Introduction

The Beneficial Rhizosphere: a dynamic entity

Abstract

This introductory paper attempts to put into perspective the papers given at the Inter-COST meeting on the Establishment of the Beneficial Rhizosphere. Although the rhizosphere concept is now relatively well understood, it is too frequently viewed as a static entity. An awareness of the short longevity of the roots of many common crop species, less than 7 days for half of the new roots of oats, and of the hyphae of arbuscular mycorrhizal fungi (AMF) bring a dynamic imperative to the rhizosphere concept. This actuality means that rhizosphere conditions need to be established and maintained on an almost continuous basis. A dynamic perspective of the rhizosphere changes views on the targets for microbial inoculation for both field grown and micropropagated plants. At the time when the concept was introduced, the rhizosphere was commonly regarded as an add-on to the normal plant. We are now aware that it is the “rhizosphere” condition which is normal. These concepts and their implications are the subjects of the papers in this special issue of Applied Soil Ecology. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Associations that occur between plant roots and soil micro-organisms have been known for many decades. Considerable efforts have been devoted to studies of ectomycorrhizal fungi, nitrogen fixing bacteria and soil-borne pathogenic fungi. With time, an awareness of the complexity of the interactions between roots and soil microbes has developed, especially as a consequence of the many investigations of the variable response of plants to different soils. In 1978, a conference was held to bring together information on interactions between roots and soils (Harley and Russell, 1979). The conference considered chemical, physical and biological aspects of interactions. Reviewing the biology of the soil–root interface, Rovira (1979) identified, as key areas, the release of organic materials from roots, microbial colonisation of roots, root associated nitrogen fixation, mycorrhizas, and interactions between root pathogens and root functioning. Summarising what was known at that time, he concluded “the ultimate agricultural goal, in studies of the biology of the soil–root interface, must be the manipulation of micro-organisms in this zone to increase plant growth”. Among subjects identified as important to allowing such manipulations, he identified endotrophic mycorrhizas, biological control, and the introduction of micro-organisms which stimulate plant growth.

In the 20 years which followed this meeting, research made it clear that arbuscular mycorrhizal fungi and other fungi, together with root-associated bacteria, play an integral role in the functioning of the plant-root system, both in vitro and in vivo. The emphasis of many of the papers in the 1979 volume indicated that rhizosphere micro-organisms were viewed as either a beneficial add-on to the normal healthy plant or, in the case of pathogens, as an impediment to growth. Studies over the past two decades have demonstrated that it is normal for plant roots to have...
a rhizosphere population and that they have evolved to function in this condition. As a consequence, that the normally mycorrhizal plant has difficulty in accessing appropriate amounts of mineral nutrients or is unsatisfactory at interacting with pathogenic fungi when non-mycorrhizal is perhaps only to be expected. This has clear implications for plants raised in field situations. In addition, it has become clear that understanding the mechanisms by which biota interact and influence root quality, and especially the ways in which they promote plant quality, is a critical factor in the development of improved micropropagation systems.

The use of microbial inoculants of any type raises a series of technical issues related to their efficacy with both micropropagated and other plants. The meeting held at Edinburgh in 1998 on the subject of the “Beneficial Rhizosphere” provided an opportunity to bring together four separate EU COST Actions all with an interest in questions related to these subjects, and to review the current state of information and thought about the rhizosphere. This paper reviews the above themes and some of the points developed during the many discussions at the conference.

1.1. The rhizosphere: a dynamic entity

The picture of the rhizosphere conveyed by earlier studies (e.g. Barber, 1979; Rovira, 1979), has been one of a relatively static entity. At the time of the 1979 meeting, the ability to study the dynamics of roots and associated micro-organisms, especially under field conditions, was severely limited by technique. The mini-rhizotron technique, which has been important to investigating root systems in situ for a range of crops, was introduced as a means of characterising rooting patterns in the late 1970s (Sanders and Brown, 1979). The combination of a small-scale means of observing roots in soil, together with appropriate technology to follow a cohort of roots from initiation to death, has allowed the longevity of roots to be assessed in situ. For many temperate tree species, this has been found to be relatively short (e.g. Black et al., 1998). However, only limited data is available for agriculturally important species in Europe. As part of a field study of crop rotations in NE Scotland (Baggs et al., 2000), roots of five crops were followed using a mini-rhizotron technique (Hooker et al., 1995). A plot of the proportion of a cohort of roots surviving for periods up to 42 days (Fig. 1), showed substantial variation between species. In white clover, around 80% of roots survived for longer than 7 days. In contrast in oats and pea, survival beyond 7 days occurred in under 50% of roots. After 42 days, whilst over 60% of clover roots remained alive, less than 20% of pea, mustard and oat roots survived. Red-clover roots were intermediate. This information is important in assessing both the significance of rhizosphere activity and the importance of the processes involved in the establishment of a functional rhizosphere. Where a significant proportion of roots (Fig. 1) survive for only a relatively short period of time, then the re-establishment of rhizosphere conditions around new roots must occur constantly and the process of the development and the establishment of the rhizosphere must be considered to be truly dynamic. This information also has significant consequences in relation to the carbon economy of the plant–soil-microbe system.

Many older studies have implied that once a root–soil-microbe interaction has been established, it will continue functioning for a considerable period of time. In the absence of suitable techniques, it has not been possible to determine the longevity of particular individual root–soil-microbe associations. The development of large-scale soil research facilities, such as the “soil biotron” established at the University of Michigan’s Biological Station, has allowed the cohort approach developed for the measurement of roots adjacent to mini-rhizotrons to be applied to soil fungi (Atkinson and Fogel, 1997). The University of Michigan Soil Biotron is surrounded by an undisturbed forest soil, with colonisation of the observation panels by the roots of a native forest flora (Fogel and Lussenhop, 1991). Extraction of the roots of common species from soil near to the biotron, followed by the use of standard staining methods (Rajapakse and Miller, 1992), established that most of the roots of most species were heavily infected (>50%) with arbuscular mycorrhizal fungi. As a consequence, there is a reasonable probability that some of the extra matricular hyphae of fungi, seen to be associated with roots visible through the biotron windows, are from arbuscular mycorrhizas. The dominant species adjacent to the area of study
Fig. 1. The survival of the roots of a range of agricultural species assessed using the mini-rhizotron method: ( Rolled red clover; (□) pea; (△) mustard; (x) white clover; (o) oats (data drawn from unpublished data).
were *Prunus pennsylvanica*, *Rubus* sp. and *Pteridium aquilinum*, all of which are known to be mycorrhizal. The survival of individual fungal hyphae was assessed by following the fate of a cohort of around 80 individual hyphae which appeared between 2 and 6 June, at a depth of 10–15 cm. The cohort of hyphae followed were from 12 separate observation areas. The survival of these hyphae was followed for a period of 24 days (Fig. 2). Survival information showed that the majority of hyphae survived for less than 7 days.

Under normal conditions, it would seem that both plant roots, and at least some of the micro-organisms with which they are associated, can turn over on a rapid basis. Understanding this dynamic element is an important complement to studies of the particular microbial species associated with roots and of the effects of microbial inoculation on root performance, rhizosphere establishment and development.

### 1.2. Microbial interactions

Discussions at the 1998 meeting (Gianinazzi and Schuepp, 1999) identified the most important aspects of an established rhizosphere as being the presence of a complex microbial population and organic substrates released from plant roots. Beneficial, detrimental and neutral relationships between plant roots and micro-organisms are all regulated by complex molecular signalling. It is clear that the total biological community, rather than just the immediate micro-flora, plays a role in rhizosphere interactions with plant roots. The existence of both microbial responses to plant exudation, and plant exudation responses to the presence of microbes, suggests a degree of co-evolution between plants and soil microbes. This has major implications for both bio-control in field and glasshouse conditions and the use of soil micro-organisms during micropropagation and the plant establishment process. Despite the large number of studies of interactions in the rhizosphere, a number of which are contained within this volume, it is clear that there remains major gaps in our knowledge of the interactions occurring in the rhizosphere. For example many of the compounds, such as flavonoids and hormones, which are produced in mycorrhizal associations are also produced during cell differentiation. This makes identifying their role in the mycorrhizal establishment process difficult. Continuing work in this area will be needed to provide a base for “rhizosphere technologies”.

#### 1.2.1. Practical applications of rhizosphere technology

Whilst the interactions between plant roots and soil microbes are of basic scientific interest and important to the dynamics of plant communities, there is also an interest in managing these interactions as a means of influencing crop production and health both in the field and under more controlled environment conditions, e.g. glasshouses, and as a major component of the micropropagation process. In relation to the latter aspect, the key questions are how a root system of good quality can be induced from a micropropagated cutting produced in vitro, and how an appropriate rhizosphere for such a root system can be established and maintained both to favour plant growth and to protect against soil-borne diseases. For micropropagated plants, a key question is how the development of the rhizosphere can help these plants in re-establishing a “normal physiology”. While it is clear that different means of propagation, and different techniques for the introduction of soil microbes have important effects, it remains impossible to define the quality of a root system, or the range of interactions between roots of different types, e.g. seminal or adventitious roots, and
their interactions with the rhizosphere. Nevertheless, despite the lack of functional understanding, it is clear that the means, type and extent of biotization of microplants has a major impact upon their establishment and growth, and on their interaction with fungal pathogens. Several papers in this volume develop this major theme.

Many previous studies of rhizosphere technology have concentrated on beneficial fungi such as arbuscular mycorrhizal fungi. Studies on soil bacteria are now illustrating the number of bacteria which can be significant components of the rhizosphere, and the range of effects which they are able to mediate both directly in relation to the response and functioning of roots, and indirectly through interactions with other soil micro-organisms. Papers in this volume illustrate the breadth of such interactions and the wide range of consequences.

Agricultural interest in farming systems, which both use complex sources of nutrients and aim to minimise the losses of soluble nutrients by leaching, have increased the level of interest in both the management of the rhizosphere around roots, and the control of the rhizosphere composition by plant inoculation. The papers in this volume illustrate a number of approaches to the inoculation of plants with desirable soil microbes. Developments in biotechnology raise the prospect that in the future, inoculation may involve the use of transgenic micro-organisms. Technical aspects of this technology were discussed at the conference. It does, however, also raise questions in respect of both safety and ethical issues. Resolution of the type of ethical issues, identified by Bruce and Bruce (1999), was seen as being crucial to gaining public support for the use of these technologies.

The complexity of rhizosphere interactions has resulted in much previous work (Rovira, 1979) having involved only relatively simple conceptual models, and commonly a static view of the rhizosphere. As indicated above, one of the key challenges for the future will be to link the dynamics of rhizosphere populations, which are now increasingly well understood, with both the dynamics of plant-root systems and their longevity. Success in the inoculation of plants, with normal or transgenic micro-organisms, and the management of rhizosphere micro-organisms, will clearly require appropriate attention to be paid to the dynamics of both micro-organisms and roots.

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References


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