Meetings

Organic nitrogen

OrgN2014 International workshop on organic nitrogen and plant nutrition – from molecular mechanisms to ecosystems, Monte Verità, Ascona, Switzerland, February 2014

Which forms of nitrogen (N) do plants acquire from soil? This question, central to understanding of plant function, was debated intensely a century ago. It was revitalized more recently with insights in plant–soil interactions and molecular biology, but the difficulties associated with dissecting rhizosphere processes – rapid absorption, uptake, conversion and release of N in the interfaces of soil, microbes and plants – have prevented resolution. In the recent past, inorganic redox reactions were discussed, while today's focus is transformations of organic N. Despite significant advances and relevance, views are diverging on the importance of organic N as a nutrient source for plants. A recent workshop brought together leading experts, early stage researchers and industry representatives to discuss and evaluate the current knowledge and on-going research to link from molecular function of plants to ecosystem processes.

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Synthetic N fertilizer has largely removed the N limitations of plant production in agriculture but has unleashed an unprecedented rise in reactive N levels in the biosphere (Smil, 2004). Given that a 5% perturbation of the global carbon (C) cycle is transforming the planet, the effects of human-driven doubling and possibly more than tripling of terrestrial N fixation in addition to biological N fixation are far reaching (Gu *et al.*, 2013). Continuous increase in the manufacture of synthetic N fertilizer is the main cause for the rising levels of reactive N. Extreme inefficiencies contribute to this problem, exemplified in China where a massive 37-fold increase in N fertilizer rates from 1961 to 2009 has achieved only a 3.4-fold increase in yield (Zhang *et al.*, 2013). Severe environmental problems result across terrestrial and aquatic environments and atmosphere, with temperate ecosystems considered more sensitive to N inputs than tropical and subtropical systems. Documented effects of N enrichment on terrestrial ecosystems include altered litter chemistry, microbial biomass and decomposition rates (Craine *et al.*, 2007; Treseder, 2008), with unknown long-term outcomes on global C and nutrient fluxes.

Historic knowledge has shaped the changing paradigm of N cycling (Fig. 1). Organic N dominates the N pool of soils (Schimel & Bennett, 2004; Visser, 2010), and plants can acquire and metabolize organic N forms (Näsholm *et al.*, 2009; Paungfoo-Lonhienne *et al.*, 2012; Schmidt *et al.*, 2013; Warren, 2014). The workshop discussions focused on: (1) the availability of organic N in soil; (2) competition between plants and microorganisms for N; (3) uptake of organic vs inorganic N by roots; (4) N remobilization during senescence and delivery to seeds; (5) regulatory networks and N–C interactions; (6) organic N in agriculture and forestry applications. The highlights from each of these themes are summarized here.

Availability of organic N in soil

Micro-dialysis of diffusive N fluxes in soil has promise to advance knowledge of N forms in soil. Probes with an outer diameter of only 500 μm (used in neurobiology) interact with the soil solution and allow quantification of N pools available to roots. Diffusive fluxes show that soil under boreal forest is dominated by organic N (amino acids were studied), contrasting traditional soil extracts that suggest a dominance of inorganic N (Inselsbacher & Näsholm, 2012). Similarly, amino acids have a consistent presence in temperate crop soils and in diffusive fluxes of subtropical soil under sugarcane, indicating that organic N has a general presence in soils with both, slow and high mineralization rates (Jämtgård *et al.*, 2010; R. Brackin *et al.*, unpublished). Capillary electrophoresis mass spectrometry shows that, in addition to proteinaceous compounds, soils contain a plethora of organic N of low molecular mass including quaternary ammonium compounds, metabolites such as betaines, ectoine and aliphatic polyamines. The presence of these compounds varies in response to drought and form part of the pool of organic N that roots can potentially take up (Warren, 2014). Organic N compounds rather than inorganic N are generated during fire as discovered by solid-state nuclear magnetic resonance NMR spectroscopy. This 'Black N' generated by pyrogenic processes includes pyrroles, pyridines and other organic N forms and indicates that peptides are precursors for Black N (De la Rosa & Knicker, 2011). This session highlighted that organic N in soils warrants further research to address questions relating to the role of organic N for plant nutrition.

New Phytologist

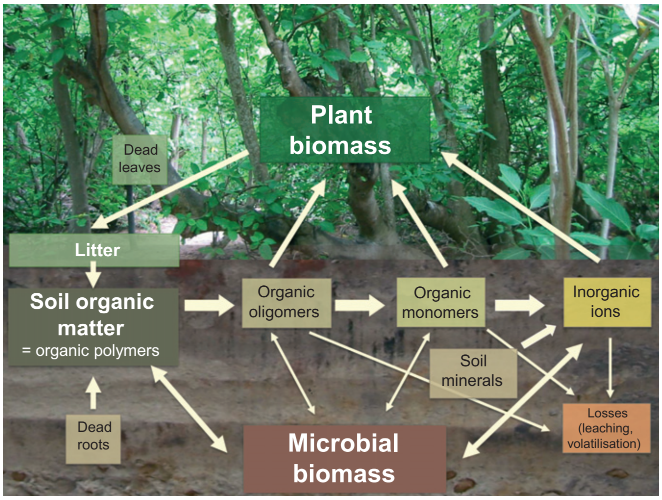

Fig. 1 Nitrogen cycling with focus on below-ground processes. Inspired by Schimel & Bennett (2004).

Competition between plants and microorganisms for N and uptake of organic vs inorganic N by roots

These topics explored the interactions of plants with microbes and mechanisms for the uptake of organic N by roots. A key concept under revision is that soil microbes have a greater ability to use organic N than plants. This concept was evaluated from different perspectives. The view that plants predominantly access inorganic N that is derived from microbial mineralization is being revised as there is evidence that plants not only take up organic N, but also compete with microbes for it. It remains debated how competitive plants are when compared with microbes for accessing organic N (Kuzyakov & Xu, 2013). Recent studies have identified genes that are involved in the uptake of organic N, including amino acids, peptides and nucleosides (e.g. Komarova *et al.*, 2008). Importantly, affinities of roots for amino acids are comparable to those of microbes. Root uptake studies demonstrate the diversity of organic N nutrition including quaternary ammonium compounds, proteins and even intact microbes (Paungfoo-Lonhienne *et al.*, 2012; Warren, 2014). The issue that the predominant N form in soils does not match the ability of crops to efficiently acquire it was illustrated with sugarcane, which receives on average twice (and up to nine-times) more N fertilizer than N removed by crops (Robinson *et al.*, 2011), questioning the sustainability of sugarcane (and other crop) production.

Nitrogen remobilization during senescence and delivery to seeds

The contribution of recently assimilated vs organic N remobilized from vegetative parts for seed filling varies among plant species and cultivars. Nitrogen remobilization processes transferring N from leaves to seeds are crucial for final seed N content and nutritional composition as demonstrated with mutants impaired in amino acid and ureides remobilization (Zhang *et al.*, 2010; M. Tegeder, unpublished). As a main component of N-efficiency measure of crops, this topic linked uptake and remobilization processes of organic N.

Regulatory networks and nitrogen–carbon interactions

Nitrogen uptake and metabolism are controlled by environmental factors and linked to C metabolism and availability of other nutrients. Regulatory networks and switches involve multiple signalling, feedback and sensing events, allowing tight control of metabolism, growth and development. Regulation occurs at the level of uptake, metabolism, storage, and re-allocation and involves regulation at the transcriptional and posttranslational level. This topic highlighted the complex interplay of N and C, and respective signalling pathways and research aimed at improving the N use efficiency of crops (Masclaux-Daubresse *et al.*, 2010; Krouk *et al.*, 2011; Tegeder, 2012).

Organic N in agriculture and forestry applications

Can organic N improve N use efficiency in bioproduction systems? This question was addressed in N-enriched temperate pasture soils which leach organic N (J. Rasmussen, unpublished). The successful formulation and commercial success of organic N fertilizers based on cationic amino acids for the production of conifer seedlings demonstrated the benefits derived from N forms that match the ability of plants for uptake, greater biomass allocation to roots that aids seedling establishment, and dramatically lowered N losses to the environment (.swetree.com).

Conclusions

In summary, we discussed present knowledge, ongoing research and development, and future needs of N research. The workshop illustrated inherent difficulties but also provided examples of recent methodological and conceptual progress that is advancing knowledge. However, the quantitative role of organic N for plants in managed systems and in natural ecosystems remains undisclosed.

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