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EDITORIAL

The potential of beneficial microorganisms in agricultural systems

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Problems and concerns in relation to the use of inorganic fertilisers, irrigation, herbicides and pesticides have led to the search for alternative strategies to combat limiting soil nutrient and water levels and the effects of weeds and pests on crops. Microorganisms can improve crop nutrition and the ability of crops to resist biotic and abiotic stress. Thus, greater utilisation of microorganisms in agricultural systems has the potential to allow reductions in the use of inorganic fertilisers, water, herbicides and pesticides. Here, we introduce a *Virtual Special Issue* of *Annals of Applied Biology* featuring seven recently published papers in this journal, which focused on the utilisation of positive plant microbial interactions in agricultural systems (Andrews *et al*., 2010, 2011; Dodd *et al*., 2010; Newton *et al*., 2010; Novak, 2010; Raven, 2010; Tikhonovich & Provorov, 2011). We also highlight cases within and outside these papers where microorganisms have been utilised as a viable alternative to chemical inputs into agricultural systems or have had a substantial impact on chemical losses from them.

Andrews *et al.* (2010) gave an overview of positive plant microbial interactions, which are currently under study in relation to assessment of their potential in agricultural systems. The interactions considered were bacterial and mycorrhizal stabilisation of soil aggregates and structure; rhizobacterial promotion of plant growth via increased nutrient availability; rhizosphere and endophytic bacterial promotion of plant growth by influencing plant hormone balance and the production of stress-protective compounds; endophytic and symbiotic bacterial nitrogen (N) fixation; mycorrhizal uptake of water and nutrients; rhizobacterial suppression of plant disease; associative fungal protection against plant parasitic nematodes; endophytic fungal protection against herbivore pests; associative microbial protection against insect pests and bacteriophage protection against disease.

Dodd *et al.* (2010) linked rhizobacterial mediation of plant hormone status with changes in root growth and architecture and ultimately plant performance. Particular attention was paid to the ability of plant growth-promoting rhizobacteria to affect plant growth via metabolising phytohormones in the rhizosphere. It was shown that rhizobacterial mediation of plant hormone status has local effects on root elongation and architecture, thereby mediating water and nutrient capture, and can also affect plant root-to-shoot hormonal signalling that regulates leaf growth and gas exchange. It was proposed that combining rhizobacterial traits (or species) that impact on plant hormone status thereby modifying root architecture (to capture existing soil resources) with traits that make additional resources available (e.g. N_2 fixation and phosphate solubilisation) may enhance the sustainability of agriculture.

There are many reports for legumes that the proportion of total plant N obtained from symbiotic N_2 fixation decreases with increased soil N availability. Cost-benefit analysis based on biochemical principles indicates that photon and water costs per unit N assimilated are greater for N_2 fixation than for utilisation of combinations of ammonium, nitrate (NO_3^-) and organic N, the main forms of N taken up from the soil (Raven, 1985; Andrews *et al*., 2009). Thus, utilisation of soil N when available is likely to be advantageous to plants. Considerable research has been carried out in attempts to improve biological N_2 fixation in legumes. One way of manipulating symbiotic N_2 fixation is based on the use of host symbiotic mutants. Novak (2010) focused on the 'supernodulating' mutants of legumes, which lack the internal regulation of the number of symbiotic root nodules that harbour the N_2-fixing nodule bacteria. This trait is often associated with resistance of nodule initiation and functioning to the inhibition by soil NO_3^- and results in more intense and stable N_2 fixation. However, it is also associated with reduced shoot growth linked to the increased carbon requirement of nodules. For grain legumes, this decreased shoot growth results in decreased seed yield. Novak (2010) argued that the deleterious effects of excessive nodulation can be neutralised or alleviated by a breeding strategy aimed at creating an ideotype N_2-fixing legume. In particular, the growth depression can be overcome by the reduction in nodule number from the 6- to 10-fold wild-type typical of 'supernodulators' to an optimal level for a particular crop that would guarantee enhanced N_2 fixation without a significant reduction in shoot growth. It was recommended that this shift should be associated with breeding aimed at increasing the photosynthetic capacity of the shoot and proposed that supernodulation has greater potential with forage than grain legumes due to their long-term breeding history for green biomass accumulation as opposed to seed production.

Andrews *et al.* (2011) reviewed the literature on positive plant microbial interactions in perennial ryegrass dairy pasture systems, and interactions that have been reported to have a substantial impact on pasture production and/or levels of chemical inputs into or losses from the system were assessed. Three very different, successful interactions were described. First, utilisation of N_2-fixing (rhizobia) white clover as the N input into a perennial ryegrass pasture is likely to give pasture and milk production similar to that with addition of 200 kg inorganic N ha^{-1} $annum^{-1}$ and avoid greenhouse gas emissions resulting from N fertiliser production (Andrews *et al.*, 2007). Second, use of the nitrification inhibitor dicyandiamide that deactivates the ammonia monooxygenase enzyme in ammonia-oxidising bacteria can substantially reduce NO_3^- leaching and nitrous oxide emissions from perennial ryegrass pastures while increasing productivity (Di & Cameron, 2005; Di *et al.*, 2007). Third, infection of perennial ryegrass plants with the fungal endophyte Neotyphodium *lolii* is very significant for the production and persistence of dairy pastures in Australasia due to the endophyte producing a range of alkaloids that confer benefit to the host plant through insect resistance/repellance. In New Zealand, novel beneficial endophytes are intentionally introduced into most grass cultivars to protect against insect pests and the pastoral economy relies on these endophytes as the primary means of protection against introduced grass pests (Goldson *et al.*, 2005). Virtually, all plants contain fungal endophytes (Stone *et al.*, 2000). However, other than forage and turf grasses (Vázquez-de-Aldana *et al.*, 2010), the extent to which microbial symbionts can be harnessed for the benefit of crop protection is uncertain, but there is growing interest in their potential (Maciá-Vicente *et al.*, 2009; Vallino *et al.*, 2009; Gurulingappa *et al.*, 2010).

Raven (2010) considered some evolutionary aspects of N_2-fixing and mycorrhizal symbioses of vascular plants, and especially the extent to which the microbial symbionts are genetically independent of, or integrated with, the host plants. Here, it was described how bacteria and fungi involved in N_2-fixing and mycorrhizal symbioses with plants have varying degrees of genetic recombination. Those with very limited, or no, recombination are at risk from the progressive accumulation of mutations ('Muller's ratchet'; Muller, 1964). This accumulation could be alleviated by complete genetic integration of the parts of the rhizobial and mycorrhizal genomes relating to their function *in hospice* (N_2 fixation and acquisition of a range of nutrients, in particular N and phosphorus, respectively) into the nuclear genome of the (usually) sexually reproducing plant. This integration is not known to have occurred and Raven (2010) asked the question 'Why are mycorrhizal fungi and symbiotic nitrogen-fixing bacteria not genetically integrated into plants?' It was argued that N_2-fixing symbioses and mycorrhizas are respectively only an advantage at low N and low N/phosphorus availability and an evolutionary and environmental possibility is that it was difficult to maintain genetically integrated N_2 fixers and mycorrhizas as environments changed with respect to the availability of combined N and phosphorus. The implications of this possibility in relation to the breeding of crops and their symbionts were considered.

Newton *et al.* (2010) emphasised that the lack of stability and system resilience in agriculture is accentuated by a 'zero tolerance' of pathogens approach to crop protection. A target of complete elimination of pathogens, whether achieved through highly expressed resistance mechanisms or pesticides, tends to impose very high selection pressure for virulence or resistance in pathogen populations, and leaves the plant as a substrate without second lines of defence when this occurs. It was argued that the phyllosphere is a rich and varied microbial community comprising organisms with diverse functional types and its composition is strongly influenced by both genotypic and environmental factors, many of which can be manipulated by breeding, agronomy and crop protection strategies in an agricultural context. These factors also affect the complex interactions between the microbes, which in turn affect their interaction with their host plant. Whether an organism becomes pathogenic, and the subsequent expression of disease, is also influenced by all these factors. Understanding the population dynamic balance between the putative pathogens and beneficial organisms of the phyllosphere as an ecological system should lead to new approaches in agronomy, crop protection and breeding, which will enhance sustainability. Here, the requirement to eliminate putative pathogens would be replaced by 'managed co-existence', management that favours dominance of beneficial organisms and contains putative pathogens in an asymptomatic or stable state.

In the final paper of the special issue, Tikhonovich & Provorov (2011) argued that utilisation of appropriate preparations of beneficial microorganisms is the most promising strategy for maintaining agricultural productivity whilst reducing the inputs of inorganic fertilisers, herbicides and pesticides and that 'microbiology is the basis of sustainable agriculture'. Here, agricultural microbiology is presented as a synthetic research field responsible for the transfer of knowledge from general microbiology and microbial ecology to the agricultural biotechnologies.

Considering work outside that highlighted in the papers of the special issue, at least 37 pathogens have been released against arthropod pests (Hajek *et al.*, 2007), and 26 pathogens released against invasive weeds (Barton, 2004) with no reported adverse environmental effects or impacts on beneficial species. Some of these programmes have been very successful. For example in the 1970s, the rust pathogen, Puccinia chondrillina, was released and successfully controlled the important agricultural weed, rush skeleton weed, *Chondrilla juncea*, in Australia. Also during the 1970s, the *Oryctes baculovirus* was released throughout the South Pacific islands and successfully controlled the coconut rhinoceros beetle, *Oryctes rhinoceros*, a devastating pest of cultivated palms. Both programmes resulted in a degree of control that required little continued management inputs and had high benefit-cost ratios (Tisdell, 1987; Hajek *et al.*, 2007). Many other pathogens have been less successful, and are perceived to be failures, as additional management inputs are necessary to reduce pests below an economic threshold. However, the value of these less successful biocontrol agents should not be dismissed, as even moderate or periodic control through occasional disease outbreaks can yield highly favourable benefit-cost ratios (Culliney, 2005). Currently, microbial biocontrol agents account for only around 2% of agents released against arthropod pests (Hajek *et al.*, 2007), and 5% of agents released against weeds (Julien & Griffiths, 1998). As demand for sustainable solutions increases, it is likely that microbes will constitute a greater proportion of biocontrol agents.

Currently, around 60 bacterial species, 60 fungal species and 29 virus/phage species are being used in biopesticide products worldwide (CPL Business Consultants, 2010). The bacterium *Bacillus thuringiensis* (Bt) is the most widely used and successful microorganism 'insecticide'. Bt produces insecticidal crystal proteins during its sporulation phase that must be ingested by pest species for effect. These proteins differ depending on the Bt subspecies and as a result there is a range of Bt types that are toxic to different insect species. Bt can be both sprayed onto or genetically engineered into crops (Lei *et al.*, 2011). The requirement for the Bt toxins to be ingested means that leaf-chewing insects (primarily phytophagous *Lepidoptera* and *Coleoptera*) are most susceptible, whereas piercing-sucking insects (e.g. aphids, leafhoppers and true bugs) avoid infection (Gurr *et al.*, 2011). This selectivity of Bt (relative to chemical pesticides) is one of its key advantages; however, more than 3000 arthropod species have been recorded as susceptible to at least one Bt isolate (Glare & O'Callaghan, 2000).

There is increasing development of biopesticides based on pathogenic fungi (Atkins *et al.*, 2009), most notably *Beauveria bassiana* and *Metarhizium anisopliae* (de Faria & Wraight, 2007). Unlike bacteria, entomopathogenic fungi do not need to be ingested, but rather upon contact, fungal hyphae penetrate the cuticle of arthropods and then grow vegetatively within the body, eventually causing death. The contact mode of action makes fungi such as *B. bassiana* and *M. anisopliae* effective against both chewing and sucking pests. The limitations of many fungal biopesticides are target specificity, inability to be mass produced on cheap substrates and sensitivity to environmental conditions such as humidity, temperature and sunlight. Compared to bacteria and fungi, relatively few biopesticides have been developed from viruses due to their extreme host specificity. However, viral biopesticides have a significant market value as they target some of the most serious economic pests such as *Spodoptera* spp., *Helicoverpa* spp. *Cydia pomonella*, and *Plutella xylostella* (CPL Business Consultants, 2010). In 2007/2008, global microbial plus nematode biopesticide sales were close to US$ 400 million and this accounted for around 1% of the total pesticide market which was worth approximately US$ 40.5 billion (CPL Business Consultants, 2010). Thus, currently, microbial pesticides are a fringe option for pest control that is typically employed only in high-value crops. The sustainability of biopesticides is one of their key advantages; however, their usage in a similar manner to chemical pesticides (frequent and widespread) risks the development of pest resistance (Lacey & Goettel, 1995). Worldwide reports of diamondback moth (*P. xylostella*) resistance to Bt highlights this threat (Shelton *et al.*, 2007).

Overall, the papers highlighted and the discussion here show that microorganisms can be utilised to increase the sustainability of agricultural systems. Further research is required to fully assess this potential in both subsistence and intensive agricultural systems.

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