Meetings

Root biology never sleeps

11th Symposium of the International Society of Root Research (ISRR11) and the 9th International Symposium on Root Development (Rooting2021), 24–28 May 2021

Emerging frontiers: root and rhizosphere research in the context of global environmental change

Natural ecosystems and agricultural production have been threatened by multifaceted global environmental changes. Soil degradation, extreme drought and flooding events, shifting climatic patterns and other challenges have prompted many disciplines within plant science to pivot to find solutions. Accordingly, root research has expanded from fundamental studies on roots, as providers of physical support, water and essential nutrients uptake, towards identification of beneficial traits for stress adaptation and control of key biological soil processes. Advances in trait identification, data acquisition, management and modelling are enabling root researchers to develop predictive models to support ecosystems in these changing environments.

Through technical presentations, posters, industry exhibits and a root phenotyping workshop, the international, jointly presented, completely virtual International Society of Root Research (ISRR) 11/Rooting2021 meeting provided a unique platform for researchers across disciplines to share recent advances in root biology, from molecular to ecosystem-level scales, in agricultural and natural ecosystems, addressing critical questions in response to climate change and its impact on crop productivity and ecosystem services. In this report, the 2021 ISRR Ambassador cohort provides an overview of the current root research landscape and reflection on the importance of frontier research for a more sustainable future.

ISRR11 and Rooting2021: A joint, virtual meeting

In response to global travel restrictions imposed by the COVID-19 pandemic, the 11th Symposium of the International Society of Root Research (ISRR11, https://www.rootresearch.org/) and the 9th International Symposium on Root Development (Rooting2021) merged into a single online event co-organised by the Interdisciplinary Plant Group at the University of Missouri (Columbia, MO, USA) and the University of Nottingham (UK). Over 700 participants representing academia, government and industry from more than 53 countries (Supporting Information Fig. S1) joined the virtual event held 24–28 May 2021. The schedule ran almost uninterrupted across international time zones, featuring 74 talks (10 plenaries, 16 keynotes, and 48 invited) and c. 300 posters, spanning a broad range of disciplines. In addition, the

2021 ISRR Lifetime Achievement Award was presented to Wendy Silk, Emeritus Professor at the University of California-Davis (USA).

The Ambassador Program

ISRR11/Rooting2021 hosted the 3rd ISRR Ambassador Program, a unique platform for early-career root researchers. The virtual ISRR11/Rooting2021 Ambassador Program provided networking activities, experience with conference organisation, interaction with professionals in diverse career areas, and opportunities to discuss advances in the field with a broadly multidisciplinary cohort (Notes S1). Ambassador tasks at the ISRR11/Rooting 2021 meeting included session note-taking, the production of this *Meeting report*, and a set of recommendations for diversity and inclusion in future scientific events (Notes S2).

Root phenotyping workshop

The ISRR11/Rooting2021 meeting concluded with a root phenotyping workshop with virtual tours of major root phenotyping facilities and demonstrations of methods. Organised by Larry York (Oak Ridge National Laboratory, TN, USA) and Darren Wells (University of Nottingham, UK), in collaboration with other experts and the ISRR Ambassadors, the workshop with a Q&A format was used to discuss the latest advances in root phenotyping techniques. The potential complementarity of image analysis software tools emerged as a key topic as depicted in Fig. S2. The availability of standardised protocols for root collection and trait measurement was also highlighted by the participants of the online survey, organised by the Ambassadors in addition to the Symposium (Delory *et al.*, 2022) and the workshop as an important issue for future research. The Root Ecology Handbook recently published in *New Phytologist* provides a comprehensive guide on root sampling, processing and measuring for a wide variety of traits in a standardised manner (Freschet *et al.*, 2021).

Stress-resilient crops as a root phenotyping target

Root phenotyping for traits related to crop performance or ecosystem services has been a main focus in the field of root biology since the 1970s (Hurd, 1974). However, quantitative analysis of plant phenotypes and their linkages to plant functions remains a major bottleneck. ISRR11/Rooting2021 highlighted the current emphasis on phenotyping root traits that will provide resilience to changing environmental conditions (Fig. 1), including traits related to root–microbial interactions (Kawasaki *et al.*, 2021). Rhizosphere processes related to root stress responses are key for sustainable food production systems, as they impact soil functioning and resource use efficiency.
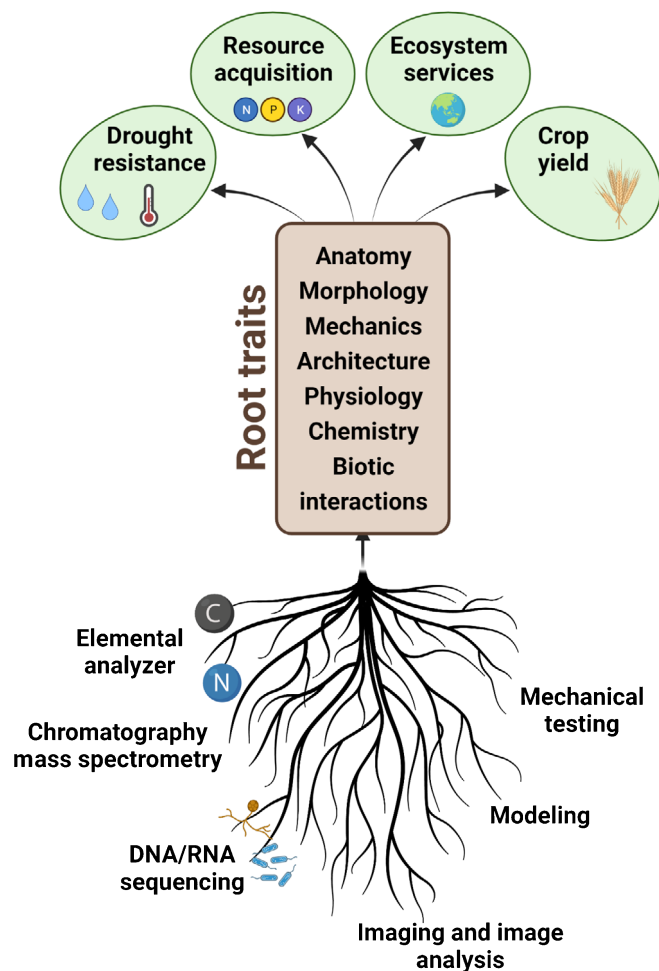
Fig. 1 Schematic overview of root phenotyping targets and methodological approaches discussed at the ISRR11/Rooting2021. The scheme highlights root system traits of interest for plant adaptation to stress, agricultural production and ecosystem services. Relevant methodological approaches to identify root traits are highlighted, including imaging techniques, rhizobiome analysis and rhizosphere metabolomics. Comprehensive collections of root image analysis and modelling tools are currently available (Lobet, 2017). Further phenotyping approaches such as the measurement of ion uptake rates and mechanical measurements were also discussed throughout the meeting. A detailed list can be found in the results of the phenotyping survey (Delory *et al.*, 2022).

The impact of drought and limited nutrient supply on plants under global climate change, and the mechanisms of root response from molecular to field scales, have prompted focussed advances on well established areas in the field of root research. Therefore, the role of auxin and cytokinin in molecular crosstalk has prompted the rise of the 'hormonics' to explore their functions in root development under drought stress (Rodriguez-Alonso *et al.*, 2018), and to identify signalling pathways that link nutrient availability to root developmental parameters (Shahzad & Amtmann, 2017). Hormonal signalling also underlies 'nutritropism', an extension of 'chemotropism' (Newcombe & Rhodes, 1904), which can now be explored with advanced imaging and microscopy technology (T. Fujiwara, University of Tokyo, Japan). Root-related strategies to mitigate drought stress related to root hydraulic architecture and water transport were also discussed (Maurel & Nacry, 2020). Root-

system-level traits linked with water and nutrient use efficiency such as wheat root axial conductance (Hendel *et al.*, 2021), architectural traits in rice (Ruangsiri *et al.*, 2021) and maize (Kistler *et al.*, 2018) have been identified with a combination of shovelomics, phenotyping, functional genomics and modelling.

The long-standing challenges of grafting for the introduction of root traits related to stress tolerance have been partially overcome by recent progress on our understanding of graft compatibility and cell-to-cell adhesion (Notaguchi *et al.*, 2020). Advancing our understanding of grafting mechanisms will certainly provide new avenues to understand the effects of specific root genotypes and/or traits on other parts of the plant body (J. Cantillo, Donald Danforth Plant Science Center, MO, USA).

Current trends in root research seek to integrate stress responses inside the root system with a better understanding of these root–soil–microbe interactions. ISRR11/Rooting2021 highlighted the role of the rhizosphere microbiome in nutrient homeostasis, for example, in root diffusion (Salas-González *et al.*, 2021), or during nitrogen acquisition (Arsova *et al.*, 2012). Root exudates were introduced as potential targets for rhizosphere engineering to promote beneficial microbiome functionalities (Kawasaki *et al.*, 2021) or to control harmful species. Novel studies looking into root–microbiome interactions have become possible due to precision genome editing, production of knocked-down lines and reconstruction of biosynthetic metabolic pathways (Huang *et al.*, 2019), and advanced imaging techniques such as positron emission tomography (Schmidt *et al.*, 2020).

Roadmap to high-throughput root phenotyping

Recent advances in imaging techniques and image analysis (Fig. 1) can support high-throughput root phenotyping of relevant structural features within the root architecture (Fig. 2). Detailed image-based root phenotyping techniques such as X-ray computed tomography (CT) scanning can improve our interpretation of in-field studies (C. Topp, Donald Danforth Plant Science Center, MO, USA). Current advances allow high-resolution and/or high-throughput phenotyping studies, even in mature crops and under field conditions (Gore *et al.*, 2020; Rich *et al.*, 2020), although methodological challenges remain (Delory *et al.*, 2022). For example, root phenotyping of rooting depth and its significance for deep water or nitrate uptake is being addressed with large-scale field experiments using minirhizotrons or soil coring on maize (A. Leakey, University of Illinois, USA), wheat (J. Christopher, University of Queensland, Australia) and potatoes (O. Popovic, Copenhagen University, Denmark). Automated, high-resolution minirhizotrons are also used for visualising the dynamics of roots and fungi interaction in experimentally warmed peatlands (C. Iversen, Oak Ridge National Laboratory, TN, USA; Defrenne *et al.*, 2020). These imaging advances are complemented by the development of free, open source and high-performance image analysis software (Fig. S2).

Pairing 3D imaging techniques (e.g. X-ray CT) with mathematical modelling is a powerful way to study plant–soil interactions on different scales, from soil pores to growing root systems (Roose *et al.*, 2016). This hybrid approach has resulted in key milestones by
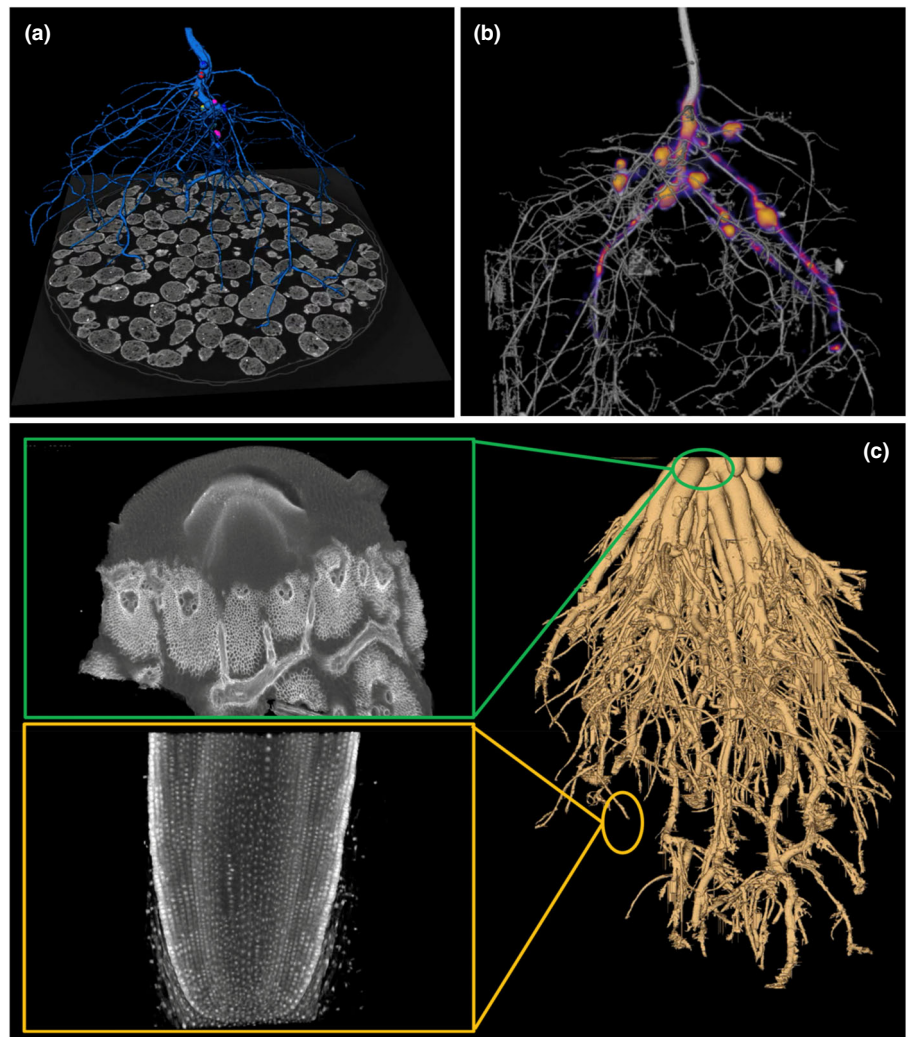
Fig. 2 Nondestructive, high-resolution and 3D imaging techniques offer new insights into the hidden half of plants. (a) Image of a soybean root system with N_2-fixing nodules obtained using X-ray computed tomography. (b) Combining positron emission tomography and X-ray computed tomography allows the visualisation of carbon allocation to the N_2-fixing nodules of a soybean root system. (c) Visualising the architecture and internal anatomy of a maize root system using X-ray computed tomography and X-ray microscope images. Photography credits: Christopher Topp (Donald Danforth Plant Science Center, MO, USA).

allowing the elucidation of how root architecture and exudation jointly affect P mobilisation and uptake (McKay Fletcher *et al.*, 2020), and to quantify the extent to which the dissolution of N fertiliser granules affects soil microbial activity (Ruiz *et al.*, 2020).

Imaging techniques can also be used for traits related to root–microbe interactions (Fig. 1), complementing other multidisciplinary approaches that seek to better understand the complex dialogue between roots, the associated microbiome and soil processes.

Unleashing the power of mathematical modelling

Mathematical modelling complements phenotyping advances by overcoming the challenges of experimental approaches and benefits from the emerging field of functional phenomics (York, 2019). Highlights from the diversity of modelling approaches presented at ISRR/Rooting2021, in both spatial and temporal scales, include: a micro-hydrological model that describes a new symplastic water pumping mechanism (Couvreur *et al.*, 2021); the dynamics and regulation of a fast brassinosteroid response pathway in Arabidopsis root tips (Großeholz *et al.*, 2021); functional–structural plant

(FSP) models to identify optimal root phenotypes for nutrient capture in contrasting environments (Rangarajan, 2021); and field-scale simulations of plant populations and communities (Postma *et al.*, 2017; Schnepf *et al.*, 2018; Faverjon *et al.*, 2019). Future mathematical models will draw on larger, more complex, datasets incorporating novel imaging technology, high-throughput phenotyping and availability of relevant environmental data. The positive feedback cycles between these models and continued advances in phenotyping are what will surely advance the field of root science.

Concluding remarks and perspectives

To meet the challenges imposed by the global COVID-19 pandemic, online communication has provided new opportunities for international multidisciplinary cooperation. The ISRR11/Rooting2021 online event brought the root research community together to share knowledge on the latest developments in root and rhizosphere research, present new technological advances and identify pressing research questions that still require answers. The adoption of a holistic approach to root research, that is, one that takes into account all categories of root traits, from anatomy to root

morphology, physiology and architecture, as well as interactions with the rhizosphere microbiota, was emphasised as a crucial step in facing the challenges posed by global change. We encourage root researchers to actively take advantage of the plethora of online resources currently available for plant phenotyping (https://quantitative-plant.org/), and to join the ISRR (https://www.rootresearch.org/). Collaborations to share knowledge, along with new technological advances, will help us further understand roots and rhizosphere processes.

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Competing interests

None declared.

Author contributions

AJM, CNT, LAG and AT coordinated the 'ISRR11 Ambassador Program' and provided valuable feedback on the manuscript. The ISRR11 Ambassadors group (CNC, GC, KKD, BMD, AD, YD, APG, QH, P-WH, MCH-S, ML, JLPN, LM, JM-M, AER, JS, TSW, PW, XW, LX, CZ) compiled and collated minutes of the sessions throughout the meeting and wrote the initial draft and the revised versions. Ambassador JS prepared Notes S2 addressing diversity and inclusion at ISRR11/Rooting2021.

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Data availability

Data sharing is not applicable to this article as no datasets were generated or analysed during the current study.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Map depicting the distribution and number of attendees to the joined Symposium ISRR11-Rooting2021.

Fig. S2 Example of root image analysis pairing RootPainter and RhizoVision explorer.

Notes S1 The ISRR11 3rd Graduate Student and Postdoc Ambassador Program.

Notes S2 Diversity and inclusion at ISRR11/Rooting2021.

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Key words: Ambassador Program, ISRR11, rhizosphere, root phenotyping, root traits, Rooting2021, roots.