Annals of Botany **136**: 1–3, 2025
https://doi.org/10.1093/aob/mcaf222, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Nonprofit since 1887

PREFACE

The hidden half in the spotlight: the diverse strategies of root systems under stress

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Received: 09 September 2025 Accepted: 09 September 2025

As the hidden half of the plant, roots provide essential anchorage and act as the lifeline of the plant. They are the primary interface between the plant and the soil, navigating a complex and often hostile environment to acquire life-sustaining water and nutrients. In an era of unprecedented climate change and increasing pressure on our agricultural and natural ecosystems, understanding how root systems respond to environmental stress has never been more critical. The challenges are immense, from prolonged droughts and frequent flooding to soil compaction, nutrient-depleted and salinized soils. Yet, with these challenges come opportunities for discovery and innovation.

This Special Issue of *Annals of Botany* was commissioned to bring together a diverse collection of research that comprehensively addresses the effects of stress on root system physiology, morphology and architecture. We were thrilled by the response from the scientific community, and the papers collected here represent the cutting edge of root biology. They make use of a remarkable array of tools, from advanced phenotyping platforms (Odone and Thorup-Kristensen, 2025; Odone *et al.*, 2025; Sillo *et al.*, 2025) and three-dimensional hydraulic models (Koch *et al.*, 2025) to multi-omics analyses (Hu *et al.*, 2024) and a bibliometric review (Zhai *et al.*, 2025), to shed new light on how plants sense, signal and strategize their reactions to challenging conditions. This issue not only delves into fundamental mechanisms but also casts a wide net, examining the adaptive strategies of crops, the ecological success of wild species and the very evolution of the traits that govern the hidden half. Although this collection significantly advances our understanding of root responses to abiotic challenges, further research is needed to address the equally critical area of biotic stress on root systems comprehensively.

A powerful theme that emerges from this collection is that there is no single ‘stress response’. Instead, roots operate on a principle of profound plasticity, whereby the outcome is contingent on genetics, development and environment. As the review by Jacob *et al.* (2025) highlights, this plasticity is orchestrated by a complex hormonal network, with auxin playing a key role in adjusting root growth in response to stimuli such as elevated temperature. Recent findings by Scott *et al.* (2024) further show the breadth of this hormonal control, demonstrating how conserved peptide signalling pathways, such as those involving CLV3/embryo-surrounding region (CLE) peptides, can simultaneously regulate shoot development and crucial below-ground symbioses. This hormonal control underpins the anatomical shifts we see elsewhere. The work of Guhr *et al.* (2025) offers a striking example, showing that wheat roots can deploy similar anatomical and architectural adaptations, such as aerenchyma formation and lateral root growth, to combat the opposing stresses of drought and flooding. Yet, this apparent convergence is layered with complexity. Koehler *et al.* (2025) caution against a monolithic view, demonstrating in maize that the anatomical and hydraulic response to drought is exquisitely specific to root class (e.g. nodal origin of the root). This context dependence extends across time, emphasizing that plant ontogenetic changes are crucial, because the selective pressures on a young seedling can be vastly different from those on a mature, reproductive plant. As Qin *et al.* (2025) show, the root economic strategy of a tree shifts throughout its life, whereas Odone and Thorup-Kristensen (2025) find that millennia of breeding have reshaped the very architecture of wheat, giving modern varieties deeper, more efficient root systems to support higher yields. Together, these studies dismantle the notion of a simple stimulus response, moving us beyond simplistic cause-and-effect assumptions. They paint a far richer picture of finely tuned strategies that reflect a dynamic calculation of costs and benefits, shaped by where a root is in the soil profile, when it is growing in the life cycle of the plant, and the unique genetic and evolutionary blueprint it carries. Indeed, a response that is advantageous for a young seedling might not be for a mature tree, almost as if they were distinct entities adapting to their specific life-stage demands; likewise, the ideal root angle for one soil type might be detrimental in another. It is this appreciation for context, from the scale of a single root tip to the grand time line of domestication, that truly advances our understanding.

When it comes to mastering environmental extremes, the papers in this issue illuminate a diverse toolkit. In facing drought, roots not only endure but actively adapt. We see this in the dynamic cycling of rice phenotypes observed by Bochmann *et al.* (2025), whereby plants shift the types of lateral roots formed (i.e. L-type vs. S-type) to recover rapidly after a dry period. The capacity for resilience is also highlighted by Li *et al.* (2025), who reveal the remarkable speed of hydraulic recovery within the root system after stress is relieved. Some species take adaptation a step further; Song *et al.* (2024) show how wild rice uses interconnected rhizomes for physiological integration, allowing connected clones to support each other through heterogeneous water stress. At the root–soil interface, plants can engineer their immediate surroundings. The work of Abdalla *et al.* (2024) and Akale *et al.* (2025) provides compelling plant-scale evidence that exudation of mucilage maintains the hydraulic connection to drying soil, a crucial buffer against failure, a finding complemented by the three-dimensional modelling by Koch *et al.* (2025) which underscores the importance of physical soil–root contact. In stark contrast, when faced with an excess of water or harsh soil chemistry, roots re-tool for survival. Sherwood *et al.* (2025) and Mondal *et al.* (2025) explore the genetic underpinnings of aerenchyma, identifying key regulatory networks in barley and showing that in rice, these air channels serve a dual purpose, not only for oxygen supply but also for restricting sodium uptake under salinity. And in wild soybean, Hu *et al.* (2024) demonstrate that resilience to alkali stress comes from strengthening cell walls through enhanced lignin and cellulose metabolism. The root, it seems, possesses a sophisticated and distinct set of strategies for every physical and chemical challenge.

The same strategic diversity is evident in the critical task of foraging for nutrients, such as phosphorus. This collection showcases a spectrum of evolutionary solutions. At the architectural level, Sillo *et al.* (2025) conclude that coordinated root traits can enhance phosphorus efficiency in wheat under deficiency and propose a novel synthetic indicator to support breeding for phosphorus tolerance. Bauer *et al.* (2024) show how phosphorus deficiency reorganizes maize root architecture with significant consequences for the water uptake capacity of the whole system. The response is also highly localized, because Sun *et al.* (2024) demonstrate how maize roots can precisely ramp up metabolic activity to fuel proliferation in nutrient-rich patches. Pushing the boundaries of current paradigms, Yan *et al.* (2025) use leaf chemistry as a proxy to reveal that dominant, mycorrhizal Myrtaceae species engage in carboxylate-driven phosphorus mining, which is a strategy previously thought to be the domain of non-mycorrhizal plants. This finding fundamentally reshapes our understanding of nutrient acquisition, proving that evolution can arrive at similar solutions through different symbiotic pathways.

These specific traits do not evolve in isolation but are woven into the broader ecological and evolutionary fabric of a species. As Münzbergová *et al.* (2025) show in a sweeping study of 65 forb species, root trait variation is directly linked to the habitat preferences of a species. Likewise, Li *et al.* (2024) identify a coordinated economic spectrum between leaf and root traits along an elevational gradient. In an alpine steppe, Zheng *et al.* (2024) provide a vivid example of this differentiation in action, showing how two grass species deploy different physiological traits and rooting depths, relating to greater adaptation during long-term drought. However, the adaptive value of these traits is not fixed. Using an innovative *in silico* approach, Rangarajan and Lynch (2024) demonstrate that the fitness landscape for root phenotypes has been dramatically reshaped by agriculture, whereby traits adaptive in native soils became less advantageous with the advent of cultivation and irrigation. Furthermore, roots are not solitary agents but hubs of vibrant ecosystems. The work presented here by Hartwig *et al.* (2025) and Würsig *et al.* (2025) reveals that drought responses are shaped by intricate, multi-year interactions between plant genotype, soil and the resident microbial community. Adopting a novel spatial lens, Galindo-Castañeda *et al.* (2025) meticulously map prokaryotic communities along the maize root system, linking the abundance of specific microbes directly to architectural phenotypes such as lateral root branching and length.

Of course, this rich, thematic tapestry is visible to us only because of the variety of methods on display in this issue. Our understanding of roots is constrained by our ability to see and measure them. The insights gathered here span scales and systems, from hydroponics (Guhr *et al.*, 2025) and mesocosms (Galindo-Castañeda *et al.*, 2025) to large-scale semi-field facilities (Odone and Thorup-Kristensen, 2025; Odone *et al.*, 2025) and multi-site European field trials (Durand-Maniclas *et al.*, 2025). We see the power of non-invasive imaging, such as the novel scanner-based analysis used by Siegwart *et al.* (2025) to assess root decomposition kinetics deep in the soil profile. We see the precision of isotope tracers Odone and Thorup-Kristensen, 2025 the depth of transcriptomics (Sherwood *et al.*, 2025) and the predictive power of sophisticated models for root system conductance (Bauer *et al.*, 2024), root water uptake (Koch *et al.*, 2025) and root mechanical properties (Yang and Ji, 2025). This diversity is not merely a detail; it is essential for uncovering the truth. The contrasting findings on the role of root hairs by Tasca *et al.* (2025) and Hartwig *et al.* (2025) illustrate how the importance of a trait is defined by its context, a context revealed only by application of different methods at different developmental stages. For example, maize root hairs are not essential for early seedling performance under stress but play a key role in modulating rhizosphere interactions and amplifying drought response dynamics. As the bibliometric review by Zhai *et al.* (2025) concludes, root ecology is moving from theory towards vital practical applications. By continuing to embrace this methodological complexity, the research community can provide the knowledge needed to breed more resilient crops, ensuring that the hidden half plays its critical role in a sustainable future.

SYNTHESIS AND FUTURE DIRECTIONS

The papers in this Special Issue collectively advance our understanding of the stress physiology of root systems on multiple fronts. A clear message emerges: there is no single, optimal root strategy. Instead, plant roots exhibit a remarkable plasticity, governed by complex trade-offs shaped by the specific environmental context, the evolutionary history of the plant and its interactions with the living soil. The latter clearly harbours numerous challenges regarding communication between kin and non-kin species/organisms.

As we look to the future, the path forwards will require an even more integrated approach, bridging the gap between the laboratory and the field, connecting below-ground processes with whole-plant performance and understanding the complex interplay between roots, soil and the microbiome. Translating these fundamental discoveries into tangible solutions, from breeding more resilient crops to managing our natural ecosystems more effectively, remains our ultimate goal.

We extend our sincere gratitude to all the authors for contributing their excellent research and to the many anonymous reviewers whose diligence and thoughtful feedback greatly enhanced the quality of this issue. We hope that you, the reader, will find this collection of articles as inspiring and insightful as we have.

REFERENCES

Abdalla M, **Carminati A**, **Cai G**, **Ahmed MA. 2024.** Mucilage facilitates root water uptake under edaphic stress: first evidence at the plant scale. *Annals of Botany* **mcae193**. doi:10.1093/aob/mcae193

Akale A, **Abdalla M**, **Koehler T**, **Sauer AM**, **Diamantopoulos E**, **Ahmed MA. 2025.** Root mucilage enhances plant water use under combined soil and atmospheric drought. *Annals of Botany* **mcaf182**. doi:10.1093/aob/mcaf182

Bauer FM, **Baker DN**, **Giraud M**, ***et al.*** **2024.** Root system architecture reorganization under decreasing soil phosphorus lowers root system conductance of Zea mays. *Annals of Botany* **mcae198**. doi:10.1093/aob/mcae198

Bochmann H, **Klein M**, **Henry A**, ***et al.*** **2025.** Rice cycles between drought and well-watered-adapted phenotypes by changing lateral root formation. *Annals of Botany* **mcaf173**. doi:10.1093/aob/mcaf173

Durand-Maniclas F, **Heinemann H**, **Seidel F**, ***et al.*** **2025.** Linking root length and surface area to yield: variety-specific root plasticity in winter wheat across contrasting European environments. *Annals of Botany* **mcaf155**. doi:10.1093/aob/mcaf155

Galindo-Castañeda T, **Kost E**, **Giuliano E**, **Conz RF**, **Six J**, **Hartmann M. 2025.** Locating the microbes along the maize root system under nitrogen limitation: a root phenotypic approach. *Annals of Botany* **mcaf185**. doi:10.1093/aob/mcaf185

Guhr T, **Song Z**, **Andersen AG**, **de la Cruz Jiménez J**, **Pedersen O. 2025.** Root morphology and anatomy respond similarly to drought and flooding in two wheat cultivars. *Annals of Botany* **mcaf152**. doi:10.1093/aob/mcaf152

Hartwig RP, **Santangeli M**, **Würsig H**, ***et al.*** **2025.** Drought response of the maize plant–soil–microbiome system is influenced by plant size and presence of root hairs. *Annals of Botany* **mcaf033**. doi:10.1093/aob/mcaf033

Hu Y, **Hu Y**, **Gao S**, ***et al.*** **2024.** Enhanced lignin and cellulose metabolism promote cell wall synthesis and growth of wild soybean HRA under alkali stress. *Annals of Botany* **mcae124**. doi:10.1093/aob/mcae124

Jacob T, **Maciel Rodrigues Junior O**, **Quint M. 2025.** Hormonal regulation of root growth under moderately elevated temperatures. *Annals of Botany* **mcaf087**. doi:10.1093/aob/mcaf087

Koch A, **Cai G**, **Ahmed MA**, ***et al.*** **2025.** On the importance of rhizosphere conductance and soil–root contact in drying soils. *Annals of Botany* **mcaf082**. doi:10.1093/aob/mcaf082

Koehler T, **Kim Y**, **Tung S-Y**, ***et al.*** **2025.** Node of origin matters: comparative analysis of soil water limitation effects on nodal root anatomy in maize (Zea mays). *Annals of Botany* **mcaf075**. doi:10.1093/aob/mcaf075

Li F-P, **Palta JA**, **Yao G-Q**, ***et al.*** **2025.** Roots go through rapid hydraulic recovery following moderate water stress. *Annals of Botany* **mcaf060**. doi:10.1093/aob/mcaf060

Li J, **Westerband AC**, **Wright IJ**, ***et al.*** **2024.** Temperature and plant-available soil phosphorus drive intraspecific variation in plant economic traits of Schima superba across an elevation gradient. *Annals of Botany* **mcae212**. doi:10.1093/aob/mcae212

Mondal S, **Panda B**, **Nayak JK**, **Pradhan C**, **Chattopadhyay K**, **Chakraborty K. 2025.** The role of aerenchymatous gas spaces in root sodium ion management under salt stress: do they matter in rice? *Annals of Botany* **mcaf134**. doi:10.1093/aob/mcaf134

Münzbergová Z, **Hanzelková V**, **Dostálek T. 2025.** Species habitat preferences and root trait variation across 65 temperate perennial forbs. *Annals of Botany* **mcaf029**. doi: 10.1093/aob/mcaf029

Odone A, **Changdar S**, **Thorup-Kristensen K. 2025.** Winter wheat phenotyping for deep root growth and function, reduced water stress and increased uptake of deep N and water. *Annals of Botany* **mcaf160**. doi:10.1093/aob/mcaf160

Odone A, **Thorup-Kristensen K. 2025.** Modern wheat has deeper roots than ancient wheats: is this an adaptation to higher productivity? *Annals of Botany* **mcaf065**. doi:10.1093/aob/mcaf065

Qin Y, **Valverde-Barrantes OJ**, **Jin G**, **Liu Z**, **Freschet GT. 2025.** Tree age affects key fine root morphological traits but does not interfere strongly with (ecto-)mycorrhizal traits. *Annals of Botany* **mcae223**. doi:10.1093/aob/mcae223

Rangarajan H, **Lynch JP. 2024.** Did crop domestication change the fitness landscape of root response to soil mechanical impedance? *An in silico analysis. Annals of Botany* **mcae201**. doi:10.1093/aob/mcae201

Scott TE, **Correa-Lozano A**, **Foo E. 2024.** Upstairs, downstairs: conserved and divergent CLAVATA signalling in shoot meristem development and root symbioses, *Annals of Botany* **mcae192**. doi:10.1093/aob/mcae192

Sherwood OL, **Burke R**, **O'Rourke J**, ***et al.*** **2025.** Transcriptional signatures associated with waterlogging stress responses and aerenchyma formation in barley root tissue. *Annals of Botany* **mcaf104**. doi:10.1093/aob/mcaf104

Siegwart L, **Saimpha G**, **Bertrand I**, **Hedde M**, **Jourdan C. 2025.** High-throughput monitoring of root diameter reveals the temporal dynamics of root decomposition. *Annals of Botany* **mcaf175**. doi:10.1093/aob/mcaf175

Sillo F, **Salon C**, **Lamboeuf M**, ***et al.*** **2025.** A novel P indicator to evaluate bread wheat (Triticum aestivum L.) genotypes to identify tolerance to phosphorus deficiency based on two distinct root phenotyping platforms. *Annals of Botany* **mcaf091**. doi:10.1093/aob/mcaf091

Song Z, **Lin C**, **Pedersen O**, **Jiménez J. 2024.** Anatomical and physiological responses of roots and rhizomes in *Oryza longistaminata* to soil water gradients. *Annals of Botany* **mcae131**. doi:10.1093/aob/mcae131

Sun Y, **Zhang J**, **Li W**, ***et al.*** **2024.** Regulation of maize root growth by local phosphorus availability, sucrose metabolism, and partitioning. *Annals of Botany* **mcae169**. doi:10.1093/aob/mcae169

Tasca A, **Alcock TD**, **Bienert GP. 2025.** The role of maize (Zea mays) radicle root hairs in seedling establishment under adverse phosphorus and water seedbed conditions. *Annals of Botany* **mcaf142**. doi:10.1093/aob/mcaf142

Würsig H, **Yim B**, **Roldán MM**, ***et al.*** **2025.** Responses of maize roots, rhizosphere enzyme kinetics and prokaryote diversity to alternating precipitation: insights from a three-year field study. *Annals of Botany* **mcaf180**. doi:10.1093/aob/mcaf180

Yan L, **Hayes PE**, **Nge FJ**, ***et al.*** **2025.** Leaf manganese concentrations reveal phosphorus-mining strategies and trait diversification of Myrtaceae in south-eastern Australia. *Annals of Botany* **mcaf129**. doi:10.1093/aob/mcaf129

Yang Y, **Ji J. 2025.** Role of stele and cortex in understanding and predicting root tensile properties. *Annals of Botany* **mcaf169**. doi:10.1093/aob/mcaf169

Zhai H, **Liu M**, **Zhang X**, ***et al.*** **2025.** Science mapping of root ecology: a bibliometric review covering 2015-2024. *Annals of Botany* **mcaf200**. doi:10.1093/aob/mcaf200

Zheng Z, **Zhang Y**, **Li Z**, **Dong F**, **Chen L. 2024.** Two grasses differ in their absorptive root physiological traits and rooting depth under drought in an alpine steppe. *Annals of Botany* **mcae151**. doi:10.1093/aob/mcae151