



Editorial: Belowground adaptation of plants to climate change

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Climate change, the long-term shift in weather patterns caused by anthropogenic release of CO₂ to the atmosphere, is an established fact and is having an impact on global temperature and precipitation patterns. According to the Intergovernmental Panel on Climate Change, surface temperature was 1.09°C higher between 2011 and 2020 than between 1850 and 1900 m with 2023 being recorded as 1.5°C above preindustrial levels, this is likely to continue to increase to mid-century causing further intensification of variation in the global water cycle, global monsoon precipitation, and the severity of wet and dry events in all ecosystems (IPCC 2023). Climate change is expected to affect almost every environment on earth and have large societal impacts.

The impacts of climate change are known to affect every organism, posing a significant risk to life on the

planet (Sergaki et al. 2018). Plant species are adapting to climate change by altering their morphology, phenology, and geographic range, with a degree of success mediated by their ecological plasticity. The combined effects on individuals, populations, and ecosystems result in altered production of agricultural systems, shifts in community composition, and interactions that might degrade the benefits and services that natural ecosystems can provide to society (Haines-Young and Potschin-Young 2018; Weiskopf et al. 2020). Agriculture ecosystems are essential for human well-being, but they are also responsible for negative alterations on climate as they contribute to emissions of greenhouse gases. Papers published in this special issue quantify the role of below-ground process governed by roots and rhizospheres of plants in mitigating the release of CO₂ into the atmosphere and adapting to the consequences of climate change.

The paper by Jebari et al. (2023) assessed the net greenhouse gas (GHG) emissions of grassland in moist temperate Northern Spain used for dairy production and concluded that under a scenario of climate change there will be a loss of soil organic carbon and an increasing emission of GHG; however, it is possible to mitigate these emissions with adequate management of manures produced by dairy cattle, namely their anaerobic digestion.

The effects of climate change on above-ground parts of plants and plant communities have been extensively studied but assessing the below-ground aspects of the plant is more challenging. Soil is a

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highly complex environment with a myriad of interdependent networks, making it difficult to determine the influence of increased atmosphere temperature, despite its correlation with soil temperature, because the soil itself buffers temperature variation increasingly with depth. The concentration of CO₂ in the soil atmosphere is several times greater than in the air; thus, it is unlikely that a higher concentration of CO₂ in the atmosphere have a direct effect on the below-ground biota (Bei et al. 2019). However, elevated CO₂ will lead to greater rhizodeposition by plants, leading to changes in the size, structure, and function of the rhizosphere.

Climate change certainly can exert its influence on the rhizosphere, the soil volume that is directly influenced by root processes and which is the home of a vast microbiome. It is the place where plants and soil organisms interact by several distinct mechanisms mediated by soil physical, chemical, and biological characteristics. The rhizosphere is a complex and dynamic zone estimated to contain tens of thousands of different microbial taxa, and their presence plays a key role in numerous interactions between plants and soils that are essential to the functions of natural and agricultural ecosystems (Dubey et al. 2019). Plant-root-microbe interactions are ubiquitous in ecosystems across the planet and control many of the key biogeochemical and resource cycles. Therefore, they are a key player in the mitigation and adaptation of natural and agroecosystems against climate change, making them a critical component of the toolbox available for dealing with the impacts of climate change.

The rhizosphere microbiome, in association with the root systems, can directly promote root growth, water and nutrient uptake, improving the plant's capacity to maintain higher rates of stomatal conductance for absorbing the CO₂ necessary for photosynthesis, even during moderate stress (Orfanoudakis et al. 2010; Henkes et al. 2018; Ulrich et al. 2019). To keep these essential functions, the root system, like other plant organs, adapt its spatial configuration and its morphology to the encountered environmental conditions (Hodge et al. 2009; Pedersen et al. 2021). The root system length and depth, root branching, root angle, and total biomass collectively form the spatial configuration of the root system, known as root system architecture. The diameter, surface area, root hairs, and specific root length are morphological

traits of individual roots that determine the ability of roots to interact directly with soil biota (Bardgett et al. 2014).

Root system architecture

The study of root system architecture (RSA) is challenging, but recent developments of multifunctional root phenotyping platforms and techniques have permitted more attention related to its study. Non-destructive root phenotyping approaches are most commonly used to phenotype RSA and examples include electrical resistance tomography (ERT), electromagnetic inductance (EMI), ground penetrating radar (GPR), magnetic resonance imaging (MRI), positron emission tomography (PET), rhizotron, and X-ray computed tomography (X-ray CT). These methodologies in combination with high resolution imaging and artificial intelligence analysis algorithms have resulted in significant advances in our understanding of the role of RSA. High-throughput techniques help to determine root system architectures, traits or ideotypes and rooting patterns (Urbanavičiūtė et al. 2022).

Gravity and light are the first drivers of germinating seeds to direct the root growth into the soil aiding seedling establishment. Further root three-dimensional growth (RSA) is shaped by biotic and abiotic signals such as water availability, soil mineral nutrient content, soil compaction, salinity, and the formation of symbiotic relationships with other organisms to optimize the uptake of water and nutrients (Morris et al. 2017; Amrani 2023). Drought is the primary abiotic signal to shape the development of roots and its influence will increase steadily, the other is soil fertility that is decreasing under pressure of all forms of land use.

Higher temperatures induce more water loss by evapotranspiration that coupled with more frequent droughts will reduce the water availability in the surface soil layers forcing the roots to grow deeper where they might find water and escape from drier and hotter surface soil and, eventually, the accumulation of soluble salts. As water percolates deeper, it carries soluble nitrates, thus the essential nitrogen plant nutrient will be found deeper in the soil too. In contrast, phosphorus (P) and some other nutrients move very slowly through the soil and tend to

accumulate in the topsoil together with most of the soil organic matter. Thus, roots must balance the influence of drought which reduces root biomass but often induces a deeper rooting structure with fewer deep axial/lateral roots (Gandullo et al. 2021; Dineny 2019) with greater lateral branching density in the topsoil to forage for the resources available at the surface (Postma et al. 2014). However, this desirable RSA ideotype might be impaired by the accumulation of soluble salts resulting from greater evapotranspiration as negative halotropism forces the roots away from saltier zones or arrests entirely the growth of primary and lateral roots (van Zelm et al. 2020).

Root system architecture is important for all land ecosystems, it becomes more relevant in crop agroecosystems which are intensively managed with the primary objective of economic productivity, and in particular in low input systems where soil resources are variable in time and space, contrary to high input systems where many of the constraints are reduced by management. Low input agricultural systems represent the majority of agriculture around the world and they need crop genotypes that better withstand the environmental conditions brought by climate change, mainly crops that are less susceptible to drought and capable of thriving in low fertility soils. These crops must have root phenotypes capable of reaching resources in both top and subsoil (Lynch 2022).

Profiling the plant root architecture is the first step for selecting more resilient crops with further breeding making them even more efficient in using water and nutrients in environments that will become ever more challenging. This special issue includes articles that show the importance of RSA deep rooting to drought tolerance and the urgency of including such RSA ideotypes on breeding programs. The paper by Wong et al. (2023) shows the potential capacity of cover crops and their root system to improve soil conditions and the storage of carbon belowground. The shoot and root biomass of a number of cover crop cultivars of grass, legume and brassica families grown in Midwest USA were analyzed. Winter cereals may provide denser canopy cover and higher root biomass, but winter triticale has a deeper rooting system that is better suited for carbon sequestration while rapeseed and kale have a C:N ratio favorable to nutrient cycling and the denser lateral root system of rapeseed can provide the absorption of excess nutrients. The

paper highlights the importance of breeding crops for root architecture that improve the ecosystem services provided by crops.

The role of deeper rooting systems is also addressed by Odone et al. (2023), one of the articles covered by this special issue. They report that the genotypes of winter wheat that grow deeper root systems are more resistance to water stress and have increased grain yield. However, greater N fertilization reduced slightly the depth of root growth. Again, they suggest that breeding efforts must attempt to develop crops with deeper rooting systems. Although it is not clear how N managements affects root depth, they recommend that breeding efforts must attempt to develop crops with deeper rooting systems.

Nevertheless, a single constraint to crop growth and its relative resistance is not sufficient to define the better rooting system ideotype as is reported by van der Bom et al. (2023) yet another article included in this issue. Some root traits are better adapted to resources available in deep soil layers, but other traits are necessary if the resources are differently located in shallow layers. The distribution of resources are certainly environmentally related but also dependent on crop system management such as fertilization and planting density.

Root exudates/metabolism and rhizosphere processes

Plants supply carbon and root exudates, mainly sugars, amino acids and organic acids, in a range of quantity and quality to soil microbes supporting higher trophic organisms that together release nutrients for plants, form symbiotic relationships with them and produce phytohormones that promote plant growth (de Vries et al. 2020; Hoang et al. 2022; Herms et al. 2022).

Elevated temperatures hinder the growth of plant roots and expedite their aging and programmed cell death by triggering a substantial production of reactive oxygen species (ROS) in the roots (Xu et al. 2016). To cope with both normal and stressful conditions, a heightened antioxidant scavenging system is crucial for preserving antioxidant metabolism. Additionally, the rearrangement and distribution of root metabolites also play significant roles in the overall

growth and survival strategy (Atkinson et al. in 2012). Here, Li et al. (2023) investigated the adaptability of cool-season creeping bentgrass (*Agrostis stolonifera*) roots to high temperatures induced by global warming, focusing on the role of γ -aminobutyric acid (GABA). The study suggests that GABA plays a crucial role in enhancing the adaptability of cool-season creeping bentgrass roots to high temperatures induced by global warming. The positive effects of GABA were attributed to increased antioxidant capacity, root vitality, and osmotic adjustment, as well as the remodelling of metabolites associated with improved energy metabolism, osmotic balance, antioxidant capacity, and cellular structures in roots under heat stress.

The rhizosphere stands out as a crucial area for the biogeochemical cycling of carbon (C) and nitrogen (N) in terrestrial ecosystems. Living-plant roots actively release a diverse range of C compounds, known as rhizodeposition, into the surrounding rhizosphere soil (Jones et al. 2009). Understanding the interactions between soil carbon (C) and nitrogen (N) mineralization in the rhizosphere is a crucial area for biogeochemical cycling in terrestrial ecosystems. In this issue, Huo et al. (2022) revealed a significant positive relationship between soil C mineralization rates (C_{min}) and net N mineralization rates (N_{min}) in the rhizosphere soils across different sites, but this was not observed in the bulk soils. Using a structural equation model, they found that the coupling of C_{min} and N_{min} in rhizosphere soils could be attributed to root-soil interactions, leading to higher levels of microbial biomass C, total organic C of soil, total N of soil, and extracellular enzyme activities. The study demonstrated that soil C and N mineralization processes are more closely coupled in the rhizosphere than in bulk soils, emphasizing the importance of considering the distinct dynamics of C and N cycling in these two soil environments. This insight suggests that the interactions between soil C and N cycling in the rhizosphere may differ significantly from those in bulk soil.

The soil, comprising the largest terrestrial C pool storing approximately 2500 Gt C, plays a critical role in the global carbon cycle, and even minor variations in the soil organic carbon (SOC) pool can have significant implications (Hopkins et al. 2012). Elevated temperatures can enhance terrestrial net primary production, leading to increased transfer of

organic matter into surface soil and potentially causing destabilization of SOC through processes known as priming effects, which can either accelerate or retard native SOC decomposition across various ecosystems (Kuzyakov et al. 2000; Frossard et al. 2021). In a meta-analysis published in this Special Issue, Dong et al. (2022) analyzed data from 39 warming experiments that utilized ¹³C or ¹⁴C isotope labeling methods and encompassed 1680 pairwise priming effects measurements. Focusing on surface soils across cropland, grassland, and forest ecosystems, the study clarified the direction and influencing factors of warming effects on priming effects, which occurs when the addition of new carbon substrates, such as plant-derived organic matter, either accelerates or restricts the decomposition of existing soil organic carbon (SOC). The results revealed a consistent pattern: warming was associated with a decrease in priming effects across different ecosystems. This reduction in priming effects was more pronounced in forest ecosystems compared to cropland and grassland. Furthermore, the decrease in priming effects was more substantial when simple substrates, such as small molecules like glucose and amino acids, were involved, compared to complex substrates (i.e. plant tissues, residues, and pyrolysis products). The study identified several influencing factors on the impact of warming on priming effects. These findings suggest that, in a warming world, the priming of surface SOC loss is likely to decrease, particularly in forest ecosystems or soils rich in organic matter, and under conditions of greater warming intensity.

Interactions with the microbiome

It is indisputable that rhizosphere microbes are essential to plant growth and health and each inhabitant of the rhizosphere has a specific role in ecological processes such as nutrient cycling and symbiosis. The soil microorganisms provide benefits to the plant host such as increased drought and salinity tolerance (de Vries et al. 2020) and improved plant nutrient absorption (Pii et al. 2016). However, the composition and structure of microbial communities are affected by environmental conditions and edaphic properties (Pascual et al. 2018) and the response of the plant-microbiome complex to extreme events such as floods and droughts is still not clearly understood (Francioli

et al. 2021). In respect to drought, some authors showed that soils afflicted by a history of droughts exhibit consistently lower microbial respiration rates, altered microbial community composition and functional response distributions (Veach and Zeglin 2020) but, on the other hand, it is possible to develop the soil microbiome through soil management to positively influence plant drought performance (Carter et al. 2023) and the use of microbes to improve ecosystem functions for specific functions has merited increased attention (de Vries et al. 2020). A combination of drought and heat stress might have a stronger negative influence on plant production (Cohen et al. 2021). The microbiome of the rhizosphere has a positive effect on soil itself as they excrete exopolysaccharides, a substance that increases soil adhesion to roots and protects soil structure, in the process soil water becomes more available to the plants (Sandhya et al. 2009).

Plant root microbe interactions are ubiquitous in ecosystems across the planet and control many of the key biogeochemical and resource cycles. Therefore, they are a key player in the mitigation and adaptation of natural and agroecosystems against climate change and are therefore a critical component of the toolbox available for dealing with the impacts of climate change. At the heart of this interaction is the role of the plant root as a source of carbon for the mainly heterotrophic microbial community it supports. This comes in the form of rhizodeposits which include exudates, secretions and lysates such as sloughed off cells (Gregory 2007), which are either actively or passively lost by the plant. These rhizodeposits can include a whole range of compounds including sugars, organic anions, nutrients, polyphenols and potential signaling molecules such as small RNAs. Therefore, their impact on the microbiome size and function is large and diverse acting both as an energy source and a catalyst for selection and recruitment of specific functional groups (Wang et al. 2022, 2023b). The interactions between plants and microbiome are complex and have a number of critical players and trophic interactions, which include critical endophytic bacteria and fungi, notably mycorrhizal fungi and nitrogen fixing bacteria, and the rhizosphere microbiome which include important bacteria, archaea and fungi which provide the plant some critical functions. Add in the complexity of the trophic interactions between plants, mycorrhizae and hyphosphere

microbiome (Li et al. 2023; Wang et al. 2023a) and it is easy to appreciate how complex this invisible belowground interaction is.

These interactions are impacted significantly by the wider environment and variation in its characteristic components. Soil type, pH, water, temperature, plant genotype, atmospheric carbon etc. all have profound impacts on the microbiome structure and function and therefore climate change will have a large impact on the function of this critical interface. The interactions of plant and microbe at the critical interface between root and soil can affect a number of essential mechanisms when it comes to mitigation and adaptation to climate change. Clearly, they are implicit in managing systems to sequester carbon to mitigate against further CO₂ accumulation in the atmosphere, but they are also implicit in the release of other greenhouse gases from soil including methane, nitrous oxides and ozone. They are critical for adaptation to low input systems to also mitigate against climate change. However, given the acceptance that global temperature is going to increase beyond 1.5 °C along with the consequent perturbations to climate and ecosystems (IPCC 2023), plant soil interactions are also implicit in the ability of plants to cope with abiotic and biotic stress caused by this and in fact can help optimise systems to be more productive under new climate conditions in some regions. With climate change there will also be shifts in the boundaries of optimal growth for ecosystems and cropping systems alike and therefore shifts into novel geographical regions with different soils. Plant soil interactions are likely to hold the key to successful shifts of cropping systems both north and south and in colonization of ecosystems in new zones of optimal production, this however also applies to weeds and invasive species, therefore posing a threat to conservation efforts.

In this special issue we pick up on some of these themes. Some of the papers highlight research which is ongoing to identify stress resistant microbial inocula, with particular reference to drought tolerance. Becker et al. (2023) demonstrate the potential of drought resistant rhizobia in forming the basis of a climate adapted N-fixing legume system. They demonstrated that water stress was a significant barrier to nodulation of legume roots with rhizobia, but

while the different drought resistant strains had no impact there was clearly an impact on nodulation of local conditions suggesting the need for assessment of inocula on a regional basis. In a similar study, Tebele et al. (2023) took the approach of trying to identify drought tolerant microbes from the rhizosphere of a notoriously drought resistant plant, *Myrothamnus flabellifolia* or resurrection plant. They found a core set of microorganisms which could form the basis of identification of an inocula with functional impacts on drought resistance in other plants. There are also papers which demonstrate the positive impact on plant microbe interactions on the resilience of plants to abiotic stress. D'Amours et al. (2022) show that selecting rhizobium which are tolerant to the impact of freeze-thaw give their associated crop (alfalfa) more tolerance to overwintering and may be critical in regions where climate change leads to more extreme winter cold or late spring frosts. This is important as it gives the cropping system resilience and allows migration into new geographic regions for production. Similarly, Arellano-Wattenberger et al. (2023) demonstrated that the presence of seed endophytic microorganisms enhanced the germination of maize landraces under drought conditions, suggesting a fundamental role of these endophytes in drought tolerance. Isolation of these endophytic bacteria and reinoculation of maize seeds also improved drought tolerance in germination.

Papers in this special issue also pick up the theme that association with mycorrhizal fungi enable plants to cope better with reduced input systems necessary to help mitigate against further CO₂ emissions and to adapt to newly agronomically favourable geographic regions as a consequence of climate change. Arcidicono et al. (2023) demonstrated that the inoculation of tomato varieties with specific mycorrhizal inocula increased the yield, shoot mass and nutrient uptake and concentration in fruits. This was associated not only with the presence of mycorrhizae, but also changes in the rhizosphere microbiome. Demonstrating that these intimate microbial trophic interactions are important to adapting systems to low-input production. Du et al. (2023) also show the importance of the plant-mycorrhizae-bacteria interaction in the invasiveness of plant species, demonstrating that the potential invasiveness is also dependent on availability of soil nutrients. This demonstrates that understanding

the trophic interactions between plants and microbes and how this is mediated by variation in the environment will be critical is managing the colonisation of newly climatically suitable geographic regions by both natural ecosystems and cropping systems.

Impacts on soil hydraulic properties

While soil water deficit is a critical factor affected by climate change that influences transpiration globally, the specific mechanisms by which soil drying and soil properties affect transpiration and stomatal regulation are not well understood. By comparing two contrasting soil textures, sand and loam, Cai et al. (2022) revealed that the transpiration rate decreased more significantly at higher soil matric potential in sand compared to loam, regardless of the vapor pressure deficit levels (1.8 and 2.8 kPa). They found that variations in canopy conductance are not solely dependent on leaf water potential but are largely affected by soil hydraulics. The findings support a model where stomatal closure is driven by a loss in soil hydraulic conductivity. The study highlights the importance of considering soil properties, specifically soil hydraulic conductance, in understanding the regulation of transpiration and stomatal behavior in response to soil drying. Whether soil-specific stomatal regulation exists among different plant species needs further exploration. It is understood that this study had no intention to separate soil hydraulics from the bulk soil and the rhizosphere. Innovative technology needs to be developed to directly measure hydraulics of the rhizosphere. Until then, the proposed models could be tested in a more accurate manner.

Precipitation and irrigation occurrences following tillage and seeding can lead to alterations in soil hydraulic properties throughout the growing season, attributable to adjustments in the soil surface and the formation of crust that serves as a key indicator of land degradation. Soil characteristics such as silt and clay content increase crusting, while factors like aggregate stability and organic matter content mitigate it, highlighting the complex interplay of soil properties in crusting susceptibility (Chen et al. 2013). In this issue, Talukder et al. (2022) investigated the temporal variation of soil hydraulic properties induced by surface crust in Mediterranean soils in NE Spain during high-frequency irrigation. Using Beerkan infiltration tests and the BEST method, this study revealed

that intensive tillage initially elevated both saturated soil hydraulic conductivity and sorptivity compared to autumn tillage, but these values declined after a 60-day period. Reduced tillage, on the other hand, maintained similar levels of these properties. Both intensive tillage and reduced tillage methods developed crusted layers after spring tillage, reducing saturated soil hydraulic conductivity, sorptivity, and number of effective pores per unit area. In contrast, long-term no-tillage practices showed an increasing trend in saturated soil hydraulic conductivity and sorptivity. Conservation tillage, encompassing both reduced tillage and long-term no-tillage approaches, improved soil structure and mitigated crust risk. Non-crusted soils within crop rows exhibited consistently higher saturated soil hydraulic conductivity and sorptivity than crusted soils between rows, emphasizing the benefits of conservation tillage and crop cover in preserving soil hydraulic conductivity.

Future perspective

To be able to fully understand the complex interactions between plants and microbes in the rhizosphere it is critical that new method development occurs to shed light on this otherwise unseen zone of the ecosystem. There are a number of novel methods that allow us to do this, such as rhizobox techniques, magnetic resonance imaging, x-ray computed tomography, isotopic tracing and transcriptomics (Gregory et al. 2022), but we also present such developments in this special issue. Patko et al. (2023) describe a new “smart soil” method where transparent soil coated with reporter chemicals are able to report in real-time and *in-situ* on changes in the properties of the rhizosphere and when coupled with the relevant light-sheet microscopy this technology can inform us on the plant-microbe dynamics in response to micro-scale changes in the rhizosphere environment.

It is clear that development of our understanding and methods to measure the complex interaction between plant roots and soil will be critical to tackling problems associated with climate change from both a mitigation and adaptation perspective. Papers

published in this special issue go some way to tackling some of these complex issues, but it is also clear that much work remains to be done.

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Data availability As an editorial there are no novel data presented in the manuscript.

Declarations

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