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| **Author(s):** |  |
| **Title:** | **Preliminary Material** |
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| **Author(s):** | Anna L. Jacobsen, R. Brandon Pratt, Martin D. Venturas and Uwe G. Hacke |
| **Title:** | **Preface: From Wood Formation to Tree Rings in Biology, Ecology and Forestry** |
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| **Author(s):** | Veronica De Micco, Marco Carrer, Cyrille B.K. Rathgeber, J. Julio Camarero, Jordi Voltas, Paolo Cherubini and Giovanna Battipaglia |
| **Title:** | **From xylogenesis to tree rings: wood traits to investigate tree response to environmental changes** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 155–182 |
| **Keywords:** | Cambium; cell differentiation; dendroecology; functional wood traits; stable isotopes; radial tree growth; water-use efficiency; wood anatomy |
| **Abstract:** | It is noteworthy that the largest part of global vegetation biomass depends on a thin layer of cells: the vascular cambium. Understanding the wood formation processes and relationships with environmental factors is a crucial and timely research question requiring interdisciplinary efforts, also to upscale the information gained and to evaluate implications for tree growth and forest productivity.  We provide an overview of wood formation processes up to tree-ring development, bearing in mind that the combined action of intrinsic factors and environmental drivers determines the anatomical traits of a tree ring formed at a specific time and position within the tree’s architecture. After briefly reviewing intrinsic factors, we focus attention on environmental drivers highlighting how a correct interpretation of environmental signals in tree rings must be grounded in a deep knowledge of xylogenesis and consequent wood anatomical traits. We provide guidelines on novel methods and approaches recently developed to study xylem formation. We refer to existing literature on established techniques for retrospective analyses in tree-ring series of anatomical and isotopic traits, to assess long-term ecophysiological responses to environmental variations, also giving advice on possible bias because of interand within-tree variability.  Finally, we highlight that, once the temporal axis of intra-annual tree-ring variability of xylem traits is established by xylogenesis analysis, a multidisciplinary approach linking classical dendro-ecology, wood functional traits (dendro-anatomy) and eco-physiology (here focusing on dendro-isotopes) allows a better interpretation of past environmental events hidden in tree rings, and more reliable forecasts of wood growth in response to climate change. |
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| **Author(s):** | Maxmira de Souza Arêdes-dos-Reis, Monique Silva Costa, Gabriel Uriel Cruz Araújo dos Santos and Cátia Henriques Callado |
| **Title:** | **Sample size and cardinal orientation in cambial activity analysis: a case study** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 183–190 |
| **Keywords:** | Cambial phenology; cambial activity sampling; tree rings; tropical trees |
| **Abstract:** | Radial growth dynamics of woody species is studied by different methods. the annual monitoring of cambial activity has been recommended as the method of greatest accuracy in research and appropriate for studies in protected areas for biological conservation, because it is largely nondestructive. Nevertheless, sampling protocols still need more standardization and precision. this study aims to investigate the influence of cardinal orientation on the number of cells in the cambial zone, and to evaluate the number of trees needed to conduct histological studies of cambial activity in Cedrela odorata, a tropical species with well-defined annual growth in the Atlantic Forest of South America/Brazil. Seventeen trees were evaluated during the period of intense cambial activity, with the sampling of four quadrants of the stem, according to cardinal orientation. the variance of cambial cell numbers was calculated for different numbers of trees. the results showed that radial growth variance was not related to cardinal orientation, but that at least 12 trees should be sampled for robust data on cambial dynamics. |
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| **Author(s):** | Larissa C. Dória, Diego S. Podadera, Rivete S. Lima, Frederic Lens and Carmen R. Marcati |
| **Title:** | **Axial sampling height outperforms site as predictor of wood trait variation** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 191–S3 |
| **Keywords:** | Caatinga; cerrado; intraspecific variation; thickness of intervessel pit membrane; Tocoyena formosa; Tabebuia aurea; vessel widening |
| **Abstract:** | Covariation amongst wood traits along the stem axis is important to maintain hydraulic integrity ensuring sufficient sap flow to the canopy. Here, we test how wood traits (co)vary along the trunk and whether two seasonally dry Brazilian habitats (cerrado and caatinga) influence this variation in two co-occurring species, Tocoyena formosa (Rubiaceae) and Tabebuia aurea (Bignoniaceae). The samples were collected at five heights along the main trunk of three individuals per species in both sites. We used light, scanning and transmission electron microscopy to observe the wood traits. Out of 13 wood traits, nine show relationships with sampling height: eight traits predict height in T. formosa and five in T. aurea. Contrastingly, only three traits show differences between sites and only for T. formosa. The intratrunk wood variation is reflected by the hydraulically weighted vessel diameter showing a curvilinear relationship, disagreeing with the prediction of a continuous vessel widening from tip to base. In both species, the largest vessels are linked to the thinnest intervessel pit membranes. Wood density increases basipetally for both species, being site-dependent and correlated with vessel traits in T. formosa, and site-independent and determined by fiber wall thickness in T. aurea. Furthermore, the functional role of rays was found to be different for each species, and may be related to the marked difference in ray composition. In conclusion, both species show a unique adaptation to deal with height-related constraints using species-specific co-variation amongst wood traits, while site does not contribute much to the wood variation. |
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| **Author(s):** | J. Julio Camarero |
| **Title:** | **Linking functional traits and climate-growth relationships in Mediterranean species through wood density** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 215–S2 |
| **Keywords:** | Dendroecology; functional traits; Mediterranean tree species; tree rings; wood anatomy |
| **Abstract:** | Functional traits are considered to influence the performance of woody plants. However, few field studies have tested this idea by using radial-growth data. Here, I test if five major traits of the leafand wood-economics spectra (height, leaf area, specific leaf area – SLA, wood density – WD and hydraulic diameter) explain climate-growth relationships in 14 Mediterranean trees and shrubs. Traits were measured for both gymnosperm (four Juniperus species plus three Pinus species) and angiosperm species (two Quercus species, two Pistacia species, Arbutus unedo, Celtis australis, and one Tamarix species). Climategrowth relationships were calculated relating ring-width indices (RWIs) and local climate data. Leaf area and SLA were high in broadleaf deciduous species (e.g., C. australis), and low in junipers. WD reached minimum and maximum values in pine and oak species, respectively. WD explained 45 % of the variation of the association observed between RWI and April precipitation, one of the main climatic variables driving radial growth. Therefore, WD is a relevant functional trait useful to predict the performance of Mediterranean woody plant species, specifically concerning their growth responses to climate. Functional traits as WD should be further explored to explain growth variability between and within woody species, and to link this variability with responsiveness to climate and ecosystem productivity. |
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| **Author(s):** | Angela Balzano, Giovanna Battipaglia and Veronica De Micco |
| **Title:** | **Wood-trait analysis to understand climatic factors triggering intra-annual density-fluctuations in co-occurring Mediterranean trees** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 241–258 |
| **Keywords:** | Pinus pinea L.; Arbutus unedo L.; false rings; functional wood traits; semi-arid climate; tree rings |
| **Abstract:** | Mediterranean trees and shrubs form intra-annual density fluctuations (IADFs) in tree rings as a sign of their plasticity in wood formation in response to intraseasonal variations of environmental conditions. Different species show a different aptitude to form IADFs, due to their diverse ability to cope with climate stressors, since the occurrence of IADFs may affect plant hydraulics. Dendroecology and quantitative wood anatomy were used to characterise IADFs in Pinus pinea and Arbutus unedo co-occurring at a Mediterranean site in Italy. The relations between climate parameters (i.e. temperature and precipitation) and intra-annual tree-ring traits (i. e. IADF frequency and conduit size) were analysed to highlight the main triggers for IADF formation and their functional role.  Data showed that both species are characterised by a high plastic response to climate and formed a high frequency of L-IADFs (occurrence of earlywoodlike conduits in latewood). The two species, although forming the same type of IADFs, showed different sensitivity to environmental factors. Pinus pinea showed a high dependence of tracheid size on temperature, while Arbutus unedo was more sensitive to precipitation in spring and autumn. Arbutus unedo promptly developed more than one IADF per year in response to rainfall events following drought periods.  The overall results were useful to compare the aptitude of the two species in forming IADFs and to highlight the factors priming their formation. This is useful to understand wood growth reactions to environmental drivers and to evaluate the adaptive capabilities in these two species, and thus to predict forest reactions after climate changes. |
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| **Author(s):** | Serena Antonucci, Sergio Rossi, Fabio Lombardi, Marco Marchetti and Roberto Tognetti |
| **Title:** | **Influence of climatic factors on silver fir xylogenesis along the Italian Peninsula** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 259–S3 |
| **Keywords:** | Abies alba; wood formation; Mediterranean area; temperature; precipitation; climate change |
| **Abstract:** | Xylem phenology has been widely recognised as an ecological indicator of the impact of environmental changes on forest ecosystems, especially at the edge of a species distribution. We investigated xylem phenology of silver fir (Abies alba Mill.) in three sites in Italy, between the 38th and 46th parallels. The phases of xylem phenology were assessed weekly on wood microcores collected from March to November 2015 to calculate timing and duration of xylem cell production. The effect of temperature and precipitation on xylem phenology were sequentially included in stepwise regressions and used to predict the duration of each phenological phase under three future climatic scenarios at different concentrations of greenhouse gases (RCP 2.6; 4. 5; 8. 5). A growing season of 163 days was detected in the southern site that was longer compared to the central (132 days) and northern (120 days) sites. A longer duration of xylogenesis was mostly related to a delayed completion of xylem differentiation in autumn rather than an earlier onset of cambium reactivation in spring. Overall, 67–76% of the duration of phenological phases was controlled by growing season precipitation, while 24 –33% was influenced by minimum temperature. Inclusion of both the above factors in the modelling exercise simulated a lengthening of the silver fir growing season during the 21st century. A longer duration of xylogenesis was envisaged in the scenario RCP 8. 5, especially in the central site. Population and climate gradients need to be considered when addressing phenological shifts and growth dynamics of silver fir in Mediterranean mountains. |
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| **Author(s):** | Marcos González-Cásares, Marín Pompa-García and Alejandro Venegas-González |
| **Title:** | **Climate signals from intra-annual wood density fluctuations in *Abies durangensis*** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 276–287 |
| **Keywords:** | Climatic change; densitometry; dendroclimatology; tree rings |
| **Abstract:** | Ongoing climate change is expected to alter forests by affecting forest productivity, with implications for the ecological functions of these systems. Despite its great dendrochronological potential, little research has been conducted into the use of wood density as a proxy for determining sensitivity to climate variability in Mexico. The response of Abies durangensis Martínez, in terms of wood density and growth ring width, to monthly climatic values (mean temperature, accumulated precipitation and the drought index SPEI) was analyzed through correlation analysis. Abies durangensis presents a high response, in terms of radial growth, to climatic conditions. Tree-ring widths are more sensitive to hydroclimatic variables, whereas wood density values are more sensitive to temperature. In particular, mean (MeanD) and minimum (MND) wood density values are more sensitive to climate than maximum (MXD). We found very marked spatial variations that indicate that A. durangensis responds differently to drought conditions depending on the indices of density. |
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| **Author(s):** | Saskia Luss, Sven-Olof Lundqvist, Robert Evans, Thomas Grahn, Lars Olsson, Giai Petit and Sabine Rosner |
| **Title:** | **Within-ring variability of wood structure and its relationship to drought sensitivity in Norway spruce trunks** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 288–310 |
| **Keywords:** | Vulnerability to cavitation; percent loss of conductivity; wood density; wood anatomy; wall thickness; tracheid dimensions; conduit wall reinforcement |
| **Abstract:** | Relationships between hydraulic vulnerability expressed as P50 (the air pressure causing 50% loss of hydraulic conductivity) and within-ring differences in wood density (WD) and anatomical features were investigated with the aim to find efficient proxies for P50 relating to functional aspects. WD and tracheid dimensions were measured with SilviScan on Norway spruce (Picea abies (L.) Karst.) trunk wood.  P50 was strongly related to mean WD (r = -0.64) and conduit wall reinforcement ((t/b)2), the square of the ratio between the tracheid double wall thickness (t) and the lumen width (b), where use of tangential lumen width ((t/bt)2) gave better results (r = -0.54) than radial lumen width (r = -0.31). The correlations of P50 with earlywood (EW), transition wood (TW) and latewood (LW) traits were lower than with the specimen averages, both for WD (r = -0.60 for WDEW, r = -0.56 for WDTW, r = -0.23 for WDLW) and all anatomical traits. The loss of hydraulic conductivity was addressed as a dynamic process and was simulated by defining consecutive phases of 5% theoretical conductivity loss. WD and tracheid traits were calculated and correlated with P50 values of each specimen. Tightest correlations were found for (t/bt)2, at relative cumulated theoretical conductivities until 45 to 50% (r = -0.75).  We conclude that WD is one of the best available proxies for P50, but does not necessarily reflect the mechanism behind resistance to cavitation. The new trait, based on estimation of conductivity loss as a dynamic process, provided even stronger correlations. |
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| **Author(s):** | Andrea Cecilia Acosta-Hernández, J. Julio Camarero and Marín Pompa-García |
| **Title:** | **Seasonal growth responses to climate in wet and dry conifer forests** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 311–S1 |
| **Keywords:** | Earlywood; dendroecology; intra-annual density fluctuations; latewood; tree rings; Mexico |
| **Abstract:** | Warming-amplified drought stress may decrease productivity and growth in both wet and dry conifer forest ecosystems. However, the seasonal radial-growth responses to climate, drought and related climate atmospheric patterns have not been compared in detail in wet and dry sites. We focus on drought-prone northern Mexico conifer forests and compare growth responses in tree species from wet (Pseudotsuga menziesii) and dry sites (Pinus leiophylla). to characterize the responsiveness to interand intra-annual changes in water availability we used dendrochronology and measured tree-ring (TRW), earlywood (EW) and latewood (LW) widths. We calculated adjusted LW (LWadj) by removing the influence of EW on LW. We identified E(narrow tracheids within the earlywood) and L-type (wide tracheids within the latewood) intra-annual density fluctuations (IADFs) and related their frequencies to seasonal climate and drought. We also related growth to atmospheric patterns related to the El NiñoSouthern Oscillation (ENSO) which drives precipitation patterns in the studied region. Wet-cool conditions during the prior winter and current spring linked to El Niño events enhanced TRW and EW, particularly in P. menziesii, whereas wet summer conditions enhanced LWadj. The formation of E(P. leiophylla) and L-type (P. menziesii) IADFs was associated with seasonal fluctuations in precipitation and temperature, suggesting different strategies to withstand drought. the sensitive P. menziesii strongly responded to short spring droughts, whereas the tolerant P. leiophylla responded to longer spring droughts. Seasonal wood measures (EW, LWadj) and IADFs are proxies of intra-annual fluctuations in water availability in similar conifer forests. |
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| **Author(s):** | C. Alvites, G. Battipaglia, G. Santopuoli, H. Hampel, R.F. Vázquez, G. Matteucci and R. Tognetti |
| **Title:** | **Dendrochronological analysis and growth patterns of Polylepis reticulata (Rosaceae) in the Ecuadorian Andes** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 331–S5 |
| **Keywords:** | Climate change; mountain forests; relict species; tree rings; dendroclimatology |
| **Abstract:** | Relict tree species in the Andean mountains are important sources of information about climate variability and climate change. This study deals with dendroclimatology and growth patterns in Polylepis reticulata Hieron., growing at high elevation (mean of 4000 m a.s.l.) in three sites of the Ecuadorian Andes. The aims of the research were: (i) characterizing tree-ring boundaries; (ii) describing tree-ring patterns of the study sites; (iii) investigating the relationships between climate and radial tree growth; and (iv) determining the spatial correlation between seasonal climatic factors and tree-ring width of P. reticulata. Tree rings were characterized by semi-ring porosity and slight differences in fibre wall thickness between latewood and subsequent earlywood. In all sampling sites, tree rings in heartwood were more clearly visible than in sapwood. Tree-ring width was more related to temperature than to precipitation, with growth being also affected by site conditions and stand structure, as well as other local factors. No significant relationships were found between tree-ring chronologies of P. reticulata and El Niño-Southern Oscillation (ENSO) and Vapour Pressure Deficit indices. The study highlights that there is not a clear driving climate factor for radial growth of P. reticulata. Additional research is needed to study growth dynamics of this species and the impacts of local environmental variables. |
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| **Author(s):** | Murat Ozturk, Kadir Alperen Coskuner, Yetkin Usta, Bedri Serdar and Ertugrul Bilgili |
| **Title:** | **The effect of mistletoe (Viscum album) on branch wood and needle anatomy of Scots pine (*Pinus sylvestris*)** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 352–365 |
| **Keywords:** | Parasitic plants; mistletoe; ecological wood anatomy; needle anatomy; Santalaceae; Viscoideae; Santalales; Pinaceae |
| **Abstract:** | Mistletoes are hemi-parasitic plants growing on many tree species. They grow on the tree branches or trunk of a tree and form root-like structures called haustoria that penetrate into the tree, taking up water and mineral nutrients. Mistletoe is capable of causing a variety of effects to its hosts, including changes in wood formation and leaf development. We investigate and discuss the effects of pine mistletoe (Viscum album ssp. austriacum, Santalaceae) on branch wood and needle anatomy of Scots pine (Pinus sylvestris, Pinaceae). Parasitized and nonparasitized branches of Scots pine were sampled from host tree crowns of trees growing on the same site. Branches were taken from mid-crown facing south. They were cut at 2 cm proximal and 2 cm distal to the mistletoe on each host branch and at the corresponding position in the case of uninfected branches from the same host. The wood anatomy at proximal and distal parts and the parts at the corresponding position in the non-parasitized section was compared. The anatomy of one-year-old needles from both parasitized and non-parasitized branches was also compared. Mistletoe had significant influences on wood and needle anatomy. The major changes were the decreases in the double wall thickness, lumen area, tangential lumen area and radial lumen area of the tracheids in the wood and a decrease in vascular area in the needles. These results help to understand how mistletoe acts on its host. |
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| **Author(s):** | Anna Dinella, Francesco Giammarchi and Giustino Tonon |
| **Title:** | **Are living peatland trees a reliable natural archive for climate reconstruction?** |
| **Source:** | IAWA Journal, Volume 40, Issue 2 |
| **Publication Year:** | 2019 |
| **Pages:** | 366–379 |
| **Keywords:** | Peatlands; tree rings; hydrology; paleoclimatology; quantitative wood anatomy |
| **Abstract:** | Peatland ecosystems are an important archive of paleoclimatic information. Within this context, tree-ring data from trees growing in such ecosystems are extremely valuable resources, and subfossil trees from peat bogs have been widely employed in dendroclimatological studies. However, there are still gaps in our understanding of the relationships among tree growth, peatland hydrology and climate factors. Here, we summarize the principal studies on living peatland trees, with a particular focus on their use as a source of information on past climatic conditions. We discuss the main factors influencing tree growth in this environment, whether it is the local hydrological cycle or climate. We put a particular focus on the reliability of the climate signal recorded by living peatland trees, comparing it with that found in subfossil trees. Finally, we discuss the relevance of quantitative wood anatomy in the context of peatland ecosystems research. |
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