



# Tree ecophysiology in the context of climate change

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**Abstract** Forest structure and function strongly depend on and concurrently influence environmental conditions. Tree performance is generally governed by its genetics and environment; thus, recent hotspots in this field include tree genotype × environment, phenotype × environment, and functional trait × environment interactions. The editorial, review, and 22 original research articles in this Special Issue, “*Tree ecophysiology in the context of climate change*”, highlight ecophysiological phenomena (e.g., climate hormesis, seed germination, tree mortality), processes (e.g., tree metabolism, photosynthate allocation, nutrient uptake and transport), indicators (e.g., carbon sequestration, pollutants), measurements (e.g., thermal time methods, soil quality indices, vegetation spectral index, and near-infrared leaf reflectance), and modeling (e.g., climate correlations with

tree growth, photosynthetic phenology, hydraulic strategies, OliveCan model) in the context of global climate change. Understanding forest–environment interactions from an ecophysiological perspective as climate changes provides insights into species fitness in suboptimal environments, species competition for limited resources, and phylogenetic divergence or convergence of species, and predicting species distributions.

**Keywords** Tree ecophysiology · Climate change · Climate hormesis · Phenology · Thermostability · Forest resilience · Hydraulics

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plants are poorly understood. In this Special Issue (SI), Erofeeva (2023) reviewed the available data on hormetic responses of woody species to the climate stressors observed in experiments and in real ecosystems and described the occurrence of climate hormesis at a low dose, direct and indirect pathways of climate hormesis, factors affecting climate hormesis, and hormetic trade-offs. This review emphasizes the importance of studies on the impacts of climatic hormesis on the stability and productivity of ecosystems, so that the effects of climate change can be more accurately assessed and predicted. Wang et al. (2021) highlight the role of environmental signals in inducing epigenetic changes; they found that climate-dependent methylation of *bHLH9* gene regulates the expression of betulin biosynthesis genes and suggest that such methylation may be useful for developing climate-resilient plants. Key issues for future work on climate hormesis include stress-mediated mechanisms that regulate methylation of the promoter region of *bHLH9* gene and potential drivers of epigenetic adaptation.

Drought in forested biomes over the past decades has caused tree mortality and rapid shifts in ecosystem structure and function (Shaw et al. 2005; Münchinger et al. 2023). In North America and Europe, moisture and drought sensitivity are major drivers of changes in tree growth and species abundance (Stern et al. 2022). Acid deposition (e.g.,  $\text{SO}_4^{2-}$ ,  $\text{NO}_3^-$ ) is a potential driver of change in tree growth (e.g., Schaberg et al. 2010). Understanding the impacts of these drivers and other climate factors on tree communities is needed to ensure and improve the health and productivity of tree species (Swanston et al. 2018). In this SI, Stern et al. (2022) analyzed correlations of climate and pollutant depositions with tree growth (positive with summer moisture and winter moisture or snow, negative with summer temperature and pollutant deposition variables) of the hardwood forests throughout Vermont (USA). Their work emphasizes the importance of growing season moisture and temperature regimes in sustaining tree growth and woody productivity in eastern North America. However, the future health and productivity of dominant and co-dominant tree species in eastern North America are still uncertain due to nonuniform changes in climate and pollution loading. In northern hardwood forests of North America, winter precipitation is an important factor determining habitat suitability for tree species in cold climates. In semi-arid conditions, changes in xylogenesis in response to seasonal drought contribute to the coexistence of tree species; commonly, species with lower climatic constraints to xylogenesis have higher tolerance to drought stress. In the study of Pompa-García et al. (2022, this SI), the tolerant species *Pinus leiophylla* had an early start of radial growth but shorter xylogenesis than *P. cembroides* and *P. engelmannii*. Temperature functions as a climate driver of xylogenesis in semi-arid forests. The capacity of tree species to adjust to climate variability is a

determinant of their vulnerability or resilience to warmer climate scenarios.

In the context of frequent and severe climatic events, particularly extreme heat and concomitant drought, Central European forests are at increasing risk of mortality of dominant tree species (i.e., *Pinus sylvestris*, *Picea abies*, and *Fagus sylvatica*), which have the narrowest thermal safety margins (O'Sullivan et al. 2017). However, less is known about other tree species in Central Europe. In this SI, Münchinger et al. (2023) analyzed thermal- and drought-resistance traits of 15 temperate coniferous and broadleaved trees and found that broadleaved species with higher drought tolerance have higher thermal tolerance. They concluded that species with drought-adapted foliage can potentially better tolerate heat stress during climatic extremes. Water relations and hydraulic processes in plants after drought are well studied; however, the role of nonstructural carbohydrates (NSC) and how their storage and allocation changes during drought events deserve further attention. Blumstein and Furze (2022) modeled and assessed the climatic drivers of total NSC concentrations in tree stems in the northeastern United States. They found a significant decrease in stemwood NSC concentrations with starch accumulation immediately following the drought and rebound to predrought levels within three years. Their work provides insight into the climatic drivers of NSC storage and highlights the importance of a tree's carbon economy in response to and recovery from drought. They proposed further work to determine the specific timeframe within which NSCs could serve as a buffer to change for temperate trees. Elevated  $\text{CO}_2$  concentrations and N deposition are important drivers of tree growth by affecting plant C cycling. Stored NSCs indicate a balance between C assimilated via photosynthesis, C released through respiration, and C invested in growth. However, the trade-offs between growth and NSC reserves under elevated  $\text{CO}_2$  and N deposition are largely unknown. Zheng et al. (2022) analyzed NSC storage in the organs of Chinese fir (*Cunninghamia lanceolata*) in southern China under  $\text{CO}_2$  elevation and N addition; they found different trade-offs between structural biomass and NSC storage among aboveground organs and roots. They also observed that timely reinvestment of carbohydrate in growth rather than in NSC reserves helps alleviate C limitation in Chinese fir under  $\text{CO}_2$  elevation and N addition. This work highlights the importance of separating biomass into structural biomass and NSC reserves.

The mechanisms of drought-related mortality involve water budget imbalance, hydraulic failure, and impaired C-dependent metabolic and hydraulic processes (Sala et al. 2010). The magnitude of drought-caused injury is species-dependent. In the study of Luo et al. (2022), the tree species *Larix gmelinii* and *Fraxinus mandshurica* displayed different hydraulic and water regulation strategies to drought stress, where the former mainly used stomata as a "safety

valve” to maintain hydraulic functions of the whole plant and delayed dehydration time under drought; whereas the latter tended to use leaves as “hydraulic fuses” (i.e., leaf-stem vulnerability segmentation) to preserve the hydraulic integrity of the stem. Their work highlights the central role of hydraulic coordination among different organs during tree responses to drought and the significance of considering different hydraulic responses of co-existing species for modelling and predicting tree growth and distribution in the context of climate change. Luz et al. (2022) reported distinct adjustments in water status and metabolic shifts underlying growth and rehydration ability of two *Hymenaea* species after short-term exposure to drought stress. *H. courbaril* invests in N to the detriment of C compounds and adjusts root growth to attenuate drought stress; *H. stigonocarpa* shows higher water potential and lower net photosynthesis to support aboveground growth during acclimation. They concluded that both mechanisms are effective with regards to water-use efficiency under suboptimal growth conditions.

Leaves are highly sensitive to environmental changes; leaf characters (e.g., leaf shape index, area, and thickness) directly reflect plant trade-off strategies in the context of climate change (Klich 2000). Yuan et al. (2023) found synergistic effects of geographical and climatic factors on leaf traits and a strong trade-off between leaf traits during the ontogenetic development of the endangered tree *Litsea coreana* var. *sinensis*. However, environmental adaptability of the offspring is alarming due to the low levels of variation within the population. To enhance protection of the wild resources and habitats of this endangered tree, they recommend the establishment of germplasm reserves and the promotion of gene exchange among populations. Ye et al. (2022) examined leaf traits and net primary productivity of the dominant species *Schima superba* and *Castanopsis carlesii* in a secondary broadleaved–evergreen forest in subtropical China. They reported species-dependent effects of fertilization with N and P on leaf traits (e.g., leaf mass per unit area, leaf N/P ratios, and N fractions in carboxylation, bioenergetics, cell wall, and other N metabolites). They highlighted that the differences between the two species in their acclimation to N deposition and to aggravated P limitation may increase the uncertainty of community succession of subtropical broadleaved evergreen forests. Yin et al. (2022) reported the interactions of N addition and photoperiod on growth and yield of *Dendrocalamopsis oldhami* through balancing C and N metabolism.

Photosynthetic phenology is genetically associated with climate factors; therefore, phenological–climatic associations are commonly used to predict plant response to climate change. In the study of Sever et al. (2022), drought negatively impacted photosynthesis and the quality of seedlings and acorns, while suboptimal N nutrition was detected as a dominant stressor for acorn mass. They highlighted the

importance of regular watering and N fertilization in maintaining plant water balance and N levels for high quality and yield of the crops. Drought tolerance is also closely correlated with the ability of trees to respond quickly and effectively to drought. In the study of de Sousa Leite et al. (2022), drought-tolerant *Mimosa tenuiflora* and *Piptadenia stipulacea* maintained a low leaf water potential during drought stress by accumulating compatible solutes, thus allowing a rapid and full recovery of water status when rehydrated. In response to drought, photosystems I and II were reversibly downregulated. In addition, morphological adaptations at the whole-plant level subsequently occurred in both species. Uncovering the intrinsic characteristics in response to and recover from drought is helpful for predicting the resilience of tropical dry forests in future warming climate scenarios. Using *Abies sachalinensis* from four seed provenances, Sugai et al. (2023) constructed a logistic model of climatic factors and photosynthetic phenology and provided a novel framework to visualize the landscape gradient in the maximal photochemical quantum yield of photosystem II ( $F_v/F_m$ ) on a map of the distribution area. Their model demonstrated that the lowest summer temperature is associated with local adaptation of autumn photosynthetic phenology and that the lower the lowest temperature in July, the higher the  $F_v/F_m$  in October and the slower the seasonal photosynthetic decline, and vice versa. Petrik et al. (2022) assessed the seasonality of photosystem II thermostability and water-use efficiency of *Picea abies* under exceptionally warm and dry conditions. Their results showed that the photosynthetic apparatus of *P. abies* at lower mountainous altitudes acclimates to higher temperatures in the summer. They concluded that the lower altitude populations might be more heat tolerant than previously thought. Temperature and photoperiod are fundamental factors affecting seedling development. Martins et al. (2022) evaluated six thermal time methods widely used to compute thermal requirements and assessed the influence of photoperiod on seedling development of three tropical forest species. They found that the phyllochron differed among the species and sowing dates. *C. myrianthum* presented the fastest development of the three species, needing less energy to produce new leaves on the main stem and complete the seedling stage. All three tropical forest species developed best in months with mild air temperatures (between 13.3 °C and 26.9 °C) and day lengths < 13 h. *Pinus koraiensis* is a dominant species in temperate forests of northeastern China. Morphophysiological dormancy following seed dispersal in autumn is an important factor limiting its natural or artificial regeneration. In this SI, Song et al. (2022) reported an optimum cold stratification temperature to stimulate the germination of *P. koraiensis* seeds at lower temperatures. They pointed out a low efficiency by breaking dormancy of *P. koraiensis* seeds in natural environments through cold overwintering in the context of increasing winter temperatures in

northeastern China. They also highlighted that seed germination at low spring temperatures is an effective measure for the growth and survival of plant species inhabiting temperate forest ecosystems.

The great amounts of atmospheric CO<sub>2</sub> captured by forests, especially old-growth forests and stored in their biomass and soils over time are critical for reducing atmospheric CO<sub>2</sub> concentrations and mitigating climate change (Yatskov et al. 2019). The study by Di Matteo et al. (2022) quantified organic C concentrations in three old-growth forest ecosystems, showing substantial variations in living trees, deadwood, and woody litterfall compartments. Their work provides a useful criterion for sustainable forest management to enhance forest adaptation to climate change. They propose further studies on structural, ecophysiological and ecological functions of old-growth forests.

Soil quality indices (SQI) are commonly used to assess the impacts of management systems on agricultural soils, but SQI-based assessments on the effects of harvest residue management on sandy forest soils are scarce. The study by de São José et al. (2022) demonstrated that removing harvest residues can lead to physical and biological degradation in eucalypt plantations on sandy soils grown in a subtropical climate. They developed a sensitive, accurate SQI-based protocol for managing *Eucalyptus* harvest residues and emphasized the importance of retaining eucalyptus harvest residues to avoid soil degradation and forest productivity losses in sandy soils. Leonel et al. (2022) evaluated the growth and physiological characteristics of pioneer (*Guazuma ulmifolia*), secondary (*Astronium fraxinifolium*), and climax (*Cariniana rubra*) tree species during rainy and dry periods with different light intensities and a soil conditioner containing a hydrogel. They demonstrated that the pioneer and secondary species under 100% luminosity had greater physiological plasticity than the climax species. They concluded that the hydrogel soil conditioning significantly stimulates photosynthesis in the pioneer and secondary species during high radiation and dry periods.

Because changes in rainfall, humidity, CO<sub>2</sub> level, and temperature fundamentally influence plant physiology and metabolism, monitoring plant nutrients status in field situations and in nurseries is essential for producing high-quality seedlings. In this SI, Gomes et al. (2022) developed a new vegetation spectral index and a near-infrared leaf reflectance model to accurately detect early variations in leaf N concentration of *Annona emarginata*. In olive stands, cover crops minimize erosion rates and provide additional ecosystem services. However, in semiarid climates, the trade-off between these benefits and their competition with the olive trees present a challenge for determining optimal management practices. López-Bernal et al. (2022) therefore developed new components for the OliveCan model to simulate the effects of cover crops on water–C balances in

olive orchards under different management strategies. The model allows the user to quantify the effect of the cover crop management strategies under different climatic, soil and orchard scenarios and will help determine the best strategy for sustainable productivity of olive orchards as the climate changes.

As the earth is subject to more extreme climate events, we must arm ourselves with the knowledge to meet all the challenges and mitigate the deleterious effects on all our ecosystems, so that the world can sustain life. As the articles demonstrate, we have much to learn and many large problems to solve. We hope that this special synthesis of recent research on critical forestry issues such as climatic hormesis, phenological–climatic associations, acclimatization in dominant tree species to climate extremes and ecological succession will inspire new ideas and research to enhance the health and productivity of our forests.

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