forests

Editorial

Physiological Responses to Abiotic and Biotic Stress in Forest Trees

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Abstract: Forests fulfill important ecological functions by sustaining nutrient cycles and providing habitats for a multitude of organisms. They further deliver ecosystem services such as carbon storage, protection from erosion, and wood as an important commodity. Trees have to cope in their environment with a multitude of natural and anthropogenic forms of stress. Resilience and resistance mechanisms to biotic and abiotic stresses are of special importance for long-lived tree species. Since trees exist for many decades or even centuries on the same spot, they have to acclimate their growth and reproduction to constantly changing atmospheric and pedospheric conditions. In this special issue, we invited contributions addressing the physiological responses of forest trees to a wide array of different stress factors. Among the eighteen papers published, seventeen covered drought or salt stress as major environmental cues, highlighting the relevance of this topic in times of climate change. Only one paper studied cold stress [1]. The dominance of drought and salt stress studies underpins the need to understand tree responses to these environmental threats from the molecular to the ecophysiological level. The papers contributing to this Special Issue cover these scientific aspects in different areas of the globe and encompass conifers as well as broadleaf tree species. In addition, two studies deal with bamboo (*Phyllostachys* sp., [1,2]). Bamboo, although botanically belonging to grasses, was included because its ecological functions and applications are similar to those of trees.

1. Drought Has Multifaceted Consequences That Impede Tree Performance

Several studies in this issue addressed traits of conifers experiencing large variations in environmental growth conditions. Fotelli et al. [3] assessed the physiological plasticity of Aleppo pine (*Pinus halepensis*), an important species in the Mediterranean area, to cope with seasonal changes in environmental conditions, especially summer drought. They found that Aleppo pine is an isohydric species, displaying a drought avoidance strategy. However, Lin et al. [4], using *Pinus massoniana*, showed significant acclimatory changes in needle carbohydrates after long-term exclusion of precipitation. This finding supports an induction of tolerance mechanisms (instead of avoidance) to prevent excessive water loss. Fan et al. [5] studied the physiology of *Pinus koraiensis*, a keystone species of temperate mountain forests, along an altitudinal gradient in China, where precipitation was among the strongest drivers for sapling growth. Interestingly, the saplings showed better growth in mixed than in pure *Pinus koraiensis* forests, suggesting facilitation effects, which obviously were not overruled by other fluctuating environmental constraints. Along similar lines, Magh et al. [6] investigated nitrogen nutrition of European beech (*Fagus sylvatica*) in pure and mixed stands with silver fir (*Abies alba*). Fir needles contained less N than beech leaves, which may dampen the competition for nitrogen in mixed stands. When soil N was low, beech benefited from the interaction with fir but not at high soil N. Together, these studies highlight the importance of distinguishing different evolutionary strategies coping with divergent nutrient and water availability and underpin that the responses of trees are context dependent.

A major issue of growing concern is the spread of pathogens in stressed forests. Therefore, the paper of Terhonen et al. [7] is particularly timely. They reported that water-deficient spruce (*Picea abies*) shows stronger disease symptoms and stronger growth suppression when exposed to *Heterobasidion* species than well-watered plants. It is, thus, urgently required to develop protective measures against forest pests.

Sudden tree death is a significant threat in many areas of the world [8]. The most likely reasons for sudden tree death are carbohydrate depletion or hydraulic failure. Here, Eckert et al. [9] provide an overview on how hardwoods acclimate their hydraulic system to cope with environmental stresses. They explain the production of basic wood structures, focusing mainly on molecular regulation, and compile information on how these structures are influenced to maintain water flow under environmental constraints. Their review is of interest for researchers who wish to obtain a glimpse into the complex regulation of wood production. Sun et al. [10] add an ecological perspective to this important topic. They studied ecophysiological markers such as ring width, $\delta^{13}C$ isotope ratios for water availability, and intrinsic water use efficiency in the wood of poplar (*Populus simonii*) to find early bio-indicators for trees that would succumb in the future. In a fragile ecosystem of the northern Chinese shelterbelt, they classified trees as dead, dying, and not affected. They report that already almost two decades before death, tree rings become smaller and $\delta^{13}C$ higher, suggesting that these traits can be used as earlier warning symptoms. Based on such traits, it is hoped that future genetic studies can develop markers that may allow the selection of resistant trees for reforestation programs in areas with strong tree decline.

2. Salinity and Combined Stresses: From Soil Amendment to Redox Balance

Salinity causes osmotic stress and, in this regard, some similarities with drought stress exist [11]. However, salinity also acts via ionic stress and, therefore, drought and salt responses are only partly overlapping [12]. Salt stressed plants often exhibit enhanced concentrations of reactive oxygen species (ROS) [13]. An overabundance of ROS, which cannot be compensated by antioxidative systems, leads to damage symptoms such as chlorophyll degradation, membrane leakage, and eventually necrosis [13]. Some examples for salt damage symptoms at the tissue and organelle levels are also demonstrated in this Special Issue [14,15]. Since soil degradation with enhanced salinization is an increasing problem, identification of salt-tolerant plant species and measures to enhance the resistance of crops and horticultural plants are urgently needed. In this Special Issue, several papers are devoted to improving salt tolerance.

Geng et al. [16] present a study on *Osmanthus fragans* (sweet olive), an ornamental plant, which has important commercial applications (e.g., for perfume production). They showed that moderate doses of γ-radiation of seeds have a long-lasting effect on the salt tolerance of seedlings that went along with a generally enhanced level of antioxidative enzyme activities and reduced superoxide accumulation. Under approximately 80 mM salt, the injury index of non-treated seedlings was twice that of γ-radiated ones, suggesting that the vitality of this horticultural species can be enhanced to cope with moderate salt stress. Further studies are required to elucidate how γ-radiation leads to this interesting effect.

Hornbeam (*Carpinus turczaninowii*) is known for its beautiful autumn colors and fine-textured wood. Zhou et al. [15,17] systematically tested the performance of this tree species as well as its European counterpart *Carpinus betulus* under moderate salt stress (up to 85 mM). They found that antioxidant systems of the European species collapsed after about 1 month and that of the Asian species after about 2 months in the presence of low salinity levels (30 to 50 mM). The plants showed distinct damage symptoms under these conditions, supporting the conclusion that both species are relatively salt sensitive. This finding calls for further research because *C. turczaninowii* is relatively drought tolerant, suggesting that the genetic basis for drought and salt tolerance diverged in this species, making it an interesting model to dissect drought and salt adaptation.

Soil amendments with hydrogels have a great potential to enhance plant performance under osmotic and ionic stress [18]. In this Special Issue, Li et al. [19] tested synthetic hydrogels and glucomannan-based biopolymer additions to salinized or dehydrated soils, in which *Metasequoia glyptostroboides* (dawn redwood) was grown. While the effects of hydrogels on growth rescue were moderate for single stress factors, all tested compounds had positive effects when drought and salinity occurred together, indicating that the performance of redwood, which is an endangered species, can be improved by retention of salt ions and better water provision.

Chemical treatments can also improve salt tolerance. Here, Rao et al. [20] showed that pre-exposure of *Populus euphratica* to salicylic acid (0.4 mM) enhanced the performance of plants under subsequent massive salt stress (300 mM). The beneficial effect was concentration dependent and disappeared in plants exposed to 1 mM salicylic acid. In another study, *Robinia pseudoacacia* seeds or seedlings were treated with 24-epibrassinolide (a brassinosteroid) and subsequently exhibited enhanced antioxidative protection and enhanced salt tolerance [14]. To obtain deeper insights into the signal transduction pathway activated by stress, the *TCP15* transcription factor (*TEOSINTE BRANCHED1, CYCLOIDEA, and PROLIFERATION CELL FACTOR*) was isolated from *Fraxinus mandshurica* (Mandchurian ash) [21]. TCP15 transient overexpression activated many downstream responses, for example, transcripts encoding antioxidative proteins and hormonal signals [21]. Along similar lines, Yuan et al. [22] tested the response of glutaredoxin *SRGRX1* of rubber (*Hevea brasiliensis*) to a large array of different hormones and stresses. Glutaredoxins are important modulators of the cellular redox state. The rubber SRGRX1 was quickly activated by ROS as well as by abscisic acid (ABA) and salicylic acid, indicating the need for redox regulation under stress [22]. These results underpin the importance of plant hormones for activating defense systems and the need for a better understanding of signaling pathways. However, for practical applications, the trees from current laboratory studies have to be transferred to the field and tested for the stability of the modified traits under natural conditions. A recent example for ABA-related transgenic trees shows that this may lead to unexpected results and novel insights into tree acclimation to their fluctuating environment [23].

3. Conclusions and Outlook

Overall, this issue covers an impressive range of trees species and their response to salinity or drought at different scales from ecophysiology to molecular mechanisms. We hope that efforts such as the current Special Issue can be used to identify similarities and divergences of stress responses, because in-depth knowledge on basal stress pathways can be exploited to develop protection strategies for trees on salt- or drought-affected soils. Furthermore, the distinctive responses of evolutionary stress-adapted tree species hold great promise for implementing specific protection measures in important crop trees.

Conflicts of Interest: The authors declare no conflict of interest.

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