

Rhizosphere 3: where plants meet soils down-under

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As the focus of the scientific community across the globe turns increasingly to issues such as food security, energy sustainability, climate change and habitat restoration, the need for a deeper understanding of the relationships between plants and soils has never been greater. The study of roots and soils has been vital for our understanding of terrestrial biogeochemical cycles and plant health and nutrition. However, it has been the recognition of the critical interface between the plants and soils that has led to major advances in both disciplines (Hartmann et al. 2008b). When Hiltner introduced the term *rhizosphere* in 1904 he dealt primarily

with the microbial ecology of the soil adjacent to the root and how this could affect plant nutrition (Hiltner 1904). While this approach remains core to modern rhizosphere research, chemical and physical processes have also become recognised as key aspects of rhizosphere science over the last century. The rhizosphere is now studied much more widely: as a sink for root exudates; a site of enhanced microbial activity and genetic exchange, nutrient transformations, mass flow and diffusion gradients; and, critically, as a home to mutualistic and pathogenic symbionts and for its more wider role in maintaining soil physical structure (Dessaux et al. 2009; Pinton et al. 2007).

The relatively recent recognition of the fundamental importance of the rhizosphere in research is reflected in the striking and prolific increase in the use of the term *rhizosphere* in titles of journal publications over the last three decades, and in this century in particular (Fig. 1). Despite its introduction in 1904, it was not until the 1930s that the term rhizosphere was first considered sufficiently important in its own right to be used in the title of a journal paper (Truffaut and Vladykov 1930). It was then used only three times in the 1930's and four times in the 1940's, so, not a meteoric rise in use for some decades. By 1961 its use reached double figures and only after the year 2000 does it consistently appear in 100 or more titles each year, which then represents more than 50 % of all occurrences or *rhizosphere* in journal paper titles. Although it makes up only a small part of the soil on the planet, the rhizosphere is arguably now considered the most important biotic-abiotic interface in the terrestrial biosphere.

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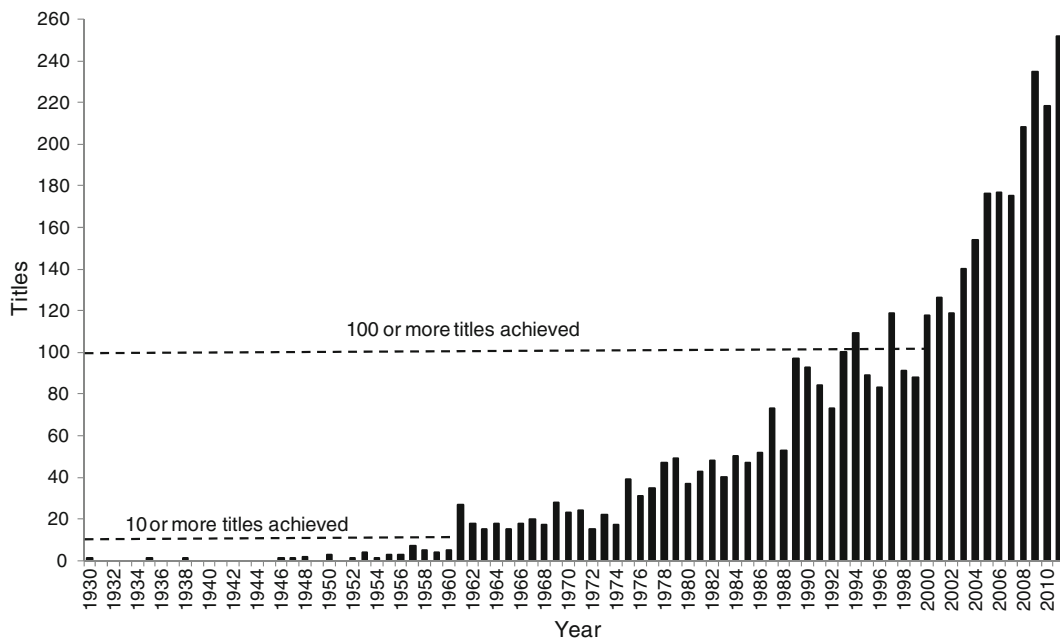


Fig. 1 Number of journal articles published annually that include the term “rhizosphere” in the title. Source: Thomson’s ISI Web of Science, accessed 13th July 2012

It is therefore not surprising that to commemorate the hundredth anniversary of the coining of the term “rhizosphere” by Hiltner (1904), an international conference series was initiated in 2004, with the first Rhizosphere conference held in Munich, Germany (Jones et al. 2006; Hinsinger and Marschner 2006). The excitement generated by bringing together the eclectic disciplines that now contribute to rhizosphere research, and the rapid pace of development in the field, led to the next conference in the series in Montpellier, France in 2007 (Jones and Hinsinger 2008; Dessaux et al. 2009; Hartmann et al. 2008a; Jones 2009) which brought together an even wider and more diverse group of scientists. Continued growth of the field has led to an increased breadth and depth of research now being undertaken globally, and the conference series has left its home in Europe and travelled to the southern hemisphere. In September 2011 the Rhizosphere 3 International Conference was held in Perth, Western Australia. The conference was attended by over 300 delegates representing four continents, with conference topics ranging from molecular communications to multitrophic interactions.

In order to capture the state-of-the-art rhizosphere research presented at the Rhizosphere 3 Conference,

selected presenters were invited to submit their work for publication in this Special Issue of *Plant and Soil*. The resulting set of papers comprise a wide range of topics that include plant phosphorus (P) uptake, control of root pests and diseases, rhizosphere nitrogen cycling, testing of a new DNA assay to quantify species-specific root biomass, rhizosphere effects of hydrocarbon contamination, sodium uptake pathways in a halophyte, and a Marschner review article on the importance of root-produced volatiles as foraging cues for entomopathogenic nematodes, which show potential to be significant biocontrol agents for insect pests of major crops.

The large proportion of contributions which address aspects of plant P uptake is appropriate to the location of the conference in Perth. The south-western corner of Australia is a biodiversity hotspot (Myers et al. 2000), whose soils are impoverished in P (Laliberte et al. 2012) and whose plants have evolved a wide range of novel mechanisms to acquire P (Handreck 1997; Lambers et al. 2010; Shane and Lambers 2005). An influential body of research on the rhizosphere and plant nutrition has originated from this region (e.g., Abbott and Robson 1978; Lambers et al. 2010; Rengel and Marschner 2005), including substantial contributions from the recently retired Vice Chancellor of the University of Western Australia

Professor Alan Robson, who opened the conference. The two papers in this special edition which focus on perennial plants native to Australia highlight unusual, but contrasting, responses to increasing P availability—no growth response in spite of enhanced P uptake by slow-growing woody acacias (He et al. 2012) and a strong growth response coupled with high accumulation of shoot P by two herbaceous species (Suriyagoda et al. 2012). The identification of Australian native plants with the capacity to accumulate high concentrations of P without toxicity presents an intriguing contrast to the large number of native species that also cannot down-regulate their P uptake, but suffer P toxicity at low levels of P availability (e.g., Johnston et al. 2006; Shane et al. 2004). In recent years, interest in Australian native plants with unusual P physiology and the relative importance of their various root adaptations to enhance P uptake, as explored by Suriyagoda et al. (2012) in this volume, has intensified as the need to improve P efficiency in crop plants has become a matter of urgency (Lambers et al. 2011; Shi et al. 2012).

It should be remembered, however, that roots are only one part of the story and the complex biology of the rhizosphere is an important factor in plant P acquisition. This is emphasised by two papers in this Special Issue. Irshad et al. (2012) show that poorly available organic P could be made available to plants only through the grazing by nematodes of phytase-producing bacteria, and Jin et al. (2012) report that elevated CO₂ may increase the amount of P immobilised by microorganisms in the rhizosphere. These complex interactions are likely to be the focus of much future research.

A second major focus of this Special Issue is control of root pests and diseases. Worldwide, root diseases in crops cause substantial yield losses (Doornbos et al. 2012). Root pests and diseases also pose a serious threat to natural ecosystems, as is currently the case with *Phytophthora cinnamomi* in south-western Australia (Cahill et al. 2008), and such threats may intensify under climate change (Pautasso et al. 2012). In this context, the papers in this Special Issue that focus on control of root pests and diseases are of particular importance.

The Marschner review by Turlings et al. (2012) is especially noteworthy, first summarising the evidence for root volatiles as foraging cues for parasitic entomopathogenic nematodes and then presenting data to show that there may be a synergistic effect of root volatiles and CO₂ as attractants for the nematodes.

They conclude that there is considerable potential to improve the effectiveness of entomopathogenic nematodes as biological agents for crop insect pests by both improvement of signalling by crops and responsiveness to specific signals by the nematodes (Turlings et al. 2012). These findings may prove critical for the development of effective control techniques for serious insect pests of major crops including the western corn rootworm (*Diabrotica virgifera virgifera*), a destructive and worsening pest of corn in the United States and Europe (Gray et al. 2009). The Marschner review is complemented in this special edition by a paper by Hiltbold et al. (2012), who show that entomopathogenic nematodes can be effectively applied to soil by encapsulating them in a polysaccharide shell with added attractants and feeding stimulants. With further development this technique could overcome constraints to adoption of nematodes as biological control agents that arise from current application methods.

The theme of plant rhizosphere signalling in response to biotic or abiotic stresses is picked up again by Kawasaki et al. (2012). Using a split-root model, they show that stressing part of the rhizosphere of a legume plant with an organic pollutant such as pyrene leads to changes in the composition of the rhizosphere fungal and bacterial community in both the stressed and unstressed parts of the rhizosphere. This demonstrates the presence of signalling pathways between different parts of the rhizosphere mediated by the plant, and suggests further questions about whether these pathways are also important for other plant stress responses or other aspects of rhizosphere function.

Finally, quantification of root biomass has always been a difficult task, due to the losses associated with removing and washing roots. Differentiation of roots belonging to co-occurring plant species is then a further difficulty. A DNA method which uses quantitative PCR to amplify species-specific DNA based on the 18S–23S (ITS) spacer region (Haling et al. 2011; Riley et al. 2010) for quantification of root biomass of individual plant species grown in field plots is an exciting step forward in this regard (Haling et al. 2012). Although considerable calibration is required, and considerable replication, the technique can show differences between plant genotypes in root growth and may be especially useful in situations where rapid processing of large numbers of samples is required (Haling et al. 2012).

Overall, the papers presented in this special issue represent a key subset of the research presented and

discussed at the Rhizosphere 3 Conference. The breadth and diversity of this research has continued to expand rapidly in recent years, fuelled by advances in technology, and intense interactions between scientists in different disciplines. The application of systems biology approaches to provide integrated and holistic analyses of plant-soil-biota interactions, and the development of high resolution, non-destructive phenomic studies, offer exciting prospects for the next Rhizosphere conference, Rhizosphere 4, to be held in the Netherlands in 2015.

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