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THE ROLE OF MICROORGANISMS IN PLANT NUTRITION

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INTRODUCTION

All plants are exposed to large numbers of microorganisms, particularly in the soil, though leaves and stems are also colonised. As far as we are aware most of the species involved do not affect the wellbeing of plants. A few species are important pathogens, some cause minor damage and others have a known role in promoting the growth of plants through their ability to provide essential nutrients. The best-known example of the latter are the nitrogen-fixing microorganisms which will be discussed elsewhere in this Proceedings by Postgate. In this brief review other aspects of the role of microorganisms in providing nutrients for plants will be discussed.

MICROORGANISMS AND THE SOIL BIOMASS

It is clear from extensive research that the fertility of arable soils is influenced strongly by the amount of organic matter present. It has a very important role in holding water and is a major reservoir of plant nutrients. Soil organic matter is formed from plant matter by extremely large numbers of microorganisms, which are responsible for decomposing plant remains and cycling the nutrients that they contain. Microorganisms decompose plant material to obtain carbon compounds and other nutrients for their own growth - they will either die and release part of these into the soil or be consumed by other organisms such as protozoa, which again will die or be consumed. Each time an organism dies there will be a release of nutrients, some of which will be taken up by plants, some will be taken up by other micro-organisms for further recycling, some will be

irreversibly lost through leaching or as gases (for example denitrification) and some will become unavailable through being incorporated into complex organic compounds which are only degraded very slowly, if at all. When microbial activity is limited, as occurs in very acid soils, organic matter builds up and nutrient cycling is very restricted. A good example of such a situation is the accumulation of peat.

The metabolic activities of microorganisms are also important in altering the chemical nature of nutrients, often making them more available to plants. Good examples of this are nitrification (the conversion of ammonia to nitrate) and the oxidation of reduced sulphur compounds to sulphate. However, under waterlogged conditions when soil is anaerobic the lack of available oxygen can lead to irreversible losses of nitrogen, through denitrification (the reduction of nitrogenous compounds to nitrogen gas or N_2O), and sulphur as H_2S and other sulphides. Some nitrogen is also lost during nitrification, though the significance of this is debatable.

MICROORGANISMS AND PHOSPHATE

The availability of phosphate in the soil to plants is often limited because too little is present in the soil solution, from which uptake occurs. This may result from strong sorption on the solid phase, as in ferruginous soils, or only a small amount being present in the labile pool, or because phosphate ions migrate only slowly through soil leading to zones of depletion around absorbing roots. Microorganisms may improve phosphate nutrition in three main ways: 1) by

producing acid which increases the solubility of phosphates; 2) by transporting phosphate across depletion zones to roots; and 3) by altering the physiology and possibly morphology of roots so that they are more able to exploit existing sources of phosphate in the soil.

Phosphate solubilizing bacteria have long been a source of interest because they appear to offer an opportunity to utilise slightly available reserves of phosphate in soil. Indeed inocula containing these bacteria have been sold. They liberate phosphate by the production of acid during their metabolism, or by producing compounds which complex with aluminium or calcium, and so cause phosphate salts with these elements to dissolve. However, as with nitrogen fixation by free-living bacteria, the potential for this activity is limited by the availability of organic substrates which are nearly always in short supply in the soil and are utilised by a wide range of other microorganisms. Further, though phosphates 'solubilization' has been shown to occur in agar or similar media, there is no good evidence for it occurring in soil, where pH is buffered.

The transport of phosphate to plant roots by mycorrhizal fungi is probably the most widespread and important interaction between plants and microorganisms that we are aware of, because it involves virtually all plant species of commercial importance (notable exceptions being brassicas and sugar beet). Mycorrhizas, which are defined as associations between roots and fungi, are of two main types: ectomycorrhizas, in which the fungi grow mainly on the surface of the root and endomycorrhizas, in which the fungi grow mainly within the root. In both types of association fungal mycelium grows in the root

and also out into the soil, extending well beyond the zone which is explored by root hairs.

It is generally accepted now that mycorrhizal fungi absorb and transport phosphate through the mycelium into plant roots, and that the plant provides the fungi with photosynthetically-fixed carbon compounds. There is no evidence available to suggest that the fungi specifically liberate unavailable phosphate; their role appears to be due mainly to their ability to explore regions of the soil beyond those from which phosphate ions can move to the root surface. There are also suggestions that their absorbing power is greater than that of roots alone in soil solutions with very low phosphate concentrations. It has also been shown that the ability of mycorrhizal plants to take up phosphate is particularly important when plants are under moisture stress, because the movement of phosphate in soil is then particularly slow.

Specific micro-organisms are now used to inoculate tree seedlings with ectomycorrhizas. This is particularly important where the tree is an introduced species, and the appropriate fungus may not be present naturally. Ectomycorrhizal fungi are often quite specific for a particular host, but the vesicular-arbuscular (VA) mycorrhizal fungi have very little specificity, and infect almost all susceptible plants. For this reason spectacular responses to inoculation with VA mycorrhizas in the field are rare, because the soil will almost certainly contain natural inoculum. The largest responses are thus found where the soil has been sterilized, e.g. for citrus nurseries in California, and for horticultural crops in Israel. In such conditions

crops can fail completely without mycorrhizal inoculation. Useful effects are also being found in non-sterilized soils, e.g. in hill-land pasture in Britain. In pot tests, inoculation of non-mycorrhizal plants has given responses corresponding to adding from 30 to several hundred kg P ha⁻¹ to the soil, depending upon crop and conditions, with the most usual values being about 100 kg P ha⁻¹.

In pot tests it has also been shown that inoculation with VA mycorrhizas allows plants to use phosphates of low solubility more effectively (Tinker, 1980). Mycorrhizal inoculation is of no benefit if the phosphate source is so 'available' that the phosphate deficiency of non-mycorrhizal plants is cured. It also does not help the plant to utilize phosphates of such low solubility that the non-mycorrhizal plant is not benefited at all, but it can greatly increase the response to moderate dressings of phosphate of intermediate solubility (Table 1).

There are particularly interesting interactions between simultaneous infections of Rhizobium and mycorrhizal fungi in legumes. The presence of the mycorrhizas increased the activity of the nitrogen fixing bacteria. It is not yet clear whether this is because Rhizobium infections are particularly susceptible to phosphate deficiency, or whether hormonal interactions are involved. Other nutrients are also transferred to plants, such as zinc, copper and some other trace elements, though there is little evidence to suggest that nitrogen and potassium are transported in the same way. There are reports that mycorrhizal fungi may have a role in making plants less susceptible to water stress, particularly tree species which form

ectomycorrhizas. If so, mycorrhizal fungi must obviously have an indirect effect on nutrient uptake in general.

OTHER ROLES FOR MICROORGANISMS

Because plant roots in nature are constantly exposed to very large populations of a wide range of different microorganisms it is difficult to determine whether particular groups or species have a direct role in plant nutrition.

Microorganisms compete with plants for nutrients, and this is best known in relation to the requirement for additional nitrogen fertilizer when cereal or other plant materials are ploughed in. Under these conditions there is a dramatic change in the amount of carbon compounds with high C/N ratio available to microorganisms. As these are utilised the microorganisms take up nitrogenous compounds, sulphur, phosphate and other nutrients from the soil. Such nutrients are, of course, eventually recycled in the organic matter.

A particularly interesting example of an organism that might have a quite unexpected role in plant nutrition has arisen from studies with Azospirillum. This is a nitrogen-fixing bacterium which has been studied in some detail recently because it grows in the region of soil closely associated with plant roots and is isolated routinely from a range of plants, especially tropical grasses, that are believed to be benefiting from biological nitrogen fixation. The potential for reducing nitrogen requirements for crops and/or increasing yields through inoculation with Azospirillum is at present unclear.

Initial optimism, usually based on rather poorly conducted experiments, has been replaced by a realization that in temperate agriculture inoculation is unlikely to provide host plants with as much as 10 kg of N per ha per annum (see O'Hara, Davey & Lucas, 1981; van Berkum, McCJung & Stoger, 1982). Under tropical and sub-tropical conditions greater amounts of nitrogen may be fixed, though it has yet to be demonstrated clearly that the amounts will be sufficient to repay the investment in purchasing and distributing inocula containing Azospirillum.

Perhaps the most interesting observation for the future that has come from work with Azospirillum is that maize plants inoculated with Azospirillum in Israel contained significantly more phosphorus (0.5% P) than uninoculated plants (Kapulnik et al., 1982). Thus it is likely that part, or possibly all of the growth response seen after inoculation is due to the role of the bacteria in modifying the ability of the plants to take up nutrients from the soil. Whether other bacteria can be isolated that will have similar attributes remains to be seen.

It is not clear at present whether the growth responses to inoculation with these bacteria are due to an increased ability of inoculated plants to take up nutrients under conditions where plant growth is nutrient-limited, or that they are due to a general increase in plant growth, leading to increased nutrient uptake. To find sensible methods for testing bacteria for their ability to facilitate plant nutrition will require that these different roles are recognized. Our understanding of what is happening to plants that are

inoculated with Azospirillum is still limited, and we cannot yet make sensible predictions about the possibility of developing bacterial strains that could improve the ability of plants to take up nutrients from the soil.

Recently Schroth and coworkers (Suslow et al., 1979; Klopper, Schroth & Miller, 1980; Suslow & Schroth 1982) have reported that some bacteria isolated from the roots of plants can promote growth (plant growth promoting rhizobacteria, PGPR), probably because they are antagonistic to minor pathogens. It is not at all clear what happens after inoculation, because 'minor pathogens' is an ill-defined term concerning largely unknown microorganisms. We assume that PGPR inhibit minor pathogens because they are not effective when added to sterile soil or to soil taken from fields in which the test plant has not been grown previously. We have no idea how minor pathogens affect plant growth. It could be through directly damaging the plants, causing damage which makes plants more susceptible to other pathogens, or by interfering with nutrient uptake. Some microorganisms may, in fact, do all of these. There is no suggestion from this work that PGPR can be used to reduce the demand for fertilizers.

CONCLUSIONS

It should be clear from this review, and that of Postgate at this meeting, that some microorganisms are of great importance in providing nutrients to plants. In the case of nitrogen-fixing microorganisms this is done by converting nitrogen gas in the air into a form usable by plants, while for the others the role is in facilitating uptake of

nutrients already present in the soil. Our knowledge of these interactions is limited, and thus our ability to manipulate many of the organisms involved is poor. However, microbial inoculants containing Rhizobium for use on legumes are widely available and can be of enormous importance in producing nitrogen-fixing root nodules when appropriate strains are absent in the soil. Mycorrhizal fungi are also produced commercially and have a definite role in forestry and some other situations. Improvements in strains used as inoculants will be made in the future and we can expect to see an expanding market for these useful organisms. Unfortunately there are also a number of other products containing microorganisms on the market which are claimed to improve plant growth. In many cases the claims are based on the supposition that, simply because the inoculants contain nitrogen-fixing bacteria, levels of soil N will be increased. This idea has been refuted earlier in this review on the basis of the very obvious constraint that sufficient reserves of energy are seldom available in soils. Whether or not such preparations contain species of microorganism that are of direct benefit to plants is uncertain and will be difficult to prove or disprove.

Further attempts to improve crop yields by inoculation with microorganisms will depend upon the isolation of species, such as Azospirillum, which appear to be beneficial, the testing of such organisms to ensure that they are useful in specific conditions and the formulation of inoculants to add enough microorganisms to be able to colonise the soil in sufficient numbers to have an effect. These inoculants will have to compete with indigenous microorganisms which are likely to be well adapted to the soil conditions, making it

difficult for the introduced organisms to grow rapidly and produce large populations. These constraints are a major barrier to the introduction of foreign microorganisms to soil. They should be considered when assessing whether formulations containing microorganisms are likely to improve plant growth, and if so whether it is due to the presence of the microorganisms or of nutrients present in the mixture.

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Table 1

Effect of inoculation with vesicular-arbuscular fungi on growth of white clover in partially sterilised soil, in presence of different rates of soluble phosphate or rock phosphates. (after Sparling & Tinker, 1978). Inocula were of fine endophytes (*Glomus tenuis*), an undefined 'coarse' endophyte, and *Glomus mosseae*

Fertiliser applied per kg soil	Inoculum	Dry weight	% P
N11	N11	6	0.08
	Fine	130	0.26
	Coarse	170	0.21
Soluble P (50 mg P)	<u>G. mosseae</u>	6	0.09
	N11	30	0.16
	Fine	370	0.31
Rock phosphate 2 g P	Coarse	140	0.28
	<u>G. mosseae</u>	30	0.19
	N11	210	0.27
Coarse	Fine	490	0.37
	Coarse	450	0.30
	<u>G. mosseae</u>	380	0.32