Editorial

Special issue: WSE symposium: Wood growth under environmental changes: the need for a multidisciplinary approach

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This special issue of \textit{Tree Physiology} presents original and review papers of the International Symposium ‘WSE: Wood Structure in Plant Biology and Ecology’, held in Naples on 17–20 April 2013 and organized by the Department of Agricultural and Food Sciences of the University of Naples Federico II and the Department of Environmental, Biological and Pharmaceutical Sciences and Technologies of the Second University of Naples on behalf of the COST Action FP 1106 STReESS, ‘Studying Tree Responses to extreme Events: a SynthesiS’.

The symposium presented a survey of current research on wood structure and tree physiology in the context of environmental changes. A challenging aim was to indicate research gaps in different disciplines and to answer key questions for future research by the integration of different research topics. During the five sessions, the conveners emphasized the relevance of wood sciences to: (i) assess past, current and future responses, as well as plasticity and adaptive traits, of trees and tree species to environmental conditions; (ii) individuate the factors driving wood formation due to both genomic-based endogenous regulation and environmental pressure; (iii) analyze plant–water relations to comprehend the structural and physiological mechanisms contributing to survival in the face of drought and other extreme events.

From these sessions, seven authors contributed research papers based on their talks for this special issue of \textit{Tree Physiology} (Eilmann et al. 2014, Jyske et al. 2014, Martin-St Paul et al. 2014, Oddo et al. 2014, Shestakova et al. 2014).

One paper not presented in Naples, but submitted in the recent months to Tree Physiology also fits the theme of this special issue: an overview of the mechanistic understanding of the isotopic fractionation process that determines the isotopic composition in the tree-ring archive over the long term (Gessler et al. 2014).

Altogether, the papers form an interesting collection of contemporary applications of wood sciences to better understand wood formation and climate-change effects on tree physiology and ecology.

Wood formation involves cambial cell division followed by a process of cell growth and differentiation that implies radial enlargement, longitudinal elongation, cell-wall deposition, thickening and lignification (Wardrop 1965, Grozditis and Ifju 1984). During wood formation, many interrelated processes are realized at three main hierarchical levels: whole tree, tissue and cell. These processes are regulated by several intrinsic factors, such as gene expression and hormonal signals, together with environmental factors, such as temperature and precipitation (Schrader et al. 2003, 2004, Deslauriers and Morin 2005, Gričar et al. 2007). The combined action of intrinsic and environmental factors is responsible for the unique structure of a tree ring formed at a specific time in a specific position within the plant architecture (Vaganov et al. 2006) (Figure 1). However, a mechanistic understanding of how these factors
Intra-annual formation of xylem and phloem of a widespread species, Picea abies (L.) Karst., growing at three temperate sites along an altitudinal gradient, was analyzed in the paper by Gricar et al. (2014). The authors aimed at: (i) verifying that cell production on the xylem side varies depending on environmental conditions (e.g., weather), while phloem formation is more stable and mainly depends on endogenous factors; (ii) testing whether the difference in seasonal cambial activity among sites is the result of the high plasticity of P. abies; and (ii) assessing the intra-annual climate—growth relationship in P. abies during the study period (2009–11). With a weekly sampling of micro-cores and a considerable effort of measurements (from cell counting to assessment of principal phenological phases of cambial activity), the authors confirmed the plasticity of xylem formation, influenced by climatic and environmental constraints. They suggested that the dynamics of phloem formation in temperate trees could also be at least partly triggered by local environmental conditions. These findings support the idea of a strong relationship between wood formation and local weather conditions and thus indicate the potentially high plasticity of trees to adapt to ongoing climate change. Further studies to investigate the plasticity of tree species should not only focus on extreme environments (such as upper tree-line or dry sites), but also include temperate habitats with moderate growing conditions.

The study by Jyske et al. (2014) focuses on the sub-cellular level by studying the orientation of cellulose microfibrils (MFs) across the cell wall in four clones of Japanese cedar. Microfibril orientation is an important trait determining wood quality in this commercial Japanese species. The authors found differences in MF orientation in consecutively formed secondary tracheid-wall layers in the four clones, although clonal variation in the phenology of tracheid production and differentiation was minor. This indicates that both endogenous and external processes, most likely through seasonality in cell formation, can influence cell-wall structure and hence wood quality.

Environmental influences, e.g., changes in climate and weather, have an effect on the anatomical structure, as well as on the physical and chemical properties of wood. Water shortage, as a result of climate change, in particular, is likely to become a major factor limiting species distribution and establishment in the near future (IPCC 2007). At present, drought is thought to be an important factor leading to increased forest decline and rapid decline-induced vegetation shifts (Breshears et al. 2005, Allen et al. 2010, Eilmann et al. 2011). Further, to cope with drought conditions, trees have evolved phenological, morphological and physiological adaptations (Baas 1976, Jacobsen et al. 2007, Battipaglia et al. 2010, 2014, Voelker et al. 2011, Pineda-Garcia et al. 2013), which often originate by specific patterns of cambial activity and are responsible for changes in xylem-hydraulic conductivity and vulnerability to cavitation (Harvey and van den Driessche 1999, Sperry

Figure 1. Schematic view summarizing how intrinsic and environmental factors are responsible for specific wood traits which can be covered by different disciplines. Wood formation is affected by intrinsic factors (such as gene expression and hormonal signals) and environmental factors (especially temperature, precipitation and nutrients) which act both directly on processes of xylogenesis and indirectly by modifying physiological processes (such as photosynthesis, respiration and transpiration), and thus the availability of resources. Environmental factors can also interact with intrinsic factors. The result is a complex tissue in which many signals (e.g., specific wood-anatomical traits, isotope composition, chemical features of cell walls, etc.) are summarized and can be ‘read’ by different disciplines which can cooperate to reach a comprehensive understanding of the physiological mechanisms involved in wood formation.

Impact of environmental factors on wood formation has not been reached yet due to difficulties in investigating this multifaceted subject using a single disciplinary perspective. The studies reviewed here emphasize the integration of several disciplines and approaches with different temporal and spatial scales, coupling wood biology, ecophysiology and hydraulic architecture to assess the physiological mechanisms behind wood formation and the related influencing factors.

Guerriero et al. (2014) reviewed the current understanding of the gene and hormonal pathways involved in wood formation, including the cambium, phloem and bark. Particular emphasis is given to the molecular analyses of cambial tissues underlying classic and emerging models to study secondary growth. The last section of the paper is dedicated to environmental constraints (salinity, drought and anthropogenic effects) affecting wood production and quality through radial growth dynamics and wood density. The paper argues the importance of an integrated view on the wood-formation process to understand carbon-flow dynamics within forest ecosystems.
Provenance trials could provide an excellent basis to compare the performance and structural adaptation (Palmroth et al. 1999) of different provenances under similar site conditions, allowing the identification and selection of productive and drought-tolerant provenances (Broadmeadow et al. 2005, Ellmann et al. 2013).

Ellmann et al. (2014) evaluated the plastic response to environmental conditions versus genetic predisposition of four beech provenances originating from European southern, potentially drought-adapted (Bulgaria, France), and northern locations (Sweden, the Netherlands) and planted in a provenance trial under moderate climate conditions in the Netherlands. The evaluation was based on variations in radial growth, wood-anatomical traits and leaf phenology. Surprisingly, the Bulgarian provenance not only showed the highest growth level but had an efficient water-conducting system which was unaffected by the drought in 2003, pointing to a high ability of this provenance to cope well with dry conditions. Altogether, the authors concluded that the similarity in ring-width variation among provenances suggests an environmental control of this trait, whereas the differences encountered in wood-anatomical traits, as well as the consistent differences in flushing pattern, support the hypothesis of a genetic control of these features. Although the results are based on four provenances at one trial location only, they indicate the potential of wood-anatomical traits to assess the adapation potential of beech and ultimately evaluate the possibility of speeding up species migration by planting well-performing provenances.

In their paper, Martin-St Paul et al. (2014) compared different methods to assess xylem vulnerability to cavitation, based on vulnerability curves (VCs). Vulnerability curves are an important tool to evaluate species adaptation to drought, particularly in the context of the ongoing climate change and increasing drought mortality risk. Three tested methods are: bench drying (BD), Cavitrone (C) and air injection (AI). Recent studies have suggested that AI and CA methods are inappropriate, in comparison with BD, if working with species with long vessels, because they produce high threshold xylem pressure for embolism compared with the ecophysiological plant condition. The authors used Quercus ilex L. as test species, and they demonstrated that the BD method provides the most reliable estimates of the VCs for this species. The CA technique was subjected to a vessel-length artifact (the so-called open vessel artifact) and the AI method furnished very variable results attributed to differences in base diameter among specimens. Consequently, the authors recommend using the CA and AI methods with great care when deriving VCs for species with long vessels.

The paper by Oddo et al. (2014) focused on the link between drought stress and plant-hydraulic conductance which depends on the geometry of the conducting elements, but can be modulated by fluctuations in the sap-solute content, in particular by potassium concentration (K⁺). Indeed, changes in K⁺ in the soil and other environmental matrices influence xylem-hydraulic capacity and vulnerability to cavitation (Harvey and van den Driessche 1999). In this context, the authors aimed at testing whether severely water-stressed laurel plants, growing under low K⁺ availability, could recover earlier from stress after short-term potassium fertilization. They performed short-term pot experiments to highlight possible hydraulic effects before the onset of other physiological responses. However, even though their findings confirmed the capacity of well-watered plants to rapidly increase potassium concentration after fertilization, the results of the experiment did not indicate significant short-term improvement in drought-stress recovery when potassium was added to the irrigation solution. The authors highlight the need for further investigate the mechanisms of reduced K⁺ uptake under drought stress.

The influence of drought on the ecophysiological performance of different co-occurring Mediterranean oak species is analyzed in the paper by Shestakova et al. (2014). The authors investigated spatio-temporal patterns of signal strength in time series of carbon and oxygen isotopes of three deciduous (Quercus faginea Lam., Quercus humilis Mill. and Quercus petraea (Matt.) Liebl.) and one evergreen oak (Q. ilex) species. By using a mixed-modeling framework, the species were grouped according to their temporal and spatial intra-annual and site variability. This method allows the identification of functional groups that can subsequently be related to climate-isotope relations. With a unique effort, a network of 24 site chronologies scattered across an aridity gradient in the northeastern Iberian Peninsula was analyzed. As expected, the deciduous oaks seemed to depend on growing-season precipitation, while the evergreen Q. ilex showed association with the seasonal recharge of ground-water reservoirs and hence less susceptibility to summer drought.

The use of stable isotope techniques in plant ecological research has grown steadily during the past decades. This trend will continue as scientists realize that stable isotope composition of wood provides insights into the ecophysiological processes involved in the response of trees to past and present environmental conditions. The review by Gessler et al. (2014) summarized the state-of-the-art knowledge on mechanisms influencing the carbon and oxygen signals in trees. The first paragraphs are dedicated to the processes at leaf level, such as photosynthetic carbon fractionation, leaf water enrichment and the variability in the primary sources of CO₂ and H₂O. In simple and effective language, the authors focus on key issues such as the effect of changing atmospheric CO₂ concentration on δ¹³C, the influence of water uptake and transport up to the leaf level, the necessity of extracting cellulose from tree-ring wood to maximize the climatic signal and the evidence of an age trend in the carbon and oxygen isotopic composition of tree rings. Detailed treatment is given to the
less-explored ‘downstream’ process related to metabolism and transport, which has the strong potential to affect isotope fractionation. At present, very few studies address the transfer of the δ13C and δ18O from the leaves to tree rings, showing clear differences between the observed species. In addition, the complex pathway of carbon and oxygen assimilation, remobilization and storage is still unclear and needs to be further investigated. The review clearly puts forward the need for new experiments, models and conceptual frameworks to increase our understanding of the long-term fate of the isotopic signals from the source to the tree-ring archive.

All the studies reported in this special issue represent emblematic examples of the importance of a multidisciplinary approach in wood sciences to provide answers to questions related to tree performance under changing environmental conditions. At the current stage, it is crucial to integrate the knowledge obtained from studies conducted in the different disciplines and with different temporal (from minutes to millennia) and spatial (from cell to landscape ranging from extreme hot and dry to cold and wet environments) resolutions to generate a basic understanding of short- to long-term physiological responses of tree species to environmental changes (Figure 2). Thus, studies that integrate across scales and where an observed process is explained through underlying mechanisms and its consequences are scaled to the next broader level likely receive results of primary importance avoiding descriptive or trivial research (Passioura 1979). The combination of information on regulation of xylogenesis and its stimuli and constraints leading to specific wood anatomy, with data on long-term variation in climate–growth relationships, as derived from dendrochronology, information derived from field and laboratory experiments on ecophysiological effects of global changes on trees, and with data derived from ecophysiological tree models, will certainly create important knowledge which can be used for conservation and engineering programs aiming at safeguarding forest health, increasing woody biomass and wood quality.

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Conflict of interest

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References


Figure 2. Conceptual framework illustrating the relationships between different disciplines with different temporal (from minutes to millennia) and spatial (from cell to landscape ranging from extreme hot and dry to cold and wet environments) resolutions. All together, those disciplines contribute to generate a basic understanding of short- to long-term physiological responses of tree species to environmental changes. Arrow on the top indicates the ‘upscaling process’ furnishing relevant information at ecosystem level, while the arrow on the bottom indicates the ‘downscaling process’ with a progressive increase of precision and high-resolution information.


