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SPECIAL ISSUE

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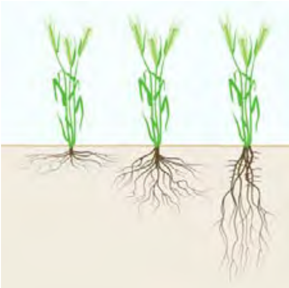
MATCHING ROOTS TO THEIR ENVIRONMENT



Matching roots to their environment (Overview)

Philip J. White, Timothy S. George, Peter J. Gregory, A. Glyn Bengough, Paul D. Hallett and Blair M. McKenzie

doi: 10.1093/aob/mct123

Plants rely on their roots to acquire the water and mineral elements necessary for their survival in nature, and their yield and nutritional quality in agriculture. **White *et al.*** examine how the roots of land plants evolved, describe how the ecology of roots and their rhizospheres affects the utilization of soil resources, and discuss the influence of plant roots on biogeochemical cycles. They then describe the roles of roots in overcoming the constraints to crop production imposed by hostile or infertile soils, illustrate root phenotypes that improve the acquisition of soil resources, and discuss high-throughput methods to screen for these traits in the laboratory, glasshouse and field. Finally, they consider how adaptations to root systems might enable sustainable agriculture in the future.

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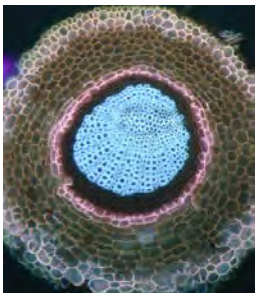

Anatomical aspects of angiosperm root evolution (Review)

James L. Seago Jr and Danilo D. Fernando

doi: 10.1093/aob/mcs266

Phylogenetic characterizations of angiosperms have been dominated by molecular, floral and above-ground shoot vegetative traits. **Seago and Fernando** utilize information from the literature and new research data to show that root anatomy can support current phylogenies and add to phylogenetic interpretations. In particular, they report that *Amborella trichopoda* and the Magnoliids have many root structural features like those of eudicots, whereas the Nymphaeales, including the recently reclassified *Trithuria* of the Hydatellaceae, very strongly exhibit traits of the monocots. However, the Austrobaileyales are enigmatic and have root structural features that do not align easily to either monocots or eudicots.

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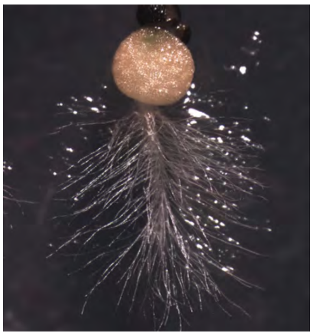

Primary root growth patterns in Cactaceae

Svetlana Shishkova, María Laura Las Peñas, Selene Napsucialy-Mendivil, Marta Matvienko, Alex Kozik, Jesús Montiel, Anallely Patiño and Joseph G. Dubrovsky

doi: 10.1093/aob/ mct100

In most species, roots are capable of indeterminate growth for extended periods. **Shishkova *et al.*** classify primary root growth of Cactaceae as being determinate or indeterminate, and explore the mechanisms underlying root meristem exhaustion. They find that species from all but one tribe of the Cactoideae exhibit determinate primary root growth. The results suggest that determinate growth of the primary root is an adaptation to aridity and became fixed after separation of Cactiodeae/Opuntioideae from Maihuenioideae/Pereskioideae lineages, and that the root meristem exhaustion in Cactoideae is co-ordinated by genes involved in the regulation of gene expression, redox and hormonal control.

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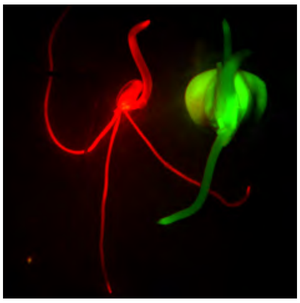

Extending perspectives on root–root interactions (Research in Context)

Marc Faget, Kerstin A. Nagel, Achim Walter, Juan M. Herrera, Siegfried Jahnke, Ulrich Schurr and Vicky M. Temperton

doi: 10.1093/aob/mcs296

Studies of root–root interactions have often suffered from being static, partly due to the lack of appropriate methodologies for *in-situ* non-destructive root characterization. **Faget *et al.*** review methods that will allow researchers to identify the roots of individual plants (or particular species) within the soil, including genotype-marking using the expression of fluorescent proteins or $^{11}CO_2$-labelling combined with positron emission tomography. They consider that the development of non-invasive methods to dynamically study root–root interactions *in vivo* will provide the necessary tools for a more inclusive conceptual framework for root–root interactions across both ecological and agronomic fields.

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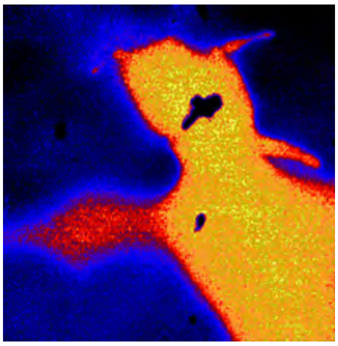

Quantitative imaging of the rhizosphere with planar optodes (Technical Article)

Stephan Blossfeld, Christina Maria Schreiber, Gregor Liebsch, Arnd Jürgen Kuhn and Philippe Hinsinger

doi: 10.1093/aob/mct047

Non-invasive measurement techniques are key to unravelling organism–environment interactions in the highly heterogeneous and difficult-to-probe environment of the rhizosphere. **Blossfeld *et al.*** introduce the application of easy-to-use planar optode systems with pH- and recently developed CO_2-sensors to produce continuous and highly resolved real-time measurements around roots of *Triticum turgidum durum* (durum wheat), *Cicer arietinum* (chickpea) and *Viminaria juncea* growing in a rhizobox system. They conclude that the technique provides a unique tool for future root research applications and overcomes limitations of previous systems by creating quantitative pH and CO_2 maps.

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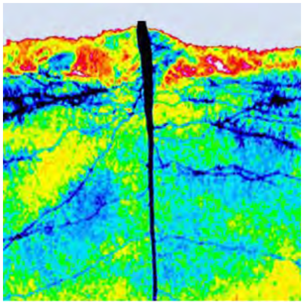

Rhizosphere plasticity helps acquisition of scarce resources (Viewpoint)

Andrea Carminati and Doris Vetterlein

doi : 10.1093/aob/mcs262

Rhizosphere properties are not constant but vary with root growth and environmental conditions. **Carminati and Vetterlein** consider such variability as an expression of rhizosphere plasticity and note that roots modify the rhizosphere in different ways. By exuding mucilage, roots maintain a wet rhizosphere and increase water availability in dry soils; however, when mucilage dries it becomes hydrophobic and limits local uptake. A similar effect is caused by root shrinkage and loss of contact with soil. Although this is a disadvantage for local uptake, looked at on a larger scale, gaps and hydrophobicity isolate roots from dry soils and avoid water losses. Manipulation of the hydraulic properties of the rhizosphere by roots could be a strategy by which plants control the part of the root system that will have greatest access to water and solutes.

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Root–shoot allometry of tropical forest trees

Amram Eshel and José M. Grünzweig

doi: 10.1093/aob/mcs275

Accurate knowledge allometric relationships between above- and below-ground tree parts is important for applications such as modelling of carbon fluxes. **Eshel and Grünzweig** develop a unique aeroponic facility that allows access to intact root systems of trees several meters high and use it to study 12-month-old saplings of two types of tropical forest trees, a fast-growing kapok, *Ceiba pentandra*, and a slow-growing African mahogany, *Khaya anthotheca*. Comparison for both species with saplings grown in 50-L soil containers shows that the biomass allometry metrics of branches and roots of different types and orders are the same in both growing systems. The ease of access to the roots in the aeroponic system allows important information to be gathered relating to the role of fine roots as carbon stores, the rates of root turnover, and the chemistry of below-ground organic inputs to soil.

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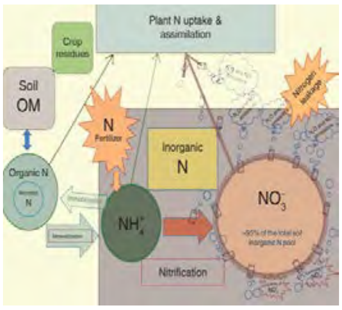

Biological nitrifictaion inhibition to improve use of nitrogen (Viewpoint)

G. V. Subbarao, K. L. Sahrawat, K. Nakahara, I. M. Rao, M. Ishitani, C. T. Hash, M. Kishii, D. G. Bonnett, W. L. Berry and J. C. Lata

doi: 10.1093/aob/mcs230

A major portion of nitrogen applied as fertilizer leaks into the environment, primarily through cycling via the soil nitrification pathway. **Subbarao *et al.*** discuss the possibilities of manipulating the release from roots of inhibitors of nitrification to limit such losses in agricultural systems. Substances effecting 'biological nitrification inhibition' (BNI) appear to be released via tightly regulated physiological process, with extensive genetic variability found in selected crops and pasture grasses. *Brachiaria* forage grasses, wheat and sorghum are used to illustrate how BNI can be utilized in order to achieve low-nitrifying agricultural systems. A fundamental shift towards ammonium (NH_4^+)-dominated systems could be brought about by using crops and pastures with high BNI capacities, thereby improving nitrogen use efficiencies and minimizing N pollution.

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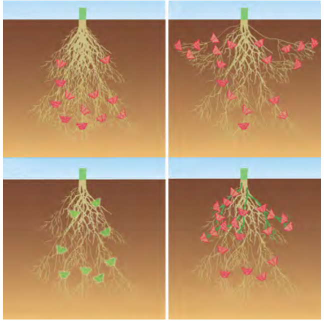

Root hair ideotypes for improved P acquistion (Viewpoint)

L. K. Brown, T. S. George, L. X. Dupuy and P. J. White

doi: 10.1093/aob/ mcs231

Phosphorus (P) often limits crop production and is frequently applied as fertilizer; however, supplies of phosphate for fertilizer production are diminishing. **Brown *et al.*** consider various root-related traits that could be deployed to improve agricultural sustainability and discuss their potential costs and benefits to the plant. They present a novel mathematical model describing the effects of length, density and longevity of root hairs on P acquisition, and calculate the relative benefit of these three root-hair traits to plant P nutrition. They conclude that the greatest gains in P-uptake efficiency are likely to be made through increased length and longevity of root hairs rather than by increasing their density, and they formulate six potential ideotypes to improve crop P acquisition that could be used to inform breeding programmes to enhance agricultural sustainability.

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Improving phosphorus and zinc acquisition by rice roots (Review)

T. J. Rose, S. M. Impa, M. T. Rose, J. Pariasca-Tanaka, A. Mori, S. Heuer, S. E. Johnson-Beebout and M. Wissuwa

doi: 10.1093/aob/mcs217

Rice, *Oryza sativa*, is the world's most important cereal crop, and phosphorus (P) and zinc (Zn) deficiency are major constraints to its production. **Rose *et al.*** review root traits that have been linked to P and Zn uptake, including those that increase mobilization of P/Zn from soils, increase the volume of soil explored by roots, enhance the rate of P/Zn uptake across the root membrane, and whole-plant traits that affect root growth. They conclude that few root traits have so far been used successfully in plant breeding for enhanced P or Zn uptake in rice or any other crop, and that insufficient genotypic variation for traits or the failure to enhance uptake under realistic field conditions are likely reasons for this limited success. More emphasis is thus needed on field studies in mapping populations or association panels to identify those traits and underlying genes that are able to enhance nutrient acquisition beyond the level already present in most cultivars.

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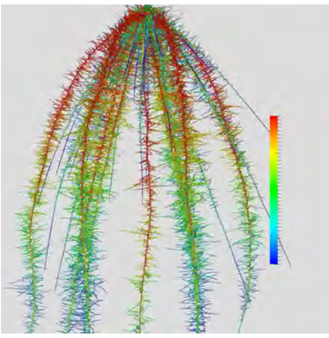

Steep, cheap and deep: an ideotype for a root system (Viewpoint)

Jonathan P. Lynch

doi: 10.1093/aob/mcs293

Since water and nitrate enter deeper soil strata over time and are initially depleted in surface soil strata, it can be presumed that root systems with rapid exploitation of deep soil would optimize water and nitrogen capture in most production environments. **Lynch** proposes an ideotype to achieve this for maize (*Zea mays*) root systems. The ideotype consists of architectural phenes that co-localize root foraging and resource availability in time and space, anatomical phenes that reduce the metabolic cost of soil exploration, and optimal nitrate uptake kinetics. Many features of this ideotype are relevant to other cereal root systems and more generally to root systems of dicotyledonous crops.

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Genotype × environment interactions for root depth of wheat (Viewpoint)

Tina L. Botwright Acuña and Len J. Wade

doi : 10.1093/aob/mcs251

Root systems are well-recognized as complex and a variety of traits have been identified as contributing to plant adaptation to the environment. **Botwright Acuña and Wade** review the use of pattern analysis for genotype × environment (G×E) interactions, with a focus on traits. Drawing on research on G×E interactions for root depth in wheat (*Triticum aestivum*), they find that the interactions account for 40 % of the variation in this trait, which is more than three times greater than that attributed to genotype alone. They conclude that with appropriate characterization of environments and genotypes, the G×E approach can be used to aid in the interpretation of the complex interactions of root systems with the environment, and hence provide supporting evidence for selecting specific root traits for target environments in crop breeding programs.

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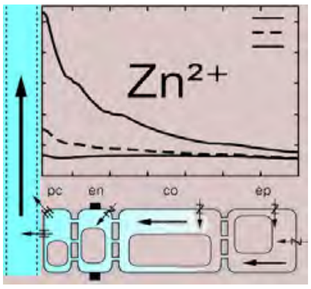

Modelling zinc uptake and radial transport in arabidopsis roots

Juliane Claus, Ansgar Bohmann and Andrés Chavarría-Krauser

doi: 10.1093/aob/mcs263

Mathematical modelling is a useful method for describing biological systems and interpreting experimental data. **Claus *et al.*** develop a comprehensive one-dimensional dynamic model of radial zinc (Zn) transport in roots of *Arabidopsis thaliana*, which accounts for the internal structure of the root and includes water flow, Zn diffusion, and cross-membrane transport via regulated ZIP transporters. They find that model simulations reproduce experimental findings very well and confirm that low abundance of a heavy metal ATPase transporter (HMA4) produces a radial gradient in Zn concentration. Transpiration is shown to be a key parameter contributing to the radial Zn gradient and the time scale of regulation appears to be faster than expected.

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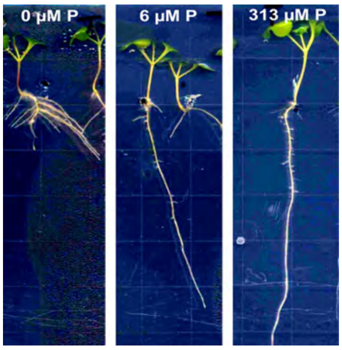

QTL for root traits under low phosphate availability

Lei Shi, Taoxiong Shi, Martin R. Broadley, Philip J. White, Yan Long, Jinling Meng, Fangsen Xu and John P. Hammond

doi: 10.1093/aob/mcs245

Breeding crops that acquire phosphate (Pi) more efficiently is one strategy to reduce the use of increasingly scarce resources, and root traits are an important source of genetic variation for breeding programs. **Shi *et al.*** use an agar-based, high-throughput root phenotyping approach to quantify seedling root architectural traits of a large *Brassica napus* double-haploid mapping population grown under contrasting Pi supply. They identify significant QTL associated with root traits and biomass at low Pi availability, providing insights to the genetic basis of plant tolerance to Pi deficiency. Whilst cross-validation with root characteristics and yield under field conditions is required, the results offer the potential for these traits to be used in crop improvement strategies.

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Root architecture development with low phosphorus supply (Review)

Yao Fang Niu, Ru Shan Chai, Gu Lei Jin, Huan Wang, Cai Xian Tang and Yong Song Zhang

doi:10.1093/aob/mcs285

Phosphorus (P) is an essential element for plant growth and development but it is often a limiting nutrient in soils. **Niu *et al.*** review current knowledge on the significance of root architecture development in response to low P availability and its beneficial effects on alleviation of P stress, with a focus on integrated physiological and molecular signalling. The mechanisms for activating alterations in root architecture in response to P deficiency depend on changes in the localized P concentration and transport of, or sensitivity to, growth regulators such as sugars, auxins, ethylene, cytokinins, nitric oxide, reactive oxygen species and abscisic acid. In the process, many genes are activated, which in turn trigger changes in molecular, physiological and cellular processes.

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Strigolactones and root responses to phosphate availability (Review)

Hinanit Koltai

doi : 10.1093/aob/mcs216

Strigolactones are a new group of plant hormones that are known to play a role in the regulation of root development, in addition to their role in suppression of lateral shoot branching. **Koltai** highlights recent findings on the activity of strigolactones, in particular in response to low phosphate stress, and discusses the different hormonal networks putatively acting with strigolactones in the response of roots to phosphate. It is suggested that strigolactones are key regulators of the adaptive responses to low phosphate in the root by impacting different developmental programs responsible for the changes in root system architecture under differential phosphate supply.

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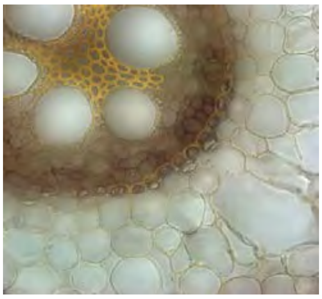

Lateral root development in maize *lrt1* mutant

Eva Husáková, Frank Hochholdinger and Ales Soukup

doi: 10.1093/aob/mct043

Maize *lrt1* (*lateral rootless1*) is a unique mutant impaired in development of lateral roots during early post-embryonic stages. **Husáková *et al.*** use detailed anatomical analysis and histological methods to characterize the effect of the mutation on initiation and subsequent development of lateral roots. Their results suggest that the *Lrt1* gene is not impaired primarily in initiation but in later development of lateral roots, and thus affects their spatial distribution and morphology, but not their abundance. The gene is also required for correct, co-ordinated cell division in the cortex and the development of the exodermis of primary roots.

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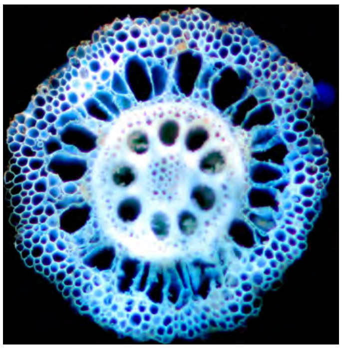

‘Cheap’ roots improve drought tolerance in maize

Raúl E. Jaramillo, Eric A. Nord, Joseph G. Chimungu, Kathleen M. Brown and Jonathan P. Lynch

doi: 10.1093/aob/mct069

The identification of traits regulating water capture from drying soil is an important step in breeding more resilient crops. **Jaramillo *et al.*** test the hypothesis that the metabolic cost of the root cortex, as measured by living cortical area (LCA), the area of living cortical tissue in root cross-sections, is one such trait. They find that, when grown under water stress in soil mesocosms, maize (*Zea mays*) lines with less LCA have less root respiration and greater root depth, water acquisition and biomass than closely related lines with more LCA. Large genetic variation for this trait suggests that it may be useful in crop breeding.

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Nodal root responses to varying soil moisture

M. Rostamza, R. A. Richards and M. Watt

doi: 10.1093/aob/ mct099

In cereals, a nodal root system can emerge from stem nodes throughout the plant's life, but its value for yield is unclear and depends on the environment. **Rostamza *et al.*** grow sorghum (*Sorghum bicolor*) and millet (*Pennisetum glaucum*) in a split-pot system that allows the primary and nodal roots to be watered separately and find that decreasing water availability to either the entire root system or just nodal roots decreases the length of the whole root system in both species, and the nodal roots of both grow more vertically in dry soil. However, millet has a more plastic response than sorghum to moisture around the nodal roots, and they conclude that nodal and primary roots have distinct responses to soil moisture that depends on the species, and these can be selected for independently in breeding programs to shape root architecture.

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Root phenotyping methods in controlled and field environments

M. Watt, S. Moosavi, S. C. Cunningham, J. A. Kirkegaard, G. J. Rebetzke and R. A. Richards

doi: 10.1093/aob/mct122

Root length and depth determine capture of water and nutrients by plants, and are targets for crop improvement. **Watt *et al.*** grow recombination inbred lines and diverse genotypes of wheat, *Triticum aestivum*, in rolled, moist germination paper in growth cabinets and measure primary root number and length when either one or two leaves are fully expanded. For comparison, plants are grown in the field and root systems are harvested at the 2-leaf stage with either a shovel or a soil core. They observe positive correlations between the sum of the lengths of the two longest seminal roots of wheat seedlings grown in germination paper and the length and depth of root systems of plants with 2–5 leaves growing in the field. They conclude that this seedling screening method is fast, repeatable and reliable for selecting lines with greater total root length in the young vegetative phase in the field.

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Root electrical capacitance to predict root mass in soil

R. C. Dietrich, A. G. Bengough, H. G. Jones and P. J. White

doi: 10.1093/aob/mct044

Electrical capacitance has often been used as an assay for root mass, and is conventionally interpreted using a model in which roots behave as cylindrical capacitors wired in parallel. In light of recent research questioning this assumption, **Dietrich *et al.*** measure capacitances of cereal plants growing in sand or potting compost in both a glasshouse and in the field, under contrasting irrigation. They find that the substrate capacitance and plant capacitance combine according to standard physical laws: for plants growing in a wet substrate, the capacitance measured is largely determined by the plant tissue between the surface of the substrate and the electrode attached to the plant. This suggests that plant tissues and the rooting substrate may behave as capacitors wired in series, and whilst the measured capacitance may be linearly correlated with root mass, it is not a direct assay of root mass.