

University of São Paulo
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Water and nutrient use efficiency of *Pinus caribaea* var. *hondurensis* and *Pinus taeda*

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Thesis presented to obtain the degree of Doctor in
Science. Area: Forest Resources, Option in: Silviculture
and Forest Management

Piracicaba
2022

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RESUMO

Eficiência hídrica e nutricional de *Pinus caribaea* var. *hondurensis* e *Pinus taeda*

O objetivo geral deste estudo foi avaliar a eficiência no uso de água e de nutrientes de *Pinus caribaea* var. *hondurensis* e *Pinus taeda*. Para essa proposta, o presente estudo foi apresentado em três capítulos. Para os capítulos I e II, o estudo utilizou árvores de *Pinus* spp., aos 13 anos, provenientes de uma área experimental do Programa Cooperativo de Pesquisa em Pinus no Brasil (PPPIB), situada no município de Itatinga, São Paulo. Dados de inventário e mensurações de bandas dendrométricas foram utilizados para avaliar o crescimento das árvores de *Pinus* spp. cultivadas sob distintos regimes de fertilização (tratamentos fertilizado e controle). Ademais, quarenta e oito árvores foram selecionadas e quatro amostras por árvore foram coletadas à aproximadamente 1,3 m de altura. No Capítulo I, o crescimento arbóreo, as relações clima-crescimento e a eficiência intrínseca do uso da água (EIUA) foram avaliados através de uma análise combinada do incremento de área seccional transversal (AST), balanço hídrico e razão isotópica de carbono ($\delta^{13}\text{C}$). No Capítulo II, a densidade da madeira foi avaliada pela técnica não-destrutiva de densitometria de raios-X. Adicionalmente, foram delimitados os anéis anuais das árvores e realizada a datação cruzada entre as árvores. As cronologias de largura do anel de crescimento e densidade da madeira foram analisadas pelo método dendrocronológico e correlacionadas com dados de precipitação e temperatura. Para o Capítulo III, foi conduzido um experimento em casa de vegetação com mudas de *Pinus caribaea* var. *hondurensis* e *Pinus taeda*, com duração de três meses, sob duas condições hídricas (bem irrigado e com déficit hídrico) e dois níveis de K do solo (suficiente e alto). Foram obtidos dados de biomassa, estado nutricional, composição isotópica foliar ($\delta^{13}\text{C}\%$, $\delta^{15}\text{N}\%$), potencial hídrico foliar (Ψ_w) e fluorescência da clorofila. Diante do exposto, alguns dos principais resultados foram: Capítulo I- a adição de fertilizante às espécies de *Pinus* afetou a abundância natural de ^{13}C , resultando em diferentes respostas de EIUA; Capítulo II- o regime de adubação aumentou a produção de madeira em *Pinus caribaea* var. *hondurensis* e aumentou a densidade da madeira em *Pinus taeda*; Capítulo III- o alto suprimento de K afetou negativamente a fisiologia das mudas de *Pinus* spp., e inibiu a fotossíntese e o crescimento.

Palavras-chave: Manejo florestal, Dendrocronologia, Estresse hídrico, Abundância isotópica

ABSTRACT

Water and nutrient use efficiency of *Pinus caribaea* var. *hondurensis* and *Pinus taeda*

The overarching purpose of this study was to evaluate the water and nutrient use effectiveness of *Pinus caribaea* var. *hondurensis* and *Pinus taeda*. To achieve this, the present study was presented in three chapters. For chapters I and II, the study used *Pinus* spp. trees, at 13 years, from the Cooperative Program on Pine Research in Brazil (PPPIB) experiment, situated in the municipality of Itatinga, São Paulo. Inventory data and measurements of dendrometer bands were used to assess tree growth of *Pinus* spp. field-grown under distinct fertilized regimes (fertilized and control treatments). Additionally, forty-eight trees were selected, and four cores per tree at approximately 1.3 m height were collected. In Chapter I, the growth, climate-growth relationships, and intrinsic water use efficiency (WUE_i) were assessed by a combined analysis of cross-sectional area increment (CSA), water balance and carbon stable isotope ratio ($\delta^{13}\text{C}$). In Chapter II, wood density was analyzed by the non-destructive technique of X-ray densitometry. Also, the annual tree-rings were delimited and the crossdating between trees was performed. Tree ring width and wood density were analyzed by dendrochronological method and correlated with rainfall and temperature. For Chapter III, a greenhouse experiment was conducted with *Pinus caribaea* var. *hondurensis* and *Pinus taeda* seedlings for three months, under two water conditions (well-watered and water deficit) and two soil K levels (sufficient and high). Plant biomass, nutritional status, leaf isotopic composition ($\delta^{13}\text{C}\text{‰}$ $\delta^{15}\text{N}\text{‰}$), leaf water potential (Ψ_w) and chlorophyll fluorescence were measured. In light of the foregoing, some of the key results were: (Chapter I) fertilizer added to *Pinus* species affected the natural abundance of ^{13}C , resulting in different responses of WUE_i; (Chapter II) the fertilization regime increased the wood production in *Pinus caribaea* var. *hondurensis* and increased wood density in *Pinus taeda*; (Chapter III) the K supply negatively affected plant's physiology, and inhibited photosynthesis and growth.

Keywords: Forest management, Dendrochronology, Water stress, Isotopic abundance

1. INTRODUCTION

In Brazil, *Pinus* is among the most economically important genus, occupying 1.6 million hectares of planted forests, the equivalent to 28% of total area (IBA, 2020). Brazilian pine forests display some of the world's highest growth rates, with an average productivity of 30 m³. ha⁻¹. year⁻¹ in about 18-year rotation cycles (IBÁ, 2020). Although more extensive plantations are concentrated in South and Southeast regions, the introduction of different species coming from a wide range of ecological conditions in their original distribution has contributed to the expansion of forests planted with pine in other regions of the country (Chaves and Corrêa, 2003). Pine wood has potential for several uses such as production of cellulose, industrial laminated products, plywood for civil construction, furniture manufacturing and resin extraction.

Loblolly pine (*Pinus taeda*), species originated from United States, is the most planted species among pine in Brazil (Oliveira et al., 2018). *P. taeda* plantations are mostly managed by large-scale forest companies to supply raw material for pulp, paper, and wood-based composite industries (Oliveira et al., 2018). The highlands of South and Southern regions present most favorable growth conditions for that species, with mild temperatures associated with no water deficit (Campoe et al., 2016a; Dobner et al., 2019). Notably, under favorable conditions, *P. taeda* can reach growth rates higher than 50 m³. ha⁻¹. yr⁻¹, at ages of 16-18 years (Elesbão and Schneider, 2011; Leite et al., 2006), more than twice as much as in its natural United States forests (Albaugh et al., 2018).

Pinus caribaea, native to the Central America, is known by its varieties *caribaea*, *bahamensis* and *hondurensis*, and has been cultivated in Brazil for over 30 years. As a tropical species, *Pinus caribaea* has a broad adaptation in Brazilian territory, extending to Southeast and Central-west regions (Campoe et al., 2016b; Araújo et al., 2012; Pirovani et al., 2018) and some areas of the North and Northeast regions (Lima et al., 2022; de Oliveira et al., 2018). *P. caribaea* var. *hondurensis* is the most commonly planted variety in Brazil, and its timber has favorable quality for manifold uses (Shimizu & Medrado, 2005). Honduran provenance climates are very variable, range from 700 mm mean annual rainfall with 6 -7 months dry season, to over 3000 mm mean annual rainfall, and 2-3 months dry season (Robbins & Hughes, 1983). Typically, *Pinus caribaea* has excellent productivity and reaches higher growth rates than the *Pinus taeda* (Campoe et al., 2016b).

Much of the *Pinus* representativeness is associated to the genus' tolerance and rusticity, which makes possible its adaptation to low fertility soils, involving low input costs (Dobner Jr., 2013; Oliveira, 2013). However, although *Pinus* forests have low nutritional demand, studies have pointed to the importance of fertilization practices for the purpose of improving the productivity and to maintain the long-term sustainability of forests (Moro et al., 2014; Samuelson et al., 2008). Additionally, despite the economic importance of *Pinus* plantations in Brazil, not much is known about the management of these on response to the factors such as climate, site, and resources availability, leading to the belief that its potential has not been well explored.

Considering this, further studies directed to the understanding of how the productivity of the main pine species (tropical and subtropical) respond to climate, silvicultural and management practices have been required. This subject is directed towards the interests of the forest managers to create management strategies aimed at increasing productivity and improving competitiveness of *Pinus* forests. The main objective of this study is to evaluate the water and nutrient use effectiveness of *Pinus taeda* and *Pinus caribaea* var. *hondurensis*. Thus, three chapters were developed to achieve the present goal.

1. Climate-growth relationships and isotopic $\Delta^{13}\text{C}$ carbon responses of field-grown *Pinus* spp. to nutrient availability. This chapter characterizes the development of *Pinus caribaea* var. *hondurensis* and *Pinus taeda* trees grown in an experimental site located in Itatinga Municipality, São Paulo state, Brazil, from a factorial design with two level of management, considering fertilization regime. Biomass variations were monthly analyzed over a 7-year period and correlated to local climate variables. Intra-annual $\delta^{13}\text{C}$ analysis was applied jointly with biomass and climate data for the in-depth assessing of water use effectiveness of *Pinus caribaea* var. *hondurensis* and *Pinus taeda* trees.

2. Effects of fertilization management on stand development and radial wood density variability of *Pinus caribaea* var. *hondurensis* and *Pinus taeda*. In this chapter, non-destructive X-ray densitometry analysis was applied to assess wood density variability of 13-year-old *Pinus caribaea* var. *hondurensis* trees, considering fertilized and unfertilized treatments. Interrelations of tree-ring width, microdensity and biomass were also assessed and correlated to local climate data.

3. Effect of high potassium supply and soil water regime on the early growth of *Pinus caribaea* var. *hondurensis* and *Pinus taeda*. Here, the objective was to evaluate the

effects of drought stress and K-fertilization on morphological and physiological responses of *Pinus caribaea* var. *hondurensis* and *Pinus taeda* seedlings. To achieve the proposed objectives a greenhouse experiment was conducted for three months. Measurements include growth, plant chemical composition, chlorophyll fluorescence, leaf water potential, and isotopic composition ($\delta^{13}\text{C}$ e $\delta^{15}\text{N}$).

REFERENCES

- Albaugh, T.J., Fox, T.R., Maier, C.A., Campoe, O.C., Rubilar, R.A., Cook, R.L., Raymond, J.E., Alvares, C.A., Stape, J.L., 2018. A common garden experiment examining light use efficiency and heat sum to explain growth differences in native and exotic *Pinus taeda*. *For. Ecol. Manage.* 425, 35–44. <https://doi.org/10.1016/j.foreco.2018.05.033>
- Araújo, R.F., Matricardi, E.A.T., Nappo, M.E., 2012. Ecological zoning for small scale traditional forest species in the federal district. *Floresta* 42, 421–430. <https://doi.org/10.5380/rf.v42i2.19570>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016a. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. *For. Ecol. Manage.* 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016b. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. *For. Ecol. Manage.* 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- Chaves, R. de Q., Corrêa, G.F., 2003. Micronutrients in the soil - *Pinus caribaea* morelet system with yellowing of the needles followed by senescence and death. *Rev. Arvore* 27, 769–778.
- Dobner Jr., M., 2013. Crown thinning effects on growth and wood quality of *Pinus taeda* stands in southern Brazil. *Fac. Environ. Nat. Resour. Albert-Ludwigs-Universität* 221.
- Dobner, M., Nicoletti, M.F., Arce, J.E., 2019. Influence of crown thinning on radial growth pattern of *Pinus taeda* in southern Brazil. *New For.* 50, 437–454. <https://doi.org/10.1007/s11056-018-9669-x>
- Elesbão, L.E.G., Schneider, P.R., 2011. Yield of *Pinus taeda* L. in thinned stand in the Brazilian southern region. *Cienc. Florest.* 21, 119–124.
- Indústria Brasileira de Árvores (IBA), 2020. Annual Report: 2020. Brazilian Tree Industry. <https://iba.org/datafiles/publicacoes/relatorios/relatorio-iba-2020>

- Leite, H.G., Nogueira, G.S., Moreira, A.M., 2006. Effect of spacing and age on stand variables of *Pinus taeda* L. Rev. Árvore 30, 603–612. <https://doi.org/10.1590/s0100-67622006000400013>
- Lima, G.M.L., Gomes, N.S.B., da Cunha, T.A., Figueiredo, A., 2022. Effects of meteorological variables on *Pinus caribaea* growth in different ages at the Amazon region. Floresta 52, 113–121. <https://doi.org/10.5380/RF.V52I1.78392>
- Moro, L., Gatiboni, L.C., Simonete, M.A., Cezar, P., 2014. Response of one-, five-, and nine-year-old *Pinus taeda* to NPK fertilization in Southern Brazil. R. Bras. Ci. Solo, 1181–1189.
- Munhoz, J.S.B. 2011. Characterization of forest productivity and growth patterns of *Pinus taeda* L. in Southern Brazil through of trunk analysis. University of São Paulo, Piracicaba. (Msc thesis).
- Oliveira, R.K., 2013. Assessment of the sustainability of agroforestry production systems in Brazil based on emergy and economic criteria. Dept. of Forest Sciences, Federal Univ. of Paraná, Curitiba. (Ph.D. thesis).
- Oliveira, R.K., Higa, A.R., Silva, L.D., Silva, I.C., da Penha Moreira Gonçalves, M., 2018. Emergy-based sustainability assessment of a Loblolly pine (*Pinus taeda*) production system in southern Brazil. Ecol. Indic. 93, 481–489. <https://doi.org/10.1016/j.ecolind.2018.05.027>
- Pirovani, D.B., Pezzopane, J.E.M., Xavier, A.C., Pezzopane, J.R.M., de Jesus Júnior, W.C., Machuca, M.A.H., dos Santos, G.M.A.D.A., da Silva, S.F., de Almeida, S.L.H., de Oliveira Peluzio, T.M., Eugenio, F.C., Moreira, T.R., Alexandre, R.S., dos Santos, A.R., 2018. Climate change impacts on the aptitude area of forest species. Ecol. Indic. 95, 405–416. <https://doi.org/10.1016/j.ecolind.2018.08.002>
- Robbins, A.M.J.; Hughes, E.E. Provenance regions for *Pinus caribaea* and *P. oocarpa* within the Republic of Honduras. 1983 Oxford : University of Oxford. 77 p. Commonwealth Forestry Institute. Unit of Tropical Silviculture. Tropical Forestry (Paper, 18).
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K., Kane, M., 2008. Growth and physiology of Loblolly pine in response to long-term resource management: Defining growth potential in the southern United States. Can. J. For. Res. 38, 721–732. <https://doi.org/10.1139/X07-191>
- Shimizu, J.Y.; Medrado, M.J.S. Pine cultivation. Embrapa Florestas Production Systems. n.5, p.1-18, 2005.

2. CLIMATE-GROWTH RELATIONSHIPS AND ISOTOPIC $\Delta^{13}\text{C}$ CARBON RESPONSES OF FIELD-GROWN *PINUS* SPP. TO NUTRIENT AVAILABILITY

2.1. Introduction

Brazilian pine plantations have one of the highest productivity rates in the world, with an average of $30 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (IBA, 2020), and consists predominantly of subtropical species as opposed to tropical species. Loblolly pine (*Pinus taeda*), native to North America, is the most planted species. The good performance of *Pinus* spp. plantations is to be largely attributed to the more favorable soil and climatic conditions (Sass et al., 2020) as well as the selection of more adapted and productive genotypes (Aspinwall et al., 2011). However, pine forests show wide regional variation in productivity, ranging from 15 to $50 \text{ m}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (IPEF, 2016), which is ascribable mainly to differences in silvicultural practices management. That is because due to genetic and environmental factors and silvicultural treatments interacts on the capacity of *Pinus* spp. production is still unclear.

Diversified responses of *Pinus* species to climate-edaphic variability are directly connected to phenotypic plasticity and to local adaptation (Corcuera et al., 2010; Richter et al., 2012; Taïbi et al., 2015; Valladares et al., 2007) and therefore are the basis for adoption of best management practices aimed at increasing pine productivity and to maintain the long-term sustainability of forests. *Pinus Caribaea* var. *hondurensis*, a tropical pine, has been drawing some attention among forest managers because it is assumed to be relatively drought resistant (Barret; Golfari, 1962) and able to adapt to various climate conditions and soil types (Chaves and Corrêa, 2003; Shimizu, 2006). In contrast, as a subtropical species, *Pinus taeda* is well established in regions with mild temperatures, where the annual water deficit is less than 50mm (Pirovani et al., 2018).

Most Brazilian pine plantations are on low-fertility and sandy soils where moisture is frequently limiting (Sass et al., 2020). Despite the genus' tolerance and rusticity (Dobner Jr., 2013; Sixel et al., 2015), soil nutrient availability in pine stands is considered one of the most important factors affecting forest yield (Allen et al., 2005; Fox et al., 2007; Maggard et al., 2016). Fertilization increases pine productivity mainly through increases in leaf area index and intercepted radiation (Albaugh et al., 2016). Furthermore, it is known that there are interactive effects of nutrient availability and water stress on the physiological processes and

tree growth (Maggard et al., 2016; Ward et al., 2015). In this sense, it has been suggested that the fertilization may be beneficial in *Pinus* spp. plantations experiencing reduced water availability (Faustino et al., 2013; Samuelson et al., 2018; Wightman et al., 2016).

Fractionations of stable carbon isotope ($\delta^{13}\text{C}$ ‰) in tree rings of *Pinus* species in sub- and tropical (Brooks and Mitchell, 2011; Fichtler et al., 2010; Ibell et al., 2013; Krepkowski et al., 2013; van der Sleen et al., 2017) zones have been analyzed at inter- and intra-annual resolutions. Linking tree growth, carbon isotopic composition provides integrated measures of both environmental conditions and plant physiological processes, and is related to the plant water use efficiency (Farquhar et al., 1982; Mateus et al., 2019; 2022). Stomatal conductance for CO_2 and the photosynthetic carbon assimilation are regulated by the partial pressure of CO_2 in the leaf intercellular spaces (Farquhar et al., 1989). The CO_2 diffusion through stomata and the carboxylation process mediated by Rubisco are the principal components of photosynthesis influencing carbon discrimination and $^{13}\text{C}/^{12}\text{C}$ isotopic ratio (O'Leary, 1988, 1993). The primary mechanism for inhibition of photosynthesis under water deficit is the decrease in intercellular CO_2 concentration and a reduced CO_2 supply to Rubisco (Marques et al., 1995). As the water availability cause variations of $\text{CO}_{2\text{plant}} / \text{CO}_{2\text{atm}}$ mainly through their effects on stomatal conductance and photosynthetic activity, these effects are measurable as either changes in $\delta^{13}\text{C}$ or carbon discrimination (Δ). Overall, water stress condition causes stomata closure, reduces stomatal conductance for CO_2 , and leads to increased water use efficiency. It is expected to be recorded in tree-rings as an increase of the ratio between ^{13}C and ^{12}C stable isotopes of carbon fixed in stem wood (McDowell et al., 2003).

The present work evaluated the climate-growth relationships of *Pinus caribaea* var. *hondurensis* and *Pinus taeda* stands grown under fertilized and unfertilized treatments, on an experimental area situated in the Southeast Brazil. These data were linked to the variation in $\delta^{13}\text{C}$ of annual rings to assess the water use efficiency of trees. The hypotheses are: (1) the fertilization regime would influence the tree cambial activity and wood production of the two studied *Pinus* species; (2) the natural abundance of ^{13}C may be an effective tool for assessing the effects of fertilization regime on tree WUE (as indicated by wood $\delta^{13}\text{C}$) and tree growth.

2.2. Conclusions

The tree growth of *Pinus caribaea* var. *hondurensis* and *Pinus taeda* showed significant relationships to meteorological variables and all tree size classes responded to multiple meteorological variables related to water availability and evapotranspiration. Considering the climate aptitude of studied *Pinus* species, the water balance analysis revealed that the tree growth performance was not significantly impacted by drought stress in most of the years of study.

Differences between treatments were recorded in $\delta^{13}\text{C}$ which showed that fertilized *Pinus* spp. trees displayed higher carbon isotope discrimination values. This indicates that the increased of nutrient availability improved the soil water absorption capacity, resulting in higher photosynthetic performance of *Pinus* spp. trees. Unfertilized trees of *Pinus caribaea* var. *hondurensis* presented lower wood productivity associated to higher WUEi. In return, fertilized trees of *P. taeda* showed higher WUEi in some drier periods, without significant changes in growth rates. In general, *P. caribaea* var. *hondurensis* has proved to be more water-use efficient than *P. taeda*, being able to use smaller amounts of water for a higher wood production.

References

- Albaugh, T.J., Albaugh, J.M., Fox, T.R., Allen, H.L., Rubilar, R.A., Trichet, P., Loustau, D., Linder, S., 2016. Tamm Review: Light use efficiency and carbon storage in nutrient and water experiments on major forest plantation species. *For. Ecol. Manage.* 376, 333–342. <https://doi.org/10.1016/j.foreco.2016.05.031>
- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192, 3–19. <https://doi.org/10.1016/j.foreco.2004.01.002>
- Albaugh, T.J., Fox, T.R., Maier, C.A., Campoe, O.C., Rubilar, R.A., Cook, R.L., Raymond, J.E., Alvares, C.A., Stape, J.L., 2018. A common garden experiment examining light use efficiency and heat sum to explain growth differences in native and exotic *Pinus taeda*. *For. Ecol. Manage.* 425, 35–44. <https://doi.org/10.1016/j.foreco.2018.05.033>
- Ali, M.A., Louche, J., Duchemin, M., Plassard, C., 2014. Positive growth response of *Pinus pinaster* seedlings in soils previously subjected to fertilization and irrigation. *For. Ecol. Manage.* 318, 62–70. <https://doi.org/10.1016/j.foreco.2014.01.006>
- Allen, C.B., Willl, R.E., Jacobson, M.A., 2005. Production Efficiency and Radiation Use efficiency of four tree species receiving irrigation and fertilization. *For. Sci.* 51, 557–569.

- Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. FAO irrigation and drainage paper N°. 56 - Crop Evapotranspiration.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. Meteorol. Zeitschrift. 22, 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Araújo, R.F., Matricardi, E.A.T., Nappo, M.E., 2012. Ecological zoning for small scale traditional forest species in the federal district. Floresta. 42, 421–430. <https://doi.org/10.5380/ufv.v42i2.19570>
- Aspinwall, M.J., King, J.S., McKeand, S.E., Bullock, B.P., 2011. Genetic effects on stand-level uniformity and above- and belowground dry mass production in juvenile loblolly pine. For. Ecol. Manage. 262, 609–619. <https://doi.org/10.1016/j.foreco.2011.04.029>
- Barbour MM, Andrews TJ, Farquhar GD. 2001. Correlations between oxygen isotope ratios of wood constituents of *Quercus* and *Pinus* samples from around the world. Australian Journal of Plant Physiology 28: 335–348.
- Barret, W. H. G.; Golfari, L. Descripción de las nuevas variabilidades del “Pino del Caribe”. Caribbean Forester, Porto Rico, v. 23, n. 2, p. 59-71, 1962.
- Barrie, A.; Prosser, S. J. Automated analysis of light-element stable isotope ratio mass spectrometry. In: Boutton, T. W.; Yamasaki, S. Mass spectrometry of soils New York: Marcel Dekker, 1996. p. 1-46.
- Begum, S., Nakaba, S., Yamagishi, Y., Oribe, Y., Funada, R., 2013. Regulation of cambial activity in relation to environmental conditions: Understanding the role of temperature in wood formation of trees. Physiol. Plant. 147, 46–54. <https://doi.org/10.1111/j.1399-3054.2012.01663.x>
- Brooks, J.R., Mitchell, A.K., 2011. Interpreting tree responses to thinning and fertilization using tree-ring stable isotopes. New Phytol. 190, 770–782. <https://doi.org/10.1111/j.1469-8137.2010.03627.x>
- Caminero, L., Génova, M., Camarero, J.J., Sánchez-Salguero, R., 2018. Growth responses to climate and drought at the southernmost European limit of Mediterranean *Pinus pinaster* forests. Dendrochronologia 48, 20–29. <https://doi.org/10.1016/j.dendro.2018.01.006>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016a. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. For. Ecol. Manage. 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016b. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. For. Ecol. Manage. 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- Carneiro, R. L. 2013. Characterization of photosynthesis and stomatal conductance in *Pinus caribaea* var. *hondurensis* and *Pinus taeda* in Itatinga, São Paulo. University of São Paulo, Piracicaba. (Msc thesis).

- Carneiro, R. L.; Conti Jr, J. L. F.; Sidorowski, F. A.; Andrade, H. B.; Stape, J. L. Effect of nutrition and irrigation on bole radial growth and basal area of *Eucalyptus* clones in northern Minas Gerais. In: International Symposium of scientific research Of São Paulo University- Agricultural – Forestry Science. 2007. Annals...Piracicaba, ESALQ-USP, 2007.
- Carpanezzi, A., Ferreira, C., Rotta, E., Namikawa, I., Sturion, J., Pereira, J., Montaigner, L., Rauen, M. de J., Silveira, R., Alves, S., 1986. Ecological zoning for forest plantations in the State of Paraná. Brasília: EMBRAPA – Centro Nacional de Pesquisa de Florestas
- Chaves, R. de Q., Corrêa, G.F., 2003. Micronutrients in the soil - *Pinus caribaea* morelet system with yellowing of the needles followed by senescence and death. Rev. Arvore 27, 769–778.
- Corcuera, L., Gil-Pelegrin, E., Notivol, E., 2010. Phenotypic plasticity in *Pinus pinaster* $\delta^{13}\text{C}$: Environment modulates genetic variation. Ann. For. Sci. 67. <https://doi.org/10.1051/forest/2010048>
- Dhirendra Singh, N., Venugopal, N., 2011. Cambial activity and annual rhythm of xylem production of *Pinus kesiya* Royle ex. Gordon (Pinaceae) in relation to phenology and climatic factors growing in sub-tropical wet forest of North East India. Flora Morphol. Distrib. Funct. Ecol. Plants 206, 198–204. <https://doi.org/10.1016/j.flora.2010.04.021>
- Dietrich, R., Bell, F.W., Silva, L.C.R., Cecile, A., Horwath, W.R., Anand, M., 2016. Climatic sensitivity, water-use efficiency, and growth decline in boreal jack pine (*Pinus banksiana*) forests in Northern Ontario. J. Geophys. Res. Biogeosciences 121, 2761–2774. <https://doi.org/10.1002/2016JG003440>
- Dobner Jr., M., 2013. Crown thinning effects on growth and wood quality of *Pinus taeda* stands in southern Brazil. Fac. Environ. Nat. Resour. Albert-Ludwigs-Universität 221.
- Dobner, M., Nicoletti, M.F., Arce, J.E., 2019. Influence of crown thinning on radial growth pattern of *Pinus taeda* in Southern Brazil. New For. 50, 437–454. <https://doi.org/10.1007/s11056-018-9669-x>
- Elesbão, L.E.G., Schneider, P.R., 2011. Yield of *Pinus taeda* L. in thinned stand in the Brazilian southern region. Cienc. Florest. 21, 119–124.
- Ellsworth, D.S., 2000. Seasonal CO₂ assimilation and stomatal limitations in a *Pinus taeda* canopy. Tree Physiol. 20, 435–445. <https://doi.org/10.1093/treephys/20.7.435>
- English, N., McDowell, N., Allen, C., Mora, C., 2011. The effects of α -cellulose extraction and blue-stain fungus on retrospective studies of carbon and oxygen isotope variation in live and dead trees. Rapid Commun. Mass Spectrom. 25, 3083–3090.
- Ewers, B.E., Oren, R., Albaugh, T.J., Dougherty, P.M., 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. Ecol. Appl. 9, 513–525. [https://doi.org/10.1890/1051-0761\(1999\)009](https://doi.org/10.1890/1051-0761(1999)009)
- Farquhar, G.D., Ehleringer, R., Hubic, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537.

- Farquhar, G.D., O'Leary, M.H., Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9, 121–137. <https://doi.org/10.1071/PP9820121>
- Faustino, L.I., Bulfe, N.M.L., Pinazo, M.A., Monteoliva, S.E., Graciano, C., 2013. Dry weight partitioning and hydraulic traits in young *Pinus taeda* trees fertilized with nitrogen and phosphorus in a subtropical area. *Tree Physiol.* 33, 241–251. <https://doi.org/10.1093/treephys/tps129>
- Fichtler, E., Helle, G., Worbes, M., 2010. Stable-carbon isotope time series from tropical tree rings indicate a precipitation signal. *Tree-Ring Res.* 66, 35–49. <https://doi.org/10.3959/2008-20.1>
- Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. *South. J. Appl. For.* 31, 5–11. <https://doi.org/10.1093/sjaf/31.1.5>
- Fyllas, N.M., Christopoulou, A., Galanidis, A., Michelaki, C.Z., Dimitrakopoulos, P.G., Fulé, P.Z., Arianoutsou, M., 2017. Tree growth-climate relationships in a forest-plot network on Mediterranean mountains. *Sci. Total Environ.* 598, 393–403. <https://doi.org/10.1016/j.scitotenv.2017.04.145>
- Helle, G., Schleser, G., 2004. Beyond CO₂-fixation by Rubisco – an interpretation of ¹³C/¹²C variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant. Cell Environ.* 27, 380.
- Golfari, L., 1975. Ecological zoning of the State of Minas Gerais for reforestation [Brazil]. PNUD/FAO/IBDF –BRA/71/545. (Série Técnica no3).
- Goldstein, G., Bucci, S.J., Scholz, F.G., 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? *Tree Physiol.* 33, 238–240. <https://doi.org/10.1093/treephys/tpt007>
- Gonçalves, J.L.D.M., Alvares, C.A., Gonçalves, T.D., 2012. Soil and productivity mapping of *Eucalyptus grandis* plantations, using a geographic information system. *Sci. For.* 40, 187–201.
- Gough, C.M., Seiler, J.R., Johnsen, K.H., Sampson, D.A., 2004. Seasonal photosynthesis in fertilized and nonfertilized loblolly pine. *For. Sci.* 50, 1–9.
- Hartl-Meier, C., Zang, C., Büntgen, U., Esper, J., Rothe, A., Göttelein, A., Dirnböck, T., Treydte, K., 2014. Uniform climate sensitivity in tree-ring stable isotopes across species and sites in a mid-latitude temperate forest. *Tree Physiol.* 35, 4–15. <https://doi.org/10.1093/treephys/tpu096>
- Hevia, A., Sánchez-Salguero, R., Camarero, J.J., Buras, A., Sangüesa-Barreda, G., Galván, J.D., Gutiérrez, E., 2018. Towards a better understanding of long-term wood-chemistry variations in old-growth forests: A case study on ancient *Pinus uncinata* trees from the Pyrenees. *Sci. Total Environ.* 625. <https://doi.org/10.1016/j.scitotenv.2017.12.229>

- Hickel, K., Zhang, L., 2006. Estimating the impact of rainfall seasonality on mean annual water balance using a top-down approach. *J. Hydrol.* 331, 409–424. <https://doi.org/10.1016/j.jhydrol.2006.05.028>
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bull.* 43, 69–78.
- IBÁ (Brazilian tree Industry), 2020. Annual Report: 2020. Brazilian Tree Industry. <<https://iba.org/datafiles/publicacoes/relatorios/relatorio-iba-2020.pdf>>
- Ibell, P.T., Xu, Z., Blumfield, T.J., 2013. The influence of weed control on foliar $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and tree growth in an 8 year-old exotic pine plantation of subtropical Australia. *Plant Soil* 369, 199–217. <https://doi.org/10.1007/s11104-012-1554-3>
- Institute of Forestry Research and Studies. 2016. The advances in productivity of pine in Brazil. Technical Bulletin (n. 242).
- Jokela, E.J., Dougherty, P.M., Martin, T.A., 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: A synthesis of seven long-term experiments. *For. Ecol. Manage.* 192, 117–130. <https://doi.org/10.1016/j.foreco.2004.01.007>
- Krepkowski, J., Gebrekirstos, A., Shibistova, O., Bräuning, A., 2013. Stable carbon isotope labeling reveals different carry-over effects between functional types of tropical trees in an Ethiopian mountain forest. *New Phytol.* 199, 431–440. <https://doi.org/10.1111/nph.12266>
- Leite, H.G., Nogueira, G.S., Moreira, A.M., 2006. Effect of spacing and age on stand variables of *Pinus taeda* L. *Rev. Árvore.* 30, 603–612. <https://doi.org/10.1590/s0100-67622006000400013>
- Lévesque, M., Saurer, M., Siegwolf, R., Eilmann, B., Brang, P., Bugmann, H., Rigling, A., 2013. Drought response of five conifer species under contrasting water availability suggests high vulnerability of Norway spruce and European larch. *Glob. Chang. Biol.* 19, 3184–3199. <https://doi.org/10.1111/gcb.12268>
- Lim, H., Oren, R., Palmroth, S., Tor-ngern, P., Mörling, T., Näsholm, T., Lundmark, T., Helmissaari, H.S., Leppälammil-Kujansuu, J., Linder, S., 2015. Inter-annual variability of precipitation constrains the production response of boreal *Pinus sylvestris* to nitrogen fertilization. *For. Ecol. Manage.* 348, 31–45. <https://doi.org/10.1016/j.foreco.2015.03.029>
- Lima, G.M.L., Gomes, N.S.B., da Cunha, T.A., Figueiredo, A., 2022. Effects of meteorological variables on *Pinus caribaea* growth in different ages at the Amazon region. *Floresta* 52, 113–121. <https://doi.org/10.5380/RF.V52I1.78392>
- Lin, Y.S., Medlyn, B.E., Duursma, R.A., Prentice, I.C., Wang, H., Baig, S., Eamus, D., De Dios, V.R., Mitchell, P., Ellsworth, D.S., De Beeck, M.O., Wallin, G., Uddling, J., Tarvainen, L., Linderson, M.L., Cernusak, L.A., Nippert, J.B., Ocheltree, T.W., Tissue, D.T., Martin-StPaul, N.K., Rogers, A., Warren, J.M., De Angelis, P., Hikosaka, K., Han, Q., Onoda, Y., Gimeno, T.E., Barton, C.V.M., Bennie, J., Bonal, D., Bosc, A., Löw, M., Macinins-Ng, C., Rey, A., Rowland, L., Setterfield, S.A., Tausz-Posch, S., Zaragoza-

- Castells, J., Broadmeadow, M.S.J., Drake, J.E., Freeman, M., Ghannoum, O., Hutley, L.B., Kelly, J.W., Kikuzawa, K., Kolari, P., Koyama, K., Limousin, J.M., Meir, P., Da Costa, A.C.L., Mikkelsen, T.N., Salinas, N., Sun, W., Wingate, L., 2015. Optimal stomatal behaviour around the world. *Nat. Clim. Chang.* 5, 459–464. <https://doi.org/10.1038/nclimate2550>
- McDowell, N., Brooks, J.R., Fitzgerald, S.A., Bond, B.J., 2003. Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. *Plant Cell Environ.* 26, 631–644.
- Maggard, A.O., Will, R.E., Wilson, D.S., Meek, C.R., Vogel, J.G., 2016. Fertilization reduced stomatal conductance but not photosynthesis of *Pinus taeda* which compensated for lower water availability in regard to growth. *For. Ecol. Manage.* 381, 37–47. <https://doi.org/10.1016/j.foreco.2016.08.046>
- Meko, D.M., Baisan, C.H., 2001. Pilot study of latewood-width of conifers as an indicator of variability of summer rainfall in the North American monsoon region. *Int. J. Climatol.* 21, 697–708. <https://doi.org/10.1002/joc.646>
- Moro, L., Gatiboni, L.C., Simonete, M.A., Cezar, P., 2014. Response of one-, five-, and nine-year-old *Pinus taeda* to NPK fertilization in southern Brazil. *R. Bras. Ci. Solo*, 1181–1189.
- Muvundja, F.A., Wüest, A., Isumbisho, M., Kaningini, M.B., Pasche, N., Rinta, P., Schmid, M., 2014. Modelling Lake Kivu water level variations over the last seven decades. *Limnologia* 47, 21–33. <https://doi.org/10.1016/j.limno.2014.02.003>
- O’Leary MH (1988). Carbon isotope in photosynthesis. *Bio. Sci.*, 38: 325-336.
- O’Leary MH (1993). Biochemical basis of carbon isotope fractionation. In: *Stable isotopes and plant carbon/water relations* (Eds. Ehleringer, J.R., Hall, A.E. and Farquhar, G.D.). Academic Press, pp. 19-20.
- Oliveira, R.K., Higa, A.R., Silva, L.D., Silva, I.C., da Penha Moreira Gonçalves, M., 2018. Emergency-based sustainability assessment of a loblolly pine (*Pinus taeda*) production system in southern Brazil. *Ecol. Indic.* 93, 481–489. <https://doi.org/10.1016/j.ecolind.2018.05.027>
- Palmroth, S., Katul, G.G., Maier, C.A., Ward, E., Manzoni, S., Vico, G., 2013. On the complementary relationship between marginal nitrogen and water-use efficiencies among *Pinus taeda* leaves grown under ambient and CO₂-enriched environments. *Ann. Bot.* 111, 467–477. <https://doi.org/10.1093/aob/mcs268>
- Panayotov, M., Bebi, P., Trouet, V., Yurukov, S., 2010. Climate signal in tree-ring chronologies of *Pinus peuce* and *Pinus heldreichii* from the Pirin mountains in Bulgaria. *Trees - Struct. Funct.* 24, 479–490. <https://doi.org/10.1007/s00468-010-0416-y>
- Pirovani, D.B., Pezzopane, J.E.M., Xavier, A.C., Pezzopane, J.R.M., de Jesus Júnior, W.C., Machuca, M.A.H., dos Santos, G.M.A.D.A., da Silva, S.F., de Almeida, S.L.H., de Oliveira Peluzio, T.M., Eugenio, F.C., Moreira, T.R., Alexandre, R.S., dos Santos, A.R., 2018. Climate change impacts on the aptitude area of forest species. *Ecol. Indic.* 95, 405–416. <https://doi.org/10.1016/j.ecolind.2018.08.002>

- Pons, T.L., Helle, G., 2011. Identification of anatomically non-distinct annual rings in tropical trees using stable isotopes. *Trees - Struct. Funct.* 25, 83–93. <https://doi.org/10.1007/s00468-010-0527-5>
- Pumijumnong, N., Songtrirat, P., Buajan, S., Preechamart, S., Chareonwong, U., Muangsong, C., 2021. Climate control of cambial dynamics and tree-ring width in two tropical pines in Thailand. *Agric. For. Meteorol.* 303, 108394. <https://doi.org/10.1016/j.agrformet.2021.108394>
- Rachid-Casnati, C., Mason, E.G., Woollons, R.C., Landsberg, J.J., 2020. Modelling growth of *Pinus taeda* and *Eucalyptus grandis* as a function of light sums modified by air temperature, vapour pressure deficit, and water balance. *New Zeal. J. For. Sci.* 50, 1–18. <https://doi.org/10.33494/nzjfs502020x17x>
- Rahman, M.H., Nugroho, W.D., Nakaba, S., Kitin, P., Kudo, K., Yamagishi, Y., Begum, S., Marsoem, S.N., Funada, R., 2019. Changes in cambial activity are related to precipitation patterns in four tropical hardwood species grown in Indonesia. *Am. J. Bot.* 106, 760–771. <https://doi.org/10.1002/ajb2.1297>
- Richter, S., Kipfer, T., Wohlgemuth, T., Guerrero, C.C., Ghazoul, J., Moser, B., 2012. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia* 169, 269–279. <https://doi.org/10.1007/s00442-011-2191-x>
- Rozas, V., García-González, I., Zas, R., 2011. Climatic control of intra-annual wood density fluctuations of *Pinus pinaster* in NW Spain. *Trees - Struct. Funct.* 25, 443–453. <https://doi.org/10.1007/s00468-010-0519-5>
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K., Kane, M., 2008. Growth and physiology of loblolly pine in response to long-term resource management: Defining growth potential in the southern United States. *Can. J. For. Res.* 38, 721–732. <https://doi.org/10.1139/X07-191>
- Samuelson, L.J., Kane, M.B., Markewitz, D., Teskey, R.O., Akers, M.K., Stokes, T.A., Pell, C.J., Qi, J., 2018. Fertilization increased leaf water use efficiency and growth of *Pinus taeda* subjected to five years of throughfall reduction. *Can. J. For. Res.* 48, 227–236. <https://doi.org/10.1139/cjfr-2017-0357>
- Samuelson, L.J., Stokes, T.A., 2006. Transpiration and canopy stomatal conductance of 5-year-old loblolly pine in response to intensive management. *For. Sci.* 52, 313–323.
- Sass, A.L., Bassaco, M.V.M., Motta, A.C.V., Maeda, S., Barbosa, J.Z., Bognola, I.A., Bosco, J.V.G., Goularte, G.D., Prior, S.A., 2020. Cellulosic industrial waste to enhance *Pinus taeda* nutrition and growth: A study in subtropical Brazil. *Sci. For. Sci.* 48, 1–16. <https://doi.org/10.18671/SCIFOR.V48N126.13>
- Shimizu, J.Y., 2006. Pine in Brazilian Silviculture. *Revista da Madeira*, 16, 4-14.
- Silva J, M., Arrabica M. C., 1995. Effect of water stress on Rubisco activity of *Setaria sphacelota*. In: *Photosynthesis: from light to Biosphere*. (Ed. P. Mathis, Kluwer), Acad. Publs. Dordrecht-Boston-London, Vol. IV, pp. 545-548.

- Sixel, R.M. de M., Arthur, J.C., Gonçalves, J.L. de M., Alvares, C.A., Andrade, G.R.P., Azevedo, A.C., Stahl, J., Moreira, A.M., 2015. Sustainability of wood productivity of *Pinus taeda* based on nutrient export and stocks in the biomass and in the soil. *Rev. Bras. Cienc. do Solo* 39, 1416–1427. <https://doi.org/10.1590/01000683rbc20140297>
- Taeger, S., Zang, C., Liesebach, M., Schneck, V., Menzel, A., 2013. Impact of climate and drought events on the growth of Scots pine (*Pinus sylvestris* L.) provenances. *For. Ecol. Manage.* 307, 30–42. <https://doi.org/10.1016/j.foreco.2013.06.053>
- Taïbi, K., del Campo, A.D., Aguado, A., Mulet, J.M., 2015. The effect of genotype by environment interaction, phenotypic plasticity and adaptation on *Pinus halepensis* reforestation establishment under expected climate drifts. *Ecol. Eng.* 84, 218–228. <https://doi.org/10.1016/j.ecoleng.2015.09.005>
- Tans, P.P., Mook, W.G., 1980. Past atmospheric CO₂ levels and the ¹³C/¹²C ratios in tree rings. *Tellus* 32, 268–283. <https://doi.org/10.1111/j.2153-3490.1980.tb00954.x>
- Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M.A., Steppe, K., 2015. Responses of tree species to heat waves and extreme heat events. *Plant Cell Environ.* 38, 1699–1712. <https://doi.org/10.1111/pce.12417>
- Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. *J. Ecol.* 99, 254–264. <https://doi.org/10.1111/j.1365-2745.2010.01741.x>
- Thornthwaite, C. W; Mather, J.R. The water balance. *Publications in Climatology*, New Jersey, v.8, n.1, p. 59–117,1955.
- Valladares, F., Gianoli, E., Gómez, M.J., 2007. Ecological limits to plant phenotypic plasticity. *New Phytol.* 176, 749–763.
- van der Sleen, P., Zuidema, P.A., Pons, T.L., 2017. Stable isotopes in tropical tree rings: theory, methods and applications. *Funct. Ecol.* 31, 1674–1689. <https://doi.org/10.1111/1365-2435.12889>
- Venegas-González, A., von Arx, G., Chagas, M.P., Filho, M.T., 2015. Plasticity in xylem anatomical traits of two tropical species in response to intra-seasonal climate variability. *Trees - Struct. Funct.* 29, 423–435. <https://doi.org/10.1007/s00468-014-1121-z>
- Waghorn, M.J., Whitehead, D., Watt, M.S., Mason, E.G., Harrington, J.J., 2015. Growth, biomass, leaf area and water-use efficiency of juvenile *Pinus radiata* in response to water deficits. *New Zeal. J. For. Sci.* 45. <https://doi.org/10.1186/s40490-015-0034-y>
- Wallinger, R.S., 2002. Intensive forest management: Growing wood and preserving biodiversity in the U.S. South and Brazil. *For. Oper. Rev.* 4 (3), 5–11.
- Ward, E.J., Domec, J.C., Laviner, M.A., Fox, T.R., Sun, G., McNulty, S., King, J., Noormets, A., 2015. Fertilization intensifies drought stress: Water use and stomatal conductance of *Pinus taeda* in a midrotation fertilization and throughfall reduction experiment. *For. Ecol. Manage.* 355, 72–82. <https://doi.org/10.1016/j.foreco.2015.04.009>

- Warren, C.R., McGrath, J.F., Adams, M.A., 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia* 127, 476–486.
- Wightman, M.G., Martin, T.A., Gonzalez-Benecke, C.A., Jokela, E.J., Cropper, W.P., Ward, E.J., 2016. Loblolly pine productivity and water relations in response to throughfall reduction and fertilizer application on a poorly drained site in northern Florida. *Forests* 7. <https://doi.org/10.3390/f7100214>

3. EFFECTS OF FERTILIZATION MANAGEMENT ON STAND DEVELOPMENT AND RADIAL WOOD DENSITY VARIABILITY OF *PINUS CARIBAEA* VAR. *HONDURENSIS* AND *PINUS TAEDA*

3.1. Introduction

Understanding the mechanisms that control growth and wood formation of trees is critical for forecasting forest stands dynamics and to overview best management practices aimed at sustainable development and increased forestry productivity. Genetic and physiological components of plants are intrinsically related to their abilities to absorb and utilize nutrients under distinct environmental and ecological conditions. These traits interact with external factors such as soil moisture and temperature (Baligar et al., 2001), and how this dynamic affects the biomass production is related to the ability of crops to take up and utilize nutrients for maximum yields (Dijkstra et al., 2016; Toca et al., 2019).

Pinus taeda, a subtropical species from southeast United States, is the most cultivated *Pinus* species in Brazil (IBÁ, 2020). Among species of tropical pines, *Pinus caribaea* var. *hondurensis* has been increasingly cultivated in Brazil (de Lima et al., 2016; Gonçalez et al., 2018). In general, the *Pinus* genus is seen as exceptionally tolerant and rusticity, based on its satisfactory adaptation to low fertility soils (Kulmann et al., 2021; Pietrzykowski, 2014; Rocha et al., 2020). However, although *Pinus* forests have considerable low nutritional demand, studies have pointed to the importance of fertilization practices aiming to improve the productivity as well as to maintain the long-term sustainability of forest plantations (Campoe et al., 2016; Moro et al., 2014; Samuelson et al., 2008). Besides, despite the economic importance of *Pinus* plantations in Brazil, not much is known about the effects of fertilization management on the growth performance associated to the factors such as climate and wood properties, leading to the belief that the productivity potential of the *Pinus* spp. plantations has not been well explored.

Radial growth of trees greatly depends on the interactions between environmental and competition dynamic (Piutti and Cescatti, 1997). Changing environmental conditions, do not only influence growth rates of the trees (and thus ring width), but can also affect the wood properties, as wood density. To comprehend the role of the fertilization regime on forest dynamics in the context of the nutritional efficiency is facilitated by understanding of

tree growth changes into a longer assessment period. Dendrochronological analysis provides tools to explore radial variability of wood establishing relationships between tree-ring width, and climate data over time (tree age) (Aragão et al., 2019; Fritts, 1976). These relationships can be used in association with radial variation in wood density, for a in depth assessment of trees development (Gao et al., 2017; Jacquin et al., 2017; Tomazello et al., 2008). In this sense, annual tree-rings being a precise tool to assess long-term growth trends and to report accurately information about the effect of fertilization on stand development and their interaction with environmental conditions.

The present work used the Cooperative Program on Pine Research in Brazil (PPPIB) experiment to determine how tree growth of *Pinus taeda* and *Pinus Caribaea* var. *hondurensis* differ in response to fertilization, and how these responses are associated to tree-ring microdensity variability and climate variables.

3.2. Conclusions

In particular for *Pinus caribaea* var. *hondurensis*, fertilized plots varied greatly from the control plots in relation to tree growth and biomass production. Significant changes in the *P. caribaea* var. *hondurensis* tree-volume trends were verified in all years by the fertilization regime, indicating a high level of responsiveness to both fertilizer application periods.

The wood microdensitometry analysis associated to the study of annual rings provided accurate data to understand the impact of fertilization regime on *Pinus* spp. stands development over the years of study, regardless species and tree size class (large, medium, small). Although no significant effect was observed on tree stem volume increment of *Pinus taeda* trees, a small increase in wood density occurred in response to fertilization. Furthermore, the precipitation was a principal climate variable related to tree ring width (positive correlation) and wood density (negative correlation).

References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192, 3–19. <https://doi.org/10.1016/j.foreco.2004.01.002>
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. *Meteorol. Zeitschrift* 22, 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>

- Aragão, J.R.V., Groenendijk, P., Lisi, C.S., 2019. Dendrochronological potential of four neotropical dry-forest tree species: Climate-growth correlations in northeast Brazil. *Dendrochronologia* 53, 5–16. <https://doi.org/10.1016/j.dendro.2018.10.011>
- Baligar, V.C., Fageria, N.K., He, Z.L., 2001. Nutrient use efficiency in plants. *Commun. Soil Sci. Plant Anal.* 32, 921–950. <https://doi.org/10.1081/CSS-100104098>
- Binkley, D., Stape, J.L., Ryan, M.G., 2004. Thinking about efficiency of resource use in forests. *For. Ecol. Manage.* 193, 5–16. <https://doi.org/10.1016/j.foreco.2004.01.019>
- Björklund, J., Seftigen, K., Fonti, P., Nievergelt, D., von Arx, G., 2020. Dendroclimatic potential of dendroanatomy in temperature-sensitive *Pinus sylvestris*. *Dendrochronologia* 60, 125673. <https://doi.org/10.1016/j.dendro.2020.125673>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. *For. Ecol. Manage.* 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- De Lima, M.C.D., Barreto-Garcia, P.A.B., Sanquetta, C.R., De Novaes, A.B., De Melo, L.C., 2016. Estoques de biomassa e carbono de *Pinus caribaea* var. *hondurensis* em plantio homogêneo no Sudoeste da Bahia. *Cienc. Rural* 46, 957–962. <https://doi.org/10.1590/0103-8478cr20150493>
- Dijkstra, F.A., Carrillo, Y., Aspinwall, M.J., Maier, C., Canarini, A., Tahaei, H., Choat, B., Tissue, D.T., 2016. Water, nitrogen and phosphorus use efficiencies of four tree species in response to variable water and nutrient supply. *Plant Soil* 406, 187–199. <https://doi.org/10.1007/s11104-016-2873-6>
- Eberhardt, T.L., Samuelson, L.J., 2015. Collection of wood quality data by X-ray densitometry: a case study with three southern pines. *Wood Sci. Technol.* 49, 739–753. <https://doi.org/10.1007/s00226-015-0732-x>
- Ewers, B.E., Oren, R., Albaugh, T.J., Dougherty, P.M., 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. *Ecol. Appl.* 9, 513–525. [https://doi.org/10.1890/1051-0761\(1999\)009\[0513:COEOWA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0513:COEOWA]2.0.CO;2)
- Ferreira, A.T.B., Filho, M.T., 2009. Characterization of tree-rings of *Pinus caribaea* var. *hondurensis* Barr. et Golf. trees by X ray densitometry. *Sci. For. Sci.* 287–298.
- Gao, S., Wang, X., Wiemann, M.C., Brashaw, B.K., Ross, R.J., Wang, L., 2017. A critical analysis of methods for rapid and nondestructive determination of wood density in standing trees. *Ann. For. Sci.* 74, 1–13. <https://doi.org/10.1007/s13595-017-0623-4>
- Gonçalez, J.C., Santos, N., Gomes, F., 2018. Growth ring width of *Pinus caribaea* var. *hondurensis* and its relationship with wood properties. *Sci. Forestalis* 46, 309–317.
- Jacquin, P., Longuetaud, F., Leban, J.M., Mothe, F., 2017. X-ray microdensitometry of wood: A review of existing principles and devices. *Dendrochronologia* 42, 42–50. <https://doi.org/10.1016/j.dendro.2017.01.004>
- Kulmann, M.S. de S., Dick, G., Schumacher, M.V., 2021. Litterfall and accumulated nutrients in *Pinus taeda* plantation and native forest in southern Brazil. *Forests* 12. <https://doi.org/10.3390/f12121791>
- Martin, T.A., Jokela, E.J., 2004. Stand development and production dynamics of loblolly pine

- under a range of cultural treatments in north-central Florida USA. *For. Ecol. Manage.* 192, 39–58. <https://doi.org/10.1016/j.foreco.2004.01.004>
- Moro, L., Gatiboni, L.C., Simonete, M.A., Cezar, P., 2014. Response of one-, five-, and nine-year-old *Pinus taeda* to NPK fertilization in Southern Brazil. *R. Bras. Ci. Solo*, 1181–1189.
- Ortega Rodriguez, D.R., Tomazello-Filho, M., 2019. Clues to wood quality and production from analyzing ring width and density variabilities of fertilized *Pinus taeda* trees. *New For.* 50, 821–843. <https://doi.org/10.1007/s11056-018-09702-9>
- Pietrzykowski, M., 2014. Soil quality index as a tool for Scots pine (*Pinus sylvestris*) monoculture conversion planning on afforested, reclaimed mine land. *J. For. Res.* 25, 63–74. <https://doi.org/10.1007/s11676-013-0418-x>
- Piutti, E., Cescatti, A., 1997. A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Can. J. For. Res.* 27, 277–284. <https://doi.org/10.1139/x96-176>
- Reich, M., 2015. Complexity of nutrient use efficiency in plants Chapter 1 Physiological basis of plant nutrient use efficiency - Concepts , Opportunities and Challenges for its Improvement.
- Rocha, S.M.G., Vidaurre, G.B., Pezzopane, J.E.M., Almeida, M.N.F., Carneiro, R.L., Campoe, O.C., Scolforo, H.F., Alvares, C.A., Neves, J.C.L., Xavier, A.C., Figura, M.A., 2020. Influence of climatic variations on production, biomass and density of wood in *Eucalyptus clones* of different species. *For. Ecol. Manage.* 473, 118290. <https://doi.org/10.1016/j.foreco.2020.118290>
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K., Kane, M., 2008. Growth and physiology of loblolly pine in response to long-term resource management: Defining growth potential in the southern United States. *Can. J. For. Res.* 38, 721–732. <https://doi.org/10.1139/X07-191>
- Samuelson, L.J., Stokes, T.A., 2006. Transpiration and canopy stomatal conductance of 5-year-old loblolly pine in response to intensive management. *For. Sci.* 52, 313–323.
- Toca, A., Oliet, J.A., Villar-Salvador, P., Martínez Catalán, R.A., Jacobs, D.F., 2019. Ecologically distinct pine species show differential root development after outplanting in response to nursery nutrient cultivation. *For. Ecol. Manage.* 451, 117562. <https://doi.org/10.1016/j.foreco.2019.117562>
- Tomazello, M., Brazolin, S., Chagas, M.P., Oliveira, J.T.S., Ballarin, A.W., Benjamin, C.A., 2008. Application of X-ray technique in nondestructive evaluation of Eucalypt wood. *Maderas Cienc. y Tecnol.* 10, 139–149. <https://doi.org/10.4067/S0718-221X2008000200006>
- Topanotti, L.R., Vaz, D.R., Carvalho, S. de P.C. e., Rios, P.D., Tomazello-Filho, M., Dobner, M., Nicoletti, M.F., 2021. Growth and wood density of *Pinus taeda* L. as affected by shelterwood harvest in a two-aged stand in Southern Brazil. *Eur. J. For. Res.* 140, 869–881. <https://doi.org/10.1007/s10342-021-01372-1>
- Wilkinson, S.R., Mays, D.A., 2015. Mineral nutrition. *Tall Fescue* 41–73. <https://doi.org/10.2134/agronmonogr20.c4>

4. EFFECT OF HIGH POTASSIUM SUPPLY AND SOIL WATER REGIME ON THE EARLY GROWTH OF *PINUS CARIBAEA* VAR. *HONDURENSIS* AND *PINUS TAEDA*

4.1. Introduction

Globally, drought stress is one of the main abiotic factors that limits crop growth and its production (Ryan et al., 2010; Booth 2013; Anderegg and Hillerislambers 2016). It is a recognized fact that the water stress adversely impacts many aspects of the physiology of plants, especially photosynthetic capacity (Osakabe et al., 2014). Under water limited conditions, plants promote the closure of stomata to avoid water losses, and although this mechanism prevents the desiccation and xylem cavitation, it also restricts CO₂ supply for photosynthesis, leading to a decrease in the tree productivity (Chaves et al., 2009; Sperry and Love 2015). In addition, due to drought, there is a significant reduction in photochemical efficiency (Mena-Petite et al., 2000; Yang et al., 2006) and different water relation parameters are affected (Cochard et al., 1996 Sargent; et al., 2020). In this sense, efforts to adapt forests to drought stress have been directed at assessment of impacts and genetic variation in traits that may be important for maintaining higher photosynthetic capacity in drought-tolerant plants.

Potassium is essential for plant nutrition and plays a key role optimization of physiological and biochemical processes involved in water content of plants and CO₂ use efficiency during drought periods (Christina et al., 2015; Battie-Laclau et al., 2016; Mateus et al., 2022). Drought tolerance of the plant as a function of K nutrition is based on the fundamental role of K in osmoregulation, enabling the maintenance of turgor and cell expansion necessary to promote root growth in conditions of water deficit (Leigh and Jones 1984; Oddo et al., 2011). Furthermore, K must be intrinsically related to the water use efficiency of plants subjected to drought stress, since it controls stomatal closure, which is the most effective way to retain water in plant tissues (Egilla et al., 2005; Jordan-Meille et al., 2018). Based on this, K supply has been adopted as a nutritional management option to attenuate drought stress in tree species plantations as *Eucalyptus* spp. (Battie-Laclau et al., 2016; Santos et al., 2021; Mateus et al., 2022). However, the results that have been reported about the effect of K in the attenuation of osmotic stress linked to photosynthetic process differ regarding species or genotype, which place high emphasis on genetic factor as source of variability.

Photosynthesis in plants greatly relies upon the photochemical processes including the chlorophyll fluorescence, an important indicator of the photosynthetic energy conversion during light reaction (Schreiber et al., 1994). Chlorophyll fluorescence has been widely used in studies of plant physiology (Murchie and Lawson 2013), and is a very promising method for providing quantitative and non-invasive information. Measuring chlorophyll fluorescence can provide various information about the photosynthetic activities of plants. The energy dissipated via light-harvesting antenna pigments when excitation energy is not being transferred to the Photosystem II (PSII) reaction centers is termed F_0 (Bresson et al., 2015). After reaching F_0 , the application of a brief saturating pulse induces a maximum value of chlorophyll, F_m , which is the level attained when maximal closure of PSII reaction centers is reached (Hsu 2007; Bresson et al., 2015). The difference between F_m and F_0 is defined as the variable fluorescence, F_v . The ratio of F_v/F_m provides an estimate of the maximum quantum efficiency of PSII photochemistry (Butler, 1978), and it has been widely used to assess alterations in the photosynthetic systems induced by stress (Toscano et al. 2016, Marias et al., 2017; Remke et al., 2020; Kunert et al., 2021). In this context, differential $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures have been also used to gain insights into the nutritional status and physiological response mechanisms to abiotic stress throughout its whole cycle (Cernusak et al. 2009, Serret et al., 2018; Mateus et al., 2021; 2022).

Although *Pinus* species are widely distributed and most of them display relative drought tolerance (Koralewski et al., 2014; Móricz et al., 2018; Hanene et al., 2021), it has been recognized that the water stress greatly limits the growth efficiency and pine stand production (Albaugh et al., 2004; Fox et al., 2007). *Pinus taeda* and *Pinus caribaea* var. *hondurensis* are important components of Brazilian conifer forests, which represent about 20% of total planted forest areas (IBA, 2019). *Pinus Caribaea* var. *hondurensis*, a tropical pine, is assumed to be relatively drought resistant (Barret and Golfari, 1962), while *P. taeda*, a subtropical species, has been well established in regions without dry season (Campoe et al., 2016; Pirovani et al., 2018). Studies describing the effect of water stress and how K can upregulate drought tolerance of different *Pinus* species are scarce. This information is also useful in choosing the strategic management of the species to fully exploit planted forests.

The research evaluated the K-dynamic nutrition in *Pinus caribaea* var. *hondurensis* and *Pinus taeda* in response to different water availabilities in the soil and established relationships among the distinct treatments and nutritional and physiological responses, as

well as yield traits. For this, the study was carried out by the following hypotheses: (1) drought induced-stress affects the physiology and K-nutritional status when plants are supplied with K; (2) K supply has the potential to alleviate the drought-induced stress in *Pinus* by up-regulating growth, physiological and biochemical parameters. This research also aims to confirm the efficacy of the methods of natural isotopic abundance ($\delta^{13}\text{C}$ ‰ and $\delta^{15}\text{N}$ ‰) and chlorophyll fluorescence as a reliable indicator of the effects of K-fertilization throughout plant metabolism cycle.

4.2. Conclusions

Pinus spp. plants showed a negative response to potassium supply, as the increase in K level affected directly the plant's growth and physiology, impairing plant dry matter production and disturbing the photosynthetic activity (Fm, Fv/Fm NDVI, chlorophyll a and anthocyanin indexes). Although this negative effect has been verified for both water regimes, it was higher for *Pinus* seedlings maintained well-watered. In this sense, K supply decreased the plant biomass in well-watered regime and did not alleviate the drought-induced stress in *Pinus* spp. seedlings.

Regardless of the K-fertilization regime, water deficit was related to substantial decrease in leaf water potential (Ψ_w) and increase in leaf carbon isotope value ($\delta^{13}\text{C}$ ‰). Differences in discrimination against ^{15}N between treatments indicated consistent relationship with N cycle processes, suggesting an antagonistic relationship between high K level and N-uptake. The information presented in present study improves our understanding of the toxicity of high potassium for *Pinus* species in detriment of other essential elements and highlights the need for plantation planning to establish a nutritional balance in order to achieve high nutrient use efficiency.

References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long term growth responses of loblolly pine to optimal nutrient and water resource availability. *For. Ecol. Manage.* 192, 3–19. <https://doi.org/10.1016/j.foreco.2004.01.002>
- Anderegg, L.D.L., Hillerislambers, J., 2016. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Glob. Chang. Biol.* 22, 1029–1045. <https://doi.org/10.1111/gcb.13148>
- Ariz, I., Cruz, C., Neves, T., Irigoyen, J.J., Garcia-Olaverri, C., Nogués, S., Aparicio-Tejo, P.M., Aranjuelo, I., 2015. Leaf $\delta^{15}\text{N}$ as a physiological indicator of the responsiveness

of N₂-fixing alfalfa plants to elevated [CO₂], temperature and low water availability. *Front. Plant Sci.* 6, 1–10. <https://doi.org/10.3389/fpls.2015.00574>

- Asensio, V., Domec, J.C., Nouvellon, Y., Laclau, J.P., Bouillet, J.P., Jordan-Meille, L., Lavres, J., Rojas, J.D., Guillemot, J., Abreu-Junior, C.H., 2020. Potassium fertilization increases hydraulic redistribution and water use efficiency for stemwood production in *Eucalyptus grandis* plantations. *Environ. Exp. Bot.* 176, 104085. <https://doi.org/10.1016/j.envexpbot.2020.104085>
- Battie-Laclau, P., Delgado-Rojas, J.S., Christina, M., Nouvellon, Y., Bouillet, J.P., Piccolo, M. de C., Moreira, M.Z., Gonçalves, J.L. de M., Roupsard, O., Laclau, J.P., 2016. Potassium fertilization increases water-use efficiency for stem biomass production without affecting intrinsic water-use efficiency in *Eucalyptus grandis* plantations. *For. Ecol. Manage.* 364, 77–89. <https://doi.org/10.1016/j.foreco.2016.01.004>
- Bolhar-Nordenkamp, H.R., Long, S.P., Baker, N.R., Oquist, G., Schreiber, U., Lechner, E.G., 1989. Chlorophyll fluorescence as a probe of the photosynthetic competence of leaves in the field: a review of current instrumentation. *Funct. Ecol.* 3, 497. <https://doi.org/10.2307/2389624>
- Booth, T.H., 2013. Eucalypt plantations and climate change. *For. Ecol. Manage.* 301, 28–34. <https://doi.org/10.1016/j.foreco.2012.04.004>
- Bredemeier, C., Schmidhalter, U., 2001. Laser-induced chlorophyll fluorescence to determine the nitrogen status of plants. *Plant Nutr.* 726–727. https://doi.org/10.1007/0-306-47624-x_352
- Bresson, J., Vasseur, F., Dauzat, M., Koch, G., Granier, C., Vile, D., 2015. Quantifying spatial heterogeneity of chlorophyll fluorescence during plant growth and in response to water stress. *Plant Methods* 11. <https://doi.org/10.1186/s13007-015-0067-5>
- Brodribb, T.J., Holbrook, N.M., 2003. Stomatal closure during leaf dehydration, correlation with other leaf physiological traits. *Plant Physiol.* 132, 2166–2173. <https://doi.org/10.1104/pp.103.023879>
- Campoe, O.C., Munhoz, J.S.B., Alvares, C.A., Carneiro, R.L., de Mattos, E.M., Ferez, A.P.C., Stape, J.L., 2016. Meteorological seasonality affecting individual tree growth in forest plantations in Brazil. *For. Ecol. Manage.* 380, 149–160. <https://doi.org/10.1016/j.foreco.2016.08.048>
- Cernusak, L.A., Winter, K., Turner, B.L., 2009. Physiological and isotopic ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) responses of three tropical tree species to water and nutrient availability. *Plant, Cell Environ.* 32, 1441–1455. <https://doi.org/10.1111/j.1365-3040.2009.02010.x>
- Chaves, M.M., Flexas, J., Pinheiro, C., 2009. Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Ann. Bot.* 103, 551–560. <https://doi.org/10.1093/aob/mcn125>
- Choi, W.J., Chang, S.X., Allen, H.L., Kelting, D.L., Ro, H.M., 2005. Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. *For. Ecol. Manage.* 213, 90–101. <https://doi.org/10.1016/j.foreco.2005.03.016>
- Christina, M., Le Maire, G., Battie-Laclau, P., Nouvellon, Y., Bouillet, J.P., Jourdan, C., de Moraes Gonçalves, J. leonardo, Laclau, J.P., 2015. Measured and modeled interactive effects of potassium deficiency and water deficit on gross primary productivity and light-

- use efficiency in *Eucalyptus grandis* plantations. Glob. Chang. Biol. 21, 2022–2039. <https://doi.org/10.1111/gcb.12817>
- Cochard, H., Bréda, N., Granier, A., 1996. Whole tree hydraulic conductance and water loss regulation in *Quercus* during drought: evidence for stomatal control of embolism? Ann. des Sci. For. 53, 197–206. <https://doi.org/10.1051/forest:19960203>
- Cochard, H., Coll, L., Le Roux, X., Améglio, T., 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. Plant Physiol. 128, 282–290. <https://doi.org/10.1104/pp.010400>
- Coskun, D., Britto, D.T., Kronzucker, H.J., 2017. The nitrogen–potassium intersection: membranes, metabolism, and mechanism. Plant Cell Environ. 40, 2029–2041. <https://doi.org/10.1111/pce.12671>
- Daoud, B., Pawelzik, E., Naumann, M., 2020. Different potassium fertilization levels influence water-use efficiency, yield, and fruit quality attributes of cocktail tomato-A comparative study of deficient-to-excessive supply. Sci. Hortic. (Amsterdam). 272, 109562. <https://doi.org/10.1016/j.scienta.2020.109562>
- de Souza Mateus, N., Oliveira Ferreira, E.V., Florentino, A.L., Vicente Ferraz, A., Domec, J.-C., Jordan-Meille, L., Bendassolli, J.A., Moraes Gonçalves, J.L., Lavres, J., 2022. Potassium supply modulates *Eucalyptus* leaf water-status under PEG-induced osmotic stress: integrating leaf gas exchange, carbon and nitrogen isotopic composition and plant growth. Tree Physiol. 42, 59–70. <https://doi.org/10.1093/treephys/tpab095>
- de Souza Mateus, N., Victor de Oliveira Ferreira, E., Arthur Junior, J.C., Domec, J.C., Jordan-Meille, L., Leonardo de Moraes Gonçalves, J., Lavres, J., 2019. The ideal percentage of K substitution by Na in *Eucalyptus* seedlings: Evidences from leaf carbon isotopic composition, leaf gas exchanges and plant growth. Plant Physiol. Biochem. 137, 102–112. <https://doi.org/10.1016/j.plaphy.2019.02.006>
- Dijkstra, F.A., Carrillo, Y., Aspinwall, M.J., Maier, C., Canarini, A., Tahaei, H., Choat, B., Tissue, D.T., 2016. Water, nitrogen and phosphorus use efficiencies of four tree species in response to variable water and nutrient supply. Plant Soil 406, 187–199. <https://doi.org/10.1007/s11104-016-2873-6>
- Edalat, M., Naderi, R., Egan, T.P., 2019. Corn nitrogen management using NDVI and SPAD sensor-based data under conventional vs. reduced tillage systems. J. Plant Nutr. 42, 2310–2322. <https://doi.org/10.1080/01904167.2019.1648686>
- Egilla, J.N., Davies, F.T., Boutton, T.W., 2005. Drought stress influences leaf water content, photosynthesis, and water-use efficiency of *Hibiscus rosa-sinensis* at three potassium concentrations. Photosynthetica 43, 135–140. <https://doi.org/10.1007/s11099-005-5140-2>
- Ewers, B.E., Oren, R., Sperry, J.S., 2000. Influence of nutrient versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant, Cell Environ. 23, 1055–1066. <https://doi.org/10.1046/j.1365-3040.2000.00625.x>
- Farhat, N., Rabhi, M., Falleh, H., Lengliz, K., Smaoui, A., Abdelly, C., Lachaâl, M., Karray-Bourouai, N., 2013. Interactive effects of excessive potassium and Mg deficiency on safflower. Acta Physiol. Plant. 35, 2737–2745. <https://doi.org/10.1007/s11738-013-1306-x>

- Fox, H., Doron-Faigenboim, A., Kelly, G., Bourstein, R., Attia, Z., Zhou, J., Moshe, Y., Moshelion, M., David-Schwartz, R., 2018. Transcriptome analysis of *Pinus halepensis* under drought stress and during recovery. *Tree Physiol.* 38, 423–441. <https://doi.org/10.1093/treephys/tpx137>
- Fox, T.R., Allen, H.L., Albaugh, T.J., Rubilar, R., Carlson, C.A., 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. *South. J. Appl. For.* 31, 5–11. <https://doi.org/10.1093/sjaf/31.1.5>
- Garriga, M., Retamales, J.B., Romero-Bravo, S., Caligari, P.D.S., Lobos, G.A., 2014. Chlorophyll, anthocyanin, and gas exchange changes assessed by spectroradiometry in *Fragaria chiloensis* under salt stress. *J. Integr. Plant Biol.* 56, 505–515. <https://doi.org/10.1111/jipb.12193>
- Gitelson, A.A., Gritz, Y., Merzlyak, M.N., 2003. Relationships between leaf chlorophyll content and spectral reflectance and algorithms for non-destructive chlorophyll assessment in higher plant leaves. *J. Plant Physiol.* 160, 271–282. <https://doi.org/10.1078/0176-1617-00887>
- Gitelson, A.A., Merzlyak, M.N., 2004. Non-destructive assessment of chlorophyll, carotenoid and anthocyanin content in higher plant leaves: Principles and algorithms. *Remote Sens. Agric. Environ.* (S. Stamatiadis, J.M. Lynch, J.S. Schepers Eds.), Greece, Ella 78–94.
- Gitelson, A.A., Merzlyak, M.N., Chivkunova, O.B., 2001. Optical properties and nondestructive estimation of anthocyanin content in plant leaves¶. *Photochem. Photobiol.* 74, 38. [https://doi.org/10.1562/0031-8655\(2001\)074<0038:opaneo>2.0.co;2](https://doi.org/10.1562/0031-8655(2001)074<0038:opaneo>2.0.co;2)
- Gitelson, A.A., Viña, A., Ciganda, V., Rundquist, D.C., Arkebauer, T.J., 2005. Remote estimation of canopy chlorophyll content in crops. *Geophys. Res. Lett.* 32, 1–4. <https://doi.org/10.1029/2005GL022688>
- Gouveia, C.S.S., Ganança, J.F.T., Slaski, J., Lebot, V., Pinheiro de Carvalho, M.Â.A., 2019. Variation of carbon and isotope natural abundances ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of whole-plant sweet potato (*Ipomoea batatas* L.) subjected to prolonged water stress. *J. Plant Physiol.* 243, 153052. <https://doi.org/10.1016/j.jplph.2019.153052>
- Hanene, G., Fkiri, S., Zouaoui, R., Aloui, M. El, Nasr, Z., 2021. Intraspecific variability to drought impacts in *Pinus halepensis* provenances trials. *J. Sustain. For.* 40, 721–732. <https://doi.org/10.1080/10549811.2020.1813595>
- Hobbie, E.A., Colpaert, J. V., 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. *New Phytol.* 157, 115–126. <https://doi.org/10.1046/j.1469-8137.2003.00657.x>
- Hsu, B.D., 2007. On the possibility of using a chlorophyll fluorescence parameter as an indirect indicator for the growth of *Phalaenopsis* seedlings. *Plant Sci.* 172, 604–608. <https://doi.org/10.1016/j.plantsci.2006.11.006>
- Ibell, P.T., Xu, Z.H., Blake, T.J., Wright, C., Blumfield, T.J., 2014. How weed control and fertilisation influence tree physiological processes and growth at early establishment in an exotic F1 hybrid pine plantation of subtropical Australia. *J. Soils Sediments* 14, 872–885. <https://doi.org/10.1007/s11368-014-0891-7>
- Jákli, B., Tavakol, E., Tränkner, M., Senbayram, M., Dittert, K., 2017. Quantitative limitations to photosynthesis in K deficient sunflower and their implications on water-

- use efficiency. *J. Plant Physiol.* 209, 20–30. <https://doi.org/10.1016/j.jplph.2016.11.010>
- Jin, S.H., Huang, J.Q., Li, X.Q., Zheng, B.S., Wu, J. Sen, Wang, Z.J., Liu, G.H., Chen, M., 2011. Effects of potassium supply on limitations of photosynthesis by mesophyll diffusion conductance in *Carya cathayensis*. *Tree Physiol.* 31, 1142–1151. <https://doi.org/10.1093/treephys/tpr095>
- Jordan-Meille, L., Martineau, E., Bornot, Y., Lavres, J., Abreu-Junior, C.H., Domec, J.C., 2018. How does water-stressed corn respond to potassium nutrition? A shoot-root scale approach study under controlled conditions. *Agric.* 8. <https://doi.org/10.3390/agriculture8110180>
- Koralewski, T.E., Brooks, J.E., Krutovsky, K. V., 2014. Molecular evolution of drought tolerance and wood strength related candidate genes in loblolly pine (*Pinus taeda* L.). *Silvae Genet.* 63, 59–66. <https://doi.org/10.1515/sg-2014-0009>
- Kunert, N., Hajek, P., Hietz, P., Morris, H., Rosner, S., Tholen, D., 2021. Summer temperatures reach the thermal tolerance threshold of photosynthetic decline in temperate conifers. *Plant Biol.* 1–8. <https://doi.org/10.1111/plb.13349>
- Leigh, R.A., Jones, R.G.W., 1984. A hypothesis relating critical potassium concentrations for growth to the distribution. *New Phytol.* 97, 1–13.
- Li, Y., Ding, X., Jiang, J., Luan, Q., 2020. Inheritance and correlation analysis of pulpwood properties, wood density, and growth traits of slash pine. *Forests* 11. <https://doi.org/10.3390/F11050493>
- Marias, D.E., Meinzer, F.C., Woodruff, D.R., McCulloh, K.A., 2017. Thermotolerance and heat stress responses of Douglas-fir and ponderosa pine seedling populations from contrasting climates. *Tree Physiol.* 37, 301–315. <https://doi.org/10.1093/treephys/tpw117>
- Martin-StPaul, N., Delzon, S., Cochard, H., 2017. Plant resistance to drought depends on timely stomatal closure. *Ecol. Lett.* 20, 1437–1447. <https://doi.org/10.1111/ele.12851>
- Mateus, N. de S., Ferreira, E.V.O., Florentino, A.L., Vicente Ferraz, A., Domec, J.-C., Jordan-Meille, L., Bendassolli, J.A., Gonçalves, J.L.M., Lavres, J., 2022. Potassium supply modulates *Eucalyptus* leaf water-status under PEG-induced osmotic stress: integrating leaf gas exchange, carbon and nitrogen isotopic composition and plant growth. *Tree Physiol.* 42, 59–70. <https://doi.org/10.1093/treephys/tpab095>
- Mateus, N.S., Florentino, A.L., Oliveira, J.B., Santos, E.F., Gaziola, S.A., Rossi, M.L., Linhares, F.S., Bendassolli, J.A., Azevedo, R.A., Lavres, J., 2021. Leaf ¹³C and ¹⁵N composition shedding light on easing drought stress through partial K substitution by Na in *Eucalyptus* species. *Sci. Rep.* 11, 1–15. <https://doi.org/10.1038/s41598-021-99710-1>
- Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence - A practical guide. *J. Exp. Bot.* 51, 659–668. <https://doi.org/10.1093/jxb/51.345.659>
- Medrano, H., Tomás, M., Martorell, S., Flexas, J., Hernández, E., Rosselló, J., Pou, A., Escalona, J.M., Bota, J., 2015. From leaf to whole-plant water use efficiency (WUE) in complex canopies: Limitations of leaf WUE as a selection target. *Crop J.* 3, 220–228. <https://doi.org/10.1016/j.cj.2015.04.002>
- Mena-Petite, A., González-Moro, B., González-Murua, C., Lacuesta, M., Rueda, A.M., 2000. Sequential effects of acidic precipitation and drought on photosynthesis and chlorophyll

fluorescence parameters of *Pinus radiata* D. Don seedlings. *J. Plant Physiol.* 156, 84–92. [https://doi.org/10.1016/S0176-1617\(00\)80276-X](https://doi.org/10.1016/S0176-1617(00)80276-X)

- Moran, J.A., Mitchell, A.K., Goodmanson, G., Stockburger, K.A., 2000. Differentiation among effects of nitrogen fertilization treatments on conifer seedlings by foliar reflectance: A comparison of methods. *Tree Physiol.* 20, 1113–1120. <https://doi.org/10.1093/treephys/20.16.1113>
- Móricz, N., Garamszegi, B., Rasztoivits, E., Bidló, A., Horváth, A., Jagicza, A., Illés, G., Vekerdy, Z., Somogyi, Z., Gálos, B., 2018. Recent drought-induced vitality decline of Black pine (*Pinus nigra* arn.) in south-west hungary-is this drought-resistant species under threat by climate change? *Forests.* 9, 1–20. <https://doi.org/10.3390/f9070414>
- Murchie, E.H., Lawson, T., 2013. Chlorophyll fluorescence analysis: A guide to good practice and understanding some new applications. *J. Exp. Bot.* 64, 3983–3998. <https://doi.org/10.1093/jxb/ert208>
- Oddo, E., Inzerillo, S., La Bella, F., Grisafi, F., Salleo, S., Nardini, A., 2011. Short-term effects of potassium fertilization on the hydraulic conductance of *Laurus nobilis* L. *Tree Physiol.* 31, 131–138. <https://doi.org/10.1093/treephys/tpq115>
- Oliveira, N.M., Medeiros, A.D. de, Nogueira, M. de L., Arthur, V., Mastrangelo, T. de A., Barboza da Silva, C., 2021. Hormetic effects of low-dose gamma rays in soybean seeds and seedlings: A detection technique using optical sensors. *Comput. Electron. Agric.* 187. <https://doi.org/10.1016/j.compag.2021.106251>
- Osakabe, Y., Osakabe, K., Shinozaki, K., Tran, L.S.P., 2014. Response of plants to water stress. *Front. Plant Sci.* 5, 1–8. <https://doi.org/10.3389/fpls.2014.00086>
- Pirovani, D.B., Pezzopane, J.E.M., Xavier, A.C., Pezzopane, J.R.M., de Jesus Júnior, W.C., Machuca, M.A.H., dos Santos, G.M.A.D.A., da Silva, S.F., de Almeida, S.L.H., de Oliveira Peluzio, T.M., Eugenio, F.C., Moreira, T.R., Alexandre, R.S., dos Santos, A.R., 2018. Climate change impacts on the aptitude area of forest species. *Ecol. Indic.* 95, 405–416. <https://doi.org/10.1016/j.ecolind.2018.08.002>
- Pons, T.L., Perreijn, K., Van Kessel, C., Werger, M.J.A., 2007. Symbiotic nitrogen fixation in a tropical rainforest: ¹⁵N natural abundance measurements supported by experimental isotopic enrichment. *New Phytol.* 173, 154–167. <https://doi.org/10.1111/j.1469-8137.2006.01895.x>
- Rambo, L., Ma, B.L., Xiong, Y., da Silvia, P.R.F., 2010. Leaf and canopy optical characteristics as crop-n-status indicators for field nitrogen management in corn. *J. Plant Nutr. Soil Sci.* 173, 434–443. <https://doi.org/10.1002/jpln.200900022>
- Remke, M.J., Hoang, T., Kolb, T., Gehring, C., Johnson, N.C., Bowker, M.A., 2020. Familiar soil conditions help *Pinus ponderosa* seedlings cope with warming and drying climate. *Restor. Ecol.* 28, S344–S354. <https://doi.org/10.1111/rec.13144>
- Rhodes, R., Miles, N., Hughes, J.C., 2018. Interactions between potassium, calcium and magnesium in sugarcane grown on two contrasting soils in South Africa. *F. Crop. Res.* 223, 1–11. <https://doi.org/10.1016/j.fcr.2018.01.001>
- Robinson, D., 2001. $\Delta^{15}\text{N}$ as an integrator of the nitrogen cycle. *Trends Ecol. Evol.* 16, 153–162. [https://doi.org/10.1016/S0169-5347\(00\)02098-X](https://doi.org/10.1016/S0169-5347(00)02098-X)
- Robinson, D., Handley, L.L., Scrimgeour, C.M., Gordon, D.C., Forster, B.P., Ellis, R.P.,

2000. Using stable isotope natural abundances ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. Koch.) genotypes. *J. Exp. Bot.* 51, 41–50. <https://doi.org/10.1093/jxb/51.342.41>
- Ryan, M.G., Stape, J.L., Binkley, D., Fonseca, S., Loos, R.A., Takahashi, E.N., Silva, C.R., Silva, S.R., Hakamada, R.E., Ferreira, J.M., Lima, A.M.N., Gava, J.L., Leite, F.P., Andrade, H.B., Alves, J.M., Silva, G.G.C., 2010. Factors controlling *Eucalyptus* productivity: How water availability and stand structure alter production and carbon allocation. *For. Ecol. Manage.* 259, 1695–1703. <https://doi.org/10.1016/j.foreco.2010.01.013>
- Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K., Kane, M., 2008. Growth and physiology of loblolly pine in response to long-term resource management: Defining growth potential in the southern United States. *Can. J. For. Res.* 38, 721–732. <https://doi.org/10.1139/X07-191>
- Santos, E.F., Mateus, N.S., Rosário, M.O., Garcez, T.B., Mazzafera, P., Lavres, J., 2021. Enhancing potassium content in leaves and stems improves drought tolerance of *Eucalyptus* clones. *Physiol. Plant.* 172, 552–563. <https://doi.org/10.1111/ppl.13228>
- Sardans, J., Peñuelas, J., 2015. Potassium: A neglected nutrient in global change. *Glob. Ecol. Biogeogr.* 24, 261–275. <https://doi.org/10.1111/geb.12259>
- Sergent, A.S., Varela, S.A., Barigah, T.S., Badel, E., Cochard, H., Dalla-Salda, G., Delzon, S., Fernández, M.E., Guillemot, J., Gyenge, J., Lamarque, L.J., Martinez-Meier, A., Rozenberg, P., Torres-Ruiz, J.M., Martin-StPaul, N.K., 2020. A comparison of five methods to assess embolism resistance in trees. *For. Ecol. Manage.* 468, 118175. <https://doi.org/10.1016/j.foreco.2020.118175>
- Serret, M.D., Yousfi, S., Vicente, R., Piñero, M.C., Otálora-Alcón, G., Del Amor, F.M., Araus, J.L., 2018. Interactive effects of CO₂ concentration and water regime on stable isotope signatures, nitrogen assimilation and growth in sweet pepper. *Front. Plant Sci.* 8, 1–18. <https://doi.org/10.3389/fpls.2017.02180>
- Silva, J.G., Gomes, M.P., Pereira, E.G., Bicalho, E.M., Garcia, Q.S., 2022. Initial growth of *Peltophorum dubium* is affected by nitrogen source and manganese concentration. *J. Soil Sci. Plant Nutr.* 22, 201–211. <https://doi.org/10.1007/s42729-021-00644-4>
- Sperry, J.S., Love, D.M., 2015. What plant hydraulics can tell us about responses to climate-change droughts. *New Phytol.* 207, 14–27. <https://doi.org/10.1111/nph.13354>
- Toscano, S., Farieri, E., Ferrante, A., Romano, D., 2016. Physiological and biochemical responses in two ornamental shrubs to drought stress. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.00645>
- Vredenberg, W., Pavlovič, A., 2013. Chlorophyll a fluorescence induction (Kautsky curve) in a Venus flytrap (*Dionaea muscipula*) leaf after mechanical trigger hair irritation. *J. Plant Physiol.* 170, 242–250. <https://doi.org/10.1016/j.jplph.2012.09.009>
- Wang, M., Zheng, Q., Shen, Q., Guo, S., 2013. The critical role of potassium in plant stress response. *Int. J. Mol. Sci.* 14, 7370–7390. <https://doi.org/10.3390/ijms14047370>
- Xie, K., Cakmak, I., Wang, S., Zhang, F., Guo, S., 2021. Synergistic and antagonistic interactions between potassium and magnesium in higher plants. *Crop J.* 9, 249–256. <https://doi.org/10.1016/j.cj.2020.10.005>

- Yang, X., Chen, X., Ge, Q., Li, B., Tong, Y., Zhang, A., Li, Z., Kuang, T., Lu, C., 2006. Tolerance of photosynthesis to photoinhibition, high temperature and drought stress in flag leaves of wheat: A comparison between a hybridization line and its parents grown under field conditions. *Plant Sci.* 171, 389–397. <https://doi.org/10.1016/j.plantsci.2006.04.010>
- Zhu, J., Liang, Y., Zhu, Y., Hao, W., Lin, X., Wu, X., Luo, A., 2012. The interactive effects of water and fertilizer on photosynthetic capacity and yield in tomato plants. *Aust. J. Crop Sci.* 6, 200–209.