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EDITORIAL

Belowground solutions to global challenges: special issue from the 9th symposium of the International Society of Root Research

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The 9th Symposium of the International Society of Root Research, "Roots down under, belowground solutions to global challenges" was held in Canberra, Australia, from 6 to 9 October, 2015. The conference attracted participants from around the world and research was presented for plant species from natural and agricultural systems, and across a broad range of topics and scales from cell membranes through to ecosystems. In 2007, Lynch proposed that roots would be the source of a new green revolution (Lynch 2007). Reflecting on this, Rebetzke (2016) has outlined how many papers at the Symposium had taken this inspiration through to impact; delivering value, better yields and water and nutrient-use efficiency, improved root phenotyping and a greater genetic understanding of root traits. Despite rapid gains in our understanding of root structure and function and their interactions with soil, it is evident that root research remains a fertile frontier for research that can deliver substantive improvements in sustainable agricultural production and the knowledge required for better management of natural ecosystems (Ryan et al. 2016).

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In this, the third and final Special Issue arising from the Symposium we are delighted to present eight papers with an agricultural focus. Globally, agricultural systems face the challenge of feeding a growing world population, whilst remaining sustainable (Fischer et al. 2014; West et al. 2014; Hertel 2015; Godfray and Garnett 2014). A key issue for future food security is nutrient-use efficiency. Food security for the current population of the world already depends on the maintenance of high crop yields through fertiliser inputs. Fertiliser production is both energy-intensive (e.g. nitrogen - N) and/or based on finite nutrient reserves (e.g. phosphorus - P). The challenge to improve P-use efficiency is the context for many of the papers in this Special Issue. Crops and pastures with the ability to maintain high yields with less P inputs than currently used would help to conserve the world's finite phosphate reserves, whilst also addressing the negative consequences of P movement off farms into waterways and estuaries (Cordell and White 2011; West et al. 2014).

Several papers in this Special Issue focus on the relationship between root morphology and uptake of P and other nutrients from soil (Erel et al. 2016; Jeffery et al. 2016; Waddell et al. 2016). In the first paper, Waddell et al. (2016) report a study of nine species of Australian native wallaby grasses (*Rytidosperma*) which differ in their P requirements (Waddell et al. 2015). The aim was to determine the contribution of root morphology to P uptake by growing species in soil containing a range of P levels. Across all species there were positive correlations between P uptake and each of root mass, root length and root hair cylinder volume, i.e. the volume of soil estimated to be under the greatest influence of the root. However, no single trait contributed to a large root system for fast-growing species at all levels of P supply. For instance, specific root length was increased at low P supply for some species through a reduction in root tissue density and for others through an increase in the proportion of fine roots.

Similar to Waddell et al. (2016), cultivars with greater soil exploration were also found to generally have superior growth and nutrient uptake by Haling et al. (2016) and Andresen et al. (2016). Andresen et al. (2016) examined the root traits, growth and nutrition of several cultivars of onion (*Allium cepa* L.), spring wheat (*Triticum aestivum* L.) and lettuce (*Lactuca sativa* L.) grown in a low nutrient status soil. The use of minirhizotrons allowed repeated measures over time. They found differences among crops and cultivars in root growth patterns, notably early root growth, total root biomass, the volume of soil explored and the spatial distribution of root systems.

Jeffery et al. (2016) examined the root response to varying soil P supply for subterranean clover (*Trifolium subterraneum* L.), the most commonly-grown annual pasture legume in southern Australia. They found that root traits varied among the cultivars, but that the differences were generally maintained among P levels. This suggests that future screening of germplasm for root traits of particular interest for improving P uptake could be undertaken at a single level of P supply. One exception, however, was the low colonisation by arbuscular mycorrhizal (AM) fungi at very low P supply. This result confirms that AM fungi, although renowned for enhancing plant P uptake (Smith and Read 2008), are themselves limited by low P (Bolan et al. 1984) and that screening of cultivars for colonisation may be best undertaken at intermediate levels of P supply.

Orchard et al. (2016a) also examined AM fungal colonisation in subterranean clover. However, their study considered the effect of post-harvest storage practises of plant material on the colonisation level and intraradial morphology of the fungi. They found that AM fungi remain active in roots during storage even under cool temperatures and when shoots are removed. It was concluded that samples should be processed within two days to ensure an accurate measurement of fungal colonisation levels and abundance of vesicles and arbuscules. This is especially important if vesicles and arbusucles are used to quantify fungal activity (McGonigle et al. 1990; Veiga et al. 2013). Orchard et al. (2016a) also noted that colonisation by fine root endophyte (*Glomus tenue*) was reduced more by storage than colonisation by AM fungi, with fine root endophyte colonisation declining greatly between the second and fourth day of storage. Fine root endophyte has recently been aligned with subphylum Mucoromycotina, rather than the phylum Glomeromycota which contains the AM fungi (Orchard et al. 2017). Storage of samples for greater than two days may have contributed to under-reporting of what could be a second ubiquitous group (Abbott and Robson 1982; Orchard et al. 2016b; Read and Haselwandter 1981; Ormsby et al. 2007) of arbuscule-producing root-colonising fungi.

Exciting findings are also reported by Giles et al. (2016). Exudation rate or rhizosphere amount of carboxylates (e.g. Jeffery et al. 2016) or phytase is often assumed to be indicative of a plant's ability to access, respectively, fixed inorganic and organic soil P. However, such conclusions are usually drawn through correlations (e.g. Veneklaas et al. (2003)) rather than data providing direct causal relationships. Giles et al. (2016) examined P uptake by transgenic plants of *Nicotiana tabacum* L. with modified single gene expression encoding a citrate transporter or a fungal phytase and crossed transgenic lines expressing both genes. They showed that plants with both genes accumulated more shoot P and that over half of the variation in shoot P accumulation was predicted based on phytase-labile soil P, citrate efflux and phytase activity. Future studies should measure additional parameters such as efflux of other organic acids and, in particular, the root morphological traits most likely to enhance P uptake (see Andresen et al. 2016; Jeffery et al. 2016; Waddell et al. 2016) to assess the relative merit of all these traits. Future studies should also consider the costs and benefits of colonisation by AM fungi and, perhaps, fine root endophyte. Key interactions with other rhizosphere organisms may also merit investigation as they may quickly metabolise plant-exuded organic acids (Menezes-Blackburn et al. 2016). Moreover, microbial community structure and function may shift with the composition of the exuded organic acids (Martin et al. 2016). If the results of these studies are to be applied through plant selection and breeding programs, it will be important to understand trade-offs among carbon-expensive traits, such as the negative impact of colonisation by AM fungi on exudation of organic acids (Ryan et al. 2012; Nazeri et al. 2014), the potential for AM fungi to negate the benefits (Brown et al. 2013) of increasing root hair length (Jakobsen et al. 2005; Caradus 1981) and the impact of reducing or removing root hairs on rhizosphere processes (Pausch et al. 2016).

Average root hair length was a key component of the "root hair cylinder volume" which was strongly correlated with plant P uptake in the reports by Waddell et al. (2016) and Haling et al. (2016). The paper by Vincent et al. (2016) reports work to substantially reduce the effort required to quantify root hair development in situ. The authors use ImageJ and R statistical software to successfully develop a novel, time-efficient method for quantifying two-dimensional root hair areas from digital images of roots of maize (*Zea mays* L.), castor (*Ricinus communis* L.) and papaya (*Carica papaya* L.) growing against a clear interface in a minirhizotron.

Whilst nutrient acquisition is a key focus for much root-orientated research, addressing soil toxicities is also important. A common soil limitation to plant growth and yield is high concentrations of aluminium (Al) due to low soil pH (Kochian et al. 2015; Von Uexküll and Mutert 1995). Ulloa-Inostroza et al. (2016) applied MeJA to the leaves of blueberry (*Vaccinium corymbosum* L.) and examined the effect of antioxidant concentration in roots and leaves on the tolerance of the plants to Al stress. They found that the application of a low dose of MeJA reduced Al toxicity by decreasing the Al concentration in tissues and strengthening the antioxidant mechanisms.

Two papers in this Special Issue examine root characteristics and P uptake of field-grown maize. In the first, Li et al. (2016) assessed how root growth varied among plots which had received 22 years of contrasting tillage practices (no-till and mouldboard ploughing) and different P fertiliser regimes. Crop management had a significant effect on root distribution, with decreased root biomass in the no-till system. The reasons for this change were complex, with the authors suggesting that changes in soil properties, such as greater bulk density and higher concentrations of nutrients and organic matter in the surface soil, did not determine the changes in root system distribution. Instead they suggest delayed early growth associated with weed competition and cooler soil temperatures as the drivers. Presumably these factors could also affect other root processes such as AM fungal colonisation, community structure or function or, perhaps, exudation of organic acids. This study joins a growing literature that suggests that crop selection and breeding for root traits must be informed by the management practices of the target farming system (e.g. Thorup-Kristensen and Kirkegaard 2016).

In the second paper to focus on field-grown maize, Erel et al. (2016) grew 23 hybrid-lines under two levels of soil P in either a neutral or an alkaline soil. They found no consistent ranking of the hybrids in the two soils since those that acquired more P in the neutral soil did not perform as well in the alkaline soil. Hybrids doing best in the neutral soil tended to have greater root length and shallower roots. In the alkaline soil, P availability in the rhizosphere was greater than in the bulk soil and phosphatase activity was higher. Thus, the best-performing lines in the neutral soil were characterised by root traits that enabled superior soil exploration for P, while in the alkaline soil there appeared to be a greater role for root traits that enhance P availability. These results suggest soil type of the target farming system as an additional consideration when undertaking crop selection and breeding for root traits.

In conclusion, the eight papers presented in this Special Issue demonstrate that significant advances are being made in our understanding of plant roots, particularly in relation to nutrient uptake. Along with the papers contained in the two other Special Issues that arose from the 9th symposium of the International Society of Root Research (Rebetzke 2016; Ryan et al. 2016), the papers in this volume contribute toward the important goal of enhancing agricultural system productivity and sustainability through strategic modification of root traits in crop breeding programs.

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