochronological knowledge of Lauraceae species. To achieve our purpose, we analyzed and compiled papers dealing the presence of tree-rings in xylem of neotropical Lauraceae species. We also present new evidences on growth and wood anatomy of lauraceous species in southern Brazilian Atlantic rainforest.

DENDROCHRONOLOGY IN NEOTROPICS

Climate drivers of seasonal growth in trees

Annual growth-rings result from periodical activity of the vascular cambium as a response to unfavorable climatic conditions in one season of the year (Schweingruber 1988). In temperate areas, low winter temperature and some consequently water stress is so limiting that leads to dormancy in most life forms. Therefore, tree growth rhythm is seasonal and xylem shows clearly annual rings. For decades, scientific community discussed and neglected the presence of visible tree-rings outside the temperate and boreal zones, due to the apparent less pronounced stressful climatic conditions in humid tropical and subtropical sites (Jacoby 1989; Stahle 1999; Rozendaal & Zuidema 2011). Nowadays, tropical tree-rings are not a myth anymore and have been noticed in several environments in whole world and water availability, air temperature and day length have been pointed as the main climate drivers of tree growth (Vlam *et al.* 2014).

In some tropical sites of Neotropics, there is a period of year of monthly rainfall below 100 mm that promotes water stress due to high levels of evapotranspiration. The water stress inhibits processes of cellular expansion, such flushing and cambial activity (Borchert 1999). Therefore visible tree-rings may occur in species of semi-arid lands, seasonal and dry forests, and even rainforests (*e.g.* Boninsegna *et al.* 1989; Détienne 1989; Worbes 1999; Dünisch *et al.* 2002; Roig *et al.* 2005; Lisi *et al.* 2008; Costa *et al.* 2013; Locosselli *et al.* 2013; Ferrero & Villalba 2009; Ferrero *et al.* 2013; Mendivelso *et al.* 2014). Periodical flood-pulses are also responsible to regulate growth pattern in many trees growing in floodprone forests (*e.g.* Callado *et al.* 2001; Schöngart *et al.* 2002). During flooding, anaerobic conditions decrease capacity of root absorption, leading to hydric stress (Kozlowski & Pallardi 1997). In the subtropics, with increase of latitude, the temperature and day length become more determinant than precipitation on the phenology of plants and in the growth dynamics (*e.g.* Morellato *et al.* 2000; Marques *et al.* 2004; Dünisch 2005; Paise & Vieira 2005; Oliveira *et al.* 2009, 2010). Cambial activity is restricted to warm conditions of spring and summer months, mainly in humid subtropical sites (*e.g.* Oliveira *et al.* 2009, 2010). Meanwhile, temperature and precipitation can interact triggering growth rhythm in trees growing in subtropical and tropical high elevation sites in Andes (*e.g.* Villalba *et al.* 1998). In these sites, increasing altitude is correlated with decreasing in temperature and precipitation. So, in summer months, higher temperature can leads to a fewer water supply to growth (Morales *et al.* 2004).

Different climate-growth relationship in the same species may be common on neotropical region since tropical and subtropical ecosystems have a great variation in rainfall, temperature and topography, and so the limiting factors are more variable. For example, Dünisch (2005) compared climate-growth relationship in *Cedrella fissilis* Vell. under subtropical and tropical Brazilian sites, and found water availability is the triggering factor to seasonal growth on tropical site. Otherwise, temperature has more importance on tree growth in the subtropical site.

Dendrochronological studies

Neotropical dendrochronology has developed mainly in the last two decades (Boninsegna *et al.* 2009) when a wide list of species with dendrochronological potential was produced (see reviews in Worbes 2002; Boninsegna *et al.* 2009; Callado *et al.* 2013, 2014). Several studies evidence annual nature of tree-rings by anatomical descriptions (Alves & Angyalossi-Alfonso 2000; Callado *et al.* 2001; Tomazello-Filho *et al.* 2004), assess wood formation timing (Worbes 1995; Dünisch *et al.* 2002;

Schöngart *et al.* 2002; Callado *et al.* 2004; Oliveira *et al.* 2009; Costa *et al.* 2013) and evaluate climate-growth relationship (Détienne 1989; Vetter & Botosso 1989; Worbes 1999; Dünisch 2005; Roig *et al.* 2005; Lisi *et al.* 2008; Oliveira *et al.* 2010; Spathelf *et al.* 2010).

LAURACEAE IN NEOTROPICS

Lauraceae is a large family driving a great ecological importance in tropical and warm subtropical ecosystems of the world (Stern 1954; Richter 1981; Rohwer 1993a, b). There are approximately 55 genera and 2,500-3,500 species; most of them are trees, less shrubs (Chanderbali *et al.* 2001), occurring mainly in the tropics and subtropics of America and Asia, with few species in Australia, Madagascar and Africa (Werff & Richter 1996). Neotropics are the most important diversity center, with approximately 30 genera and more than 800 species, where Lauraceae occur over tropical and subtropical regions, in wet forests from sea level to high altitudes of Andes (Werff & Richter 1996), being therefore one of the most frequent group inhabiting the upper stratum of both in number of individuals and species (Gentry 1988; Werff & Richter 1996). This wide distribution and frequency in neotropical ecosystems would make it a powerful family to dendrochronological studies because of the facility in finding individuals enough to compute a site chronology.

Studies bringing evidence about tree-ring appearance and formation

Data about tree-ring appearance in neotropical Lauraceae species is relatively prolific in the literature. We compiled 156 species cited in 23 studies (Table 1), it corresponds to approximately 20% species and 17 of total 30 genera of neotropical Lauraceae. Studies are mainly in the scope of wood anatomy descriptions. In general, such papers may be useful as a starting point for dendrochronological studies because they describe the anatomical features that allowing recognize growth-rings in each species. In our review we compiled 14 papers in Lauraceae wood anatomy that indicated presence or absence of growth-rings and described the anatomical features of such growth zones (e.g. Callado & Costa 1997; León-Hernández 2000; León-Hernández & Espinoza-de-Pernía 2000a; León-Hernández & Espinoza-de-Pernía 2001; León-Hernández 2002; Oliveira 2005). Such studies comprised 117 species, approximately 15% of neotropical Lauraceae species (see Table 1),

Specific studies on tree-ring anatomical features provided another relevant source of information about Lauraceae tree-rings. Alves & Angyalossi-Alfonso (2000) evaluate ecological trends in the appearance and anatomical features of growth-rings in 491 Brazilian species from different environments, including 39 Lauraceae. Other studies make available lists of species and their growth-rings anatomical features, including 10 Lauraceae, in Mexico, Venezuela, Brazil and Argentina (Worbes 2002; Tomazello-Filho *et al.* 2004; Roig *et al.* 2005; Marcati *et al.* 2006; Lisi *et al.* 2008; Ferrero *et al.* 2014).

Lauraceae species have already applied in dendroecology and growth rate estimation. Spathelf et al. (2000, 2010) analyzed growth synchrony and climate-growth relationship of *Ocotea pulchella* (Nees & Mart.) Mez and *Nectandra megapotamica* (Spreng.) Mez in southern Brazil. Grau *et al. (*2002) dated tree falls dynamics in Argentina by counting tree-rings in xylem of *Cinnamomum porphyrium* (Griseb.) Kosterm. trees that resprout after the formation of a canopy gap. Mattos *et al.* (2010) verified past growth rate of *Ocotea porosa* (Nees & Mart.) Barroso, *O. pulchella* and *Ocotea puberula* (Rich.) Nees by dendrochronology techniques.

The geographical amplitude of information about Lauraceae neotropical tree-rings comprise from northern part of Neotropics (Mexico, *e.g.* Roig *et al.* 2005; Richter

1981; Pulido & Tapia 2007), through central Brazilian savanna (Tomazello-Filho *et al.* 2004; Lisi *et al.* 2008) and Atlantic coastal rainforest (*e.g.* Oliveira 2005), to subtropical southern Brazil and Argentina (*e.g.* Castiglioni 1962; Grau *et al.* 2002; Spathelf *et al.* 2010).

Anatomical features of tree-rings

According our compiled data, formation of growth-rings in xylem of Lauraceae is very frequent in tropics and subtropics (Table 1). At least 80 species (out of 156) reported by literature have clearly distinct tree-rings. Authors described another 15 species as mostly distinct, sometimes distinct, indistinct to distinct or poorly distinct to distinct. Approximately 50 species have poorly distinct and only 17 of 156 species do not have or have indistinct tree-rings. The presence of growth-rings in the majority neotropical Lauraceae could also be a conserved character that is a positive point to its applicability in tree-ring science. The genetic factors determine the period of cambium activity according to the availability of growth requirements and are influenced by the past evolution of group (Van Schaik *et al.* 1993). We noted, however, some species was studied by different authors and they diverged in respect of appearance of growth-rings (for example *Nectandra cuspidata*, see Table 1). This variability can in general be explained by the fact that the environmental limiting factors (mainly light, water availability and air temperature) interact with genotype to determine the growth dynamic (Van Schaik *et al.* 1993). Consequently, in situations when resources and conditions are not scarce to growth, several trees may be nonseasonal or do not show anatomical marks in the xylem, consequently growth-rings are poorly apparent or absent (Fritts 1976; Jacoby 1989). Additionally, the conspicuous of tree-rings may vary between individuals of the same species at different site conditions or between young and adult trees (*e.g.* Dünisch *et al.* 2003).

In respect to anatomical characteristics of tree-ring boundaries, the majority of reported species show variations in fiber density with radial flattened and thick-walled latewood fibres. Axial marginal parenchyma band is also present in several species. Some species present a fiberzone with fewer vessel elements and a greater concentration of fiber cells.

Findings in Lauraceae cambial activity and dendroecology

The previous section described the presence of distinct growth layers in a large portion of neotropical Lauraceae species. However, the dendrochronological suitability of a species also depends on the annual nature of those structures. In this sense, there are studies evidencing seasonal growth and proving annual nature of growth-rings in neotropical laurels. Ávila *et al.* (1975) investigated cambial activity of *Cryptocarya alba* (Molina) Looser*,* a sclerophyllous evergreen shrub growing in a high elevation site in Chile. They found wood formation was restricted to a short period between spring and early summer months (Aug-Dec). Among other seven species, Botosso and Vetter (1991) explored periodicity and growth rate of *Aniba rosodora* Ducke (pau-rosa), a Lauraceae tree of high commercial value, using dendrometer bands and annual cambial marks in five plantation trees (of known age) in amazonian terra firme forests. They found cambial activity followed a seasonal pattern in response to water stress. During the dry season (Jun-Nov), they measured low lateral growth but, after the first rainfalls, increment rates increased. Also with dendrometer bands, Figueiredo-Filho *et al.* (2008) analyzed growth rate of southern Brazilian species including three Lauraceae: *Cinnamomum vesiculosum* (Nees) Kosterm., *Nectandra grandiflora* Nees & Mart. ex Nees and *O. porosa*, found growth decreased sharply in the autumn and winter months and the reaching maximum values in summer months. All these studies showed the periodical lateral growth follows a seasonal pattern in Lauraceae trees.

Climate-growth relationship was studied by Spathelf *et al.* (2010), whose evaluated crossdating quality and climate signal in chronologies of *O. pulchella* and *N. megapotamica* in southern Brazil. Based on wood structure, crossdating between trees and seasonality of air temperature in the studied site, they concluded *O. pulchella* and *N. magapotamica* formed annual rings. Nevertheless, ring width index correlation to water balance and evapotranspiration did not indicate any significant climatic signal.

Cinnamomum porphyrium is a long-lived tree reaching 200 years in mesic-humid Yungas forest at 400-700 m of elevation (Grau *et al.* 2003). Annual rings of *C. porphyrium* was successfully used to reconstruct history of treefalls because of its ability to produce datable resprouts after stem falls (Grau 2002). In addition, fire scars present in tree-rings were used to reconstruct fire history (Grau *et al.* 2003).

TREE-RINGS OF LAURACEAE IN SOUTHERN ATLANTIC RAINFOREST

We have focused our efforts in studying tree-rings of Lauraceae in southern Brazilian Atlantic rainforest due to its physiognomic and ecological importance in such ecosystems. In phytosociological surveys, Lauraceae appears as one of the most frequent family both in number of individuals and species inhabiting the upper stratum of Atlantic rainforest remnants.

Recognizing periodic anatomical patterns in xylem of trees is the first step to understand the growth rhythm, and identifying which anatomical structure defines tree-rings is a primordial step to its application in dendroecological studies. Stahle *et al.* (1999) suggest that we need analyzing phenology, ring anatomy, crossdating and climate-growth correlation to obtain indications whether increment zones are truly annual. Therefore, we analyzed wood cores of 14 Lauraceae species to describe tree-ring anatomy (Table 2). We observed under magnification transversal sections deposited in Porto Alegre Colégio Anchieta Herbarium (PACA) and wood samples collected with the help of an increment borer.

Sampled individuals are from two study areas in southern Brazil. First area is approximately 300 m a.s.l, corresponds to municipalities of Aratiba and Itá, and the original vegetation is characterized by seasonal forests (Fig. 1). Climate in this site is Cfa, according to Köppen classification, humid temperate with warm summers (mean air temperature in the hottest month above 22 °C). According to local meteorological data (2002-2010), the mean air temperature was 23.1°C (25.3°C in the hottest month, January and 19.7 °C in the coldest, August) and total annual precipitation was 2106 mm (Fig. 2). Rainfall, however, was concentrated in springer and summer months, while in the winter, precipitation decreased below 150 mm (in June, it was below 100 mm). The second area corresponds to municipalities of Caxias do Sul, Campo Belo do Sul and São Francisco de Paula (700 - 900 m a.s.l) and indigenous vegetation is mixed rainforest (*Araucaria* forest) (Fig. 1). Climate is Cfb, humid temperate with mild summers (mean air temperature in the hottest month bellow 22 °C). According to long-term local meteorological data, the annual sum of precipitation was between 1700 and 2300 mm. Despite the precipitation being constant over the year, the mean air temperature follows a seasonal pattern. The mean annual temperature was between 16 and 17 °C (approximately 20°C in the hottest month, January and 11 °C in the coldest, July) and from May until September it decreased to less than 15°C (Fig. 2).

We observed all fourteen species had a similar anatomical pattern in xylem, for example: change in fiber density between early and latewood, diffuse porous wood, vessels more predominantly solitary or in radial multiples of 2-3 elements, presence of paratracheal parenchyma and narrow rays with less than three cells. Other authors have observed that wood structures of lauraceous trees are similar and cited the pattern mentioned above as the main characteristics of the family (Stern 1954; Richter 1981; León-Hernández 2000; Oliveira 2001). There was no clear distinction between early and latewood, since the transition was gradual. However, some characteristics as vessel size and grouping and kind of paratracheal parenchyma changed between early and latewood, allowing the recognition of such zones. In some rings of *Nectandra lanceolata* Nees & Mart., *O. pulchella* and *Persea wildenowii* Kosterm., for example, vessels decreased slightly in diameter and/or frequency in the latewood, but they are not typically a semi-porous wood. *Cinnamomum amoenum* (Nees) Kosterm., *Cinnamomum glaziovii* (Mez) Kosterm., *N. grandiflora*, *N. megapotamica*, *Ocotea bicolor* Vattimo-Gil and *O. porosa* presented earlywood vessels solitaries and latewood ones grouped in radial-multiples of 2-3 elements. *Ocotea odorifera* Rohwer had both solitary vessels and grouped vessels; however, clusters up to four elements occurred in latewood of the older portion of sample. Vasicentric paratracheal parenchyma was the most common, but others like scanty, unilateral and aliform also occurred. *C. glaziovii* had scanty and vasicentric paratracheal parenchyma in earlywood and winged-aliform in latewood. *N. grandiflora* showed vasicentric in earlywood and lozengle-aliform or occasionally confluent in latewood. *Ocotea elegans* Mez and *O. pulchella* presented in earlywood vasicentric, scanty or unilateral parenchyma, but winged-aliform pattern also occurred in latewood. Table 3 resumes wood anatomical features of studied species.

All species showed growth layers in xylem, although in some species they were distinct with some difficulty. In *N. megapotamica* fuzzy rings appeared in the inner part of sample meanwhile in *O. odorifera* they appeared in the outer part. Two anatomical structures defined the boundary of tree-rings: in genus *Cinnamomum*, *Nectandra, Ocotea* and *Persea*, boundary was marked by an abrupt transition between thick-walled and radial flattened fibres in latewood of a ring and thin-walled earlywood fibres of consecutive ring; in genus C*ryptocarya,* a marginal parenchyma band delimited tree-rings. Change in fiber density is common to Lauraceae species as a whole (Stern 1954; Richter 1981; León-Hernández 2000, 2002; Tomazello-Filho *et al.* 2004) and marginal parenchyma is characteristic of *Cryptocarya* (Richter 1981). False-ring formation was common in several species for example *C. amoenum*, *N. megapotamica* and *O. pulchella.* False rings appeared as latewood-like cells (thick-walled and radial-flattened fibres) in the earlywood and often were present in consecutive rings. However, we can easily recognize them because the boundary of a false ring is more diffuse then a true ring. Wedging rings were noted in *Cryptocarya moschata* Nees & Mart. and *O. pulchella*. Figure 3 illustrates growth-rings of studied species.

Although we did not test the annual nature of tree-rings in these species, the formation of periodical structures, the growth bands, provides evidences that Lauraceae species have periodical growth due to environmental seasonality. A study of wood anatomy of a large number of Brazilian species showed a positive correlation between the presence of annual rings and the subtropical climatic conditions (Alves & Angyalossi-Alfonso 2000). Several other studies with subtropical species have proven the annual seasonality of growth-rings (*e.g.* Dünisch 2005; Oliveira *et al.* 2009) and pointed the temperature and day length are responsible to regulate the timing of wood formation (Figueiredo-Filho *et al.* 2008; Oliveira *et al.* 2009, 2010). In our study areas, climate diagrams based on meteorological records bring out two distinct types of climates. First, in seasonal forest, precipitation decreases in winter months (May-Aug) and may reach less than 100 mm, threshold to hydric stress. Second, in mixed rainforest, rainfall is well distributed but temperature in winter months may be limiting for growth. Thereby, in both sites, trees should be growing in the favorable months of spring and summer, responding to different climatic drivers. However, leaf phenology, strongly linked to cambial activity, apparently does not follow a seasonal pattern since our studied trees are evergreen or semi-deciduous (see Table 2). Because of it, even when it seems to be highly likely to be annual, the growth rhythm should be accompanied in further investigations.

One way to prove the regulation of climatic conditions on growth is to analyze growth synchrony of trees in a population. The technique of crossdating is based on the idea that, if climate is the limiting factor for tree growth, trees under the same climatic conditions would show convergent growth patterns. In this context, we analyzed two of our fourteen species: *O. pulchella* (n=5) and *C. amoenum* (n=2) growing in the same site in municipality of Caxias do Sul. We measured and standardized tree-ring widths following dendrochronological procedures (Stokes & Smiley 1968; Cook & Kairukstis 1990) and correlated them by Pearson's correlation in order to evaluate growth synchronism. Comparing trees of same species, Pearson's correlation coefficients were 0.33 and 0.34 for *O. pulchella* and *C. amoenum*, respectively. Spathelf *et al.* (2010) found intercorrelation between trees of *O. pulchella* with a coefficient about 0.61, above what we found. However, Oliveira *et al.* (2010) exploring growth synchronism of *Araucaria angustifolia* (Bertol.) Kuntze in the same region detected a mean correlation of 0.25 between trees. The same authors brought out a review of correlation coefficients and founded in several dendrochronological studies with different species and environments a mean correlation of 0.33. Surprisingly, intercorrelation between species was also 0.34. Indeed, individuals of both species showed similar growth patterns (see Fig. 4). Therefore, *O. pulchella* and *C. amoenum* in southern Brazil have similar growth pattern and this is probably due to climatic influence.

Another interesting point is the influence of climatic conditions on total annual growth. In subtropical sites, both temperature and precipitation have power over total annual growth, but it depends on how strong is rainfall seasonality. In subtropical humid mountains in China, no significant relationship was found between precipitation and annual tree growth whereas spring and summer temperatures are positive related with it (Zheng *et al.* 2012). At high elevations in subtropical Andes treelines, increasing in altitude is accompanied by decreasing in precipitation and air temperature. The radial growth of some tree species is strongly influenced by rainfall and the temperature is important regulating the evapotranspiration, leading to more or less water availability in growing season (Morales *et al.* 2004). Similar growth response was found for *A. angustifolia* growing in subtropical southern Brazil (Oliveira *et al.* 2010; Cattaneo *et al.* 2013). Moreover, the relationship between annual increment and temperature at the beginning and at the end of growing season (Dünisch 2005; Oliveira *et al.* 2010) indicates that air temperature controls extent of cambial division (Dünisch 2005) and producing wider or narrower rings. We also investigated climatic signals in the chronology of *O. pulchella* through correlation profiles that evidence periods of months that most influenced the growth (Fig. 5). We noted both temperature and precipitation had influence on annual growth. Lower temperatures in late summer and early autumn in the previous growing season had positive influence in current growth. Low temperatures can induce early reduction of cambial activity and therefore a greater stock of carbohydrates for wood formation becomes available (Kozlowski & Pallardi 1997), resulting in wider rings in the next growing season. Consequently, higher temperatures prolong the previous year's growth and reduce the reserves of nutrients available for the next year, leading to narrower rings. Similarly, a positive effect of air temperature in the end of current growing season indicates that higher temperatures in late summer and early autumn prolong the growing season, forming larger growth-rings. Positive correlations with rainfall and negative with maximum temperature evinced that growth of *O. pulchella* is positively associated with the water availability in the current growing season. High temperatures increase evapotranspiration rates and producing less favorable water conditions during the late spring and early summer, leading to the formation of narrow rings (Fig. 5).

CONCLUSION

Here, we reviewed papers dealing tree-rings of neotropical Lauraceae species and showed most species records its growth cycle as tree-rings in xylem. Annual nature of tree-rings and seasonal growth were also showed for some tropical and subtropical species by cambial activity studies and by measurements of monthly increment rates. It is right in stating Lauraceae species have seasonal cambium activity due to climate drivers that in Neotropics may be variable according to latitude, altitude and continentally. In tropical region of America, rainfall seasonality drives the seasonal cycles of plant growth. In seasonal forests and savannas, dry period with a mean precipitation below 100 mm/month induces dormancy or decrease in cambium activity after rainy season in deciduous or even evergreen species (Roig et al. 2005; Worbes 1995, 1999). During the flooding in forest plains several species have dormancy to tolerate hydric stress, showing distinct increment layers (Callado et al. 2001; Schöngart et al. 2002). In higher latitudes and altitudes, low temperatures of cold season is the triggering factor of growing reduction leading many species to form distinct increment layers (Jacoby 1989; Oliveira et al. 2009, 2010). In this sense, it is likely that the species of Lauraceae family respond to ecosystem seasonality through the cambial periodicity and, therefore, show tree-rings in xylem.

The high biodiversity in tropical environments is considered to be one of the main factors that slow the advance of dendrochronology because of the difficulty in exploring which species have at least visible tree-rings and for those gather sufficient trees to sample to build tree-ring chronologies (Jacoby 1989). Our study compiled a list of species that represents approximately 20% of total neotropical laurel species and the vast majority of them with at least scarce distinct tree-rings. Furthermore, the large occurrence and sometimes high density of laurels in neotropical forests allows to get a statistically significant sample easier.

Finally, the wide distribution of the group throughout several types of biomes and climates are another stimulus for the application of Lauraceae in dendrochronology because it permits the implementation of chronologies networks. Our study permits improving ecological knowledge of a diverse and rich system as Neotropics that remain poorly understood. Moreover, these data allow us to develop studies on forest ecology and general climatology.

Table 1. List of neotropical Lauraceae species registered in papers, tree-ring characteristics, origin (when present) and type of study.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Aiouea costaricensis (Mez) Kosterm.	-	PD	-	Costa Rica	T	WA	1
Aiouea dubia (Kunth) Mez	-	D	-	Colômbia	T	WA	18
--	-	PD	-	Peru	T	WA	1
Anaueria brasiliensis Kosterm.	2	I	-	Brazil	T	WA	4
--	1	D	FD	-	-	WA	12
--	-	I	-	Brazil	T	WA	1
Aniba affinis (Meisn.) Mez	2	I-D	FD	-	-	WA	7
Aniba burchellii Kosterm.	3	D	FD	-	-	WA	7
Aniba canelilla (Kunth) Mez	2	I-D	FD, MP	-	-	WA	7
Aniba cylindriflora Kosterm.	1	PD	FD	-	-	WA	7
Aniba guianensis Aubl.	1	D	FD	-	-	WA	7
Aniba hypoglauca Sandwith	3	D	FD	-	-	WA	7
Aniba kappleri Mez	1	D	FD, MP	-	-	WA	7
Aniba robusta (Klotzsch & H. Karst.) Mez	1	PD	FD	-	-	WA	7
--	3	D	FD	Venezuela	T	WA	20
Aniba spp. (*A. affinis, A. citrifolia, A. terminalis, A. taubertiana, A. excelsa, A. williamsii, A. bracteata, A. hostmaniana, A. burchelli, A. intermedia, A. robusta, A. jenmani, A. guianensis, A. megaphylla, A. riparia, A. kappleri, A. pichurri-minor, A. perutilis, A. santaladora, A. panurensis, A.roseadora, A. percoriaceae, A. parviflora, A. cylindriflora, A. permollis, A. firmula, A. coto, A. canelilla, A. ferrea*)	-	D+	-	Brazil, Colômbia, Guyanas and Peru	T	WA	3
Aniba spp. (*A. perutillis, A. roseadora, A. canelilla, A.parviflora, A. terminalis*)	-	D+	FZ	-	-	WA	1

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Beilschmiedia emarginata (Meisn.) Kosterm.	1	D	FD, MP	Brazil	T	WA	4
Beilschmiedia latifolia (Nees) Sach. Nishida	3	D	MP	Venezuela	T	WA	20
Beilschmiedia louisii Robyns & R. Wilczek	1	D	MP	-	-	WA	8
Beilschmiedia mexicana (Mez) Kosterm.	1	D	FD, MP	-	-	WA	8
Beilschmiedia obtusifolia (F. Muell. ex Meissner) F. Muell.	1	D	MP	-	-	WA	8
Beilschmiedia pendula (Sw.) Hemsl.	2	D	MP	-	-	WA	8
--	-	I	-	Colômbia	T	WA	18
--	-	D-	MP	-	-	WA	1
Beilschmiedia rigida (Mez) Kosterm.	4	D	FD, MP	Brazil	T	WA	4
Beilschmiedia sulcata (Ruiz & Pav.) Kosterm.	2	D	MP	-	-	WA	8
Beilschmiedia tarairi (A. Cunn.) Kirk	1	D	MP	-	-	WA	8
Beilschmiedia taubertiana (Schwacke & Mez) Kosterm.	1	D	FD, MP	Brazil	T	WA	4
Beilschmiedia tawa (A. Cunn.) Kirk	1	D	MP	-	-	WA	8
Chlorocardium rodiei (R.H. Schomb.) Rohwer, H.G. Richt. & van der Werff	2	I	-	-	-	WA	12
--	-	I-PD	-	-	-	WA	1
Cinnamomum porphyrium (Griseb.) Kosterm.	>1	D	FD	Argentina	S	TR	23
Cinnamomum stenophyllum (Meisn.) Vattimo-Gil	1	D		Brazil	S	TR	5
Cinnamomum triplinerve (Ruiz & Pav.) Kosterm.	3	D	FD	Venezuela	T	WA	20
Cryptocarya alba (Molina) Looser	-	D	-	-	-	WA	1
Cryptocarya moschata Nees & Mart.	5	I	-	Brazil	T, S	TR	5

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Cryptocarya sp.	3	D	-	Brazil	T, S	TR	5
Dicypellium caryophyllatum Nees	-	D	FD	Brazil	T	WA	1
--	1	D	-	Brazil	T	TR	5
Dicypellium sp.	1	D	-	Brazil	T	TR	5
Endlicheria arunciflora (Meisn.) Mez	-	D	FD	Venezuela	T	TR	13
Endlicheria sp.	-	D	-	Colômbia	T	WA	18
Endlicheria spp. (*E. browniana, E. sericea, E. anomala, E. williamsii, E. multiflora*)	-	PD	-	-	-	WA	1
Licaria aurea (Huber) Kosterm.	1	I-D	FD	-	-	WA	12
Licaria campechiana (Standl.) Kosterm.	1	I-D	FD	-	-	WA	12
Licaria cannella (Meisn.) Kosterm.	1	D	-	Brazil	T	TR	5
--	3	I-D	FD	-	-	WA	12
Licaria guianensis Aubl.	1	I-D	FD	-	-	WA	12
Licaria multiflora (Kosterm.) Kosterm.	1	I-D	FD	-	-	WA	12
Licaria rigida (Kosterm.) Kosterm.	1	I	-	Brazil	T	TR	5
Licaria spp. (*L. triandra*, *L. campechiana*, *L. armeniaca*, *L. limbosa*, *L. appelli*, *L. canella*)	-	I-D	FD, MP	-	-	WA	1
Licaria triandra (Sw.) Kosterm.	1	I-D	FD	-	-	WA	12
Licaria vernicosa (Mez) Kosterm.	1	I-D	FD	-	-	WA	12
Mezilaurus itauba (Meisn.) Taub. ex Mez	1	I	-	Brazil	T	TR	5
Mezilaurus lindaviana Schwacke & Mez	1	I	-	Brazil	T	TR	5
Mezilaurus mahuba (A. Samp.) van der Werff	1	I	-	Brazil	T	TR	5

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Mezilaurus sp.	2	I-D	-	Brazil	T	TR	5
Mezilaurus spp. (*M. itauba, M. navalium. M. synandra*)	-	PD	-	-	-	WA	1
Nectandra acutifolia (Ruiz & Pav.) Mez	1	PD	FD	-	-	WA	10
Nectandra amazonum Nees	1	PD	FD	-	-	WA	10
--	-	D	FD	Venezuela	T	TR	13
Nectandra angustifolia (Schrad.) Nees & Mart.	4	D-	FD	Argentina	S	WA	2
Nectandra cissiflora Nees	1	D	-	Brazil	T	TR	5
--	2	PD	FD	-	-	WA	10
Nectandra coriacea (Sw.) Griseb.	1	D	FD, MP	-	-	WA	10
Nectandra cuspidata Nees & Mart.	2	PD	FD	Argentina	S	WA	2
--	2	D	FZ	Brazil	T	WA	9
--	7	I	-	-	-	WA	10
--	1	D	FD	Brazil	T	WA	11
Nectandra globosa (Aubl.) Mez	3	D	FD, MP	-	-	WA	10
Nectandra grandiflora Nees & Mart. ex Nees	1	D	FD, MP	-	-	WA	10
--	2	D	-	Brazil	T	TR	5
Nectandra grandis (Mez) Kosterm.	1	I	-	-	-	WA	10
Nectandra hihua (Ruiz & Pav.) Rohwer	3	D	FD, MP	-	-	WA	10
Nectandra lanceolata Nees & Mart.	5	D	FD	Argentina	S	WA	2

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Nectandra laurel Klotzsch ex Nees	2	PD	FD	-	-	WA	10
--	3	D	FD	Venezuela	T	WA	20
Nectandra leucantha Nees & Mart.	1	D	FD	Brazil	T	WA	11
Nectandra martinicensis Mez	2	D	FD, MP	-	-	WA	10
Nectandra megapotamica (Spreng.) Mez	2	D	FD	Brazil	S	DC	22
Nectandra oppositifolia Nees & Mart.	3	D	FD	Brazil	T	WA	15
--	1	D	-	Brazil	T	TR	5
Nectandra pardo	1	D	FD, MP	-	-	WA	10
Nectandra puberula (Schott) Nees	1	I	-	-	-	WA	10
--	2	PD-D	FD	Brazil	T	WA	11
--	1	D	-	Brazil	T	TR	5
Nectandra reticulata (Ruiz & Pav.) Mez	4	D	FD, MP	-	-	WA	10
--	3	I-D	FD	Brazil	T	WA	11
--	-	D	-	Colômbia	T	WA	18
--	1	D	-	Brazil	T	TR	5
Nectandra saligna Nees & Mart.	4	D	FD	Argentina	S	WA	2
Nectandra sp.	5	I-D	-	Brazil	T, S	TR	5
Nectandra sp.	-	D	-	Colômbia	T	WA	18
Nectandra sp.	1	D	FD	Brazil	T	TR	17
Nectandra spp.	-	D	FD	-	-	WA	1

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Nectandra surinamensis Rottb. ex Bercht. & J. Presl	1	D	FD, MP	-	-	WA	10
Nectandra turbacensis (Kunth) Nees	6	D	FD, MP	-	-	WA	10
Ocotea aciphylla (Nees & Mart.) Mez	2	PD	-	Brazil	T	WA	9
--	8	D	FD	-	-	WA	6
--	2	D	FD	Brazil	T	WA	15
--	2	D	-	Brazil	T	TR	5
Ocotea acutangula (Miq.) Mez	1	D	FD	-	-	WA	6
Ocotea adenotrachelium (Nees) Mez	2	D	FD	-	-	WA	6
Ocotea amplissima Mez	1	PD	FD	-	-	WA	6
Ocotea argentea Mez	1	D	-	Brazil	T	TR	5
Ocotea aurantiodora (Ruiz & Pav.) Mez	3	D	FD	-	-	WA	6
Ocotea babosa C.K. Allen	1	I	-	-	-	WA	6
Ocotea barcellensis (Meisn.) Mez	4	D	FD	-	-	WA	6
Ocotea bofo Kunth	2	D	FD	-	-	WA	6
Ocotea calophylla Mez	4	I-PD	FD	-	-	WA	6
--	-	D	-	Colômbia	T	WA	18
Ocotea canaliculata (Rich.) Mez	5	I-D	FD	-	-	WA	6
--	1	D	-	Brazil	T	TR	5
Ocotea caracasana (Nees) Mez	1	PD	FD	-	-	WA	6

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Ocotea catharinensis Mez	1	D	FD	-	-	WA	6
--	1	I	-	Brazil	S	TR	5
Ocotea cernua (Nees) Mez	3	D	FD	-	-	WA	6
Ocotea corymbosa (Meisn.) Mez	1	D	FD	-	-	WA	6
--	1	PD	FD	Brazil	T	TR	17
Ocotea cymbarum Kunth	1	I	-	Brazil	T	TR	5
Ocotea divaricata (Nees) Mez	2	D	FD	Brazil	T	WA	15
Ocotea elegans Mez	2	D	FD	Brazil	T	WA	15
Ocotea floribunda (Sw.) Mez	3	D	FD, MP	Venezuela	T	WA	20
Ocotea fragrantissima Ducke	2	D	FZ	Brazil	T	WA	9
Ocotea guianensis Aubl.	5	D	FD	-	-	WA	6
--	-	D	FD	Venezuela	T	TR	13
--	5	D	-	Brazil	T	TR	5
Ocotea indecora (Schott) Mez	3	D	FD	Brazil	T	WA	15
Ocotea itatiaiae Vattimo-Gil	5	PD	FD	Brazil	T	WA	15
Ocotea lanata (Nees & Mart.) Mez	1	D	-	Brazil	T	TR	5
Ocotea longifolia Kunth	3	D	-	Brazil	T	TR	5
Ocotea magnilimba Kosterm.	1	D	-	Brazil	T	TR	5
Ocotea neesiana (Miq.) Kosterm.	2	D	FZ	Brazil	T	WA	9
--	1	D	-	Brazil	T	TR	5

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Ocotea nitida (Meisn.) Rohwer	1	D	-	Brazil	T	TR	5
Ocotea odorifera Rohwer	5	D	FD	Brazil	T	WA	15
--	1	D	-	Brazil	T	TR	5
Ocotea porosa (Nees & Mart.) Barroso	6	D	MP	Brazil	T	TR	19
--	10	D	FD	Brazil	S	GR	21
--	3	D	FD	Brazil	T	TR	14
Ocotea puberula (Rich.) Nees	8	D	FD	Brazil	S	GR	21
--	3	D	FD	Brazil	T	TR	14
--	1	D	-	Brazil	S	TR	5
--	1	D	FD	Brazil	T	WA	15
--	5	D-	FD	Venezuela	T	WA	20
Ocotea pulchella (Nees & Mart.) Mez	7	D	FD	Brazil	S	GR	21
--	1	D	-	Brazil	T	TR	5
Ocotea rigens (Nees & Mart.) Rohwer	1	D	-	Brazil	T	TR	5
Ocotea rubra Mez	3	I	-	Brazil	T	TR	5
Ocotea sp.	4	D	-	Brazil	T	TR	5
Ocotea splendens (Meisn.) Baill.	1	D	-	Brazil	T	TR	5
Ocotea spp.	-	D	FD	-	-	WA	1
Ocotea tenuiflora (Nees) Mez	4	PD	FD, MP	Brazil	T	WA	15
Ocotea tristis (Nees & Mart.) Mez	1	D	-	Brazil	T	TR	5

Continue.

Table 1. Cont.

Species	**N**	**GR**	**RB**	**Origin**	**Zone**	**Study**	**Source**
Persea americana Mill.	1	I	-	-	-	WA	12
--	-	D	FD, VD	Mexico	T	TR	16
Persea borbonia (L.) Spreng.	1	PD	FD	-	-	WA	12
Persea ferruginea Kunth	1	I	-	-	-	WA	12
Persea indica (L.) Spreng.	1	PD	FD	-	-	WA	12
Persea lingue (Ruiz & Pav.) Nees	1	PD	FD	-	-	WA	12
Persea mutisii Kunth	-	D	-	Colômbia	T	WA	18
Persea pyrifolia (D. Don) Spreng.	1	D	-	Brazil	T	TR	5
Persea sp.	3	I-D	-	Brazil	T, S	TR	5
Persea spp.	-	D	FD	-	-	WA	1
Phoebe paniculata (Nees) Nees	1	D	-	Brazil	T	TR	5
Phoebe porosa (Nees & Mart.) Mez	-	D	FD	-	-	WA	1
Pleurothyrium densiflorum A.C. Sm.	-	I-PD	-	-	-	WA	1
Pleurothyrium parviflorum Ducke	1	D	FD	-	-	WA	6
Sextonia rubra (Mez) van der Werff	-	I-PD	-	-	-	WA	1

GR: growth-ring = D: distinct, PD: poorly distinct, I: Indistinct, D+: mostly distinct, D-: sometimes distinct. **RB**: ring boundary = FD: change in fiber density, MP: marginal parenchyma, FZ: fiberzone, VD: change in vessel diameter. **Zone** = T: tropical, S: subtropical. **Study** = WA: wood anatomy, GR: growth-rate by tree-ring analysis, TR: tree-ring anatomical description, DC: dendroecology. **Source** = 1: Record and Hess (1942), 2: Castiglioni (1962), 3: Richter (1981), 4: Callado and Costa (1997), 5: Alves and Angyalossi-Alfonso (2000), 6: León-Hernández (2000), 7: León-Hernández and Espinoza-de-Pernía (2000a), 8: León-Hernández and Espinoza-de-Pernía (2000b), 9: Czarneski *et al.* (2001), 10: León-Hernández and Espinoza-de-Pernía (2001), 11: Oliveira *et al.* (2001), 12: León-Hernández (2002), 13: Worbes (2002), 14: Tomazello-Filho *et al.* (2004), 15: Oliveira (2005), 16: Roig *et al.* (2005), 17: Marcati *et al.* (2006), 18: Pulida and Tapia (2007), 19: Lisi *et al.* (2008), 20: Parra (2009), 21: Mattos *et al.* (2010), 22: Spathelf *et al.* (2010), 23: Ferrero *et al.* (2014).

-- Indicates the same species of above line.

Table 2. Tree species studied from subtropical forests formations in southern Brazil.

Species	**Wood core**	**N**	**Wood collection (PACA herbarium)**	**Leaf phenology**	**Municipality**
Cinnamomum amoenum	TS	2	372, 412	-	CSU
Cinnamomum glaziovii	TS, IB	2	711	S	SFP
Cryptocaria aschersoniana	IB	3		E	SFP
Cryptocaria moschata	TS	1	662	-	ARA
Nectandra grandiflora	TS	1	1017	E	ARA
--	IB	5		E	SFP
Nectandra lanceolata	TS	2	685, 849, 597	S	Itá, ARA
Nectandra megapotamica	TS	3	603, 681, 1000	E-S	Itá, ARA
--	TS	1	525	E-S	SFP
Ocotea bicolor	IB	5		S	SFP
Ocotea elegans	IB	5		E	SFP
Ocotea odorifera	TS	2	629, 758	E	ARA
Ocotea porosa	IB	5		S	SFP
Ocotea puberula	TS	3	732, 713, 587	S	SFP
--	TS	2	627, 876	S	ARA
Ocotea pulchella	TS	6	312, 374, 408, 411, 287, 297	E-S	CSU
Persea willdenovii	IB	1		S	CBS

Wood core = TS: transversal section, IB: core by increment borer. N = number of trees. Leaf phenology = E: evergreen, S: semideciduous. Municipality = CSU: Caxias do Sul, SFP: São Francisco de Paula, ARA: Aratiba, CBS: Campo Belo do Sul.

-- Indicates the same species of above line.

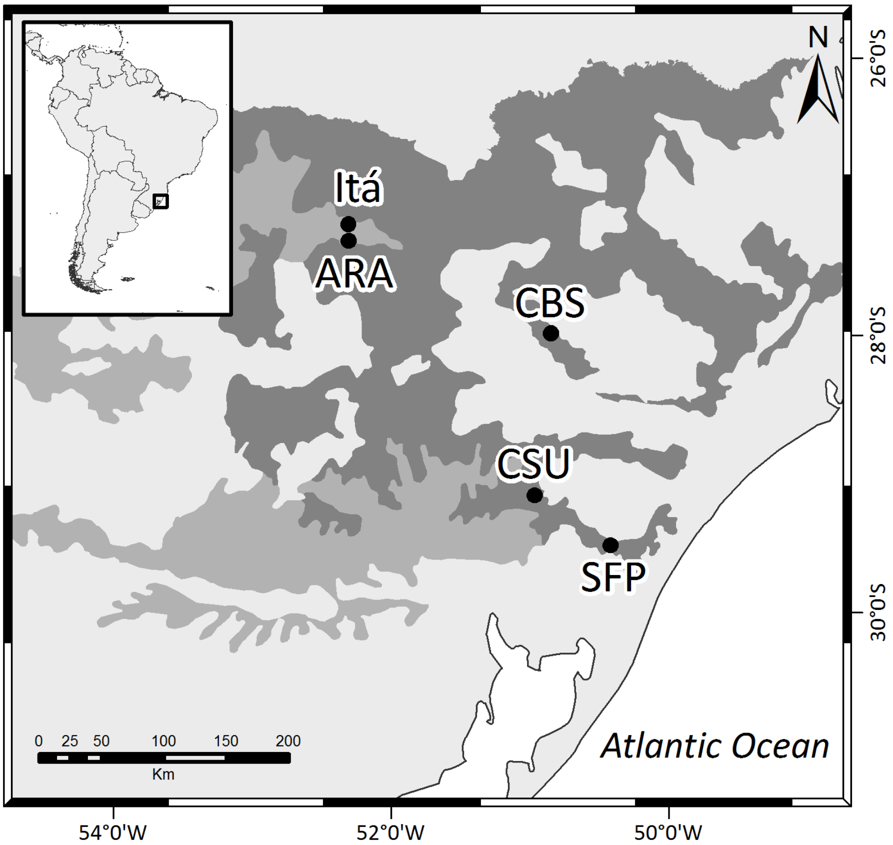

Fig. 1. Original distribution of seasonal (grey) and mixed forests (dark grey). Locations of wood sampling in southern Brazil are indicated: Itá (seasonal forest), ARA: Aratiba (seasonal forest), CSU: Caxias do Sul (mixed rainforest), SFP: São Francisco de Paula (mixed rainforest), CBS: Campo Belo do Sul (mixed rainforest).

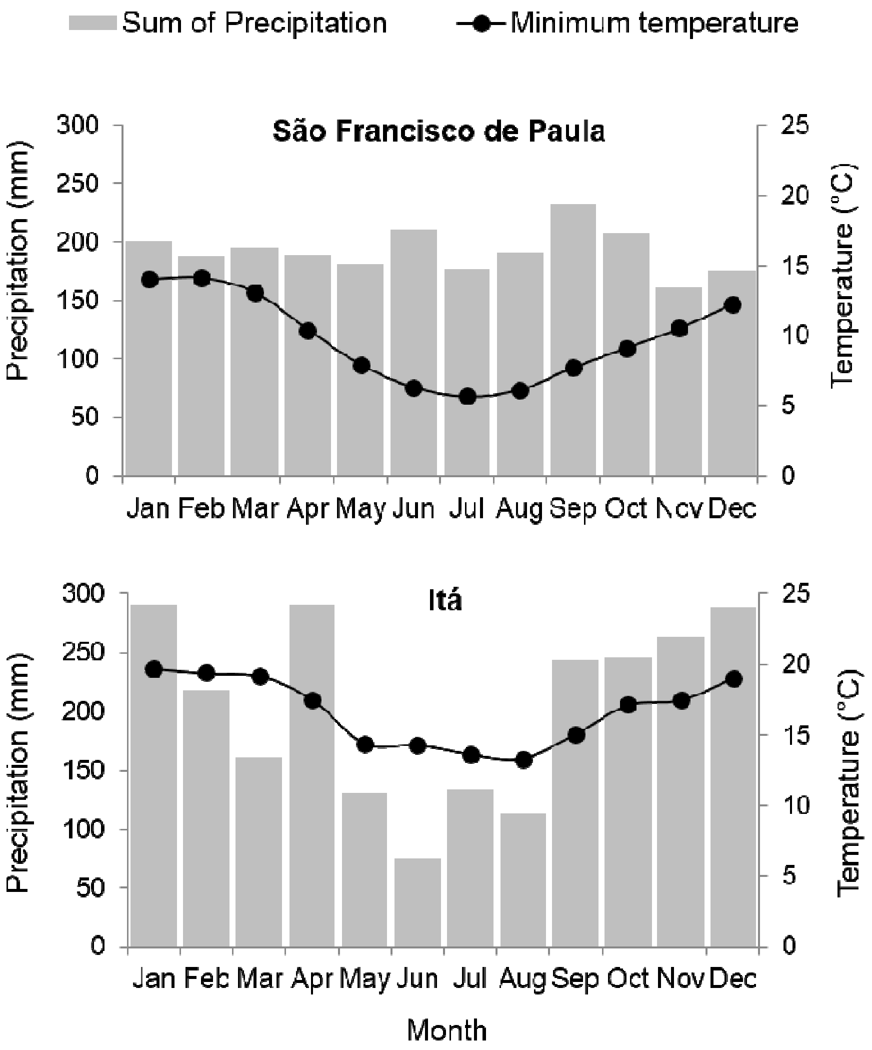

Fig. 2. Long-term monthly averages of temperature and precipitation for the two study regions. Above: climate diagram of São Francisco de Paula representing also Caxias do Sul and Campo Belo do Sul. Below: climate diagram of Itá representing also Aratiba.

Table 3. Tree species studied from subtropical forests in southern Brazil and growth-ring characteristics.

Species	**Forest type**	**Wood characters**					
		GR	**FR**	**RB**	**POR**	**VG**	**PAR**
Cinnamomum amoenum	MR	D	+	FD	D	S - M	(S) – V
Cinnamomum glaziovii	MR	D-	+	FD	D	S - M	(S) - V – W
Cryptocaria aschersoniana	MR	D		MP	D	(S) - M	V
*Cryptocaria moschata**	SF	D-		MP	D	(S) - M	V
Nectandra grandiflora	MR, SF	D	+	FD	D	S - M	(V) - L – C
Nectandra lanceolata	SF	D	+	FD	(D)	(S) - M	V
Nectandra megapotamica	MR, SF	D	+	FD	D	S - M	V
Ocotea bicolor	MR	D	+	FD	(D)	S - M	(S) – V
Ocotea elegans	MR	D	+	FD	(D)	(S) - M	(V) - S - U – W
Ocotea odorifera	SF	D-		FD	D	(S - M) - C	V
Ocotea porosa	MR	D	+	FD	D	S – M	V
Ocotea puberula	MR, SF	D	+	FD	D	(S) – M	V
Ocotea pulchella	MR	D	+	FD	(D)	S – M	(V) - S - U – W
*Persea willdenovii**	MR	D		FD	D	(S) – M	V

Forest type = MR: mixed rainforest, SF: seasonal forest. **GR**: growth-rings = D: distinct, D-: distinct with difficulty. **FR**: false ring = +: present. **RB**: ring boundary = FD: fiber density, MP: marginal parenchyma. **POR**: porosity = D: diffuse porous. **VG**: vessel grouping = S: solitary, M: radial multiple, C: clusters. **PAR**: paratracheal parenchyma = S: scanty, U: unilateral, V: vasicentric, L: lozangle-aliform, W: winged-aliform, C: confluent. ( ) Indicates mostly. * Indicates only one tree studied.

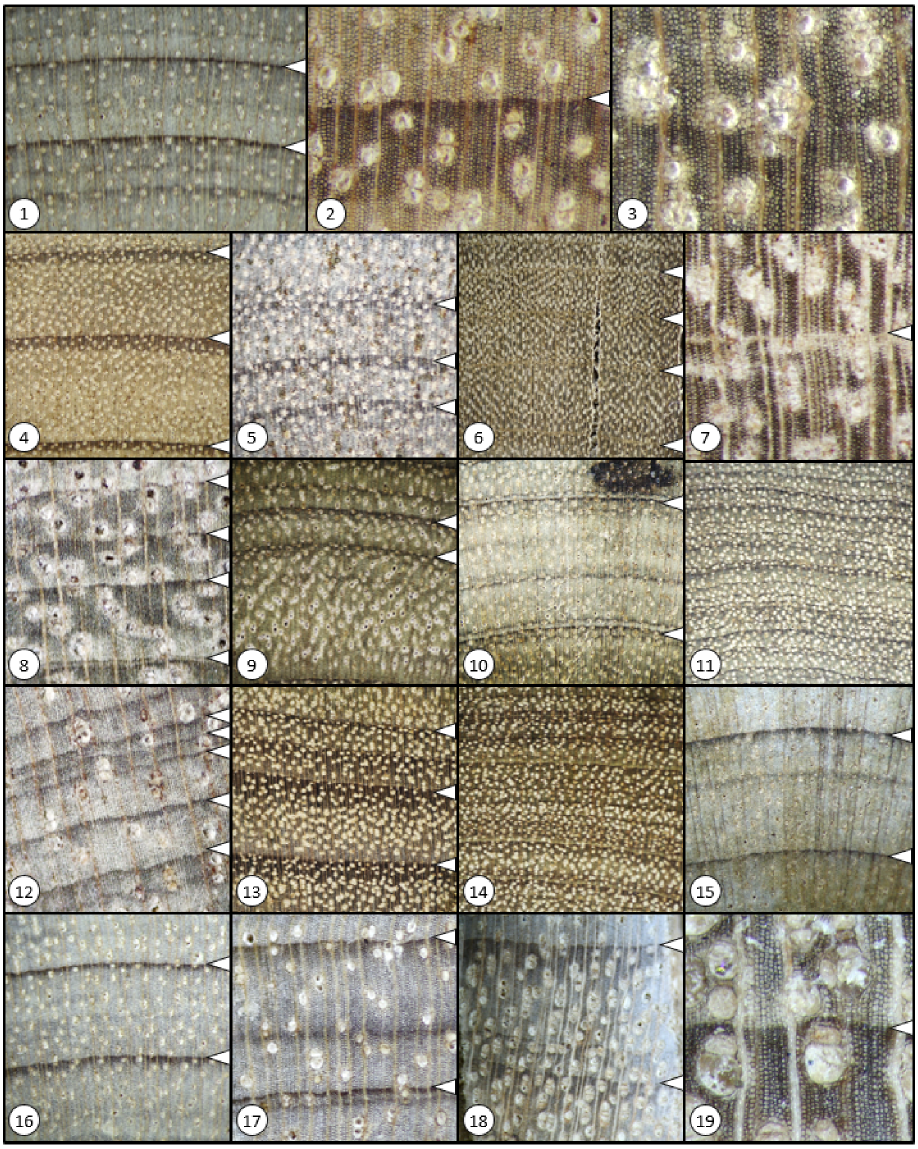

Fig. 3. Anatomical features of tree-rings from cross sections of Lauraceae species from southern Atlantic rainforest. – 1: Distinct growth-rings (*Ocotea pulchella*, 16x). – 2: Solitary vessels predominantly (*Cinnamomum amoenum*, 64x). – 3: Vasicentric parenchyma and narrow rays (*Ocotea odorifera*, 80x). – 4: *C. amoenum* (10.4x). – 5: *Cinnamomum glaziovii* (16x). – 6—7: *Cryptocarya moschata* (16x, 64x). – 8: *Nectandra grandiflora* (64x). – 9: *Nectandra lanceolata* (16x). – 10—11: *Nectandra megapotamica* (16x). – 12: *Ocotea bicolor* (16x). – 13—14: *Ocotea odorífera* (16x). – 15: *Ocotea puberula* (16x). – 16—17: *Ocotea pulchella* (16x, 32x). – 18—19: *Persea wildenowii* (16x, 80x).

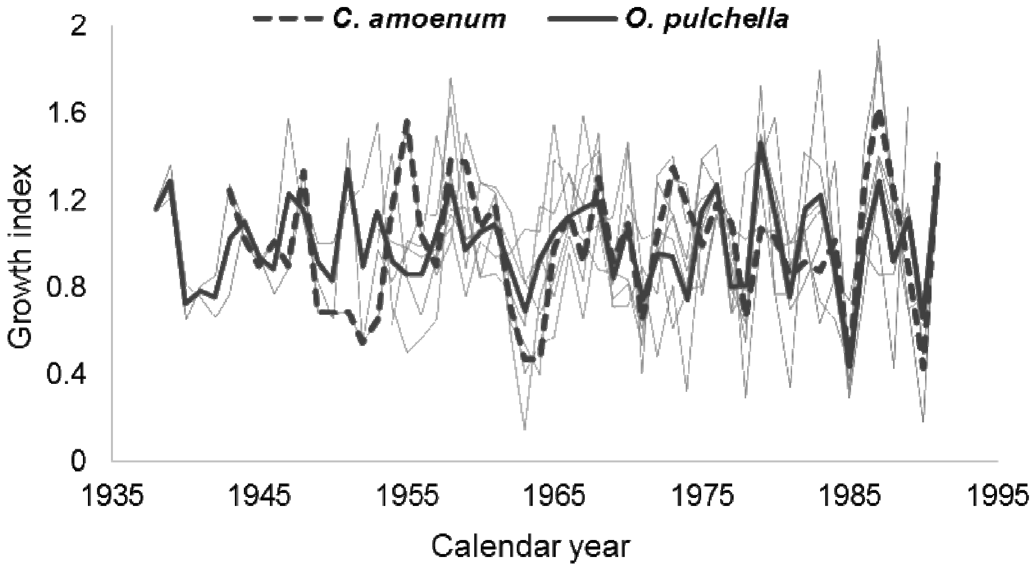

Fig. 4. Series of growth-ring width index of two *Cinnamomum amoenum* and five *Ocotea pulchella* trees analyzed. Mean index series of both species are discriminated.

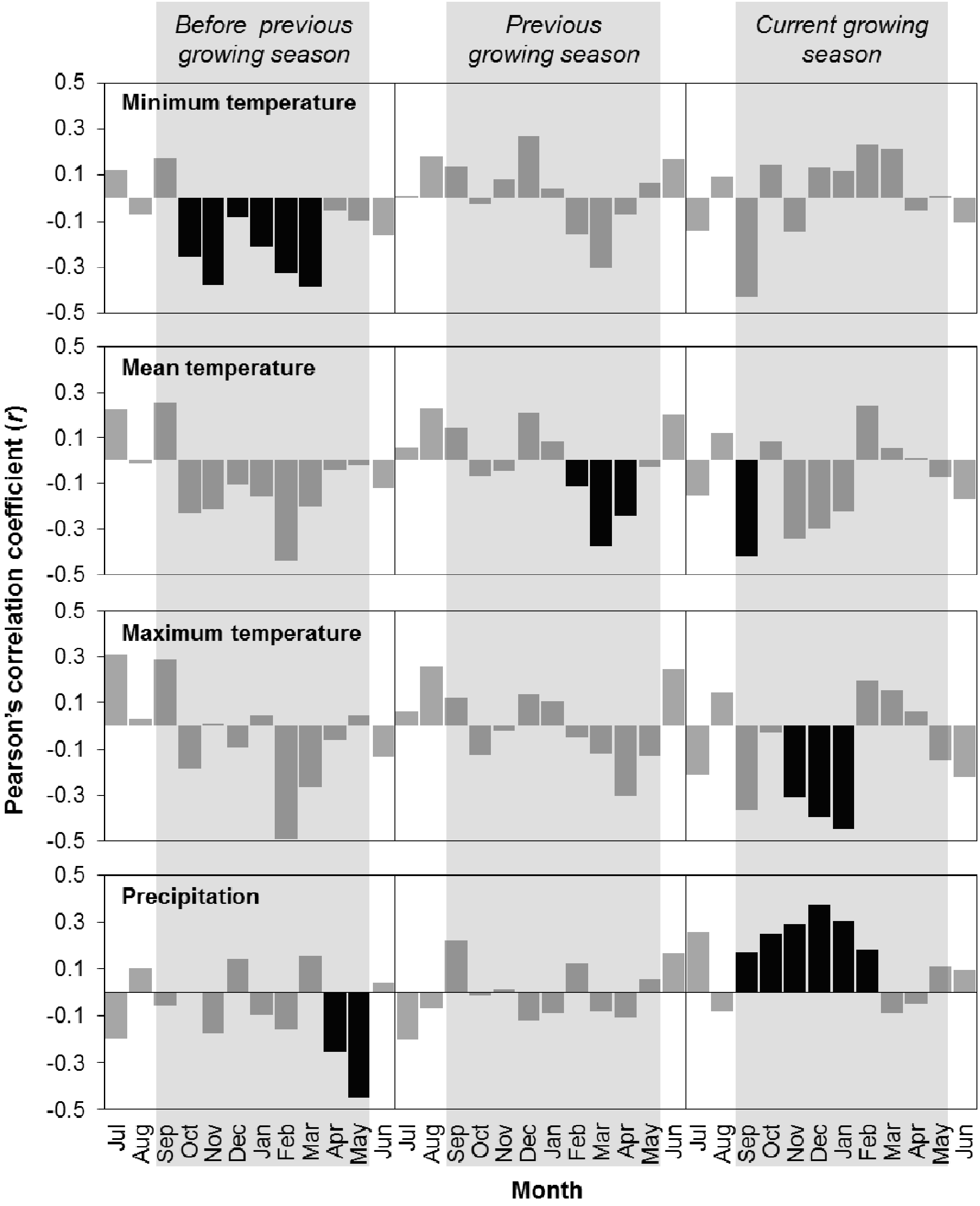

Fig. 5. Correlation profile between growth-ring width index of *Ocotea pulchella* and the monthly climate variables for common time 1953-1989. Periods with Pearson's correlation coefficient above confidence level of 95% are discriminated.

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CAPÍTULO 2

TREE-RING APPEARANCE AND CLIMATE-GROWTH RELATIONSHIP IN *Ocotea elegans* Mez (Lauraceae) GROWING IN SUBTROPICAL MONTANE RAINFOREST†

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ABSTRACT

Tree-rings are the major reliable data source for long-term analysis on tree growth, forest dynamics and climate growth-relationship. It is necessary to encourage and develop researches/studies involving tropics and subtropics wood plants in order to provide clearer information in autoecology, forest ecology and climatology. *Ocotea elegans* Mez is an evergreen Lauraceae tree that has wide distribution in southeastern and southern Brazilian Atlantic Forest, occurring in seasonal forests, mixed rainforest and coastal rainforests. In this study, we assessed growth-ring appearance, tree growth synchrony and climate-growth relationship of *O. elegans* in a montane mixed rainforest in subtropical Brazil in order to evaluate the annual nature of increment layers. We evaluated annual nature of growth-rings by anatomical inspection in search of distinct increment layers, by crossdating growth-ring index series within and between trees and by relating annual tree growth and monthly climatic variables. *O. elegans* showed clearly tree-rings marked by thick-walled and radial flattened latewood versus thin-walled early wood fibres. Even with anatomical irregularities hindering identification of true growth-rings, we considered we successfully crossdated trees. Synchronization of tree-ring width within and among trees in both study sites pointed out a common regional and local growth trend. Regional patterns of annual tree growth was related with both precipitation and temperature. We can assert that *O. elegans* has seasonal growth in subtropical montane *Araucaria* forest in southern brazilian plateau. The evidences are presence of distinct increment layers, tree growth synchronism (crossdating) and climate signal in annual growth. This study evidenced the suitability of *O. elegans* for dendrochronological purposes.

Introduction

Tree-rings are the major reliable data source for long-term analysis on tree growth, forest dynamics and climate growth-relationship. In spite of more than two decades of dendroecological research development in extra-temperate regions, those mentioned issues still remain less known in tropical and subtropical humid ecosystems (Worbes 2002; Boninsegna et al. 2009). High biodiversity in such ecosystems is one of the main factors hindering the dendrochronological advance due to difficulty of exploring which species have at least visible tree-rings and finding a significant population number in the study area to compute chronologies (Jacoby 1989). Although, a large list of species with visible tree-rings and with dendrochronological potential has been produced (*e.g.* Worbes 2002; Callado et al. 2013; 2014), a huge portion of the high diversity remains available to analysis in basic and advanced studies. Furthermore, variability in growth pattern and climate response within a species growing in different environmental conditions is something relevant to investigation. It is necessary to encourage and develop researches/studies involving tropics and subtropics wood plants in order to provide clearer information in autoecology, forest ecology and climatology.

Ocotea elegans Mez is an evergreen Lauraceae tree, a pantropical family that has great importance on tropical and warm subtropical ecosystems of South America (Werff and Richter 1996). *O. elegans* has wide distribution in southeastern and southern Brazilian Atlantic Forest, occurring in seasonal forests, mixed rainforest (*Araucaria* forest) and coastal rainforests (Baitello et al. 2003), from 10 to 1200 m a.s.l (Broto 2010). In this study, we assessed growth-ring appearance, tree growth synchrony and climate-growth relationship of *O. elegans* in a montane mixed rainforest in subtropical Brazil in order to evaluate the annual nature of increment layers.

Distinct increment layers and annual nature of tree-rings in some species of Lauraceae Jussieu were already proved in literature both in tropical and subtropical zones (see chapter 1). In tropics, water availability is the limiting factor for growth and induces seasonal rhythms in several species, including members of Lauraceae. Botosso and Vetter (1991) observed the Amazonian tree *Aniba rosodora* Ducke has seasonal cambial activity, decreasing its growth in the dry season. In subtropics, however, with increase in latitude the air temperature becomes more determinant than precipitation on plant phenology (Marques et al. 2004; Morellato et al. 2000; Paise and Vieira 2005) and growth periodicity (Dünisch 2005; Oliveira et al. 2009, 2010). Temperature and day length are responsible to regulate the timing of wood formation (Oliveira et al. 2009, 2010), but both temperature and precipitation have power over total annual growth. In high montane site in Chile, for example, Ávila et al. (1975) showed *Cryptocaria alba* (Molina) Looser, grows exclusively in a short period between spring and early summer months (Aug-Dec), since autumn and winter are cold for maintenance of metabolic activity and in summer hydric stress may occurs. In high elevation treelines in Andes, the increasing in altitude is accompanied by the decreasing in precipitation and air temperature. Radial growth of some species is strongly influenced by rainfall, and the temperature is important for regulating the evapotranspiration, leading to more or less water availability in growing season (Morales et al. 2004). In subtropical montane rainforest, *Cinnamomum vesiculosum* (Nees) Kosterm., *Nectandra grandiflora* Nees & Mart. ex Nees and *Ocotea porosa* (Nees & Mart.) Barroso reduce their growth in winter months and have growth rate peak in summer (Figueiredo-Filho et al. 2008). Spathelf et al. (2010) evaluated growth synchrony and climate signal in chronologies of *Ocotea pulchella* (Nees & Mart.) Mez and *Nectandra megapotamica* (Spreng.) Mez in southern Brazil. Based on wood structure, crossdating between trees and seasonality of air temperature in the studied site, they concluded those species formed annual rings. Nevertheless, they correlated water balance and evapotranspiration with ring width index and did not find influence of them on total annual growth.

Therefore, we hypothesized the seasonal condition of air temperature in subtropics (Jacoby 1989) determines the presence of annual growth-rings in *O. elegans.* We assess annual nature of growth-rings by anatomical inspection in search of distinct increment layers, by crossdating trees and by relationship between annual tree growth and climate. We surmise both temperature and precipitation may have influence on growth as pointed out by other authors to some subtropical South America species (*e.g.* Dünisch 2005; Morales *et al.* 2004; Oliveira *et al.* 2010; Villalba *et al.* 1998).

Methods

Study area and climate

We investigated growth-ring appearance, common trends among trees growth patterns and climate-growth relationship of *O. elegans* in a subtropical montane mixed rainforest from southern Brazil. This rainforest called *Araucaria* forest is characterized by the endemic coniferous *Araucaria angustifolia* Bertol. (Kuntze) and other austral-antarctic components (temperate origin), and shares many floristic features with Atlantic rainforest such as Lauraceae species that has a tropical origin (Klein 1960, 1984; Rambo 1953). *Araucaria* forest occurs in subtropical Brazil. Historically, it occupied also the northern Argentina and eastern Paraguay. Our study area corresponds to southtern Brazilian plateau. It is an ecotone zone between subtropical Atlantic coastal rainforest, *Araucaria* forest (mixed rainforest) and *Campos* (grasslands). Grasslands occur on the high plateaus, forming a mosaic with *Araucaria* forest that occupies lower and humid sites. Atlantic rainforest occurs on the slopes and in the valleys of the rivers from where it permeates and gradually enters *Araucaria* forest (Fig. 1). The study sites are the Parque Nacional de Aparados da Serra (PARNA; 29°07’ - 29°15’ S, 50°01’ - 50°10’ W; 950 m a.s.l), a federal conservation unit (since 1959) in Cambará do Sul municipality; and the Centro de Pesquisas e Conservação da Natureza – Pró-Mata (CPCN; 29°26’S and 50°08’ - 50°14’W; 800-950 m a.s.l) in São Francisco de Paula municipality (Fig. 2). Distance between the sites is about 40 km. Selective logging of some species, mainly *Araucaria angustifolia* occurred up to 1994 at CPCN and was extended after 1959 at PARNA.

The regional climate is mild-mesothermic, with well-distributed rainfall over the year and moderate to cold temperatures with mild summers (mean air temperature in the hottest month bellow 22 °C) (Nimer 1989). Due to elevation and influence of Atlantic Polar Front, humidity is high and precipitation is constant over the year, despite it, mean air temperature follows a seasonal pattern. According to long-term local meteorological data (São Francisco de Paula municipality, 1931–1960), annual sum of precipitation varies between 1750 and 2500 mm mean annual and temperature was 16 °C (20 °C in the hottest month, January and 11 °C in the coldest, July) and from May until September it may decreased to less than 10°C (Fig. 3). Frosts is common in at least 30 days in winter.

Sampling and analysis of wood cores

We analyzed 15 trees, seven at CPCN and eight at PARNA. The average trunk diameter at breast high of these trees was 21.1 cm and the average total height was 13.9 m. For each tree, four or five transversal wood cores were collected with the help of an increment borer, totaling 31 cores at CPCN and 32 at PARNA. For information about trees see Table 1. The sampling was carried out in April 2009 at CPCN and January 2013 at PARNA.

The cores were mounted on wooden supports, air-dried and mechanically polished with sandpaper of gradually finer grades of grit (from 80 to 600 grains), evidencing the wood anatomical markers. We inspected the samples under a stereomicroscope to observe the distinctiveness and to describe the anatomical markers of increment layers according to IAWA Committee (1989). Then, we dated the increment layers from its outermost ring corresponding to the last year of growth when the individual was sampled, following standard methods (Stokes and Smiley 1968). For the CPCN samples, we measured growth-ring width with a Velmex® Measuring System (precision of 0.01 mm). For PARNA tree cores we scanned them in a table scanner (1,200 dpi of resolution) and measured growth-ring width with the help of Image-Pro Plus software (v4.5, Media Cybernetics, USA). In order to check dating accuracy, we compared the resulting ring-width time series within and among trees by synchronizing patterns of wide and narrow growth-ring (crossdating), with the help of printed graphics and COFECHA software (Holmes 1983; Stokes and Smiley 1968). Crossdating is possible only if the tree growth is regulated by seasonal climatic conditions, leading to similar growth patterns among individuals in a population. Therefore, possible errors of dating caused by anatomical irregularities such as false rings and partial rings may be corrected (Fritts 1976; Schweingruber 1988; Stokes and Smiley 1968). Thus, the good quality of crossdating gives us an indication that the trees growth is synchronic and influenced by climatic periodicity.

Standardization and site chronology

Chronologies are crossdated time series of growth-rings. Numerical methods (usually cubic smoothing spline and regional curves) are employed to maximize the common signal of the sampled population that is possibly determined by climate, filtering age and individual growth trends (Cook and Kairukstis 1990). We averaged the crossdated series of ring-width for each tree and standardized them by fitting a cubic smoothing spline function, 20 years of segment length and 50% frequency-response cutoff, and computed the growth indices ratios between observed and predicted values (Cook and Kairukstis 1990). In the series of growth index (ratios), the serial autocorrelation was filtered using autoregressive linear modeling, resulting in residual series (Cook 1985). These procedures of standardization decreases the variance of data, giving the required normal distribution values, removes individual and long-term growth trends while retaining the climatically induced year-to-year variations and eliminates the autocorrelation present in the time series. This standardization also maximized the mean correlation between trees and climatic signal on growth. Finally, we obtained the site chronologies by combining the standardized series on a bi-weighted robust mean series (Cook and Kairukstis 1990). We standardized the series and computed the chronology on ARSTAN software (Cook and Krusic 2005).

We evaluated the synchronism between trees and the quality of site chronologies by computed the mean correlation between trees (r_b) and mean correlation within trees (r_w) and Pearson's correlation coefficient between site chronologies. We assess the relationship between chronologies using correlation analysis, computed for the common time-span. We performed an ordination (principal component analysis) to assess similar growth patterns among the 15 trees, computed for the time span that included at least eight trees (1946-2007). We used years as sample units and the growth ring index (residuals) as descriptors to compute the matrix of correlation between trees (variables). The ordination axes stability was verified through randomization test. We conducted correlations and ordination on MULTIV (Pillar 2006), r_b *and* r_w on COFECHA software.

Climate-growth relationship

To examine the climate-growth relations we utilized the first principal component (PC1) of ordination analysis as response variable in correlation functions and regression analysis with climate data. Ordination summarizes the variance of data on the principal components (PC's); as a result, PC's represent the common tendency between variables. In our study, PC1 represents the regional convergent growth trend between all trees like a chronology. The climatic variables were maximum and minimum temperature and total annual precipitation recorded monthly between 1961 and 2013 (with missing values) in three meteorological stations near the sampled sites (Fig. 2; BDMEP, available in http://www.inmet.gov.br). After centering, we averaged climate series among the three meteorological stations to produce a single regional annual series for each monthly climatic variable. The PC1 was correlated to each of these climatic series, matching the series by the same year (lag=0) and by the previous year (lag=1). We observed the results through correlation profiles that evidence periods of months that most influenced the growth.

Results

Appearance of growth-rings

Distinct increment wood layers founded in all samples pointed out the presence of tree-rings in *O. elegans*. The growth-rings were marked by thick-walled and radial flattened latewood versus thin-walled early wood fibres. This character also gives differentiation between early wood creamy to yellow-gray and latewood dark-brown color. The wood had diffuse porosity with solitary vessels or less frequently grouped in radial-multiples of two elements. In some growth-rings, diameter and frequency of vessels tended to decrease slightly, but this was not a pattern to the samples inspected. Anatomical irregularities, mainly false-rings, periods of fuzzy growth-ring boundaries (diffuse tree-rings) and missing rings caused difficulties for crossdating. False rings occurred in the early and latewood, more often in the first, and in consecutive juvenile rings. When present in early wood appeared as bands of flattened fibres with thickened walls like latewood fibres. These gradually became fibres with thin walls and wide lumen, followed by latewood. In latewood fibres they formed bands of earlywood-like cells. Missing rings and fuzzy growth-ring boundaries occurred mainly in the last decade (2000's). Figure 4 illustrates the anatomical features of growth-rings in the species.

Tree growth patterns and site chronologies

Synchronization of tree-ring width within and among trees in both study sites pointed out a common regional and local growth trend in *O. elegans*. Despite anatomical irregularities, the fifteen trees were crossdating but only 48 cores (out of 63) were included in further analysis. The uncorrelated cores were excluded from the chronology. In total, we analyzed 1184 tree-rings, covering the time-span of 1793-2011. Age of each tree ranged 47-215 (mean of 79, SD=42). The mean correlation within trees was r_w=0.58 (SD=0.2), and the mean correlation between the fifteen trees was r_b=0.29 (SD=0.11), demonstrating that these trees tend to grow fairly uniform around the whole circumference of the trunk and have similar growth patterns. Table 1 summarizes information about the fifteen studied trees.

Time-span represented by three or more trees was 1920-2007 (88 years) at CPCN and 1947-2011 (65 years) at PARNA. The correlation between trees of CPCN chronology was *r*=0.22 and between trees of PARNA was *r*=0.12. Considering common period between CPCN and PARNA chronologies (1932-2007, 76 years) correlation coefficient was *r*=0.39 (p=0.01). Descriptive statistics and graphical representation of CPCN and PARNA chronologies are shown in Table 2, Figure 5 and 6.

Results of ordination analysis showed common loading in the first eigenvector between CPCN and PARNA trees, implying that there are environmental factors operating similarly on the entire region producing a common growth pattern between trees. The first principal component (PC1) defined a convergent trend between all trees and explained 19.6% of growth variance (p=0.001). The second principal component (PC2) indicated a divergent trend but it was not stable (Fig. 7).

Relationship between annual growth and climate

The correlation profiles describing the relationship between principal component, representing regional growth trend in *O. elegans,* and monthly climate variables pointed out that both sum of precipitation and air temperature influenced total annual growth (Fig. 8). The correlation between PC1 and sum of precipitation tended to positive for the previous spring and summer (Oct-Jan), previous May and current autumn and was negative for the current October. Minimum temperature had a positive relationship for the previous March and current autumn, and a negative relationship for previous winter. Maximum temperature apparently influenced negatively in all periods.

Discussion

Tree-ring appearance and growth patterns

O. elegans showed clearly tree-rings marked by thick-walled and radial flattened latewood versus thin-walled early wood fibres. This pattern is the most common in Lauraceae species and occurs in genus *Ocotea* Aubl., *Nectandra* Rol. ex Rottb., *Cinnamomum* Schaeff. and *Persea* Mill.(Record and Hess 1942; Stern 1954; Richter 1981; León-Hernández 1999; 2002).

False-rings occurred mainly in juvenile rings and appeared as bands of flattened fibres with thickened walls like latewood fibres. These gradually became fibres with thin walls and wide lumen, followed by latewood. Diffuse growth-ring boundaries was also frequent, but occurred mainly in last decades. Extremely reduction in radial growth in 2000's years, resulting in diffuse rings was also noted in other species, but was not discussed (*e.g.* Souza et al. 2009; Cavalli and Oliveira unpub. data). Anatomical trickies were often cited as one of the obstacle to dendrochronological investigations of tropical and subtropical species (Jacoby 1989; Roig 2000; Worbes 2002).

False-rings are frequently linked to climatic fluctuations within the growing season, which leads to an abnormal physiological stress (Fritts 1976; Wimmer et al. 2000), so some trees cease their growth resuming when environmental conditions become milder. Despite the high humidity and constant precipitation over the year, we conjecture that false-ring formation in *O.elegans* is linked to a dry period in the growing season. Oliveira et al. (2010) studying climatic signal in *Araucaria angustifolia* tree-rings chronologies also found false-rings in trees growing near our study site and subject to similar climate conditions. False-ring occurrence was also investigated in *Ocotea pulchella*, another Lauraceae species in the same region (Ávila and Oliveira, unpub.

data). They found the synchronic formation of false-rings in five individuals of a population is linked to low water availability in spring months, early growing season. Studies in Europe and Patagonia summarized false-ring formation is related to abnormal elevation in temperature in the beginning of growing season (Rigling et al. 2002; Masiokas and Villalba 2004; Copenheaver et al. 2006; Martin et al. 2011). The increase in temperature promotes increase in evapotranspiration and consequently decrease in water availability in growing season. Hydric stress reduces cambial activity and, therefore, processes like cell elongation (Fritts 1976) This results in a change of cell structure within a tree-ring that resembles the boundary of the true increment layer (Priya and Bhat 1998; Lorimer et al. 1999) but can be distinguished by its discontinuous character or diffuse structure (Brienen et al. 2009). According to Copenheaver et al. 2006, occurrence of such structures in juvenile trees more than in adult, as we found, is due to the young trees be more susceptible to drought during the growing season than adults ones. We suggest further dendroclimatic studies to investigate false-ring formation in *O. elegans.*

Even with those irregularities hindering identification of true growth-rings, we considered we successfully crossdated trees. All trees and the most of cores (48 out of 63) were included in chronologies that covered together a long period of time (1793-2011, 218 years). The correlation within trees (r_w=0.58) was similar to the results of other studies with tropical and subtropical species. However, correlation between trees was somewhat lower (r_b=0.29). If we analyzed correlation among trees within each site, this relationship decreases more (r=0.22 at CPCN, r=0.12 at PARNA), but still exists. Spathelf et al. (2010), studying five *O. pulchella* and two *N. megapotamica* trees found higher correlations between trees than in our study (r between 0.36 and 0.74). *A. angustifolia* trees growing near the study site have an internal intercorrelation between

0.49 and 0.57 and a mean correlation among trees between 0.25 and 0.34 (Oliveira et al. 2009). Dünisch (2005) investigated climate influence on radial growth of *Cedrella fissilis* Vell., a deciduous Meliaceae tree, growing in the *Araucaria* forest in Paraná (Brazil). He showed a correlation of 0.65 within trees and of 0.31 in subtropical and 0.43 in tropical sites. On the face of it, our results may indicate that tree growth was strongly influenced by environmental factors that promotes divergent growth trends such as site disturbs. We, however, cannot rule remaining crossdating errors. Nevertheless, the degree of synchronism within and between trees of both sites is sufficient to state that there is local and regional common growth trend between *O. elegans* trees. Corroborating with these assumption, ordination analysis showed common loading in the first eigenvector. First principal component (PC1) defined a convergent trend between all trees explaining 19.6% of growth variance.

Climate-growth relationship

Convergent regional growth patterns is a strong preditor of the influence of environmental factors operating on the entire population in the same way (Fritts 1976; Schweingruber 1996).

Regional patterns of annual tree growth in *Ocotea elegans* was related with both precipitation and temperature. This relationship occurred for previous and current year, indicating there is a lag between a climatic conditions change and growth response, and also climatic conditions of years before are determinant to current growth. Moreover, our results reinforce the relevance of climatic conditions for inter-annual variation of *O. elegans* growth.

Correlation profiles between annual tree growth and climatic variables showed that precipitation of previous year are positively associated with current year of increment, indicating the trees would mobilize the water supply available in the previous year for growth in the next season. Dendroclimatic analysis in subtropical New Zealand found that *Agathis australis* (D. Don) Loudon (Araucariaceae) has diameter increment controlled also by rainfall of previous growing season (Buckley et al. 2000). A strong negative effect of precipitation in current October may be explained by the decrease in light intensity due to cloudiness in the beginning of growing season. Positive relationship between minimum temperature of the previous and current end of growing season and annual growth indicates that higher temperatures in summer and autumn would prolong the growing season, forming larger growth-rings (Kozlowski and Pallardy 1997). Moreover the relationship between annual increment and temperature at the beginning and at the end of growing season (Dünisch 2005; Oliveira et al. 2010) indicates that air temperature controls extent of cambial division (Dünisch 2005) and producing wider or narrower rings. These relationships were similar to those found for chronologies of *A. angustifolia* established in forest and field near our study area in southern brazilian plateau (Oliveira et al. 2010). At subtropical humid mountains in China no significant relationship was found between precipitation and annual tree growth still the spring and summer temperatures are positive related with it (Zheng et al. 2012). Maximum temperature apparently influenced negatively in all periods. Elevation in temperatures increase evapotranspiration rates, and producing less favorable water conditions, leading to the formation of narrow rings. Similar growth response was found for *Araucaria angustifolia* growing in subtropical southern Brazil (Cattaneo et al. 2013; Oliveira et al. 2010). However, the study of Spathelf et al. (2010) with *O. pulchella*, growing in an ecotone between seasonal and *Araucaria* forest in Rio Grande do Sul (Brazil) found weak relationship between water availability and growth.

Findings of this study

We can assert that *O. elegans* has seasonal growth in subtropical montane *Araucaria* forest in southern brazilian plateau. The evidences are presence of distinct increment layers, tree growth synchronism (crossdating) and climate signal in annual growth. Despite the influence of precipitation on annual growth, the triggering factor leading to cambial periodicity should be temperature. In agreement, Gomes et al. (2008) showed that seven Lauraceae species (*Cinnamomum amoenum* (Nees) Kosterm., *Cinnamomum glaziovii* (Mez) Kosterm., *Cryptocarya aschersoniana* Mez, *N. megapotamica*, *Ocotea indecora* (Schott.) Mez, *Ocotea puberula* (Rich.) Mez and *O. pulchella*) growing in *Araucaria* forest near our study site reduce the amount of lateral growth up to half in autumn and winter months.. An anatomical study of about 400 species in all regions of Brazil noted that the presence of growth-rings is correlated mild and medium mesothermic climates. In such climates, typical of southern Brazil, thermal seasonality influences cambial activity, leading to the formation of growth-rings (Alves and Angyalossi-Alfonso 2000). In addition, studies have proven the seasonal growth in several species in subtropical Brazil, pointing out temperature and photoperiod as the main drivers to tree periodical growth (*e.g.* Figueiredo Filho et al. 2008; Oliveira et al. 2009; Oliveira et al. 2010). However, *O. elegans,* as well as other Lauraceae species migrated from the north and reached its southern limit of distribution in the state of Rio Grande do Sul (Brazil). In tropical Brazil, it experience a drought period during the winter months from May to September (Spathelf et al. 2010). Therefore, formation of growth-rings would be a conservative genetic caracter.

This study evidenced the suitability of *Ocotea elegans* for dendrochronological purposes. Simply counting of tree-rings provides first knowledge in the age structure of a population. Apllying dating methods it is possible to determine year of establishment of individuals, populations and tree communities. Construction of growth-ring chronologies allows us to understand climate-growth relationship and thus modeling tree response to climate change. Such issues are important for proper forest management, for planning conservation of biodiversity, for understand and mitigate the impacts of global change. We believe that *Ocotea elegans* may provide high resolution data source for future dendroecology research of long-term ecological factors, over its whole distribution area, due to the distinct growth-ring boundaries, synchronic growth pattern and climate-growth relationship observed in this study. Additionally, monitoring cambial activity in this specie may further enhance the knowledge of growth dynamics in subtropical ecosystems.

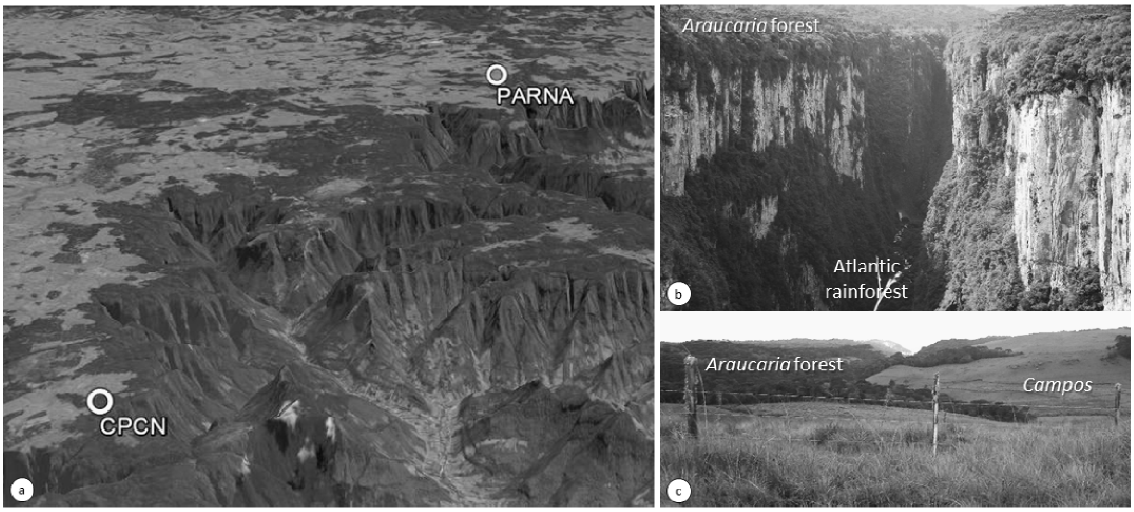

Fig. 1. Study area. Regional aspect in the southern brazilian plateau (a) and representation of vegetation ecotone at Parque Nacional de Aparados da Serra – PARNA (b); and near Centro de Pesquisas e Conservação da Natureza Pró-Mata – CPCN (c).

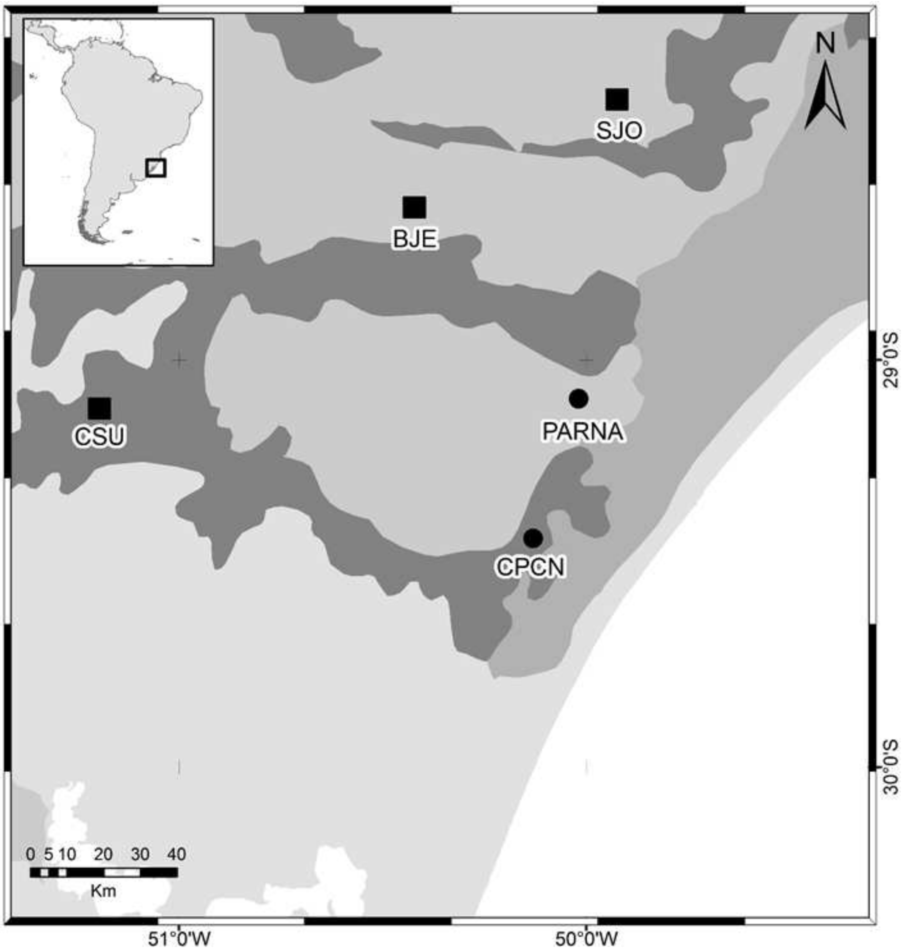

Fig. 2. Study sites (dots), meteorological stations (squares) and the distribution of *Araucaria* forest (dark grey patches), *Campos* (light grey) and Atlantic coastal rainforest (grey). CPCN: Centro de Pesquisas e Conservação da Natureza Pró-Mata; PARNA: Parque Nacional de Aparados da Serra; BJE: Bom Jardim; CSU: Caxias do Sul; SJO: São Joaquim.

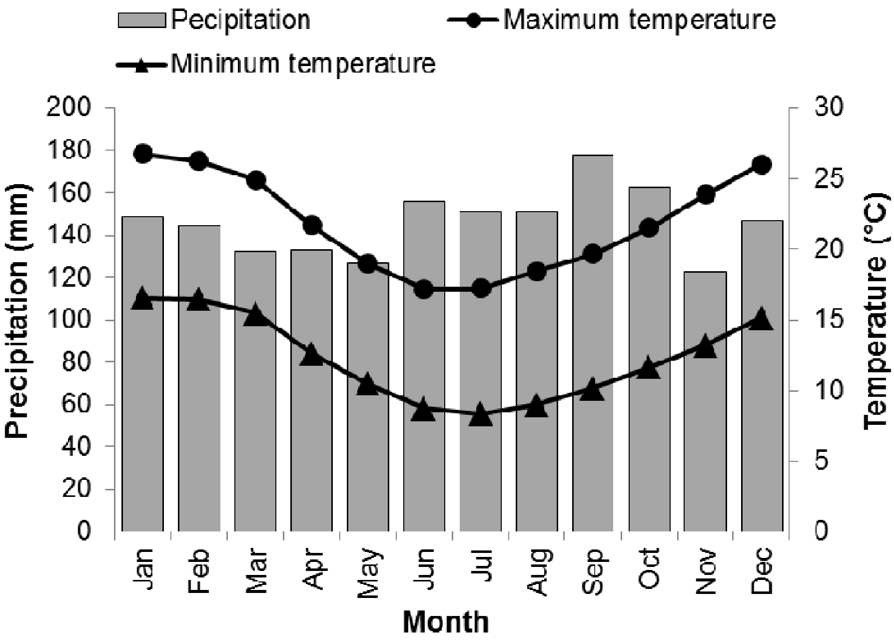

Fig. 3. Long-term monthly averages (1938-1961) of maximum and minimum temperature (lines) and total precipitation (bars) for the study region (dada from São Francisco de Paula municipality).

Table 1. Data from fifteen studied *Ocotea elegans*. DBH: Diameter at breast height; H: height; r_w: mean correlation of growth-ring width within trees (between cores); r_b: correlation of growth-ring width between tree and master chronology.

Site	Tree	DBH (cm)	H (m)	Time-span	N rings	N cores	*rw*	*Rb*
CPCN	1	25.5	13.5	1793-2008	216	2	0.22	0.22
CPCN	2	28.0	13.0	1932-2007	76	5	0.80	0.37
CPCN	3	10.0	13.0	1936-2007	72	4	0.85	0.53
CPCN	4	10.0	18.0	1959-2007	49	4	0.70	0.23
CPCN	5	24.5	13.0	1920-2007	88	3	0.40	0.23
CPCN	6	22.8	9.0	1891-2007	117	2	0.46	0.21
CPCN	7	40.4	12.0	1941-2007	67	5	0.82	0.41
PARNA	8	14.0	12.0	1947-2011	65	2	0.53	0.25
PARNA	9	14.5	9.0	1964-2011	48	3	0.33	0.22
PARNA	10	27.0	15.0	1932-2011	80	2	0.53	0.43
PARNA	11	14.3	16.0	1946-2011	66	2	0.67	0.18
PARNA	12	23.1	17.0	1955-2011	57	4	0.66	0.26
PARNA	13	27.1	17.0	1956-2011	56	3	0.63	0.42
PARNA	14	20.6	15.0	1947-2011	65	4	0.67	0.21
PARNA	15	14.2	15.0	1950-2011	62	3	0.33	0.38

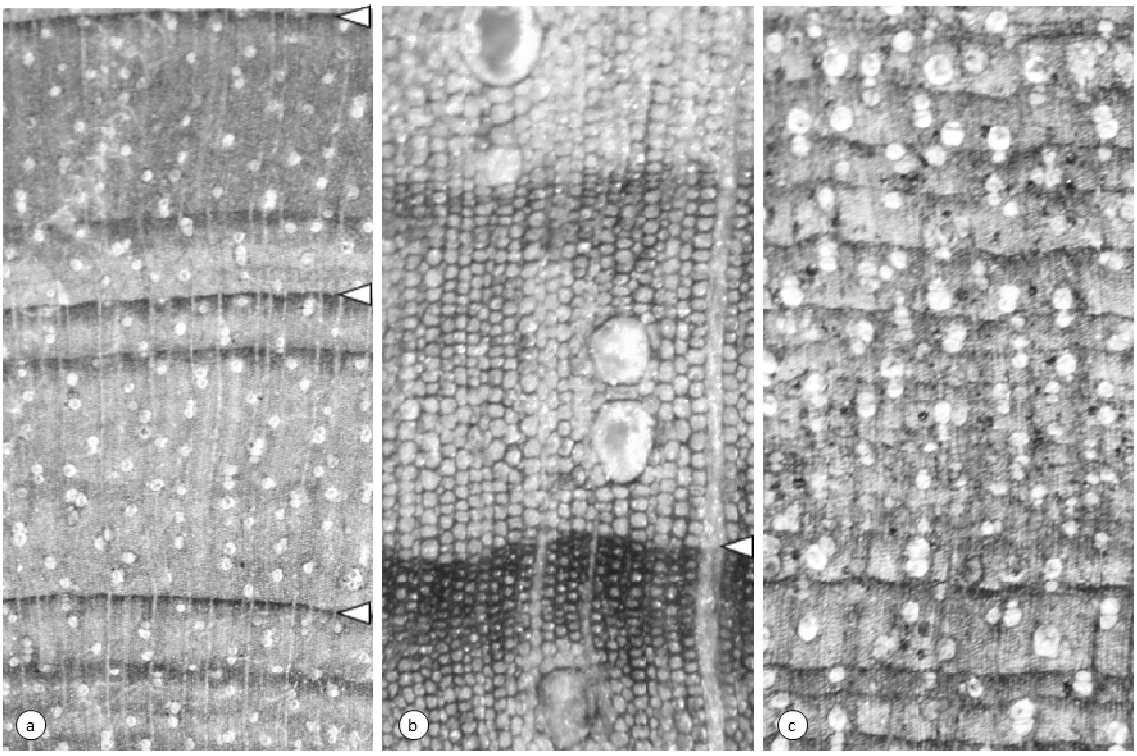

Fig. 4. Growth-ring features of *Ocotea elegans*. Tree-ring boundaries indicated by mark and intra-annual density fluctuations (false-rings) appear in (a) and (b). Fuzzy rings that occurred mainly in last decade (2000’s) in (c). Zoom (a): 16x, (b):80x, (c): 80x.

Table 2. Descriptive statistics of *Ocotea elegans* tree-ring width chronologies from both sites (CPCN) and (PARNA).

	CPCN	PARNA
Time-span	1793-2007 (215 years)	1932-2011 (80 years)
Number of trees	7	8
Number of cores	25	23
Number of growth-rings	685	499
Mean series length	98 years (SD=55)	62 years (SD=9)
rb	0.22	0.12

CPCN: Centro de Pesquisas e Conservação da Natureza Pró-Mata, PARNA: Parque Nacional de Aparados da Serra , *rb:* mean correlation between trees.

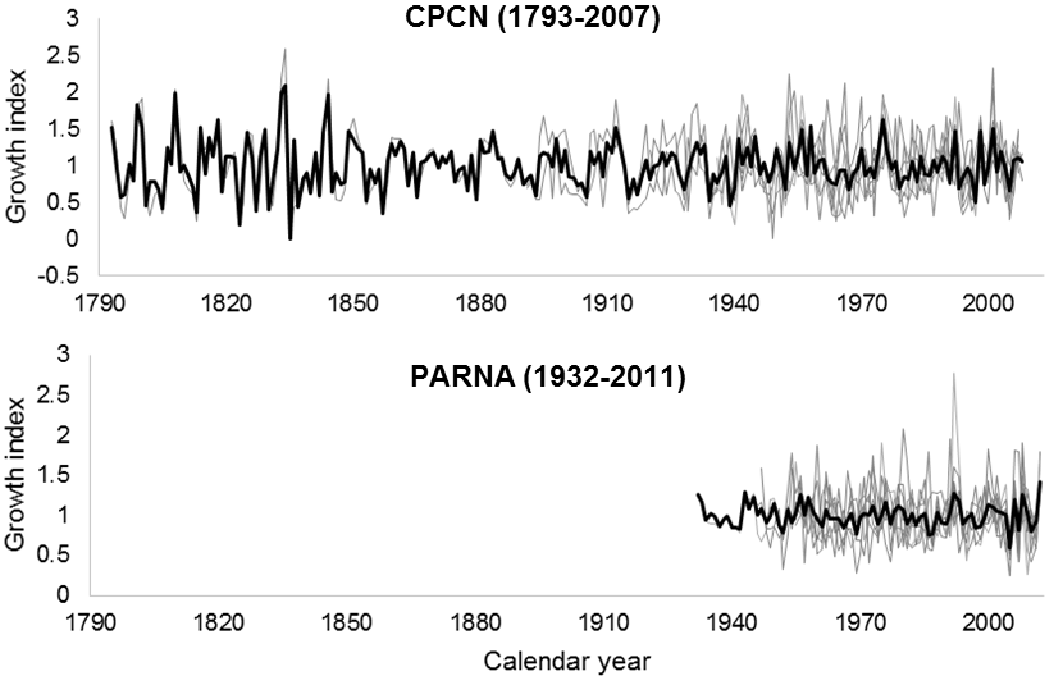

Fig. 5. Tree-ring width chronologies of *Ocotea pulchella* from Centro de Pesquisas e Conservação da Natureza (CPCN) and Parque Nacional de Aparados da Serra (PARNA). Residual chronologies (black lines) and series of growth index per tree in each site chronology (grey lines) are included.

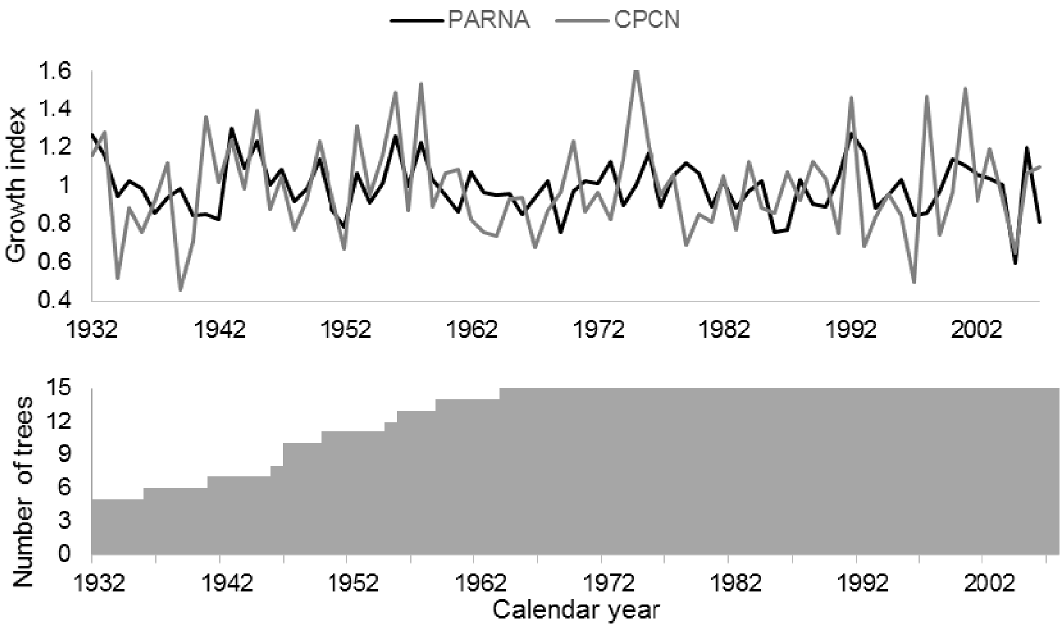

Fig. 6. Common period between site chronologies of *Ocotea pulchella* from Centro de Pesquisas e Conservação da Natureza (CPCN) and Parque Nacional de Aparados da Serra (PARNA). Sample size (number of trees included) are shown.

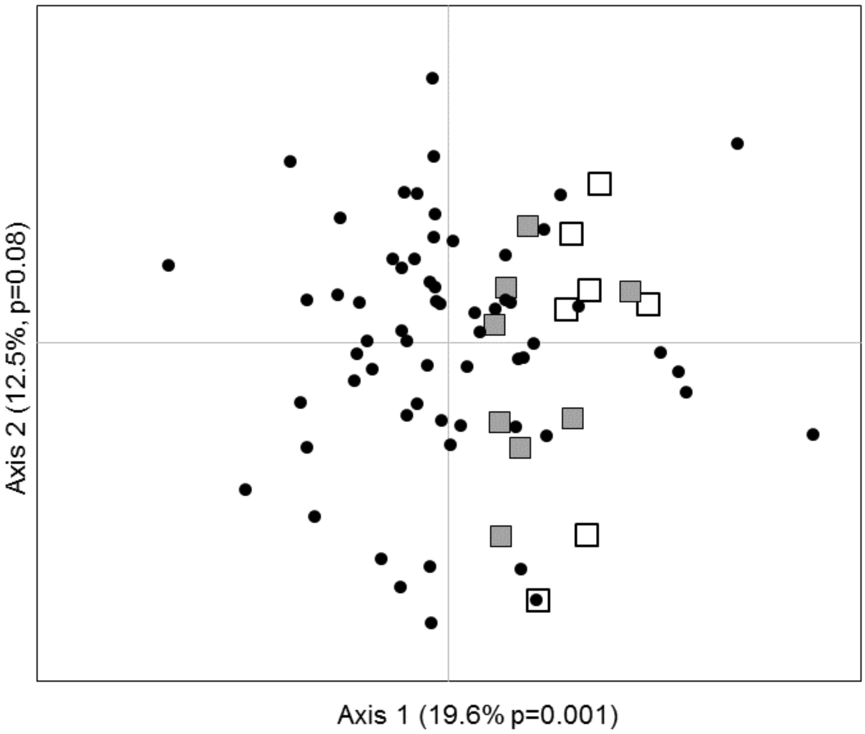

Fig. 7. Ordination analyses of years (dots) described by standardized growth-ring series of trees from Centro de Pesquisas e Conservação da Natureza Pró-Mata (white squares) and Parque Nacional de Aparados da Serra (grey squares).

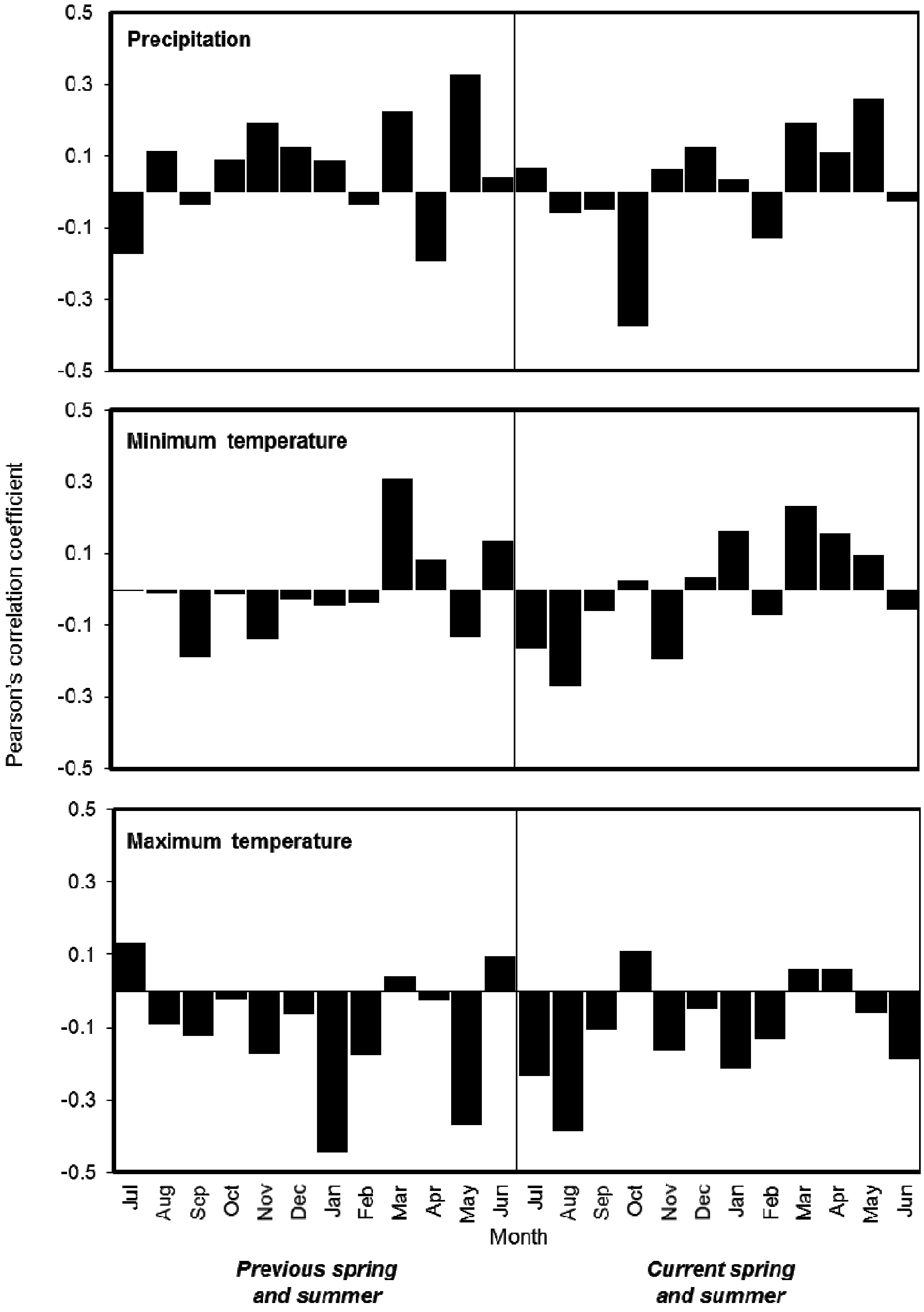

Fig. 8. Pearson's correlation coefficient between total annual tree growth (principal component) and monthly climatic variable (total precipitation, minimum and maximum temperature).

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