

PREFACE: PART OF A SPECIAL ISSUE ON ROOT BIOLOGY

Plant roots: understanding structure and function in an ocean of complexity

Peter R. Ryan^{1,*}, Emmanuel Delhaize¹, Michelle Watt² and Alan E. Richardson¹

¹CSIRO Agriculture and Food, GPO Box 1600, Canberra, ACT 2601, Australia and ²Plant Sciences Institute, Bio and Geo Sciences, Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

*For correspondence. E-mail peter.ryan@csiro.au

Received: 3 August 2016 Returned for revision: 6 August 2016 Accepted: 19 August 2016

- **Background** The structure and function of plant roots and their interactions with soil are exciting scientific frontiers that will ultimately reveal much about our natural systems, global water and mineral and carbon cycles, and help secure food supplies into the future. This Special Issue presents a collection of papers that address topics at the forefront of our understanding of root biology.
- **Scope** These papers investigate how roots cope with drought, nutrient deficiencies, toxicities and soil compaction as well as the interactions that roots have with soil microorganisms. Roots of model plant species, annual crops and perennial species are studied in short-term experiments through to multi-year trials. Spatial scales range from the gene up to farming systems and nutrient cycling. The diverse, integrated approaches described by these studies encompass root genetics as applied to soil management, as well as documenting the signalling processes occurring between roots and shoots and between roots and soil.
- **Conclusions** This Special Issue on roots presents invited reviews and research papers covering a span of topics ranging from fundamental aspects of anatomy, growth and water uptake to roots in crop and pasture systems. Understanding root structure and function and adaptation to the abiotic and biotic stresses encountered in field conditions is important for sustainable agricultural production and better management of natural systems.

Key words: Rhizosphere, water, nutrients, perennial, signals, plant-microbe interactions, abiotic stress, growth.

INTRODUCTION

It is staggering how much we have learnt about the natural world over recent decades. Much of the research progress in biological systems has been driven by new technologies that enable them to be investigated in greater detail at every scale: from genomes, transcriptomes and metabolomes at the subcellular level, all the way up to fields, forests and ecosystems. Yet the deeper we probe, the greater our surprise at the gaps that remain. This is as true for the commonplace weeds in our gardens as it is for our iconic species. For instance, it is bewildering how little is known about the blue whale (*Balaenoptera musculus*), the largest animal that has ever lived on the planet and a creature that still swims along the coastline of every continent on Earth. Zoologists don't know how long blue whales live for, how they communicate, nor much at all about their courtship and reproduction. Equally bewildering for plant biologists are the gaps in our knowledge about basic plant processes and their interactions with the environment, considering the critical role plants play in the air we breathe, the food we eat and the fibres we use. Our understanding of roots, the 'hidden half' of plants (Eshel and Beeckman, 2013), is even more rudimentary than that of shoots or flowers. Much of the biology controlling roots' functions in anchorage, storage, resource acquisition and communication remains a mystery. Apart from specific root crops like carrot and cassava (Stein and Nothnagel, 1995; Nassar and Ortiz, 2007), below-ground traits are rarely considered by plant breeders and dendrologists because roots are so difficult to observe and study *in situ*. The pressing challenge for plant biologists is not only to improve our understanding of root functions

and how they influence shoots and seed production, but to do so in the context of the surrounding soil and biomes. In one sense the issues hampering the study of blue whales and plant roots are similar – they are both surrounded by an ocean of complexity with enormous spatial and temporal variability. Nevertheless, the mysteries surrounding roots are gradually being unravelled, as described by the articles presented in this Special Issue. The genetic and phenotypic variability of roots remains to be fully exploited by breeders to benefit agricultural productivity and sustain natural plant systems. Filling the knowledge gaps in root research will bring opportunities for improving food security and environmental sustainability.

ROOTS AND WATER

Drought is the major limitation to the growth of crops and the distribution of natural plant communities globally, and several papers address the physics and physiology of water uptake by roots. Zarebanadkouki *et al.* (2016) remind us how little is known about basic aspects of water uptake. Hydraulic conductance is a critical parameter for understanding water uptake by roots, yet few models take into account the variation in conductance that is likely to occur along roots and radially within roots. This uncertainty was examined by mapping the spatial variation of water uptake in lupin (*Lupinus albus*) roots. Using neutron radiography the authors demonstrate that water uptake varies significantly between different types of roots as well as along roots. This information is useful for developing realistic models for water uptake from soil. Pioneering work by Gardner (1960)

considered the moisture gradients in soil immediately adjacent to roots, but a clear understanding of the behaviour of water at that interface is still lacking. This topic was addressed by Carminati *et al.* (2016), who developed a biophysical model to explain the changes that occur in the xylem water potential as the soil dries. Their model provides a framework for estimating the water potential across the rhizosphere and for predicting moisture levels directly adjacent to the root surface.

Root hydraulic conductivity in a drying soil was also investigated experimentally by Henry *et al.* (2016) using drought-susceptible and drought-tolerant cultivars of rice (*Oryza sativa*). Bleeding rates (sap exuded from a cut stem) were compared with vapour pressure deficit and transpiration rates during diurnal and seasonal cycles. They show how changes in these environmental factors affect root hydraulic conductivity and suggest a link between suberin content of roots and drought tolerance. Meng *et al.* (2016) investigated how rice plants balance the demand for water from the shoots with the supply of water by the roots. They show that changes in water demand alter the expression of aquaporins in the roots. Removing the shoots rapidly decreased the hydraulic conductance of the roots and decreased transcript levels of six aquaporin genes. These responses were reduced if xylem tension was maintained after excision by quickly applying a vacuum to the cut stems. The authors propose that xylem water tension acts as a signal between shoots and roots to coordinate water supply with demand. Aquaporin function was investigated in barley (*Hordeum vulgare*) roots by Sharipova *et al.* (2016) with an immunochemical approach. They applied abscisic acid (ABA) treatments to wild-type plants and an ABA-deficient mutant and successfully linked local ABA concentrations with the abundance of aquaporins and changes in root hydraulic conductivity.

Many fundamental questions concerning how water moves from the soil to the shoots remain to be answered. The studies mentioned above share the central objective of understanding how water movement is controlled by roots, but the scale of the investigations varies widely, from analysis of the root–soil interface and specific transporter proteins on root-cell membranes, to total hydraulic conductivity. *In situ* measurements using tracers showed fine spatial control of water flow along roots that was influenced by age and soil moisture. This likely reflects further levels of regulation. These studies confirm roles for hormones, protein transporters and cell-wall structure in water uptake, indicating the necessity for complex signals to coordinate these factors.

PERENNIAL ROOT SYSTEMS

Roots of some perennial species can pose additional hurdles to researchers because of their size, depth and difficulty of manipulation. These challenges are considered in a detailed review by Pierret *et al.* (2016) that explores the complex physiology of deep roots, including the different functions they perform at various depths. The authors critically examine popular models describing the structures and functions of deep roots. They conclude that most current models are supported by scant evidence and suggest priority areas for future research to improve these models. Rooting depth is important for the perennial pastures so central to the grazing systems that support milk and meat

production. White clover (*Trifolium repens*) is one of the most important forage species in temperate zones yet is prone to drought stress due to its relatively small and shallow root system. White clover also competes poorly for nutrients when included in swards with grasses. Nichols *et al.* (2016) describe their strategies for improving the root structure of white clover by crosses to a range of *Trifolium uniflorum* accessions. Several characteristics of the backcross hybrids were altered, including root depth and root length density. The results demonstrate that targeted breeding strategies can be used to alter root architecture to improve pasture production. An important role of roots is to provide support and stability to the plant shoots. Dorval *et al.* (2016) examined how root architecture affects stability and anchorage in young *Pinus pinaster* trees. They identify several root shapes that are particularly beneficial on sandy soils and conclude that a large proportion of the anchorage can be attributed to the distal region of the tap root and associated laterals. In agro-forestry production systems, competition between roots from different perennials could limit the productivity of either one or both species. This idea was tested in a mixed coffee (*Coffea arabica*)/tree (*Erythrina poeppigiana*) plantation by Defrenet *et al.* (2016). This group monitored root biomass and fine-root density to 4 m depth in different parts of the plantation with contrasting light environments. No significant effects of the larger shading trees on the fine roots of coffee were found and the study concludes that coffee roots are very competitive in this system. Finally, Bastos *et al.* (2016) provide the first detailed anatomical study of roots from the woody vines collectively called lianas. Using traditional techniques and X-ray microtomography analysis, they compare and contrast mature roots from 14 species in the Paullinieae tribe (Sapindaceae) and highlight differences from known tissue anatomies in the stems of these species.

Such studies on perennial roots are arguably at the forefront of root biology and function, and constitute an exciting field for root research in the future. Much of our knowledge on roots to date has come from observations of annual, short-lived plants, and has been particularly focused upon the roots of relatively young plants. The roots of plants that live over several seasons, re-colonizing soil profiles year after year, decaying and interacting with microorganisms and cycling nutrients and water over years, are difficult to investigate but present opportunities for many discoveries. Such discoveries have wide and important implications for global productivity. For example, perennial biofuel crops are potentially more energy-efficient because they don't need to be re-sown annually. Forests, trees and perennial shrubs regulate water and carbon cycling to many metres below ground, and while roots are critical to these processes very little detail is known about their regulatory roles.

RESPONSES TO ABIOTIC STRESSES

Several papers examine how roots respond to abiotic stresses, including nutritional limitations, elemental toxicities, waterlogging and physical constraints. Soil acidity affects more than 30 % of arable land and continues to limit agricultural productivity globally. Aluminium and manganese toxicities are largely responsible for poor plant growth but nutrient deficiencies also contribute. Many species have evolved strategies to

cope with these stresses, and Rao *et al.* (2016) comprehensively review the adaptive changes in root structure and function that provide protection from these hostile soils. They encourage further breeding strategies to select for additional root traits. Líška *et al.* (2016) demonstrate how exposure of roots to air, or to toxic metals such as cadmium, influences the development of suberin lamella. Suberin is a wax-like cell-wall polymer that provides a barrier to the movement of water and solutes. They find that suberin is preferentially deposited on the side of the root exposed to these treatments, presumably as a means of protecting the plant from these stresses. Metabolic responses to phosphorus deficiency in rice (*O. sativa*) were investigated by Zhu *et al.* (2016). This paper examines phosphorus recycling from roots to the shoots, where the phosphorus supply is restricted, and reports that ethylene regulates this process. Raising ethylene concentrations in phosphorus-deficient rice plants increased cell wall pectin content and the expression of the phosphate transporter OsPT2; both of these changes accelerated phosphorus release from the root cell walls, which increased phosphorus translocation to the shoots. Compaction is another major soil constraint that affects root penetration and final rooting depth. Popova *et al.* (2016) studied the effect of soil strength on elongation rate and diameter of maize (*Zea mays*) roots. Their paper describes how final root shape and tortuosity in compacted soil results not only from mechanical deflections but also from tropic responses via touch stimuli. Mechanical stress is also the topic of a study by De Zio *et al.* (2016). They examined roots of the woody perennial *Populus nigra* and compared the anatomy, lignin content and hormone concentrations on the convex and concave sides of roots forced to turn a tight corner. Lignin content and xylem thickness increased on the concave side whereas more lateral roots appeared on the convex side. Hormone analysis indicates that auxin and abscisic acid concentrations were likely to be responsible for regulating these changes. Interestingly, the responses of roots to mechanical stress contrasts with the modifications known to occur in the stems of poplar plants (Plomion *et al.*, 2001).

Waterlogging presents a number of physical and chemical stresses to plants but the reduction in oxygen availability can limit growth and survival. Some species, such as alligator weed (*Alternanthera philoxeroides*), are well adapted to flooded conditions because they have evolved specific mechanisms to overcome this limitation, and consequently have become a major threat to wetlands, rivers and irrigation systems around the world. Alligator weed is a perennial, growing vigorously and forming an intricate root system of adventitious roots that suspend in water. Ayi *et al.* (2016) investigated the adventitious roots that develop on alligator weed in submerged conditions. They measured the oxygen gradients in the unstirred layers adjacent to these roots and provide evidence that they are capable of absorbing oxygen from the water. They also demonstrate that oxygen concentration within stem nodes having adventitious roots increased compared with stem nodes without adventitious roots, suggesting that oxygen may intimately regulate their development, possibly helping to supply carbohydrate for vigorous root growth. It remains to be shown whether the development of these adventitious roots offers alligator weed greater capacity to absorb oxygen from water than similar roots in other species.

Phenotypic screens for single, abiotic soil constraints, such as those in the studies summarized above, can reveal the genetic and physiological basis of tolerance mechanisms. Similar studies have identified many new membrane transport proteins that regulate the uptake of nutrients and the exclusion of toxic ions through specific root exudates (Schroeder *et al.*, 2013). The next step will be to combine these treatments and score performance with the multiple stresses encountered in the field. This will accelerate progress towards improving agricultural production and provide management options for forestry and natural systems (Rich and Watt, 2013).

GROWTH AND DEVELOPMENT

Several papers investigate root growth and development with mathematical models and by examining the mechanisms that control growth. Le Deunff *et al.* (2016) surmise that root growth relies on a specific set of signals involving hormones, nutrients and carbon supply. They generated a fractal-based model for root development that accounts for specific interactions between ethylene levels, nitrogen availability and energy supply. Pacheco-Escobedo *et al.* (2016) also adopted a mathematical approach to map the developmental zones at the root apices using a ‘multiple structural change’ algorithm. A spatial model was developed that predicted three main developmental regions they named the proliferation, transition and elongation domains. These domains represent stages of differentiation, and the position of the transition zone was confirmed with transgenic *Arabidopsis* lines that expressed the green fluorescent protein at specific stages of the cell cycle. These domains are controlled by interacting regulatory networks of signals and transcription factors. Pacheco-Escobedo *et al.* (2016) further show that a transcription factor encoded by the MADS-box family gene *XAANTALI* (*XALI*) affects the size of the proliferation zone and critical length of dividing cells. This same MADS-box gene was investigated by García-Cruz *et al.* (2016). They describe how the loss-of-function *Arabidopsis* mutant *xall* had altered expression of several key cell-cycle genes, disrupted tissue differentiation patterns and reduced cortical cell length. Reverse genetics approaches like this one will help to untangle the complex networks controlling root growth.

Cluster roots are specific root types that form in some species in response to phosphorus deficiency. They are viewed as an effective strategy for plants to extract phosphorus from soil pools not usually available to other plants. Cluster roots typically comprise a region of densely arranged short secondary laterals thickly covered with root hairs. In addition to providing a large surface area for absorbing nutrients, cluster roots exude protons, organic anions and phosphatases to increase the concentration of available phosphate in that region (Neumann and Martinoia, 2002). The efflux of citrate and malate from cluster roots is dependent, in part, on the activity of phosphoenolpyruvate carboxylase (PEPC). Shane *et al.* (2016) investigated the regulation of PEPC in the cluster roots of white lupin (*L. albus*) by monitoring the effect of light and sugar supply on organic anion exudation. They report that PEPC activity in these tissues is post-translationally regulated by the light-dependent, reversible phosphorylation of the PEPC proteins. Their findings

demonstrate that sucrose translocated from source leaves down to the roots influences the activity of this enzyme in sink tissues.

PLANT–MICROBE INTERACTIONS

Signalling processes associated with root development and the cross-talk between roots and soil microorganisms has emerged as an exciting topic in plant biology. A paper by Lamont and Pérez-Fernández (2016) describes how the emergence of the cluster roots in three distinct species from different genera and geographic origin (*Leucadendron salicifolium*, *Viminaria juncea* and *Lupinus albus*) was affected by inoculation with seven different bacterial strains and nitrogen treatments. The paper reports that six of the bacterial strains induced greater cluster root production than the aseptic controls. This response was not correlated with the relative ability of these bacterial strains to produce indole-3-acetic acid, a hormone previously linked with cluster root production. Microorganisms trigger other responses in roots, and Koroney *et al.* (2016) examine how a pathogen can affect the composition of root exudates. They challenged potato (*Solanum tuberosum*) roots with an elicitor isolated from *Pectobacterium atrosepticum*, a soil-borne pathogen of potato. They found that these inoculations altered the composition of the galactose-containing compounds and arabinogalactan proteins exuded from the root border cells of potato. They show that the *in vitro* growth rate of the pathogen depended on whether it was exposed to exudates collected from induced or non-induced border cells. These results illustrate the dynamic nature of the stimulus–response interactions that likely occur continually between roots and the microbiome. Song *et al.* (2016) contribute a further study on signalling in roots. In this paper, systemic acquired resistance (SAR) was induced in shoots of tobacco plants (*Nicotiana benthamiana*) by application of benzthiadiazole, and transmission of SAR between neighbouring plants was subsequently shown to occur by root-to-root transmission via a salicylic acid-mediated pathway. This was tested by challenging the adjoining plants with root (*Pseudomonas syringae*) and leaf (*Ralstonia solanacearum*) pathogens and showing that the disease severity of the neighbouring plants, not directly treated with benzthiadiazole, was reduced. These three papers reveal some of the connections between roots and the wider soil microbiome and highlight their involvement in elaborate communication pathways both within and between plants. Understanding how roots interact and communicate with the soil microbiome through the release of exudates and other metabolites is a rapidly emerging area of research that offers new opportunities for plant protection and growth promotion. Indeed, the root microbiome, which encompasses root endophytes and microorganisms that colonize the rhizoplane, rhizosphere and mycorrhizosphere, is now recognized as being part of the ‘extended phenotype’ of the plant.

FARMING SYSTEMS

A long-term aim of much plant research is to identify root traits that can be exploited to improve agricultural production, and Thorup-Kristensen and Kirkegaard (2016) emphasize in their review some of the practical considerations for achieving this

goal. The authors compare two cropping systems in Australia and Denmark, where deep roots can benefit wheat yields by enabling access to stored soil water and nitrogen late in the season. They argue that the preceding crop, management during the fallow period, and sowing date have a large influence on subsequent wheat yields. While screens to optimize root systems should benefit productivity, the authors conclude that the target traits need to be carefully matched with the local conditions and management practices. Screening methodologies are central to the contribution by Thomas *et al.* (2016). This project scored canola (*Brassica napus*) varieties for shoot and root characters in the laboratory and in the field over three seasons. They conclude that primary root length and field performance were correlated with early vigour, which is more easily scored for in the shoots. However, they find that lateral root density was correlated with calcium and zinc concentrations in the leaves, and these analyses could potentially be used as a surrogate screen for root traits. These papers illustrate the value of designing screens for root traits that match the field conditions where they need to function. By matching root and rhizosphere phenotypes with the soil, climate and regional management practices, root researchers will contribute more directly to the productivity and efficiency gains needed for global food, water and land security.

CONCLUSIONS

While the new tools afforded by biotechnology, computing power and satellite imagery have allowed unprecedented progress in root research, basic measurements remain a challenge. Phenotyping roots *in situ* is still a major obstacle. The intricate communication between roots and microorganisms is emerging as another frontier in root research. Much has been achieved in laboratory-based studies, but it is clear that the shape and function of roots grown in the field can be quite distinct from that of those grown in pots or hydroponics. The challenge is not only to understand how roots function but to do so in soil with all its physical, chemical and biological complexity. This is an exciting time to be involved in root research, but we need to acknowledge, with some humility, that our understanding of organisms as commonplace as a weed or as grand as a blue whale remains in its infancy.

DEDICATION

This Special Issue is dedicated to the memory of Michael Shane, the lead author of Shane *et al.* (2016), who sadly passed away shortly after this manuscript was accepted for publication. Mike studied at the Carleton University in Ottawa before continuing his commitment to root research for many years at the University of Western Australia. The Editors of this Special Issue knew Mike and his excellent research on so many aspects of root biology very well. Our thoughts and condolences are extended to Mike’s family, friends and many colleagues.

ACKNOWLEDGEMENTS

We acknowledge the International Society of Root Research for the ninth and most recent symposium entitled ‘Roots

Down Under: Belowground Solutions for Global Challenges', held in Canberra, Australia, on 6–9 October 2015. This symposium provided a forum for root researchers to share the latest results and ideas about the fundamentals of how roots function and provided the stimulus for this Special Issue.

LITERATURE CITED

- Eshel A, Beeckman T. 2013. *Plant roots: the hidden half*, 4th edn. Boca Raton: CRC Press, 848.
- Ayi Q, Zeng B, Liu J, Li S, van Bodegom PM, Cornelissen JHC. 2016. Oxygen absorption by adventitious roots promotes the survival of completely submerged terrestrial plants. *Annals of Botany* 118: 675–683.
- Bastos CL, Tamaio N, Angyalossy V. 2016. Unravelling roots of lianas: a case study in Sapindaceae. *Annals of Botany* 118: 733–746.
- Carminati A, Zarebanadkouki M, Kroener E, Ahmed MA, Holz M. 2016. Biophysical rhizosphere processes affecting root water uptake. *Annals of Botany* 118: 561–571.
- Defrenet E, Rouspard O, Van den Meersche K, et al. 2016. Root biomass, turnover and net primary productivity of a coffee agroforestry system in Costa Rica: effects of soil depth, shade tree, distance to row and coffee age. *Annals of Botany* 118: 833–851.
- Le Deunff E, Lecourt J, Malagoli P. 2016. Fine-tuning of root elongation by ethylene: a tool to study dynamic structure-function relationships between root architecture and nitrate absorption. *Annals of Botany* 118: 607–620.
- Dorval AD, Meredieu C, Danjon F. 2016. Anchorage failure of young trees in sandy soils is prevented by a rigid central part of the root system with various designs. *Annals of Botany* 118: 747–762.
- García-Cruz KV, García-Ponce B, Garay-Arroyo A, et al. 2016. The MADS-box *XAANTAL1* increases proliferation at the *Arabidopsis* root stem-cell niche and participates in transition to differentiation by regulating cell-cycle components. *Annals of Botany* 118: 787–796.
- Gardner WR. 1960. Dynamic aspects of water availability to plants. *Soil Science* 89: 63–73.
- Henry A, Wehler R, Grondin A, Franke R, Quintana M. 2016. Environmental and physiological effects on grouping of drought-tolerant and susceptible rice varieties related to rice (*Oryza sativa*) root hydraulics under drought. *Annals of Botany* 118: 711–724.
- Koroney AS, Plasson C, Pawlak B, et al. 2016. Root exudate of *Solanum tuberosum* is enriched in galactose-containing molecules and impacts the growth of *Pectobacterium atrosepticum*. *Annals of Botany* 118: 797–808.
- Lamont BB, Pérez-Fernández M. 2016. Total growth and root-cluster production by legumes and proteas depends on rhizobacterial strain, host species and nitrogen level. *Annals of Botany* 118: 725–732.
- Líška D, Martinka M, Kohanová J, Lux A. 2016. Asymmetrical development of root endodermis and exodermis in reaction to abiotic stresses. *Annals of Botany* 118: 667–674.
- Meng D, Walsh M, Fricke W. 2016. Rapid changes in root hydraulic conductivity and aquaporin expression in rice (*Oryza sativa* L.) in response to shoot removal – xylem tension as a possible signal. *Annals of Botany* 118: 809–819.
- Nassar NMA, Ortíz R. 2007. Cassava improvement: challenges and impacts. *Journal of Agricultural Science* 145: 163–171.
- Nichols SN, Hofmann RW, Williams WM, van Koten C. 2016. Rooting depth and root depth distribution of *Trifolium repens* × *T. uniflorum* interspecific hybrids. *Annals of Botany* 118: 699–710.
- Neumann G, Martinoia E. 2002. Cluster roots – an underground adaptation for survival in extreme environments. *Trends in Plant Science* 7: 162–167.
- Pacheco-Escobedo MA, Ivanov VB, Ransom-Rodríguez I, et al. 2016. Longitudinal zonation pattern in *Arabidopsis* root tip defined by a multiple structural change algorithm. *Annals of Botany* 118: 763–776.
- Pierret A, Maeght J-L, Clément C, Montoro J-P, Hartmann C, Gonkhamdee S. 2016. Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. *Annals of Botany* 118: 621–635.
- Plomion C, Leprovost G, Stokes A. 2001. Wood formation in trees. *Plant Physiology* 127: 1513–1523.
- Popova L, van Dusschoten D, Nagel A, Fiorani F, Mazzolai B (2016). Plant root tortuosity: an indicator of root path formation in soil with different composition and density. *Annals of Botany* 118: 685–698.
- Rao IM, Miles JW, Beebe SE, Horst WJ. 2016. Root adaptations to soils with low fertility and aluminum toxicity. *Annals of Botany* 118: 593–605.
- Rich SM, Watt M. 2013. Soil conditions and cereal root system architecture: review and considerations for linking Darwin and Weaver. *Journal of Experimental Botany* 64: 1193–1208.
- Schroeder JI, Delhaize E, Frommer WB, et al. 2013. Using membrane transporters to improve crops for sustainable food production. *Nature* 497: 60–66.
- Shane MW, Feil R, Lunn JE, Plaxton WC. 2016. Light-dependent activation of phosphoenolpyruvate carboxylase by reversible phosphorylation in cluster roots of white lupin plants: diurnal control in response to photosynthate supply. *Annals of Botany* 118: 777–785.
- Sharipova G, Veselov D, Kudoyarova G, et al. 2016. Exogenous application of abscisic acid (ABA) increases root and cell hydraulic conductivity and abundance of some aquaporin isoforms in the ABA deficient barley mutant *Az34*. *Annals of Botany* 118: 777–785.
- Song GC, Sim H-J, Kim S-G, Ryu C-M. 2016. Root-mediated signal transmission of systemic acquired resistance against above-ground and below-ground pathogens. *Annals of Botany* 118: 821–831.
- Stein M, Nothnagel T. 1995. Some remarks on carrot breeding (*Daucus carota sativus* Hoffm.). *Plant Breeding* 114: 1–11.
- Thomas CL, Graham NS, Hayden R, et al. 2016. High throughput phenotyping (HTP) identifies seedling root traits linked to variation in seed yield and nutrient capture in field-grown oilseed rape (*Brassica napus* L.). *Annals of Botany* 118: 655–665.
- Thorup-Kristensen K, Kirkegaard J. 2016. Root system-based limits to agricultural productivity and efficiency: the farming systems context. *Annals of Botany* 118: 573–592.
- Zarebanadkouki M, Meunier F, Couvreur V, Cesar J, Javaux M, Carminati A. 2016. Estimation of the hydraulic conductivities of lupine roots by inverse modelling of high-resolution measurements of root water uptake. *Annals of Botany* 118: 853–864.
- Zhu XF, Zhu CQ, Zhao XS, Zheng SJ, Shen RF. 2016. Ethylene is involved in root phosphorus remobilization in rice (*Oryza sativa*) by regulating cell wall pectin and enhancing phosphate translocation to shoots. *Annals of Botany* 118: 645–653.
- De Zio E, Trupiano D, Montagnoli A, et al. 2016. Poplar woody taproot under bending stress: the asymmetric response of the convex and concave sides. *Annals of Botany* 118: 865–883.