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PREFACE

# Plant root research: the past, the present and the future

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This special issue is dedicated to root biologists past and present who have been exploring all aspects of root structure and function with an extensive publication record going over 100 years. The content of the Special Issue on Root Biology covers a wide scale of contributions, spanning interactions of roots with microorganisms in the rhizosphere, the anatomy of root cells and tissues, the subcellular components of root cells, and aspects of metal accumulation and stresses on root function and structure. We have organized the papers into three topic categories: (1) root ecology, interactions with microbes, root architecture and the rhizosphere; (2) experimental root biology, root structure and physiology; and (3) applications of new technology to study root biology. Finally, we will speculate on root research for the future.

## INTRODUCTION

The study of root biology is certainly not new, with research papers going back in the literature over 100 years (e.g. Hanstein, 1870; Janczewski, 1874; Vines, 1888; Pfeffer,1894; Němec, 1900). Root interaction with the soil, the rhizosphere, symbiotic interactions with bacteria and fungi, exploitation of soil and increased surface by root hairs, and even more specific root characteristics such as Casparian bands in the endodermis, cellular characteristics of the root apex and the root cap all represent the basic knowledge of root biology. Regardless of long-standing observations and intensive research over generations, the biology of roots has largely been ignored by mainline plant scientists and has remained 'The hidden half' of the plant body (Waisel *et al.*, 2002). This somehow neglected part of plant research – in comparison with stems, leaves, flowers or fruits – was realized by the organizers of the first root biology meeting organized more than 40 years ago in Slovakia. The symposium, held in the High Tatra Mountains, was organized by a group from the Institute of Botany, Slovak Academy of Sciences, Bratislava, Slovakia, and was called 'Structure and Function of Primary Root Tissues'. It was the first specialized scientific meeting focused on roots. The Proceedings from this Symposium were published in 1974 (Kolek, 1974), and the first paper in the proceedings was written by J. G. Torrey and H. I. Philips Jr., Harvard University, Cambridge, MA, USA (Torrey and Philips, 1974). Numerous international collaborations were established during this and following root symposia and the books published from them represent valuable sources of information about roots (Brouwer *et al.*, 1981; Loughman *et al.*, 1989; Baluška *et al.*, 1995; Gašparíková *et al.*, 2001; Mistrík *et al.*, 2004). In addition to the authors of the papers in this current issue and those mentioned above, we would like to dedicate this Special Issue to those scientists around the world who have worked tirelessly on all aspects of root biology.

Interestingly, during 2011 there were four important international meetings dealing with roots, perhaps indicating a critical change in the attitude of plant scientists worldwide as to the importance of roots to the well-being and function of plants.

Australia: *Rhizosphere3*, International Conference, http://rhizosphere3.com.

Slovakia: 7th International Symposium on Structure and Function of Roots, http://www.rootsymposium2011.sav.sk/index.html.

Japan: The Latest Frontiers of Root Research in Asia, http://www.jsrr.jp/20th/index.htm.

Canada: 6th International Symposium on Root Development: Adventitious, lateral and primary roots, http://root2011.uqat.ca/.

Specialized societies joining people interested in root research have been created. The best known is the International Society of Root Research (ISRR), established in 1982 by the late Professor Eleonore Kutschera and her scientific group, and the first symposium of the ISRR, focusing on 'Root ecology and its practical application', took place in Austria in the same year. Kutschera is well known as an author and co-author of a series of books documenting the root systems of various plants and their root anatomy, the last volume, number 7, being published in 2009 (Kutschera *et al.*, 2009). Regular meetings of this society not only brought scientists together, but contribute to moving the focus of root investigations. Several specialized monographs were published from these symposia or are available online (Abe, 2003; http://asrr.boku.ac.at/fileadmin/files/RRcd/index.html). One of these meetings has been organized for 2012 ('Roots to the Future', http://www.rootresearch.org/meetings/isrr2012). Less known in Europe, and partially also in the US, is the very active Japanese Society for Root Research (JSRR), which publishes its own online journal *Plant Root* (http://www.plantroot.org/) and sponsors some international symposia, as mentioned above.

The 40 years since the first specialized root conference has brought a completely new age in science. Undergraduate university students learn many new concepts that weren't even dreamed about 40 years ago. Science is in permanent 'repair', and new information is added daily so that we can hardly follow the constant flow of news in our very narrow fields of specialization. As an example, in 2011 there were more than 7000 papers published that mentioned plant roots in their topic (http://webofknowledge.com/WOS). What was published 10 years ago may not be true any longer, but on the other hand the older literature may hold the exact truth you would need to understand a new observation. Our root biologist ancestors might provide inspiration to again read books published a hundred years ago. Collections of papers published from some of the previous specialized root meetings helped to educate the new generation of root scientists. It is always satisfying for an older scientist and teacher to meet young, enthusiastic students at conferences introducing themselves and adding the words, 'I know your publications'. We hope that this Special Issue on Root Biology will be a new source of information for new researchers and students.

## SPECIAL ISSUE ORGANIZATION

The stimulus for creating this Special Issue is to highlight recent progress in root research and to trigger new research and attention to root biology traditionally ignored but now in resurgence. What follows is a brief narrative of the content of this Special Issue on Root Biology.

### *Content summaries*

*Root ecology, interactions with microbes, root architecture and the rhizosphere.* Papers of the first category in this Special Issue focus on the rhizosphere, root interactions with the soil microbes, root evolution and ecology, and the development of root systems in reaction to nutrients, stresses and subterranean communication between roots.

Jones and Dolan (2012) report on a study of gene regulatory networks that are similar in rhizoids in moss gametophytes and the root hairs of vascular plant sporophytes. They discuss the implications of this relative to the morphological diversity of plants radiating to the land. Rout and Callaway (2012) review the literature on human-induced exotic plant invasions and the consequences for microbial biogeography. Even though microbes are not limited by dispersal, the data collected indicate, that 'everything may not be everywhere'. The importance of these findings for roots and whole plants influenced by soil microbes is discussed. Soil pollution represents another human-made impact on plants, and roots in particular. Huang *et al.* (2012) report on the reconstruction of biologically functional root zones for re-vegetation of mine tailings. Integration of knowledge from soil and plant subsystems is necessary to develop functional concepts required for rehabilitation and remediation of these destroyed areas. Close to this topic is the report by Remans *et al.* (2012), which points out the neglected aspect of root system architecture as influenced by toxic soil contaminants. A split-root experimental system is used to investigate the local effects of cadmium and copper on roots in combination with plant-associated bacteria. To separate the role of roots and soil microbes in rhizosphere is a difficult task. Graham *et al.* (2012) report on partitioning of heterotrophic respiration by soil microbes from autotrophic respiration by roots in relation to rhizosphere priming. The importance of roots in regulation the temperature response is emphasized. Finally in this section, Valentine *et al.* (2012) describe an extensive comparative study of soil types in Scotland and how the physical and chemical characteristics of soil influence root elongation in laboratory and field experiments. They show that root elongation is linked especially to physical rather than the chemical properties of soils.

The next set of papers focuses on communication between plants, their reaction to biotic stress and to external factors. Falik *et al.* (2012) report on responses of unstressed plants to signals communicated to them by stressed neighbours. In this study the split-root system is designed with several plant species sharing rooting compartments between stressed and unstressed plants: osmotic stress or drought induced stomatal closure in both stressed plants and their unstressed neighbours. These results demonstrate a novel and unexplained type of plant communication through the root system. The contribution by Lee *et al.* (2012) shows elicitation of plant resistance and increased beneficial populations of rhizosphere bacteria caused by above-ground phloem-sucking aphids. This helps the plant to cope with and survive the subsequent biotic stress. Specialized root morphology is related to edaphic specialization, enabling survival of numerous species with a high level of endemism in shallow soil and rocky habitats. The investigation by Poot *et al.* (2012) concerns root system traits of woody perennials from Australian granite outcrops and elucidates the narrow endemism of these species. Barlow and Fisahn (2012) correlate gravitational acceleration caused by the sun and moon with plant growth, leaf movements and dilatation of tree stems. Based on experimental observation of the rate of root elongation by *Arabidopsis*, they indicate a putative lunar-based relationship of root growth and lunisolar tidal force.

The last section in this category of papers deals with the response of roots and root systems to nutrients. Phosphorus as a limiting factor in plant nutrition is investigated by Brown *et al.* (2012). They use a mutant population of barley to demonstrate the importance of root hairs for plant yield under P deficiency and also when combined with drought. Lambers *et al.* (2012) compare cluster roots in plants from the family Proteaceae growing in Australia and Chile and discuss their role as 'ecosystem engineers', related to their capacities to take up phosphorus by utilizing different strategies.

*Experimental root biology, root structure and physiology.* Papers in this next topic category focus on aspects of root anatomy, physiology and the effects of stresses on root growth. Mironova *et al.* (2012) report on the root apical meristem of *Arabidopsis thaliana* and the role of auxin gradients in meristem behavior. They suggest a dual mechanism model for auxin movement, called reverse fountain and reflective flow, and suggest how this can be used to study the role of auxin in roots. Martinka *et al.* (2012) follow the development of the endodermis in wild-type and mutant *Arabidopsis thaliana*. They report that cell-to-cell contact is required for the spatial control of Casparian band development. Additionally, endodermal cells in the vicinity of developing lateral root primordia develop suberin lamellae earlier and thicker compared to the neighbouring endodermal cells, and thus the protruding primordia are protected by an endodermal pocket covered by suberin lamellae. Tanimoto (2012) reviews the literature on the plant growth regulator gibberellin (GA), which was first identified as a fungal toxin in rice shoots and has been primarily associated with the regulation of shoot elongation. In this short review, he shows that low concentrations of GA can also regulate root elongation. In another review, Nguema-Ona *et al.* (2012) examine the structural and functional properties of arabinogalactan proteins (AGPs) in cell walls of roots and pollen tubes. They discuss many aspects including the observations that AGPs are released from roots into the rhizosphere where they interact with soil microorganisms.

The remaining papers in this category examine the effects of various stresses: flooding, tree growth on slopes, silicon, cadmium and zinc. Rich *et al.* (2012) report on the tolerance of root growth to flooding of the aquatic plants *Cotula coronopifolia* and *Meionectes brownii*. Plants are grown in large pots with 'sediment' roots in nutrient solution and then placed in large tanks where the shoots are left in air or submerged. Both species tolerated 4 weeks of submergence. When submerged, both species responded by growing photosynthetically active adventitious roots contributing up to 90 % of the root system dry weight, and removal of these roots negatively affected shoot growth. Trupiano *et al.* (2012) study the effects of slope on root growth pattern in the forest tree *Populus nigra*. In their paper they examine the proteome of roots of 1-year-old trees that are bent to 90 ° using a steel net. The protein profiles above, at and below the bend are analysed, and 207 proteins are identified. Some of these proteins are involved in plant defence, reaction wood formation and lateral root development, suggesting that mechanical stress stimulates the defence machinery of the tap root. Vaculík *et al.* (2012) show that treatment with silicon reduces the negative effects of cadmium on plant development. The distribution of Si and Cd is investigated with special attention to the development of root apoplasmic barriers and lignification of xylem elements within the vascular cylinder. They also suggest that alleviation of Cd toxicity by Si might be attributed to enhanced binding of Cd to the apoplasmic fraction of the maize shoots. Kendérešová *et al.* (2012) examine the electro-physiological responses of the plasma membranes in three species of *Arabidopsis*, *A. thaliana*, *A. halleri* and *A. arenosa.* Using these traits they confirm that *A. thaliana* is sensitive to zinc exposure while the other two species show high tolerance.

*Applications of new technology to study root biology.* The last topic category deals with papers using new technology to study root biology. Domozych (2012) surveys many aspects of microscopy, and although his paper doesn't specifically address roots, it does offer many ideas on applications and their future use. Zelko *et al.* (2012) describe a new method to prepare plant material for free-hand sectioning followed by staining with fluorescent dyes. Fine, small roots fixed in methanol, pre-stained in toluidine blue and then embedded in a mould in a 6 % solution of agarose can then be free-hand sectioned, to produce sections even as thick as 1 mm, and then successfully stained with fluorescent stains to observe such features as Casparian bands. Ilina *et al.* (2012) use *Agrobacterium rhizogenes*-transformed cucurbits plus various molecular markers to study lateral root initiation. They propose the application of this technique to study root meristem development and lateral root branching. In another study of lateral root development, Szymanowska-Pułka *et al.* (2012) describe the developmental anatomy of lateral roots in *Arabidopsis thaliana* and then use a computer model to show how principal growth directions and tensors lead to patterned development. Karahara *et al.* (2012) study the development of aerenchyma in rice roots exposed to water stress conditions and use unique growth conditions, called a sandwich method, so that one root can be exposed to different conditions at the same time and then viewed by X-ray computed tomography. Tracy *et al.* (2012) also use X-ray micro-computed tomography, but to study effects of soil compaction on root system development. Roots growing in more densely compacted soil tend to have reductions in root surface area, but increased root diameters. Postma and Lynch (2012) investigate polycultures, a traditional way of crop cultivation during their domestication. The results of this study explain the fact that polycultures over-yield corresponding monocultures on low fertility soils due to the differences in root architecture of individual species. This paper is included in this new techniques section of the Special Issue because of the use of the modelling software *SimRoot*.

## CONCLUSIONS

The study of root biology has been ongoing for over 100 years, but has often been ignored by mainstream biologists. In recent times, however, the application of new technologies and the study of simple roots such as in *Arabidopsis* has led to many new insights and has directly led to stimulating a new generation of root biologists. Possible reasons for this renewal also have been the flood of molecular genetic studies using root models in several laboratories, and the appearance of some new discoveries on topics such as polarity mechanisms and regulators in plants (for overview see Dettmer and Friml, 2011), regulation of lateral root initiation (Blilou *et al.*, 2005; for review see for example De Smet, 2012), discovery of polar localization of some transporters in roots (Ma *et al.*, 2007; Takano *et al.*, 2010), a novel protein family mediating Casparian band formation in endodermis (Roppolo *et al.*, 2011) and many others. In addition, roots are now used as model systems to study pollution, soil remediation, nutrient cycling, genetics, tissue growth patterns and modelling, and other emerging fields where a simple biological system is needed. The future for root research is very bright. We hope that in this Special Issue you will find both information about the current state of art in plant root biology and an inspiration for future work in this dynamic area of biological sciences.

## LITERATURE CITED

**Abe J. (Ed.) 2003.** *Root: the dynamic interface between plant and the Earth*. Dordrecht: Kluwer Academic Publishers.

**Baluška F, Čiamporová M, Gašparíková O, Barlow PW. (Eds.) 1995.** *Structure and function of roots*. Dordrecht: Kluwer Academic Publishers.

**Barlow PW, Fisahn J. 2012.** Lunisolar tidal force and the growth of plant roots, and some other of its effects on plant movements. *Annals of Botany* **110**: 301–318.

**Blilou I, Xu J, Wildwater M, *et al.* 2005.** The PIN auxin efflux facilitator network controls growth and patterning in *Arabidopsis* roots. *Nature* **433**: 39–44.

**Brouwer R, Gašparíková O, Kolek J, Loughman BC. (Eds.) 1981.** *Structure and function of plant roots*. The Hague: Kluwer Academic Publishers.

**Brown LK, George TS, Thompson JA, Wright G, Lyon J, Dupuy L, Hubbard SF, White PJ. 2012.** What are the implications of variation in root hair length on tolerance to phosphorus deficiency in combination with water stress in barley (*Hordeum vulgare*)? *Annals of Botany* **110**: 319–328.

**De Smet I. 2012.** Lateral root initiation: one step at a time. *New Phytologist* **193**: 867–873.

**Dettmer J, Friml J. 2011.** Cell polarity in plants: when two do the same, it is not the same. *Current Opinion in Cell Biology* **23**: 686–696.

**Domozych DS. 2012.** The quest for four-dimensional imaging in plant cell biology: it's just a matter of time. *Annals of Botany* **110**: 461–474.

**Falik O, Mordoch Y, Ben-Natan D, Vanunu M, Goldstein O, Novoplansky A. 2012.** Plant responsiveness to root–root communication of stress cues. *Annals of Botany* **110**: 271–280.

**Gašparíková O, Čiamporová M, Mistrík I, Baluška F. (Eds.) 2001.** *Recent advances of plant root structure and function*. Dordrecht: Kluwer Academic Publishers.

**Graham SL, Millard P, Hunt JE, Rogers GND, Whitehead D. 2012.** Roots affect the response of heterotrophic soil respiration to temperature in tussock grass microcosms. *Annals of Botany* **110**: 253–258.

**Hanstein J. 1870.** *Die Entwicklung des Keimes der Monokotylen und Dikotylen*, Bonn: A. Marcus.

**Huang L, Baumgartl T, Mulligan D. 2012.** Is rhizosphere remediation sufficient for sustainable revegetation of mine tailings? *Annals of Botany* **110**: 223–238.

**Ilina EL, Logachov AA, Laplaze L, Demchenko NP, Pawlowski K, Demchenko KN. 2012.** Composite *Cucurbita pepo* plants with transgenic roots as a tool to study root development. *Annals of Botany* **110**: 479–489.

**Janczewski E. 1874.** Recherches sur l'accroissement terminal des racine dans les phanerogames. *Annales des Sciences Naturelles Cinquieme Serie Botanique* **20**: 162–201.

**Jones VAS, Dolan L. 2012.** The evolution of root hairs and rhizoids. *Annals of Botany* **110**: 205–212.

**Karahara I, Umemura K, Soga Y, Akai Y, Bando T, Ito Y, Tamaoki D, Uesugi K, Abe J, Yamauchi D, Mineyuki Y. 2012.** Demonstration of osmotically dependent promotion of aerenchyma formation at different levels in the primary roots of rice using a 'sandwich' method and X-ray computed tomography. *Annals of Botany* **110**: 503–509.

**Kenderešová L, Staňová A, Pavlovkin J, Ďurišová E, Nadubinská M, Čiamporová M, Ovečka M. 2012.** Early $Zn^{2+}$-induced effects on membrane potential account for primary heavy metal susceptibility in tolerant and sensitive *Arabidopsis* species. *Annals of Botany* **110**: 445–459.

**Kolek J. (Ed.) 1974.** *Structure and function of primary root tissues*. Slovak Academy of Sciences Bratislava: Veda.

**Kutschera LE, Lichtenegger E, Sobotik M. 2009.** *Wurzelatlas der Kulturpflanzen gemäßigter Gebiete mit Arten des Feldgemüsebaues. 7. Band der Wurzelatlas-Reihe*. Frankfurt am Main: DLG-Verlag.

**Lambers H, Bishop JG, Hopper SD, Laliberté E, Zúñiga-Feest A. 2012.** Phosphorus-mobilization ecosystem engineering: the roles of cluster roots and carboxylate exudation in young P-limited ecosystems. *Annals of Botany* **110**: 329–348.

**Lee B, Lee S, Ryu C-M. 2012.** Foliar aphid feeding recruits rhizosphere bacteria and primes plant immunity against pathogenic and non-pathogenic bacteria in pepper. *Annals of Botany* **110**: 281–290.

**Loughman BC, Gašparíková O, Kolek J. (Eds.) 1989.** *Structural and functional aspects of transport in roots*. Dordrecht: Kluwer Academic Publishers.

**Ma JF, Yamaji N, Mitani N, *et al*. 2007.** An efflux transporter of silicon in rice. *Nature* **448**: 209–212.

**Martinka M, Dolan L, Pernas M, Abe J, Lux A. 2012.** Endodermal cell–cell contact is required for the spatial control of Casparian band development in *Arabidopsis thaliana*. *Annals of Botany* **110**: 361–371.

**Mironova VV, Omelyanchuk NA, Novoselova ES, Doroshkov AV, Kazantsev FV, Kochetov AV, Kolchanov NA, Mjolsness E, Likhoshvai VA. 2012.** Combined *in silico/in vivo* analysis of mechanisms providing for root apical meristem self-organization and maintenance. *Annals of Botany* **110**: 349–360.

**Mistrík I, Gašparíková O, Čiamporová M.** (eds.) **2004.** Plant root development and adaptation to stresses. *Biologia* **59**: Suppl. 13.

**Němec B. 1900.** *Ueber die Art der Wahrnehmung des Schwerkraftreizes bei den Pflanzen*. Berichte der deutschen botanischen Gesselschaft 18: H.6.

**Nguema-Ona E, Coimbra S, Vicré-Gibouin M, Mollet J, Driouich A. 2012.** Arabinogalactan proteins in root and pollen-tube cells: distribution and functional aspects. *Annals of Botany* **110**: 383–403.

**Pfeffer W. 1894.** Geotropic sensitiveness of the root-tip. *Annals of Botany* **8**: 317–320.

**Poot P, Hopper SD, van Diggelen JMH. 2012.** Exploring rock fissures: does a specialized root morphology explain endemism on granite outcrops? *Annals of Botany* **110**: 291–300.

**Postma JA, Lynch JP. 2012.** Complementarity in root architecture for nutrient uptake in ancient maize/bean and maize/bean/squash polycultures. *Annals of Botany* **110**: 521–534.

**Remans T, Thijs S, Truyens S, Weyens N, Schellingen K, Keunen E, Gielen H, Cuypers A, Vangronsveld J. 2012.** Understanding the development of roots exposed to contaminants and the potential of plant-associated bacteria for optimization of growth. *Annals of Botany* **110**: 239–252.

**Rich SM, Ludwig M, Colmer TD. 2012.** Aquatic adventitious root development in partially and completely submerged wetland plants *Cotula coronopifolia* and *Meionectes brownii*. *Annals of Botany* **110**: 405–414.

**Roppolo D, De Rybel B, Tendon VD, *et al*. 2011.** A novel protein family mediates Casparian strip formation in the endodermis. *Nature* **473**: 380–383.

**Rout ME, Callaway RM. 2012.** Interactions between exotic invasive plants and soil microbes in the rhizosphere suggest that 'everything is *not* everywhere'. *Annals of Botany* **110**: 213–222.

**Szymanowska-Pułka J, Potocka I, Karczewski J, Jiang K, Nakielski J, Feldman LJ. 2012.** Principal growth directions in development of the lateral root in *Arabidopsis thaliana*. *Annals of Botany* **110**: 491–501.

**Takano J, Tanaka M, Toyoda A, *et al*. 2010.** Polar localization and degradation of *Arabidopsis* boron transporters through distinct trafficking pathways. *Proceedings of the National Academy of Sciences, USA* **107**: 5220–5225.

**Tanimoto E. 2012.** Tall or short? Slender or thick? A plant strategy for regulating elongation growth of roots by low concentrations of gibberellin. *Annals of Botany* **110**: 373–381.

**Torrey JG, Philips HI Jr. 1974.** The organization of the root apex. In: Kolek J. ed. Structure and function of primary root tissues. *Slovak Academy of Sciences*, 17–21.

**Tracy SR, Black CR, Roberts JA, Sturrock C, Mairhofer S, Craigon J, Mooney SJ. 2012.** Quantifying the impact of soil compaction on root system architecture in tomato (*Solanum lycopersicum*) by X-ray micro-computed tomography. *Annals of Botany* **110**: 511–519.

**Trupiano D, Rocco M, Renzone G, Scaloni A, Viscosi V, Chiatante D, Scippa GS. 2012.** The proteome of *Populus nigra* woody root: response to bending. *Annals of Botany* **110**: 415–432.

**Vaculík M, Landberg T, Greger M, Luxová M, Stoláriková M, Lux A. 2012.** Silicon modifies root anatomy, and uptake and subcellular distribution of cadmium in young maize plants. *Annals of Botany* **110**: 433–443.

**Valentine TA, Hallett PD, Binnie K, Young M, Squire GR, Hawes K, Bengough AG. 2012.** Soil strength and macropore volume limit root elongation rates in many UK agricultural soils. *Annals of Botany* **110**: 259–270.

**Vines SH. 1888.** On the relation between the formation of tubercles on the roots of Leguminosae and the presence of nitrogen in the soil. *Annals of Botany* **2**: 386–389.

**Waisel T, Eshel A, Beeckman T, Kafkafi U. 2002.** *Plant roots: the hidden half*, 3rd edn. NewYork/Basel: Marcel Dekker, Inc.

**Zelko I, Lux A, Sterckeman T, Martinka M, Kollárová K, Lišková D. 2012.** An easy method for cutting and fluorescent staining of thin roots. *Annals of Botany* **110**: 475–478.