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Annual Meeting

Root and Rhizosphere Processes under Drought: Digging Deeper to Enhance Ecosystem Resilience

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Global ecosystems face severe challenges from climate change, environmental pollution, and intensive farming. Among these challenges, frequent and intense drought presents a significant threat to plants in both natural and managed ecosystems. Roots and the rhizosphere, including countless microorganisms, can shape plant responses to drought and hence ecosystem health and resilience. This ESA symposium focused on how root traits and rhizosphere microbiomes respond to drought in diverse ecosystems. More profound knowledge of these vital connections between rhizosphere processes and ecosystem health under drought stress can help us formulate sustainable ecosystem management practices and impart drought resilience in plants. Forests are essential in sustaining life on earth as they contribute to many ecosystem services, including soil carbon sequestration. Fine roots of trees and the associated mycorrhizae which contribute to a majority of soil carbon exhibit a high level of plasticity under drought. The different talks in this symposium examined recent advances on the morphological, physiological, and chemical plasticity

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of plant roots under drought, which is indispensable for plant health. The talks also focused on the impact of drought on mycorrhizae and the associated changes in plant–fungal interactions. The symposium also highlighted the importance of root phenotypes that mitigate drought stress in grasses and harnessing the rhizosphere microbiome to impart drought resilience in agroecosystems. The speakers in this symposium represented wider disciplines, including soil ecology, plant physiology, and microbiology.

Vidya Suseela from Clemson University, USA, focused on the effect of fine root chemical plasticity on drought tolerance in trees. The environment stress-induced morphological and physiological plasticity is often accompanied by chemical plasticity, which includes changes in the quantity, composition, and localization of heteropolymers such as lignins, tannins, and suberin. These heteropolymers have biological activity in both green and senesced tissues and the composition of these heteropolymers (e.g., identity and number of monomer units, linkages connecting the monomers) regulates much of this biological activity than their quantity. Environmental stress such as drought can alter the quantity, composition and localization of the heteropolymers within the three-dimensional root matrix with implications on important ecosystem functions (Suseela et al. 2017, Suseela and Tharayil 2018). The chemistry of roots regulates their decomposition that recycles nutrients in senesced tissues, thus facilitating ecosystem productivity and soil carbon sequestration. The chemical plasticity of fine roots also has implications in plant-mycorrhizal symbiotic associations. Fine roots of trees (diameter ≤2 mm) adapt to their soil environment through changes in root morphology and physiology, which is relatively well studied. However, the associated changes in root chemistry are less known. In the fine roots of white oak (*Quercus alba*), drought altered the quantity and composition of tannins (Suseela et al. 2020). Under drought conditions, the white oak had lower content of ellagitannins. Since ellagitannins have antimicrobial properties, their lower content indicates an adaptive response of fine roots to promote the ectomycorrhizal association. The chemical construct of fine roots can thus vary with the type and extent of mycorrhizal association (Xia et al. 2021, Kaur et al. 2022). Drought did not alter the content and composition of lignin while they varied across root orders. Despite lower lignin in the distal order roots, these roots are better protected against stress due to the higher content of guaiacyl lignin and bound phenolics that integrate the lignocellulosic matrix (Suseela et al. 2020). Overall, the chemical content and composition of fine roots varied across root orders, mycorrhizal association, and with drought. The chemical plasticity of fine roots in reponse to drought indicated a strategy to maximize resource uptake while concurrenlty adapting to environmental stress. These changes in root chemistry have implications for root decomposition and soil carbon sequestration. The talk also briefly focused on the analysis techniques, including a sequential extraction of tissues followed by gas/liquid chromatography-mass spectrometry to estimate the biologically relevant carbon fractions in plant tissues (Suseela and Tharayil 2018).

Alex Williams from the University of Sheffield, UK, spoke about harnessing rhizosphere processes for drought resilience in ecosystems. His talk focused first on the role and importance of root exudates in the rhizosphere, followed by a discussion and description of the different techniques available for collecting and analyzing the chemical constituents of exudates. He then described work undertaken at the University of Manchester, in collaboration with Prof. Franciska de Vries, where root exudation was studied across 15 grassland species of different functional groups and found to be strongly associated with nutrient outsourcing to microbial collaborators. With more detailed analysis, he determined that there were functional-group and species-level differences within the exudate chemical profile, indicating niche specificity of exuded metabolites is likely occurring at a species level (Williams et al. 2020). Considering the plasticity of root-exudate expression during drought is likely also species-specific, which informs the microbial community response in the rhizosphere, which in turn tailors the plant resistance to drought, this

work indicates that species with less active exudation strategies are less likely to overcome drought with high fitness. He concluded his talk by highlighting the potential of leveraging these exudation processes to generate healthier and more drought-resilient soils in natural and managed ecosystems.

Cheng Gao, from the Institute of Microbiology, Chinese Academy of Sciences, presented the responses of the fungal and bacterial microbiome to drought stress. Due to the increasing demand but decreasing supply of water resources, drought is becoming one of the most important factors limiting the sustainability of our planet, causing the cascading global crisis. The realized niches of plants are largely defined by their fungal and bacterial microbiome, and together, the plant and the microbiome form a holobiont that responds to and adapts to environmental perturbation. Recently, researchers have highlighted the roles of the microbiome for drought-resilient crop production. He advocates developing a unified framework that begins with Vellend's four basic processes of microbial community assembly (selection, dispersal, diversification, and drift; Vellend 2010) and integrates the several frameworks that have been proposed for microbial response to stress, including the Resistance-Resilience-Redundant (RRR) framework that explicitly decomposes different components of the stability of microbiome to stress (Allison and Martiny 2008); the Competitor-Stress-tolerator-Ruderal (CSR) and high Yield-resource Acquisition-Stress tolerance (YAS) frameworks that focus on the tradeoff of functional traits in response to stress and disturbance (Grime 1974, Malik et al. 2020); the Stress-Gradient hypothesis (SGH) that examines the biotic interaction in response to stress (Bertness and Callaway 1994), and the Cry-For-Help (CRH) model that focuses on how the host regulates its microbiome in response to stress (Rolfe et al. 2019). He also advocates that harnessing the microbiome for modern agriculture may be fostered by integrating a multi-Omics approach, advanced ecological theory, and modern informatics technology. Finally, using the EPICON project (https://phytozome-next.jgi.doe.gov/epicon/) as an example, he highlighted their progress on understanding the response of the sorghum microbiome to the drought that has emerged from collaboratively investigating the fungal mycobiome, the bacterial microbiome, the meta-genome and meta-transcriptome, and the host sorghum transcriptome and metabolome (Xu et al. 2018, 2021*a*, *b*, Gao et al. 2019, 2020, 2022, Zhou et al. 2020).

Hannah Schneider from the Wageningen University presented on the topic of root phenotypic plasticity for drought tolerance and crop improvement. Phenotypic plasticity is a widespread and important phenomenon for the strategic capture of nutrients and water. She conducted genome-wide association mapping on root traits and their plasticity on a large maize association panel grown in the field with and without water deficit. Specifically, she presented several examples of anatomical and architectural root traits that respond to drought, including metaxylem number, root cortical aerenchyma, stele diameter, multiseriate cortical sclerenchyma, root angle, and lateral branching density and length (Schneider et al. 2020*a*, *b*, 2021). She reported that the genetic control of phenotypic plasticity was highly quantitative, and loci associated with plastic responses were distinct from loci controlling trait expression in stress and non-stress. In drought, many of these plastic responses were adaptive and were associated with deeper rooting, yield stability, and greater plant performance. However, the adaptive value of plastic responses of root traits depended on the spatial and temporal distribution of water and nutrients in the soil. Understanding the adaptive value and genetic control of root plasticity will provide an array of tools to better understand adaptive strategies for enhanced plant productivity.

The live discussion of the symposium involved conversations about the salient features imparting drought tolerance in plants and answering questions from the audience, panel members, and the

moderator. An important topic revisited during the discussion was related to research advances in utilizing microbiomes for plant drought tolerance. The panel agreed that manipulating the microbiome is an important component along with other plant adaptive traits for drought tolerance and could be targets for plant breeding. The panel discussed the importance of inoculating the entire microbiome vs. single species in imparting plant drought tolerance. Inoculating the entire microbiome may be an ideal strategy for drought tolerance than single species inoculation. However, at a field level, the inoculation of the entire microbiome may pose unique challenges that need to be further evaluated. Another approach is to utilize the plant to select the drought-tolerant microbiome by manipulating root exudates. There was also discussion about the possibility of inoculating the endosphere of the plant with drought-tolerant microbiome. However, this approach has challenges, including the lack of persistence of this microbiome over the entire growth period of the plant. Another discussion point centered around the complexity of different plastic responses of plants. Phenotypic plasticity is a trait-specific characteristic and how the various root traits interact with the environmental conditions at different spatial and temporal scales affects plant performance under abiotic stress. Further, these plastic responses to drought can influence other trophic level processes. For example, the chemical plasticity can alter plant defense against pests and pathogens. The interaction of the different plastic responses is complex, and further research is vital to unravel plastic responses of roots to environmental stress and harness them for plant drought tolerance.

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Data Availability

No data were collected for this review.

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