

Could trees change future behaviour in xylogenesis to improve fitness based on past and current conditions? A tropical case of study

Poderiam as árvores mudar o comportamento futuro na xilogénese para melhorar a condição física com base nas condições passadas e actuais? Um caso de estudo tropical

¿Podrían los árboles cambiar el comportamiento future en xilogénesis para mejora la aptitude en función de las condiciones pasadas y actuales? Un caso de estudo tropical

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Abstract

Carbon allocation is the Achilles' heel of forest models, due to the difficulty to predict responses induced by environmental changes. Structural-functional models involve the plant's strategy to split its resources between organs and functions. An important functional characteristic is xylem architecture, which is connected to water use strategy and plant productivity besides one of the most important C-sink (that absorbs carbon). Our goal is to use the information present in the tree rings of *Schizolobium parahyba*, to expand the possibilities of teleonomic approaches in structural-functional models of tree species. In a comparative xylem rings analyses, we established relationships among specific gravity, vessel traits as hydraulic conductivity potential, double wall thickness, and autofluorescence intensity of lignin. The analyses showed that growth ring characteristics seem to have been modulated not only by water availability of the period of wood formation but also by the water availability of previous years. This relationship would be occurring due to the greater capacity of accumulation of reserve carbohydrates in years whose climatic conditions were favourable. This pattern of behaviour entails the formation of two distinct growth ring patterns, one with high and the other with low structural cost. This case study shows that the species can change future behaviour in xylogenesis to improve fitness based on past and current conditions. Our study may help to extend the possibilities of teleonomic approaches in structural-functional models of tree species, which will assist in a greater understanding of how trees balance their carbon allocation in wood according to changes in the environment.

Keywords: Carbon allocation; Lignin; Rainfall; Specific Gravity; Wood traits.

Resumo

A alocação de carbono é o calcanhar de Aquiles dos modelos florestais, devido à dificuldade em prever as respostas induzidas pelas mudanças ambientais. Os modelos estruturais-funcionais envolvem a estratégia da planta para dividir os seus recursos entre órgãos e funções. Uma característica funcional importante é a arquitetura do xilema, que está ligada à estratégia de uso da água e produtividade da planta, além de um dos mais importantes C-sink (que absorve

carbono). O nosso objetivo é utilizar a informação presente nos anéis de árvores de *Schizolobium parahyba*, para expandir as possibilidades de abordagens teleonômicas em modelos estruturais-funcionais de espécies arbóreas. Numa análise comparativa de anéis do xilema, estabelecemos relações entre densidade aparente, características dos vasos como potencial de condutividade hidráulica, espessura de parede dupla, e intensidade de autofluorescência da lignina. As análises mostraram que as características dos anéis de crescimento parecem ter sido moduladas não só pela disponibilidade de água do período de formação da madeira, mas também pela disponibilidade de água dos anos anteriores. Esta relação ocorreu devido à maior capacidade de acumulação de carboidratos de reserva em anos cujas condições climáticas eram favoráveis. Este padrão de comportamento implica a formação de dois padrões de anéis de crescimento distintos, um com elevado e o outro com baixo custo estrutural. Este estudo de caso mostra que a espécie pode alterar o comportamento futuro em xilogênese para melhorar a aptidão física com base nas condições passadas e atuais. O nosso estudo pode ajudar a ampliar as possibilidades de abordagens teleonômicas em modelos estruturais-funcionais de espécies de árvores, o que ajudará a uma maior compreensão de como as árvores equilibram a sua alocação de carbono na madeira de acordo com as mudanças no ambiente.

Palavras-chave: Atribuição de carbono; Lignina; Chuva; Massa Específica; Características da madeira.

Resumen

La asignación de carbono es el talón de Aquiles de los modelos forestales, debido a la dificultad de predecir las respuestas inducidas por los cambios ambientales. Los modelos estructurales-funcionales involucran la estrategia de la planta para dividir sus recursos entre órganos y funciones. Una característica funcional importante es la arquitectura del xilema, que está relacionada con la estrategia de uso del agua y la productividad de la planta, además de uno de los más importantes C-sink (que absorbe carbono). Nuestro objetivo es utilizar la información presente en los anillos de los árboles de *Schizolobium parahyba*, para ampliar las posibilidades de enfoques teleonómicos en modelos estructurales-funcionales de especies arbóreas. En un análisis comparativo de los anillos del xilema, establecimos relaciones entre la gravedad específica, las características de los vasos como potencial de conductividad hidráulica, el espesor de doble pared y la intensidad de autofluorescencia de la lignina. Los análisis mostraron que las características del anillo de crecimiento parecen haber sido moduladas no solo por la disponibilidad de agua del período de formación de la madera, sino también por la disponibilidad de agua de años anteriores. Esta relación se estaría dando debido a la mayor capacidad de acumulación de carbohidratos de reserva en años cuyas condiciones climáticas fueran favorables. Este patrón de comportamiento implica la formación de dos patrones de anillos de crecimiento distintos, uno con alto costo estructural y otro con bajo costo estructural. Este estudio de caso nos mostró que la especie puede cambiar el comportamiento futuro en xilogénesis para mejorar la aptitud en función de las condiciones pasadas y actuales. Nuestro estudio puede ayudar a ampliar las posibilidades de los enfoques teleonómicos en modelos estructurales-funcionales de especies arbóreas, ayudando a comprender mejor cómo los árboles equilibran la asignación de carbono en la madera de acuerdo con los cambios en el medio ambiente.

Palabras clave: Asignación de carbono; Lignina; Lluvia; Gravedad específica; Características de la madera.

1. Introduction

Allocation of carbon assimilated during the process of photosynthesis influences the re-cycling of chemical elements in the forest ecosystem. How this carbon allocation occurs in plants is of great ecological interest for a long Franklin et al. (2012), and this knowledge is essential for studies of ecosystem productivity and changes in the forest ecosystem of the global carbon cycle Henry et al. (2010). Once variability of tree growth could be related by diverse factors Henry et al. (2010) Guillemot et al. (2015), carbon allocation becomes the Achilles' heel of forest research mainly in the tropical regions, where the availability of information and studies is still scarce

The phenology of plants plays important role in carbon storage, and it represents a trade-off between environmental factors and the source-sink relationship Rossi et al. (2013). Environmental conditions are important factors for the investment of the carbohydrates synthesized by a tree and its allocation occurs in the best way possible to maintain a harmony between different growing parts of a plant so that total growth could be optimized Le Roux et al. (2001) to provide longer life and a higher chance of reproduction Lacoite (2000).

Plant height is in response to apical meristem while radial growth is achieved by the cell division activity of the vascular cambium. It is the secondary meristem of plants that produces phloem and xylem cells and results in an increase in stem diameter Rossi et al. (2013). During the development process, the xylem experiences several different biochemical processes through its sequential stages of maturation Prislán et al. (2009). Although water storage occasionally affects cell

growth, the differentiation of tracheary elements and fibres in the secondary xylem is driven mainly by phytohormones Rathgeber et al. (2016) which is also related to the tree phenology. However, cambial activity is influenced by numerous physiological processes that are modulated by environmental conditions (Fritts, 1976). In tropical regions, the cambium of some species undergoes dormancy during the dry season and produce annual tree rings Rathgeber et al. (2016).

Among the products of cambium, the secondary xylem reflects the functional balance between water transport, carbon allocation, mechanical support and storage of non-structural carbohydrates and water Von Arx et al. (2012). Its structural characteristics remain archived chronologically in tree rings that offer a temporal understanding of its dynamics towards the environmental changes Fonti and Jansen (2012) and represents the principal above-ground carbon accumulation pool Babst et al. (2014)

The allometric approach is the principle widely used in tree growth modelling (Mäkelä, 2012) since changes in the allometry are directly related to a plant's carbon reserve status Ogle ND Pacala (2009). However, this kind of approach provides a simple description of carbon allocation, and it has high levels of empiricism, which is influenced by the environment is not considered. These factors limit the model's quality and knowledge of dynamics about the allocation and fluctuations in carbon due to a lack of mechanistic and quantitative information Marcelis and Heuvelink (2007).

The dynamic mechanism of carbon allocation in growth rings implies differences in wood anatomy Palacio et al. (2011). Consequently, tree rings may contain precious information about the influence of the environment on carbon allocation in wood, which assist in the progress of studies related to structural-functional mechanisms of a tree. Therefore, there is an urgent need to understand how radial growth influences carbon allocation and the wood anatomy of tropical deciduous trees. This may be achieved by quantifying the wood anatomical traits such as specific gravity, tree ring width, vessel frequency and content of lignin in them by correlating these traits with the climatic variables.

The objective of this study was to exploit the information present in the tree rings of a tropical deciduous species to expand the possibilities of teleonomic approaches in structural-functional models of tree species.

2. Methodology

2.1 Field site and sampling

The study was conducted in a tropical rain forest of Montana Alberto Löfgren State Park (23°27'S – 46°38'W and 814m ALT.) located in São Paulo, SP, Brazil. This area represents a mean annual temperature around 26°C and the mean annual precipitation is 1687 mm. The period of the rainy season is October to March and the dry season is from April to September while January remains the wettest month and August is the driest (Rossi *et al.* 2009). Rainfall data were obtained from INMET (National Institute of Meteorology), a meteorological station, which is located four kilometres from Alberto Löfgren State Park.

Schizolobium parahyba (Vell.) Blake var. *parahyba* (Fabaceae), popularly known as “Brazilian Fern Tree” is a deciduous, emerging, fast-growing and diffuse-porous tree with distinct annual rings. According to Marcati et al. (2008), cambial activity in this species initiates in August/September, reaches its peak with the arrival of new leaves from January to March. During this period, groundwater availability is also higher. Cambium activity declines in May that directly corresponds to the beginning of the dry season and defoliation and the activity remains low until October. Therefore, August was considered as the beginning of growth for the current year and the previous months to August as the reserve period of previous year.

Samples from thirty-three trees of *S. parahyba* were collected for this study. From each tree, 15 cm thick discs were obtained at breast height (1.3 m from the ground). Since the marking of tree rings over wood discs were homogeneous, we

selected only one radius of each sample and cores were sanded until wood cells were visible for anatomical and physicochemical analysis.

2.2 Crossdating

Images of wood samples were captured using a Canon EOS Digital camera (Rebel XTI) with EF 100 mm macro lens, coupled to photographic support. The tree rings width was determined with the Image-Pro Plus 6.3. program A cross-dating quality control was made using the statistical program COFECHA (Holmes 1983).

Data of tree ring width was standardized by detrending with linear regression; the quality of chronology was analyzed by the expressed population signal (EPS) using R 3.1.3 (R Core Team, 2015) package BootRes Zang and Biondi (2013). After that, we sequenced the remaining analysis.

2.3 Vessel traits

Ten trees from two diameter classes (22 to 40 cm and 50 to 70 cm), that showed the best intercorrelation values were selected. The diameter and vessel frequency of each tree ring was, measured in a radius with 29 mm wide macroscopic images. The hydraulic conductivity potential (Kp) of tree rings was obtained by the following formula:

$$Kp = (\pi\rho/128\eta) \sum (d_i^4)$$
 where $i = 1$ or n vessels, ρ = density of water ($998,2 \text{ kg m}^{-3}$ to 20°C and η is viscosity of water ($1,002 \times 10^{-9} \text{ MPa s}^{-1}$ a 20°C), K_p , $\text{kg m}^{-1} \text{ MPa}^{-1} \text{ s}^{-1}$ Tyree ND Ewers (1991).

We selected five samples at random among these ten trees to measure the vessel double wall thickness and vessel lignin content by autofluorescence intensity. In each sample, the last ten tree rings were analyzed. Transverse sections of $25 \mu\text{m}$ thickness were obtained from each tree ring by using a sliding microtome. Subsequently, the sections were clarified with 60% sodium hypochlorite and washed thoroughly with distilled water.

For vessel double wall thickness, sections were stained with an aqueous solution (9:1) of Astra blue and safranin 1% Chaffey (2002) and mounted in glycerin (50 %). Anatomical analysis was carried out using an Olympus BX51 microscope attached with a digital camera and computer. Image analysis was carried out using Image-Pro Plus 6.3 software.

To measure the autofluorescence intensity of lignin deposition in vessel walls, sections were infiltrated in 50% glycerin solution with 0,01 M phosphate buffer pH 9.0 Donaldson (2013).

The Z Stack images were captured using a Confocal LSM 510 microscope, emitting at an excitation wavelength of 364 nm (UV) and the emission spectrum of 400-650 nm. In each section, we captured the image of five vessels. Longitudinal symmetry of vessel walls along the z-axis enable us to perform 2D measurements in all-optical cuts and obtained five measurements along each vessel wall while quantitative analysis was done using Zen software 2012 (Blue Edition)

2.4 Specific gravity

For x-ray densitometry analysis, samples were maintained in an acclimatization chamber (20°C , 60% RH, 12:0 am) until they reach 12% moisture content. Then, tree rings were scanned from pith to bark every $80 \mu\text{m}$ by equipment QTRS 01X model. The intensity of X-rays was turned in specific gravity values and specific gravity profiles were built. These data were also standardized by detrending with linear regression. Chronology of the quality was analyzed by EPS using R 3.1.3 (R Core Team, 2015) package BootRes Zang AND Biondi (2013).

2.5 Leaflet size data

Fully grown, mature leaves were collected from *S. parahyba* during dry and wet periods and fixed in FAA⁷⁰ for 48 hrs and stored in 70% alcohol. The middle leaflet of adult leaves at the fourth node below the apex was used to measure the length and width of the leaflet using the millimetre rule to establish the leaflet area unit (cm²).

2.6 Statistical analyses

Pearson correlations were calculated for all pairwise combinations of wood features: vessel diameter, vessel frequency, the potential of hydraulic conductivity, vessel double wall thickness, vessel wall fluorescence and specific gravity – and between wood characteristics and monthly precipitation data. Results with $p < 0.05$ were considered significant.

Based on the significant results of correlations, we further tested the linear regression model and multiple regression models. All variables were standardized before analysis. Differences between leaflet unit areas formed during wet and dry periods were compared with Tukey's test. Statistical analyses were also performed using R 3.1.3 R Core Team (2015) package Vegan Oksanen et al. (2015).

3. Results

In *Schizolobium parahyba*, wood is diffuse-porous with distinct growth rings. The average tree ring width was 14.11 mm and it was satisfactorily cross dated with an intercorrelation of 0.582 and mean sensibility of 0.410. The expressed population signal (EPS) values for tree ring width and specific gravity was 0.90 and 0.92 respectively.

Linear regression model between ring width and wood characteristics revealed that the tree ring width had an inverse relationship with the vessel wall fluorescence ($r^2 = 0.38$, $P = 0.01$; Figure 1a). The vessel wall autofluorescence was positively related with average specific gravity ($r^2 = 0.37$, $P = 0.01$; Fig. 1b) while negatively correlated with vessel frequency ($r^2 = 0.69$, $P = 0.0002$; Fig. 1c). Therefore, wider tree rings showed a reduction in deposition of lignin on the vessel wall and increasing vessel frequency. In contrast, narrower tree rings showed a higher deposition of lignin on the vessel wall and possessed a lower vessel frequency. When cross-verified, the greater intensity of lignin autofluorescence of vessel wall, showed a higher lignification as compared to that of fibres and parenchyma (axial and radial) cells (Figure 2). Multiple regression models revealed that the increase in specific gravity was accompanied by an increase of hydraulic conductivity potential and an increase of vessel double wall thickness (Figure 3).

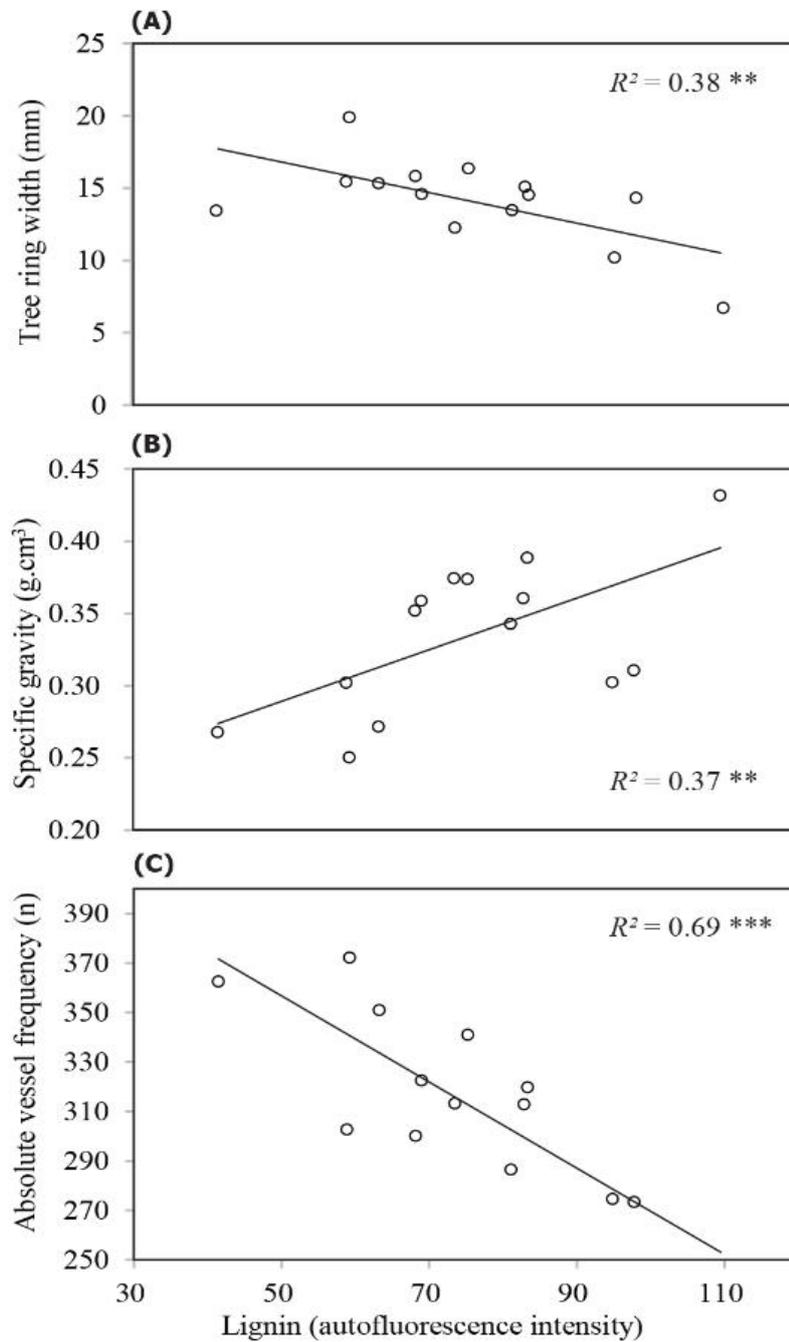
Figure 4 shows the temporal changes in specific gravity using one predominant tree out of ten trees. Lower values of specific gravity were observed at the beginning of the growing season and higher values at the end of the growing season. However, we observed some variations in the density profiles which is correlated with the seasonal alterations in the environment. A significant correlation between tree ring width and mean specific gravity was found with October and April, and rainfall respectively (Figure 5a, b). After correlation analysis, linear regression showed a negative relationship between the tree ring width and rainfall in October ($r^2 = 0.44$, $P = 0.01$; Figure 6a). Therefore, less rainfall during this month increased tree ring width. Average specific gravity showed a positive relationship with the April month of the previous year's rainfall ($r^2 = 0.44$, $P = 0.01$; Fig. 6b) suggesting the period of non-structural carbohydrate production.

According to regression analysis, it was likely to verify two different patterns of tree rings in *S. parahyba*: one with lower and another with higher structural construction costs. The first one was narrower vessels with less lignin deposition on the cell walls, lower density and higher vessel frequency. In contrast, the second one was with wider vessels with increased lignin deposition on the cell walls, higher density and higher hydraulic conductivity potential, both influenced mainly by October rainfall during the leaf expansion growth phase of the trees.

In Tukey's test, a difference in the leaflet unit area between leaves that had developed during the wet periods was

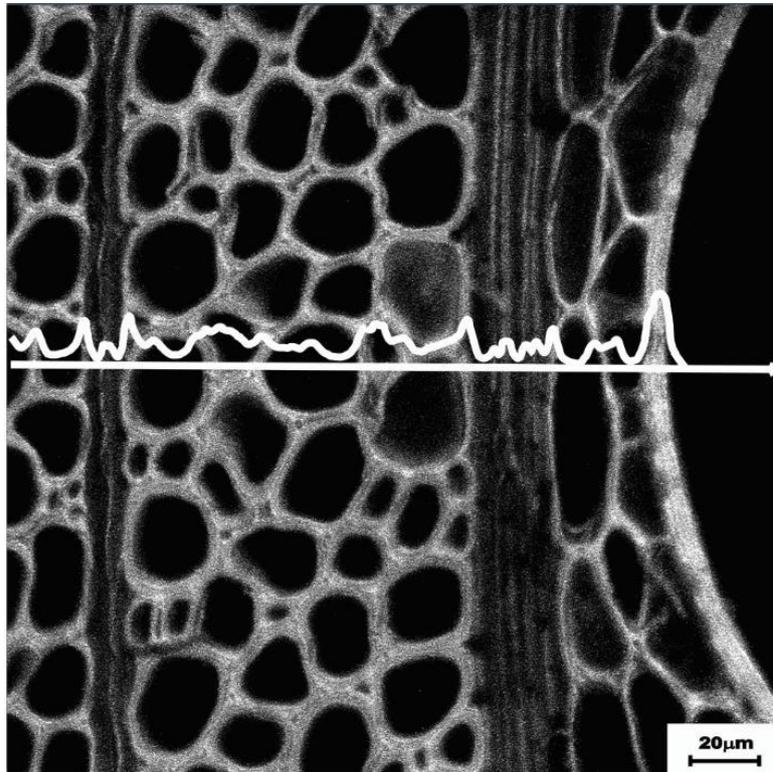
found higher ($P=0.001$), wherein leaves formed during drier periods possessed less leaflet area (Figure 7)

Figure 1. Linear regression between (A) tree ring width, (B) specific gravity and (C) absolute vessel frequency and lignin autofluorescence intensity of vessel walls.



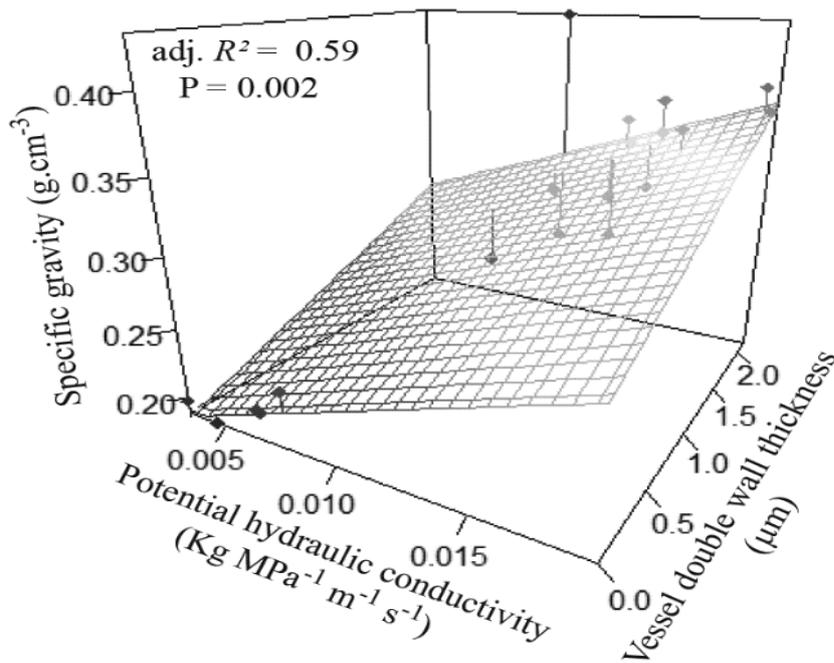
Source: Authors (2022).

Figure 2. Fluorescence intensity profile of transversal section wood of *Schizolobium parahyba* with 364 nm (UV) excitation showing the greater brightness of vessel wall lignin content.



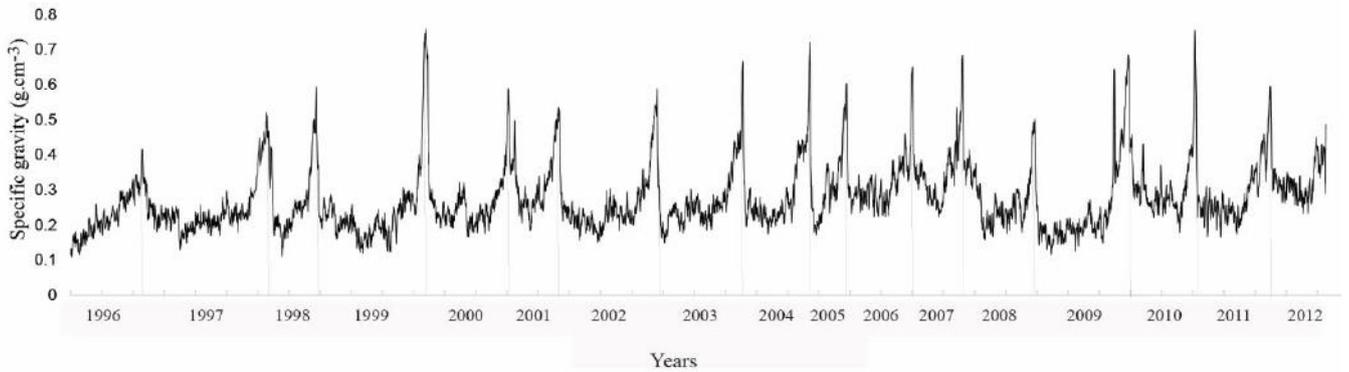
Source: Authors (2022).

Figure 3. Multiple regression between specific gravity, conductivity hydraulic potential and vessel double-wall thickness.



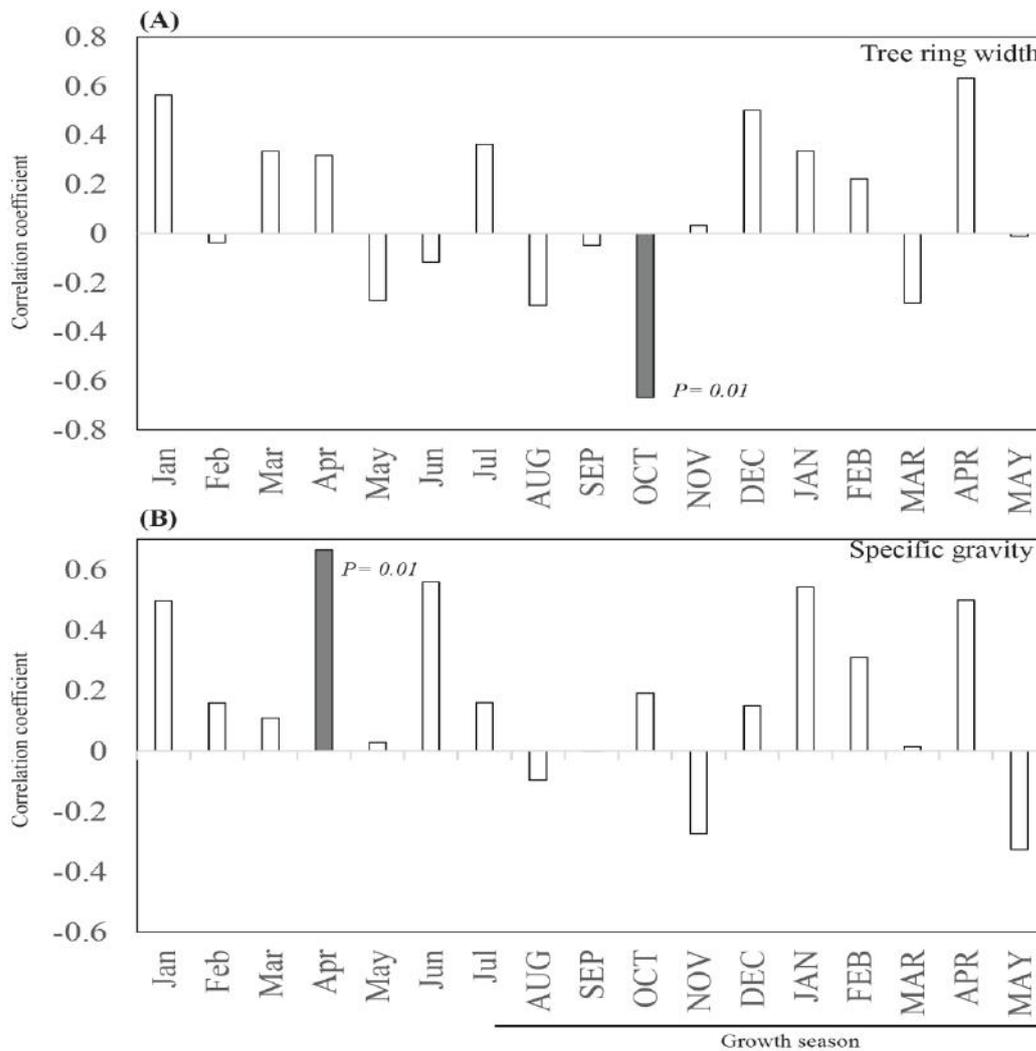
Source: Authors (2022).

Figure 4. Example for intra-annual variations of specific gravity profile.



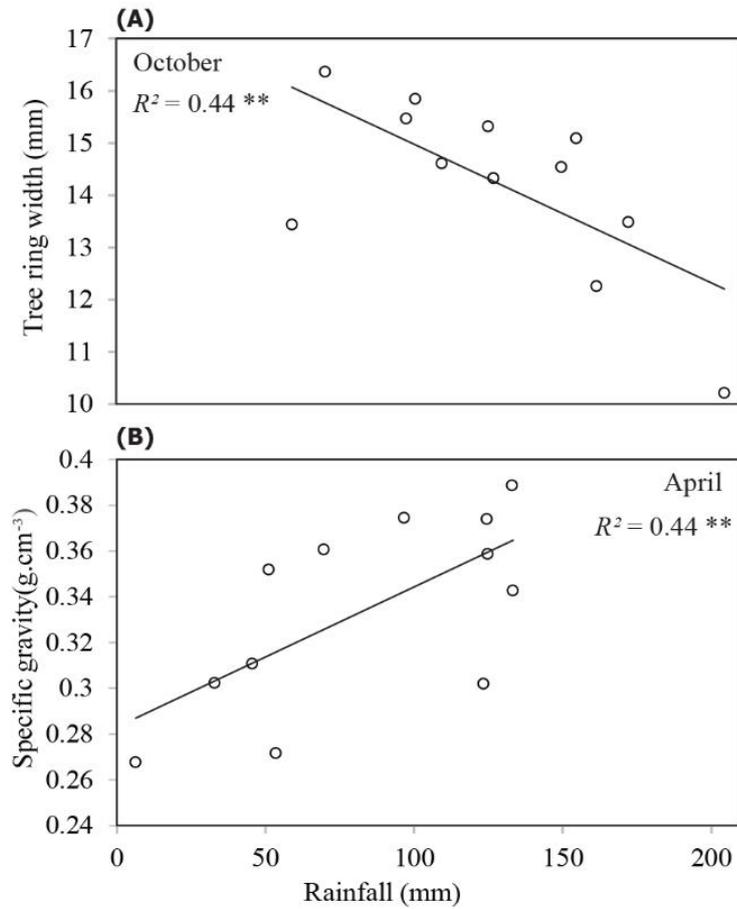
Source: Authors (2022).

Figure 5. Pearson correlations of tree (A) ring width and (B) specific gravity chronologies of *Schizolobium parahyba* with the accumulated rainfall from January (previous year) to May (current year). Months with an uppercase letter indicate the current growing season. Filled bars indicates significant results.



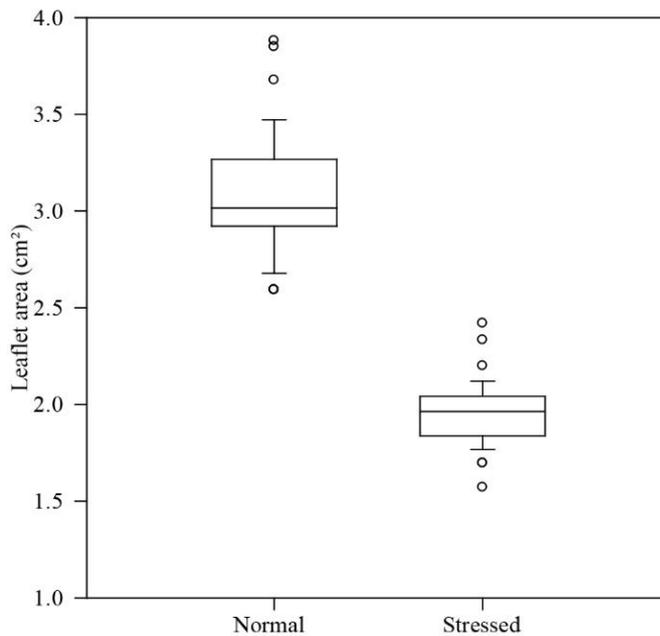
Source: Authors (2022).

Figure 6. Linear regression between (a) tree ring width and October rainfall and (b) specific gravity and April rainfall.



Source: Authors (2022).

Figure 7. The difference in the leaflet area unit between leaves that had developed during dry (stressed leaves) and wet periods (normal leaves).



Source: Authors (2022).

4. Discussions

The series of intercorrelation between all the investigated trees showed a significant influence of the climate on the *S. parahyba* growth. Tree ring width presented a positive relationship with the rainfall of October month, which is a leaf-expansion period of the species Marcati et al. (2008). Therefore, dry spells during the early growing season resulted in the production of tree rings with a greater number of less expanded cells with thinner walls and lower deposition of lignin, which indicates the reduction of structural cost. It is a well-known fact that during the early period of growth, newly developing leaves provide enough quantity of growth hormones responsible for the development of the secondary xylem and climatic conditions (like temperature, humidity and precipitation) are conducive factors for the growth (Rao & Rajput 2001; Marcati et al. 2008; Johansson et al. 2019). Lignins are large and complex polymers with a high metabolic cost of their synthesis with about 65-67% carbon content (Amthor, 2003). Simple carbohydrates are the main substrates of lignin biosynthesis and these substrates may be available directly from the previously-stored compounds like starch and also from photosynthesis (Amthor, 2003).

Our analysis also showed a significant reduction in the leaflets area that have been developed during the dry season under the water stress. According to Kalve et al. (2014), leaf development is significantly affected by environmental factors such as water availability, which influences the activity of proteins linked to expansion and incorporation of polymers in the cell wall Pantin et al. (2012). Lower leaf expansion leads to the reduction of intercellular space, which results in a slow gas diffusion through the leaf tissues. Therefore, it potentially reduces the photosynthetic rate (Levitt, 1980), which consequently influence the availability of the structural carbon compounds (Letort et al. 2008; Fatichi et al. 2014). Furthermore, biosynthesis of auxin, a hormone responsible for differentiation and cell expansion (Wang & Yong-Ling, 2013; Mähönen et al. 2014) is also affected by the lesser production of carbohydrates (LeClere et al. 2010; Sairanen et al. 2012; Kramer, 1964).

Cell expansion involves changes in the wall structure (McCann *et al.* 2001) and turgor pressure, which is necessary to drive cell expansion pressure (Ortega, 2010). However, biochemical loosening of the cell wall is the primary determinant for this process McCann et al. (2001). Auxin produced by young leaves is responsible for expansins activation, wall acidification (Acid Growth Theory), K⁺ pump regulation and separation of cellulose microfibrils allowing the insertion of newly synthesized polymers in the cell wall (MacCann et al. 2001; McQueen-Mason et al. 1992; Cosgrove 2005; Vanneste and Friml 2013). Thus, reduction in auxin availability can directly affect the cell expansion in the wood. In the present study, we believe that reduction of leaf area, that may influence the auxin availability and consequently resulting in less expanded vessels with the narrow lumen diameter. Reduction in auxin synthesis also enables increased cytokinin concentration in the cambial zone (Aloni, 2013), and leads to an increase in cell division (Nieminem et al. 2008; Matsumoto-Kitano et al. 2008), which consequently results in the formation of wider tree rings, as we could see in *S. parahyba*.

After cell expansion, secondary wall deposition begins with an extremely conservative process Macadam & Nelson (2002). Generally, in angiosperms, the secondary wall is mainly composed of 40-50% of cellulose, 20-30% of hemicelluloses, and 25-30% of lignin Schuetz et al. (2012). High levels of carbohydrates available to the cambial zone for the cell division activity coincide with periods of high cambial metabolic activity, possibly because of a continual demand of sucrose required during cell wall biosynthesis Simard et al. (2013). The cellulose chains incorporated into primary and secondary walls differ in some aspects; for example, the amount of glucose needed for their formation is higher. The cellulose chain incorporated in the primary wall consists of about 500 to 2000 glucose molecules, while the secondary wall is composed of more than 10,000 molecules Joshi and Mandsfield (2007) highlighting the increased demand for carbon compounds for their formation.

Our results suggest that rainfall in the month of April of the previous growing season is directly related to the specific gravity of the wood indicating the importance of reserved metabolites in wood production. Available literature also indicates that in deciduous species, newly produced photosynthates are used in conjunction with reserve food to produce new xylem

tissue (Palacio et al. 2011; Wiley & Helliker 2012; Simard et al. 2013), and to produce new leaves at the beginning of the growing season (Bréda et al. 2006; Millard et al. 2007; Dietze et al. 2014).

This can be verified with the fact that alterations in the leaf expansion in *S. parahyba* may be consequently leading to a reduction in carbon availability. Moreover, the species that produced wood with lower specific gravity and thinner cell walls indicates low-cost investment in the cell structure. In contrast, when the leaf expansion was adequate at the beginning of the growing season, the wood produced over the years was composed of high-cost structural cells resulting in higher specific gravity, higher lignification. It also showed greater conductivity, hydraulic potential since vessel diameter was not affected due to reduced turgor pressure and reduced auxin availability. However, in this case, the tree ring formed was narrower possibly due to less amount of cytokinin present in the cambial zone (Nieminem et al. 2008; Matsumoto-Kitano et al. 2008).

Novaes *et al.* (2010) found a very high negative correlation between plant growth and lignin content, whereas the relationship between growth and cellulose content was positive. Lignin has a higher energy content than hemicelluloses and cellulose, wherein one gram of lignin has 30% more energy than cellulosic carbohydrates. It suggests that more wood could be formed if the lignin content is reduced. Therefore, a compensatory regulation of lignin and cellulose ratio could represent an adaptation to sustain mechanical strength by reducing lignin biosynthesis (Hu *et al.* 1999). Reduction in lignin content also directly affects the resistance of wood against mechanical injuries (Novaes *et al.* 2010).

According to Larjavaara and Muller-Landau (2010), different tree species can produce two different patterns of wood: i) characterized by low cost and high rate of the radial growth, and ii) featured by high structural cost and low rate of radial growth. In our study, we found that both the patterns of wood in the inter-annual wood variation in the same species. This variation of mechanical design link safety and survival because is the result of the need to resist forces like fresh biomass, crown load, interaction with wind speed and gravity Fournier et al. (2013). Indeed, carbon structural cost along the tree life can help us to understand how trees allocate carbon to maintain the self-supporting habit and optimal mechanical performance.

Our approach of dendrochronological analysis offered new insights into understanding the carbon allocation dynamics in the wood of *S. parahyba*. The species showed two distinct tree ring patterns: one with high and the other with low structural cost. It indicates that rainfall in the early growing season during the period of leaves expansion influenced the carbon sequestration rate. Further studies on a similar line can help to extend the possibilities of teleonomic approaches in structural-functional models of tree species. It will also assist in a greater understanding of how trees balance their carbon allocation in wood according to changes in the environment and enhancing the accuracy of tree growth modelling.

5. Conclusion

In consecutive periods of higher water availability, *S. parahyba* reconciled the increase in density with the increase of the potential of hydraulic conductivity, which is not a pattern usually observed in tree species. This association benefited the efficiency in hydraulic conductivity while providing greater mechanical resistance to the tree, ensuring its permanence above the canopy as an emerging species.

The analyses showed that characteristics of the growth ring such as density, diameter and wall thickness of vessels seem to have been modulated not only by the water availability of the period of wood formation but also by the water availability of previous years. This relationship would be occurring due to the greater capacity of accumulation of reserve carbohydrates in years whose climatic conditions were favourable. Such favourable periods would provide resources for the plant to invest in the production of higher quality wood, providing more safety against hydraulic failures and mechanical injuries.

This pattern of behaviour entails the formation of two distinct growth ring patterns, one with high and the other with low structural cost, depending mainly on the water conditions of the site during the last and the present year.

This case study showed us that the species *S. parahyba* can change future behaviour in xylogenesis to improve fitness based on past and current conditions. Our study may help extend the possibilities of teleonomic approaches in structural-functional models of tree species, assisting in a greater understanding of how trees balance carbon allocation in wood according to changes in the environment and enhance tree growth modelling accuracy.

As a suggestion for further research, we believe it is relevant to collect samples of trees/species in the same environment in which we studied *S. parahyba*, especially phylogenetically close species. Thus, it would be possible to test whether the pattern repeats itself due to a strong environmental influence or the responses are more linked to genetics.

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References

- Aloni, R. (2013). The role of hormones in controlling vascular differentiation. In: Fromm J, ed. *Cellular Aspects of Wood Formation*, Heidelberg, Germany: Springer-Verlag, 99-140. <https://doi.org/10.1007/s00425-013-1927-8>
- Amthor, J.S. (2003). Efficiency of lignin biosynthesis: a quantitative analysis. *Annals of Botany*, 91(6), 673-695. <https://doi.org/10.1093/aob/mcg073>
- Bréda, N., R. Huc., A. Granier., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63(6), 625-644. <https://doi.org/10.1051/forest:2006042>
- Chaffey, N. (2002). *Wood formation in trees: Cell and Molecular Biology Techniques*. Taylor & Francis Inc. <https://10.1093/aob/mcf216>
- Cosgrove, D. J. (2005). Growth of the plant cell wall. *Nature Reviews Molecular Cell Biology*, 6, 850-861. <https://doi.org/10.1038/nrm1746>
- Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooh, J. A., Richardson, A. D., & Vargas, R. (2014). Nonstructural Carbon in Wood Plants. *Annual Review of Plant Biology*, 65, 667-687. <https://doi.org/10.1146/annurev-arplant-050213-040054>
- Donaldson, L. (2013). Softwood and hardwood lignin fluorescence spectra of wood cell walls in different mounting media. *IAWA Journal*, 34(1), 3-19. <https://doi.org/10.1163/22941932-00000002>
- Epron, D., Nouvellon, Y., & Ryan, M. G. (2012). Introduction to the invited issue on carbon allocation of trees and forests. *Tree Physiology*, 32(6), 639-643. <https://doi.org/10.1093/treephys/tps055>
- Faticchi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: from carbon source to sink-driven vegetation modelling. *New Phytologist*, 201(4), 1086-1095. <https://doi.org/10.1111/nph.12614>
- Fonti, P., & Jansen, S. (2012). Xylem plasticity in response to climate. *New Phytologist*, 195(4), 734-736. <https://doi.org/10.1111/j.1469-8137.2012.04252.x>
- Fournier, M., Dlouhá, J., Jaouen, G., & Almeras, T. (2013). Integrative biomechanics for tree ecology: beyond wood density and strength. *Journal of Experimental Botany*, 64 (15), 4793-4815. <https://doi.org/10.1093/jxb/ert279>
- Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, A., & Dybzinski, R. (2012). Modelling carbon allocation in trees: a search for principles. *Tree Physiology*, 32(6):648-666. <https://doi.org/10.1093/treephys/tpr138>
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43, 69-78.
- Hu, W., Harding, S. A., Lung, J., Popko, J. L., Ralph, J., Stokke, D. D., Tsai, C., & Chiang, V. L. (1999). Repression of lignin biosynthesis promotes cellulose accumulation and growth in transgenic trees. *Nature Biotechnology*, 17, 808-812. <https://doi.org/10.1038/11758>
- Johnssona, C., Xu, J., Xuea, W., Dubreuil, C., Lezhneva, L., & Fischera, U. (2019). The plant hormone auxin directs the timing of xylem development by inhibition of secondary cell wall deposition through repression of secondary wall NAC-domain transcription factors. *Physiologia Plantarum*, 165(4), 673-689. <https://doi.org/10.1111/ppl.12766>
- Joshi, C. P., & Mandsfield, S. D. (2007). The cellulose paradox: simple, molecule, complex biosynthesis. *Current Opinion in Plant Biology*, 10(3), 220-226. <https://doi.org/10.1016/j.pbi.2007.04.013>
- Kalve, S., De Vos, D., & Beemster, G. T. S. (2014). Leaf development: a cellular perspective. *Frontiers in Plant Science*, 5:(362), 1-25. <https://doi.org/10.3389/fpls.2014.00362>

- Kramer, P. J. (1964). The role of water and wood formation. In: Zimmermann MH, ed. *The Formation of Wood in Forest Trees*. Academic Press Inc., 519-532.
- Lacointe, A. (2000). Carbon allocation among tree organs: A review of basic processes and representation in functional-structural tree models. *Annals of Forest Science*, 57(5-6), 521-533. <https://doi.org/10.1051/forest:2000139>
- Larjavaara, M., & Muller-Landau, H. (2010). Rethinking the value of high wood density. *Functional Ecology*, 24(4): 701-705. <https://doi.org/10.1111/j.1365-2435.2010.01698.x>
- Le Clere, S., Schmelz, E. A., & Chourey, P. S. (2010). Sugar Levels Regulate Tryptophan-Dependent Auxin Biosynthesis in Developing Maize Kernels. *Plant Physiology*, 153(1), 306-318. <https://doi.org/10.1104/pp.110.155226>
- Le Roux, X., Lacointe, A., Escobar-Gutiérrez, A., & Le Dizès, S. (2001). Carbon-based models of individual tree growth: A critical appraisal. *Annals of Forest Science*, 58 (5), 469-506. <https://doi.org/10.1051/forest:2001140>
- Letort, V., Cournède, P., Mathieu, A., Reffye, P., Constant, T. (2008). Parametric Identification of a Functional-Structural Tree Growth Model and Application to Beech Trees (*Fagus Sylvatica*). *Functional Plant Biology*, 35, 951-963. <https://doi.org/arXiv:1010.5145>
- Levitt, J. (1980). *Responses of Plants to Environmental Stresses: Water, Radiation, Salt, and Other Stresses*. Michigan: Academic Press. 607 p.
- Macadam, J. W., & Nelson, C. J. (2002). Secondary cell wall deposition causes radial growth of fibre cells in the maturation zone of elongating tall fescue leaf blades. *Annals of Botany*, 89(1), 89-96. <https://doi.org/10.1093/aob/mcf010>
- Mähönen, A. P., Tusscher, K., Siligato, R., Smetana, O., Diaz-Triviño, S., Salojärvi, J., Waschsmann, G., Prasad, K., Heidstra, R., & Scheres, B. (2014). PLETHORA gradient formation mechanism separates auxin responses. *Nature*, 515(6), 125-129. <https://doi.org/10.1038/nature13663>
- Mäkelä, A. (2012). On guiding principles for carbon allocation in eco-physiological growth models. *Tree Physiology*, 32(6), 644-647. <https://doi.org/10.1093/treephys/tps033>
- Marcati, C. R., Milanez, C. R. D., & Machado, S. R. (2008). Seasonal development of secondary xylem and phloem in *Schizolobium parahyba* (Vell.) Blake (Leguminosae: Caesalpinioideae). *Trees*, 22, 3–12. <https://doi.org/10.1007/s00468-007-0173-8>
- Marcelis, L. F. M., & Heuvelink, E. (2007). Concepts of modelling carbon allocation among plant organs. In: Vos J, Marcelis LFM, de Visser PHB, Struik PC, Evers JB, eds. *Functional-Structural Plant Modelling in Crop Production*, Netherlands: Springer, pp. 103-111.
- Matsumoto-Kitano, M., Kusumoto, T., Tarkowshi, P., Kinoshita-Tsujimura, K., & Václavíková, K. (2008). Cytokinins are central regulators of cambial activity. *PNAS*, 105(50), 20027-20031. <https://doi.org/10.1073/pnas.0805619105>
- McCann, M. C., Roberts, K., Carpita, N. C. (2001). Plant Cell Growth and Elongation. *eLS*. <https://doi.org/10.1038/npge.els.0001688>
- McQueen-Mason, S., Durachko, D. M., & Cosgrove, D. J. (1992). Two endogenous proteins that induce cell wall extension in plants. *The Plant Cell*, 4(11), 1425-1433. <https://doi.org/10.1105/tpc.4.11.1425>
- Millard, P., Sommerkorn, M., & Grelet, G. (2007). Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. *New Phytologist*, 175(1), 11-28. <https://doi.org/10.1111/j.1469-8137.2007.02079.x>
- Nieminen, K., Immanen, J., Laxell, M., Kauppinen, L., Tarkowski, P., Dolezal, K., Tähtiharju, S., Elo, A., Decourteix, M., Ljung, K., Bhalerao, R., Keinonen, K., Albert, V. A., & Helariutta, Y. (2008). Cytokinin signaling regulates cambial development in poplar. *PNAS*, 105(50), 20032-20037. <https://doi.org/10.1073/pnas.0805617106>
- Novaes, E., Kirst, M., Chiang, V., Winter-Sederoff, H., & Sederoff, R. (2010). Lignin and Biomass: A Negative Correlation for Wood Formation and Lignin Content in Trees. *Plant Physiology*, 154(2), 555-561. <https://doi.org/10.1104/pp.110.161281>
- Ogle, K., & Pacala, S. W. (2009). A modelling framework for inferring tree growth and allocation from physiological, morphological and allometric traits. *Tree Physiology*, 29(4), 587-605. <https://doi.org/10.1093/treephys/tpn051>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Henry, M., Stevens, H., & Wagner, H. (2015). *Vegan: Community Ecology Package*. R package version 2.3-0. <http://CRAN.R-project.org/package=vegan>
- Ortega, J. K. E. (2010). Plant Cell Growth in Tissue. *Plant Physiology*, 154(3), 1244-1253. <https://doi.org/10.1104/pp.110.162644>
- Palacio, S., Paterson, E., Sim, A., Hester, A. J., & Millard, P. (2011). Browsing affects intra-ring carbon allocation in species with contrasting wood anatomy. *Tree Physiology*, 31(2), 150-159. <https://doi.org/10.1093/treephys/tpq110>
- Pantin, F., Simonneau, T., & Muller, B. (2012). Coming of leaf age: control of growth by hydraulics and metabolics during leaf ontogeny. *New Phytologist* 196 (2), 349-366. <https://doi.org/10.1111/j.1469-8137.2012.04273.x>
- Rao, K. S., & Rajput, K. S. (2001). Relationship between seasonal cambial activity, development of xylem and phenology in *Azadirachta indica* growing in different forests of Gujarat State. *Annals Forest Science*, 58(6), 691-698. <https://doi.org/10.1051/forest:2001156>
- R Core Team. (2015). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rossi, M., Faria, A. J., Wenzel, R., Câmara, C. D., Arcova, F. C. S., Cicco, V., Ranzini, M., Luiz, R. A. F., Santos, J. B. A., Souza, LFS, & Veneziani, Y. (2009). Avaliação do meio físico. In: Leonel C, ed. *Plano de Manejo do Parque Estadual Alberto Löffgren*. São Paulo: *Instituto Florestal*, p. 11-16.

- Sairanen, I., Novák, O., Pencík, A., Ikeda, Y., Jones, B., Sandberg, G., & Ljung, K. (2012). Soluble Carbohydrates Regulate Auxin Biosynthesis via PIF Proteins in Arabidopsis. *The Plant Cell*, 24(12), 4907-4916. <https://doi.org/10.1105/tpc.112.104794>
- Schuetz, M., Smith, R., & Ellis, B. (2012). Xylem tissue specification, patterning, and differentiation mechanisms. *Journal of Experimental Botany*, 64(1), 11-31. <https://doi.org/10.1093/jxb/ers287>
- Simard, S., Giovannelli, A., Treydte, K., Traversi, M. L., King, G. M., Frank, D., & Fonti, P. (2013). Intra-annual dynamics of non-structural carbohydrates in the cambium of mature conifer trees reflects radial growth demands. *Tree Physiology*, 33 (9), 913-923. <https://doi.org/10.1093/treephys/tpt075>
- Tyree, M. T., & Ewers, F. W. (1991). The hydraulic architecture of trees and other woody plants. *New Phytologist*, 119(34), 345-360. <https://doi.org/10.1111/j.1469-8137.1991.tb00035.x>
- Vanneste, S., & Friml J. (2013). Calcium: the missing link in auxin action. *Plants*, 2 (24), 650-675. <https://doi.org/10.3390/plants2040650>
- Van Wijk, M. T., Willians, M., Gough, L., Hobbie, S. E., & Shaver, G. R. (2003). Luxury consumption of soil nutrients: a possible competitive strategy in above-ground and below-ground biomass allocation and root morphology for slow-growing arctic vegetation? *Journal of Ecology*, 91(4), 664-676. <https://doi.org/10.1046/j.1365-2745.2003.00788.x>
- Von Arx, G., Archer, S. R., & Hughes, M. K. (2012). Long-term functional plasticity in plant hydraulic architecture in response to supplemental moisture. *Annals of Botany*, 109(6), 1091-1100. <https://doi.org/10.1093/aob/mcs030>
- Wang, L., & Yong-Ling R. (2013). Regulation of cell division and expansion by sugar and auxin signalling. *Frontiers in Plant Science*, 4(163), <https://doi.org/10.3389/fpls.2013.00163>.
- Wile, E., & Helliker, B. (2012). A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New phytologist*, 195(2), 285-289. <https://doi.org/10.1111/j.1469-8137.2012.04180.x>
- Zang, C., & Biondi, F. (2013). Dendroclimatic calibration in R: The *bootRes* package for response and correlation function analysis. *Dendrochronologia*, 31(1), 68-74. <https://doi.org/10.1016/j.dendro.2012.08.001>
- Zweifel, R., Zimmermann, L., Zeugin, F., & Newbery, D. M. (2006). Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *Journal of Experimental Botany*, 57(6), 1445-1459. <https://doi.org/10.1093/jxb/erj125>