Chapter 8

Relevance of Plant Root Pathogens to Soil Biological Fertility

V.V.S.R. Gupta[1]and K. Sivasithamparam[2]
[1] *CSIRO Land and Water, Glen Osmond, SA,5064, Australia*
[2] *School of Earth and Geographical Sciences, Faculty of Natural and Agricultural Sciences, The University of Western Australia, Crawley, 6009, Western Australia*

1. INTRODUCTION

In this chapter we use the term soil biological fertility to describe the ability of soil biota to perform various (1) plant essential functions to support the growing plant with its nutritional and other biological requirements, and (2) ecosystem functions that maintain the quality of soil resource. A number of soil functions essential for plant growth and crop productivity are regulated by different groups of biota. These include (i) mineralisation and uptake of major nutrients (e.g. N, P and S) and trace elements (e.g. Zn), (ii) beneficial, pathogenic and associative interactions affecting root and shoot growth, (iii) degradation of chemicals harmful for plant growth (e.g. herbicides from a previous cropping season), and (iv) formation of soil structural components that provide optimal aeration and water-filled pore space for plant growth.

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A unique balance between the three components of a soil system, i.e. physical, chemical and biological, is necessary for long-term sustainability of crop production, soil health and other essential ecosystem functions. Soil biota regulate processes that impact on the physical and chemical properties of soil and conversely the physical and chemical attributes of soil greatly influence the populations and activities of soil biota. The optimum functioning of the biological components of soil requires both a suitable habitat (pH, habitable pore space, oxygen concentration etc.) and optimum environmental conditions (temperature, moisture level etc.). For example, the activities of different groups of soil biota have important roles in various components of soil structure i.e. the burrowing activities of macrofauna influencing soil pore structure (Lee and Foster 1991) and binding and entanglement of soil particles by microflora (including pathogenic fungi) in the aggregate formation and stabilisation (Gupta and Germida 1988, Tisdall 1991, Tisdall *et al.* 1997). Conversely stable aggregates are an important component of soil structure for maintaining aeration and porosity for favourable microbial growth including that of plant pathogenic fungi. These activities may affect the physical and chemical properties, which are known to determine suppressiveness of soils to plant root diseases (Hoper and Alabouvette 1996).

Management practices involving surface retention of crop residues are recommended for improving soil organic matter, soil structure and biota populations. However, they can result in providing food source for the survival of some pathogenic microorganisms especially during off-season. In addition, the surface retention of residues has increased the potential for the movement of residues around the farm and across farms and might have increased the carryover of soilborne root pathogens (Neate 1994, Allen and Lonergan 1998). Allen (2000) summarised the trends in diseases in Australian cotton based on 17 years of survey data on disease incidence and severity. Results show that there has been a steady decline in the mean seedling mortality during the 10-year period ending in 1998, i.e. from 50% mean seeding mortality in 1987/88 to <30% seedling mortality in 1997/98. The incidence of diseases such as bacterial blight (*Xanthomonas campestris*) and verticillium wilt (*Verticillium dahliae*) has declined whereas diseases such as black root rot (*Thielaviopsis basicola*) and fusarium blight (*Fusarium oxysporum* f.sp. *vasinfectum*) have become a severe threat to the sustainability of Australian cotton industry.

Presence of the inoculum of a pathogen does not necessarily result in the outbreak of the disease and the severity of the disease is ultimately determined by the environmental conditions. Irrigated wheat often succumbs to pathogens different to rainfed crops. In the Pacific northwest (Cook and Baker 1983) fusarium crown rot dominated rainfed crop while take-all (caused by *Gaeumannomyces graminis* var. *tritici*) was the major problem in irrigated wheat. *Fusarium* dominates in soils that are relatively dry and with relatively low microbial (mainly bacterial) activity, while the take-all fungus although not as saprophytically competent as *Fusarium* spp., is active in moist soils. The extent of threat from major pathogens varies with crops and regions of Australia (Murray and Brennan 2001, unpublished). For example, Fusarium crown rot of wheat, especially that caused by *F. pseudograminearum*, is predominantly a problem in the north and central cropping regions of Australia, while the crops in the south central wheat growing region are more severely affected by pathogens such as *Rhizoctonia solani* AG8 and take-all fungus (*Gaeumannomyces graminis* var. *tritici*).

2. NATURE OF RELATIONSHIP BETWEEN PLANT ROOT PATHOGENS AND SOIL BIOLOGICAL FERTILITY

2.1 Interactions between Root Health and Nutrient and Water Uptake by Crops

Soil borne plant pathogens affect biological fertility directly and indirectly. Directly, they affect the efficiency of root's capacity to acquire water and nutrients. Indirectly, the reduction in plant biomass resulting from disabling the host leads to reduced input of the quality and quantity of organic matter that eventually enters the soil. Neate (unpublished data, personal communication) working with rhizoctonia bare patch soils in Spalding, South Australia observed that the unused water by the wheat plants in the rhizoctonia bare patch areas exceeded 50mm, also there was 56 kg N /ha unused nitrate nitrogen in the surface one meter soil profile. The 50 mm unused water accounts for more than 25% of growing season rainfall. Deep leaching of this unused water and mineral nitrogen below root zone could lead to a number of environmental problems and degradation of landscape at a large scale. Inadequate usage of available water by the disease-affected crops is one of the critical reasons for the increased drainage under dryland agricultural crops. Thus, plant pathogens and plant disease management play an important role in the fertility of the cropped land and also the health of the whole agroecosystem.

The value of soil fertility to the plant is only of value if plants can access this fertility. Root health and vigour is of critical importance to the nutrition of the plant. With wheat for example, under the Mediterranean conditions of southern Australia, the five seminal roots it produces are critical especially in accessing stored water. They are the only root system available for the first 21 days of the seedling's life and hence are targeted by most soil-borne root pathogens. Early infections debilitate the young plant which becomes nutrient impoverished because of dysfunctional roots. This predisposes the plant to additional attacks by other necrotrophic plant pathogens, which favour weak, nutrient-deficient plants.

In any given environment, for each farming system, a dynamic equilibrium exists between disease severity, soil biological fertility and plant production. A change in one or more components, in particular the one most limiting, may be required for any production system that is performing below optimum in order to improve productivity and resource use efficiency. Management of disease-affected crops by merely targeting the pathogen attack is unlikely to be adequate. For instance, in the wheat fields on highly calcareous soils of the Eyre Peninsula in South Australia where biological fertility of soils, especially relating to root growth and nutrient availability are limiting, just tackling the pathogen alone is not likely to significantly improve crop production until other major nutrient and biological constraints related to poor soil fertility are overcome.

2.2 Interactions between Beneficial Bacteria and Root Pathogens

Rhizobacteria capable of increasing shoot and root growth through a number of different mechanisms have been described both for dryland and irrigated agricultural crops and horticultural plants. These bacteria, known as plant growth promoting rhizobacteria (PGPR), are considered to improve plant growth either through biocontrol of plant pathogens or by increasing root and shoot growth both in the presence or absence of a disease. Some PGPR strains have also been shown to induce systemic resistance against multiple pathogens including bacteria, fungi, viruses and nematodes (Kloepper *et al.* 1999, 2000). The development of an integrated disease management approach which incorporates both the PGPR and induced systemic resistance (ISR) has greater chance of success for consistent disease suppression of both major and minor pathogens. *Rhizobium* spp. have also shown excellent potential as plant growth promoting rhizobacteria (PGPR) with non-legumes (Antoun *et al.* 1998). On colonisation of non-legumes they may produce phytohormones, siderophores and HCN. Some strains of rhizobia are also antagonistic towards some plant pathogenic fungi. *Rhizobium* may also directly compete with fungal pathogens resulting in the reduced severity of root-rots (Tu 1978).

Most of the research on beneficial effects of biocontrol microorganisms and other PGPR has been done with organisms that have been selected for effective performance in rhizosphere environments. Recently, there has been scientific and commercial interest in the use of endophytic microorganisms.

Endophytes, because of their intimate association with their host plants, their location and action, avoid environmental adversities that exist in the rhizosphere and bulk soil (Sivasithamparam 1998). However, rhizosphere microorganisms capable of endophytic activity could confer a distinct benefit to the host plant against a pathogen before it reaches the plant itself, thus providing a dual control mechanism (Kobayashi and Palumbo 2000, Sturtz *et al.* 2000). A variety of stimuli, both biotic and abiotic, appear to induce resistance against a wide spectrum of plant pathogens (Van Loon *et al.* 1998). In many cases the induced resistance appears to be effective against a broad spectrum of targeted pathogens.

2.3 Interactions between Mycorrhizae and Root Pathogens

In addition to the nutritional benefits (e.g. P and Zn) from mycorrhizal colonisation, mycorrhizal plants are also known to better withstand adverse environmental conditions, such as drought and salinity, due to the increased accessibility of soil water by the mycorrhizal roots and hyphal networks (Davies *et al.* 1992, Subramanian and Charest 1999). Another important benefit from mycorrhizal symbiosis is the protection from plant pathogenic fungi (Fernando and Linderman 1997) and nematodes. Although a cascade of biochemical changes occur in roots colonised by mycorrhizal fungi (Smith and Read 1997) it is likely that the reduction in root diseases in mycorrhizal plants is predominantly due to improved nutrition and vigour of the plant host. The improved phosphorus status of the wheat plant leading to a decrease in the net leakage of root exudates and thereby reduced pathogen growth in the rhizosphere has been suggested as the basis of reduced take-all severity in wheat plants inoculated with mycorrhizal fungi (Graham and Menge 1982).

2.4 Interactions between Soil Fauna and Root Pathogens

Soil fauna influence plant disease incidence through i) their effects on the survival, growth and transportation/dispersal of pathogen inoculum including fungal propagules, ii) host plant-pathogen interaction and, iii) the nutrition of the host plant (Lussenhop and Wicklow 1984, Old 1986, Curl 1988, Gupta 1994). The presence of high levels of mycophagous amoebae has been associated with disease suppression or reduced disease caused by take-all fungus, verticillum wilt fungus and *Rhizoctonia* causing bare-patch, in laboratory and glasshouse trials (Old 1986, Gupta *et al.* 1996). Mesofaunal grazing selectively on pathogenic fungal hyphae (e.g. Collembola grazing on *R. solani*; Lartey *et al.* 1989) and altering of rhizosphere fungal community structure has also been reported (Curl *et al.*

1983). Such reports also show the effects of macrofauna on pathogenic fungi. However, most of these reports are based on controlled environment studies and limited evidence is available showing direct relationships under field conditions. In general, management systems that support high and diverse soil faunal communities do not favour the proliferation of certain pathogenic fungi. Gupta *et al.* (1995) observed, in field based studies, that the reduction in the survival of *Rhizoctonia solani* and take-all fungal inoculum was associated with high populations of mycophagous amoebae and fungal feeding nematodes (mycophagous effects), suggesting that they could have a significant role in the broad spectrum disease suppression observed in a long-term farming systems trial at Avon, South Australia (Roget 1995).

Predation of microflora by soil fauna, in particular microfauna, releases plant available nutrients tied up in microorganisms. Better nutrition of plants could result in reduced overall negative effects from plant disease incidence. Gupta *et al.* (1999) observed that wheat plants grew better in soil cores even after inoculation with *R. solani* fungus in the presence of mesofauna. High populations of mesofauna resulted in higher levels of nutrients in plants (eg concentration and total uptake of nitrogen) suggesting that better nutrition in the presence of mesofauna could be a reason for reduced *Rhizoctonia* disease severity.

3. PLANT PATHOGENS AS COMPONENTS OF THE SOIL FOOD-WEB

Many biological processes in terrestrial ecosystems are mediated or regulated by multiple species or trophic groups of organisms. Therefore, successful functioning of most soil biological processes requires a balance of interactions in a complex soil biota community (detritus food web). In a detritus food web, organisms across trophic levels are linked on the basis of the flow of energy and food preference. While simple microbial-faunal interactions have been used to explain the effectiveness of an introduced biocontrol microorganism, complex food-web structures are needed to delineate mechanisms or predict changes in biological functions such as crop residue decomposition, nutrient (N, S and P) cycling and disease suppression. In a detrital food web, microflora including beneficial and pathogenic bacteria and fungi form the primary decomposer groups that transfer the carbon and nutrients from crop residues into the soil biota component. A conceptual framework indicating the various groups of soil biota and their linkages along with the different biological functions they might influence, based on published information, is given in Figure 1.

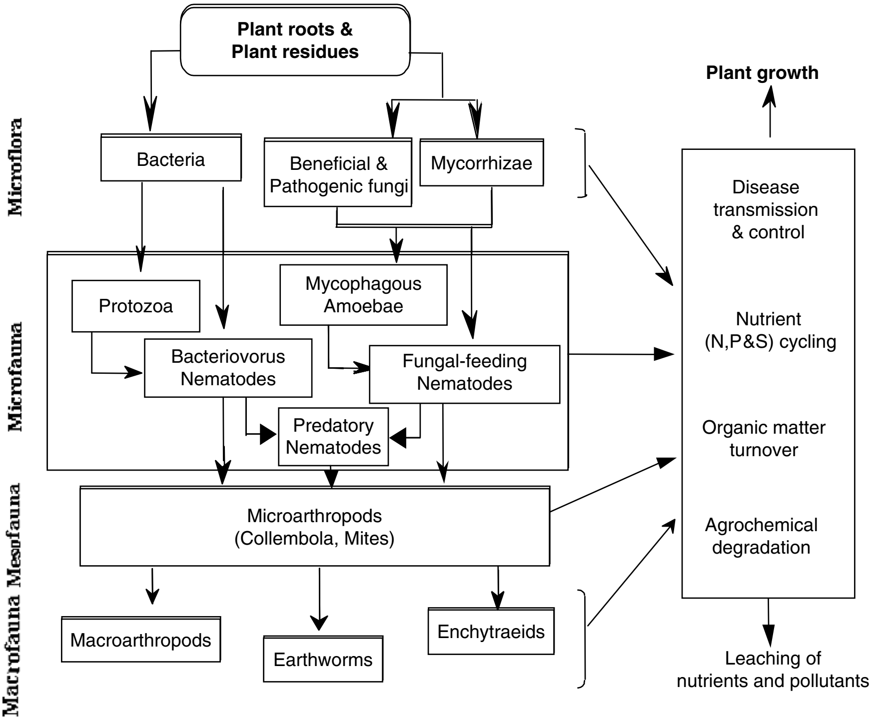

Figure 1 The different groups of soil biota are linked in a detritus food-web model in order to express their role in key soil biological processes. This model is based on published information (based on information from Hendrix *et al.* 1986, Beare *et al.* 1995, Roper and Gupta 1995 and Gupta and Neate 1999).

Carbon compounds from root exudates provide the energy source for the rhizosphere food-web complex whereas decomposing crop residues form one of the critical microsites for the food-web community in the bulk soil. Predation by protozoa and nematodes (microfauna) on microflora can lead to the release of plant available forms of nitrogen, phosphorus and sulfur and contributes to a significant portion of nutrient uptake by plants (Gupta and Yeates 1997). Predation by microfauna can also modify the community structure of bacteria and fungi in the rhizosphere. As bacteria are a major food source for microfauna, bacterial pathogens in the rhizosphere of infected plants could also become a major component of the primary food source for the higher trophic levels. Thus, these pathogens may play a significant role in the rhizosphere processes. Similarly, pathogenic fungi may form a major component of the rhizosphere food-web due to their external hyphae both pre- or post infection of a host plant. Many root pathogens maintain an ectotrophic root habit and / or their soil phase pre- and post-infection, i.e. both in their saprophytic and pathogenic phases. The take-all fungus is heavily dependant on ectotrophic spread on wheat roots for lesion extension (Garrett 1970) whilst *Armillaria mellea* spreads via rhizomorphs (Shaw and Kile 1991) through soil and establishes a widespread soil network of mycelia with the help of this habit.

Rhizoctonia solani AG8 also appears to have an extensive soil network although to a much lesser extent than some other fungi (Gill *et al.* 2002). In addition, by infecting plants, pathogenic fungi could influence the quality and quantity of root exudates thereby influencing the composition and activity of rhizosphere food-web components. For example, certain *Pythium* spp. favour the rhizosphere colonisation by certain *Pseudomonas* strains (Mazzola and Cook 1991). Similarly, pathogen-mediated changes in the rhizosphere influence the competence of biocontrol bacteria (Duffy and Defago, 2000). Fungal extracts of different soil fungi, including pathogenic fungi such as *R. solani,* have been observed to varyingly influence (positive or negative) different species of soil protozoa (Gupta *et al.* 1995). Differences in the composition of protozoan species associated with hyphae of different pathogenic fungi have also been observed (Chakraborty and Warcup 1985, Gupta *et al.* 1995). Thus, the activities of certain plant pathogens have the potential to modulate the rhizosphere microbiota composition and associated food-web dynamics and thereby influence general biological fertility of the rhizosphere soil.

4. PLANT PATHOGENS AND SOIL BIOTA IN THE PRESENCE OR ABSENCE OF A PLANT

Some pathogenic microorganisms participate in general soil biological functions, e.g. decomposition, nutrient cycling and soil aggregation, in their saprophytic phase especially in the absence of their specific host plant. This could happen during the off-season or under rotations with non-hosts. Such beneficial functions may be significant for pathogenic fungi and bacteria but are not applicable for organisms such as plant parasitic nematodes. Does this mean the beneficial functions of pathogenic microorganisms have hitherto been under-rated in relation to their role in soil biological fertility?

Soil-borne necrotrophic fungal pathogens may vary in their saprophytic competency. The take-all fungus, a pathogen considered to have a relatively low level of competitive saprophytic ability (Garrett 1970) depends heavily on its survival in the residues of cereal roots and crowns colonised during its pathogenic phase. *Rhizoctonia solani,* on the other hand, may also depend on the hyphal network in soil, which is essential for disease establishment

(MacDonald and Rovira 1985). Gill *et al.* (2002) demonstrated that the area of the bare-patch of wheat caused by *R. solani* AG8 is determined by the extent to which the mycelial network is established prior to sowing. This may explain the sensitivity of this pathogen to cultivation prior to seeding. Crop residues are important microsites for the survival during off-season for the cotton pathogen *Fusarium oxysporum* f.sp. *vasinfectum* (Allen and Lonergan 1998). In contrast to the take-all fungus, *Fusarium* and *Rhizoctonia* fungi survive well outside infected plant tissues, as they establish hyphal networks in the bulk soil as well as colonise crop residues i.e. high degree of saprophytic competency. This suggests that these fungi could form a significant proportion of fungal biomass in the soil following a susceptible host crop.

Saprophytically competent pathogens (e.g. *Fusarium* and *Rhizoctonia solani*) can thus compete with non-pathogenic soil microbes for colonisation and mineralisation of organic matter. These fungi have been found to have relatively high cellulose adequacy indices (Garrett 1970). Hyphal networks of pathogenic fungi are thought to facilitate the formation of water stable aggregates. An increase in the number of aggregates >50 μm diam. due to the saprophytic growth of the pathogen *R. solani* is shown in Figure 2 (Tisdall *et al.* 1997). Decomposing crop residues and associated fungal networks support the formation of water stable aggregates which would help reduce the loss of surface soil due to wind erosion. Potential benefits from such microbial functions may reduce soil degradation, maintain or improve the quality of the soil resource and reduce environmental problems associated with wind erosion in southern Australian environments.

Another important point in evaluating the relevance of plant pathogens in the absence of their specific or major host plant is their ability to grow on rotation crops either as a minor pathogen, asymptomatic cortical coloniser or as general rhizosphere microorganisms. Pathogens of grain legumes can be minor pathogens on pasture legumes such as clovers and medics, e.g. *Fusarium*, *Pythium* spp., *Phoma medicaginis* (field peas and medics) and *Rhizoctonia solani*. This poses a problem in planning rotations which are commonly expected to reduce disease hazards (Sivasithamparam 1993). *Rhizoctonia solani* AG 8 and the take-all fungus can attack pasture grasses after a cereal crop. It is common to see a dominance of ryegrass in wheat crops affected by take-all early in the season. This could be due to low virulence of the cereal pathogen on the grass (Nilsson 1969) or to the ability of certain wheat attacking strains of the pathogen to promote the growth of rye-grass (Dewan and Sivasithamparam 1990). This may at least partly explain the dominance of rye-grass in take-all patches. Although considered to be a weed-species within crops, this grass is an important component of pastures that form a common rotation in southern Australian farms, which rely both on crops as well as sheep to be economically viable. If the grass pathogens reduce the growth of pasture grasses they may help pasture legumes to out-compete grasses for resources (e.g. water), thus enhancing the benefits from nitrogen fixation by pasture legumes. However, these benefits may not be useful if the diseased pasture grasses maintain or increase the pathogen inoculum in the non-wheat season, resulting in higher disease incidence and severity in the following crop. Therefore, when evaluating the relevance of plant pathogens to soil biological fertility, it is necessary not only to view their role in the presence of the specific host plant but also consider their importance during the periods of host plant absence.

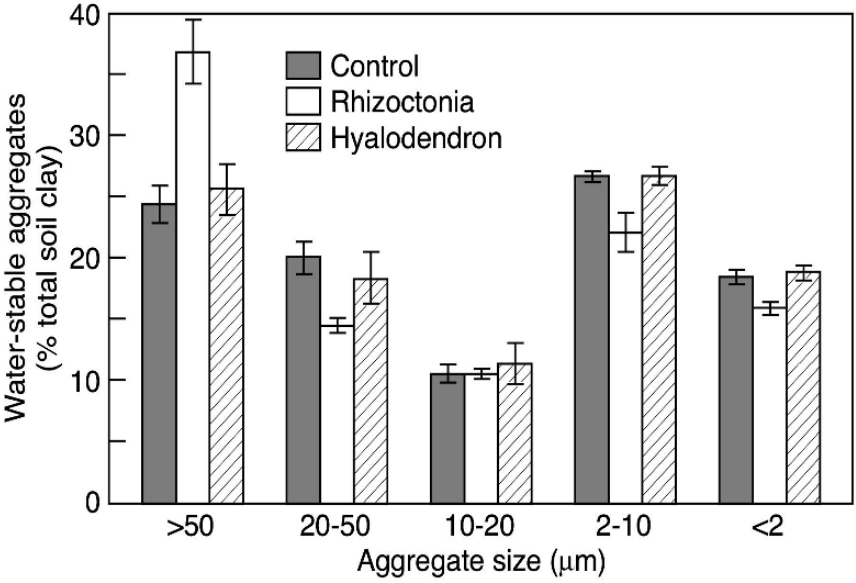

Figure 2 Effect of the saprophytic growth of fungi (for 15 days) on the size distribution of water-stable aggregates in Wiesenboden soil clay. Each error bar represents 2 x s.e.m. (from Tisdall *et al.* 1997).

5. MANAGEMENT EFFECTS ON PLANT PATHOGENS AND CONSEQUENCES TO SOIL BIOLOGICAL FERTILITY

In recent years the use of disease break crops (e.g. broadleaf crops) along with the availability of selective grass herbicides has resulted in significant increases in wheat yields, both productivity and profitability, in

Australia, USA and Canada. In addition, during the last 10-15 years, Australian farms have also seen a general reduction in the number of cultivations per season, specialised tillage practices to reduce specific diseases such as rhizoctonia bare patch (Roget *et al.* 1996), retention of crop residues and the use of fungicides to control plant diseases. Burning crop residues and intensive cultivation of Australian agricultural soils has resulted in significant decline in soil organic matter levels including nitrogen and phosphorus concentrations (Dalal 1997, Dalal and Chan 2001) and has contributed to the loss of surface soil from severe wind erosion events. Retention of crop residues instead of burning them and a reduction in number of cultivations (generally known as conservation tillage practices) improve soil organic matter levels and reduce soil erosion. Significant improvements in total biological activity, microbial biomass as well as populations and activities of different groups of soil biota as a result of crop residue retention and reduced tillage practices have been reported in soils from different agroecological zones in Australia (Mele and Carter 1993, Pankhurst *et al.* 1995, Roper and Gupta 1995).

The widespread implementation of reduced tillage practices has been made possible by the availability of specialised herbicides, e.g. sulphonyl urea (SU) herbicides, for weed management in broadacre cereal crops, in particular in the dryland agricultural regions of southern Australia. However, both the reduced tillage and the use of SU herbicides has resulted in an increase in the incidence of rhizoctonia bare patch disease. *Rhizoctonia solani*, with its high saprophytic competency and ability to form hyphal networks, thrives well in reduced till systems, in particular with the availability of crop residues under residue retention systems. This increase in rhizoctonia bare patch has been a major limitation to the widespread implementation of conservation till systems in southern and western Australian agricultural regions. Thus, residue retention coupled with reduced cultivation provide ideal conditions for the survival and proliferation of pathogenic fungi such as *Rhizoctonia solani*. Even though stubble retention in the short-term results in an increase in the biological activity in the low fertility agricultural soils, any changes in the composition of biological community i.e. microflora and soil fauna, may require long term implementation of these practices. Roget (1995) reported the development of a broad based disease suppression phenomenon in a long-term farming system trial in South Australia. This disease suppression phenomenon was observed across different crop rotation and tillage treatments that retained crop residues and took 3-4 years to develop and a further 7 years for complete disease suppression (Figure 3). The observed disease suppression was biological in nature and active against a number of diseases including rhizoctonia root-rot, take-all, fusarium root rot (Wiseman *et al.* 1996). These observations suggest that any benefits that rhizoctonia fungi received from reduced tillage were counteracted by the changes in overall biota composition (biodiversity) when carbon supply was maintained over long periods. These soils also became suppressive to the take-all fungus over the same period (David Roget, CSIRO, personal communication).

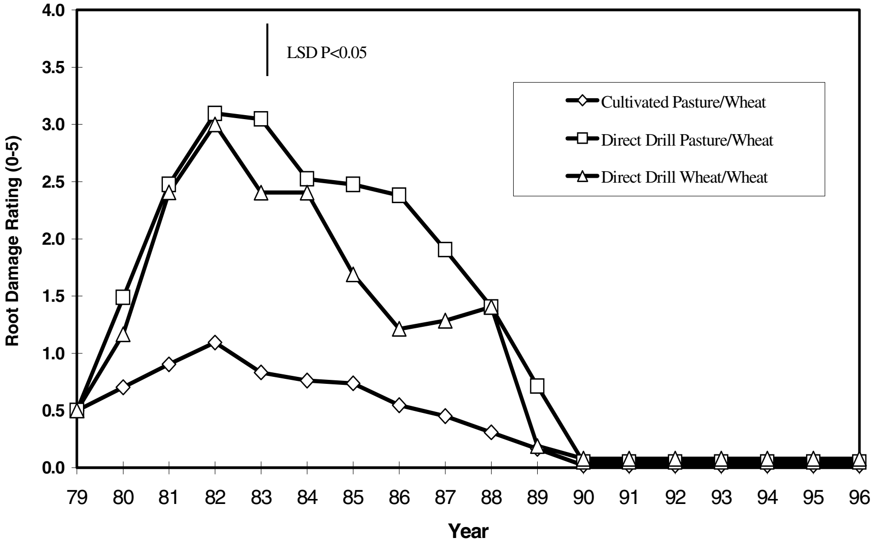

Figure 3. The development of disease suppression as indicated by the line in the rhizoctonia root rot of wheat at Avon, South Australia during 1979 to 1996 (adapted from Roget, 1995).

The nutrient-impoverished soils of southern Australia are highly conducive to diseases caused by necrotrophic plant pathogens. Rotations and fertiliser amendments to rectify these deficiencies will not only reduce the severity of diseases but also enhance the general fertility of the soils. In addition to increased yields, fertiliser applications that increase the inputs of carbon from roots and through crop residues also benefit soil biological activity. However, some negative effects from the application of specific fertilisers have been reported. For example, application of ammoniacal N suppresses take-all but leads to the acidification of bulk soil. Acidification may render the soil unsuitable for much of the bacterial activity necessary for nutrient turnover. Application of lime to enhance microbial activity in soil however renders the soil conducive to take-all (Simon and Sivasithamparam 1989).

Thus not all management practices that are recommended for improving soil biological fertility are useful to control plant diseases and vice versa. These differences in the response of specific groups of soil biota are also influenced by soil type and environmental conditions. For example, in the light textured soils in low rainfall regions of southern Australia, summer rainfall events that support higher levels of microbial activity result in the reduction of take-all fungus inoculum including those under residue retention systems (Sivasithamparam 1993, Roget 2001). In these carbon impoverished soils most of the general microbial activity including that of the take-all fungus is associated with the same microsite, i.e. fresh crop residues, and thus the take-all fungus that is resident in it is subjected to intense competition and predation by soil fauna. However, this may not apply to the heavier soils (red brown earths and heavy clay soils) in the summer rainfall regions of southeastern Australia because of the existence of adequate numbers of microsites to support both the pathogenic fungus and other microorganisms. The environment in these regions favours *Fusarium* and common root rot but not take-all.

Gupta and Neate (1999) discussed a conceptual framework which includes the factors that influence, at various stages in the pre-crop and crop growing season, the survival of pathogen inoculum from one season to the next and its effectiveness in causing disease on the susceptible plant (Figure 4). At each stage of pathogen survival and disease development, both specific organisms (micro- and macro) and general interactions between different groups are involved. For example, during the off-season (or in the absence of a suitable host plant), in order to survive in and near the substrate, the pathogen has to successfully compete (for carbon and nutrients) with other saprophytes and withstand predation by micro-, meso- and macro fauna (Gupta *et al.* 1996, Curl 1998). The distribution of microorganisms in soil is patchy; they are clumped near carbon and nutrient rich locations such as plant roots, decomposing crop residues and in micropores accessible to soluble organics. The environment is extremely heterogeneous. Pathogenic fungi have to withstand predation and competition in the carbon-poor bulk soil during their growth from the inoculum base to the host plant root. Similarly, for effective use of antagonists of pathogenic fungi (e.g. biocontrol organisms), their interaction with other microflora and predators need to be thoroughly understood (van Veen and Heijnin 1994, Bowen and Rovira 1999).

These complex biotic interactions which the pathogen needs to negotiate, necessitates the application of an integrated ecological approach (combination of functional and trophic groups and utilising the food-web model) in order to understand the mechanisms behind the reduced disease expression in disease suppressive soils. This approach may also help the development of management practices that allow the transfer of disease suppression to other soils and environments.

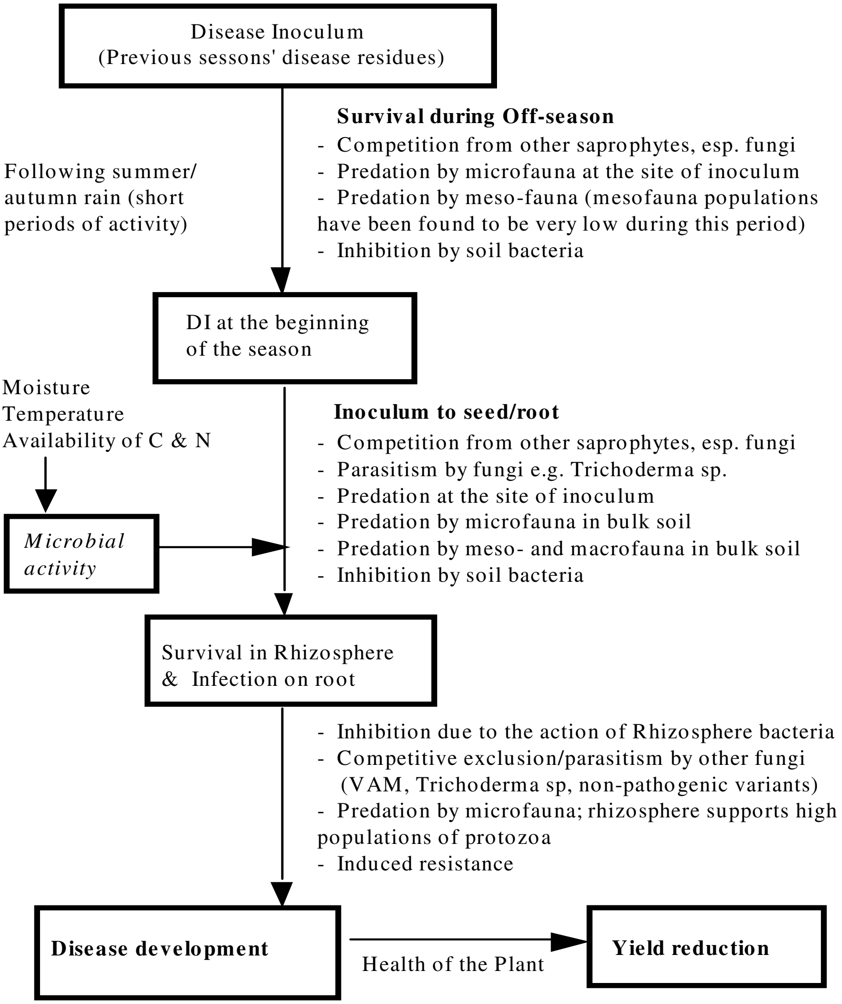

Figure 4 A conceptual frame work indicating the various factors that influence the survival and effectiveness of soil-borne root disease inoculum from one season to the next (from Gupta and Neate 1999).

6. MANAGEMENT OF SOIL BIOTA AND BIOLOGICAL FERTILITY WHICH INFLUENCES THE ROLE OF PLANT PATHOGENS IN AGRICULTURAL SYSTEMS

In the mediterranean regions of Australia, minimum tillage and stubble retention practices have led to not just the conservation of inoculum of some plant root pathogens but also to the concentration of inoculum of necrotrophic foliar pathogens at the surface of soil. Such concentration leads to early and severe seedling infections of both shoots and roots.

One of the reasons put forward for the introduction of legumes in rotation with cereals in southern Australia has been its potential to be a 'break crop' capable of reducing the carry-over of inoculum of some cereal pathogens. While this may be true of the take-all pathogen, which attacks only graminaceous hosts, it may not apply to necrotrophic pathogens such as *Pythium* spp. and *Rhizoctonia solani* AG8. In the nitrogen deficient soils of southern Australia, legumes in rotation provide the nitrogen necessary for the soil survival of fungal pathogen attacking cereals (Garrett 1970).

To conclude, many plant pathogenic fungi in their saprophytic phase may perform a number of soil functions such as the decomposition of organic matter, mineralisation - immobilisation of nutrients, degradation of agrochemicals and soil aggregation. For example, the hyphal networks of *Rhizoctonia solani* could play a beneficial role in soil aggregation during its saprophytic stage on crop residues and in bulk soil e.g. in the absence of a host plant (Tisdall *et al.* 1997). Similarly, pathogenic fungi colonising diseased crop residues play a key role in residue decomposition and the turnover of carbon and nutrients. Such activity may play a useful role in the general soil biological fertility in the absence of a host plant i.e. off-season and in the presence of alternate crops. However, these perceived benefits may not be significant for the overall soil biological fertility of the ecosystem as plant diseases have negative effects on the key source of carbon (energy) inputs through crop residues for soil biological activity. In addition, proliferation of pathogenic fungal inoculum in the absence of a host plant is not beneficial as it may lead to higher levels of disease incidence when the host plant returns. The negative effects of plant pathogens on the grain yield, above ground and below ground biomass production, carbon inputs to the soil and reduced use of water and nutrients, finally result in soil and environmental problems within the ecosystem. These generally outweigh any beneficial role of pathogenic fungi in soil functions, in particular in Australian soils low in organic matter.

7. A MEASUREMENT OF PLANT ROOT PATHOGENS AS AN INDICATOR OF SOIL BIOLOGICAL FERTILITY

The term soil health is generally referred to 'the continued capacity of soil to function as a vital living system, within ecosystem and landscape boundaries, to sustain biological productivity, promote the quality of air and water environments, and maintain plant, animal and human health' (Doran and Safley 1997). In all definitions of soil health its ability to perform plant essential functions and productivity are considered an integral part of the concept of soil biological health. Much of the literature discussing the potential indicators of soil health generally includes beneficial soil fungi such as those which form mycorrhiza, and basidiomycetes (as pollution indicators), but pathogens however are rarely considered. Hornby and Bateman (1997) discussed in detail the advantages and limitations for using plant root pathogens as bioindicators of soil health and Pankhurst *et al.* (1997) suggested that the presence of disease might indicate the existence of a major constraint to productivity and biological fertility of soil.

An ideal indicator of soil health, including soil biological fertility, should i) be linked with ecosystem processes, ii) integrate various components, iii) respond to management and climate at an appropriate time scale, iv) be easy and cost effective to measure, and v) work well in a broad spectrum of agricultural environments. Plant pathogen related measurements e.g. the level of pathogen inoculum and the incidence of plant disease, are linked to one of the principal ecosystem processes i.e. plant growth and productivity (Hornby and Bateman 1997, Pankhurst *et al.* 1995). The level of disease incidence and severity does integrate various soil, plant and environment related factors such as the amount of pathogen inoculum, plant nutrient status and plant-beneficial biota-pathogenic fungi interactions. The amount of inoculum that reaches the plant is influenced by various soil and environmental factors e.g. pH, structure, moisture etc. Thus, the level of plant disease is an integrative indicator of different plant-soil-environmental components. In addition to being integrative, plant disease incidence and severity responds to soil management and climate in time scales that are relevant to land users and thus may be one of the useful indicators of soil biological fertility i.e. one of the members of a ‘minimum data set’ to evaluate soil biological fertility.

Pathogen levels in soil are dynamic and assays of pathogen at one time of the year may not reflect correctly the biological fertility or biological health of soil at other times of the season or year. Some pathogens are host specific and their surviving inoculum status during the rotation period may not be significant. For example, the inoculum status in the stubble of *Diaporthe toxica* in the absence of a lupin crop or that of *Leptosphaeria maculans* in the absence of a canola crop may not pose a threat to the crop in rotation. Even within the cropping season, the soil-borne inoculum status of damping-off pathogens (e.g. species of *Pythium, Rhizoctonia* etc.) pose little hazard to the crop once the plants have passed the seedling stage. Thus the selection of a single pathogenic organism as an indicator may not be possible and site or crop specific pathogen selection may be necessary. Since one of the important criteria for an ideal bioindicator is its suitability or usefulness in different environments, not all plant pathogen measurements meet this essential property. Even though pathogen measurements lack this universal applicability they may be successfully used in specific environments. Following evaluation of field environmental and disease data, covering over 25 years, Roget (2001) proposed a model for pre-season prediction of potential losses from take-all disease, utilising a DNA based assay to quantify *Gaeumannomyces graminis* var. *tritici* (Herdina and Roget 2000) coupled with the rainfall and crop rotation data.

In Figure 5 we describe a conceptual scheme indicating the various factors to consider when discussing the relevance of plant pathogens to evaluate soil biological fertility. This scheme is based on the current knowledge of the interactions among environment, management practices, plant, soil biota and pathogenic organisms since disease incidence is not just an interaction between the host plant and pathogen. The presence of plant pathogenic microorganisms alone does not result in the disease incidence even in a susceptible host plant in natural soil environments.

Soil and environmental factors that influence the pathogen reaching the host plant root and establish disease affect the usefulness of pathogen assays as bioindicators. With take-all for instance, the environment decides the extent of disease even where the resident inoculum levels are high (Cotterill and Sivasithamparam 1989). Pathogen level at any particular time of the season is not only influenced by the previous presence of a susceptible host but also by the environmental factors prior to the measurement which may have had a significant influence. For example, Roget (2001) indicated the role of summer rainfall, both amount and time of occurrence, on the level of take-all fungus at the start of the crop season in the Southern Australian soils. The influence of different crop and soil management practices on plant pathogen levels and incidence of various diseases is well documented (Rovira 1986, Neate 1994). Similarly rhizosphere interactions between beneficial and pathogenic microorganisms have a significant influence on the establishment of disease (Rovira *et al.* 1990, Bowen and Rovira 1999). Soil fertility levels (availability of N, P, K, Zn and Mn) often have greater effects on the severity of root diseases rather than on disease incidence (Huber 1981, Cotterill and Sivasithamparam 1989, Thongbai *et al.* 1993, Wilhelm *et al.* 1990).

Disease suppressiveness of soil is the ability of a soil to suppress disease severity even in the presence of a pathogen, host plant and favourable climatic conditions (Baker and Cook 1974, Simon and Sivasithamparam 1989, Roget 1995, Lemanceau *et al.* 2000). The different types of disease suppression mechanisms are related to the establishment of the pathogen, reduced parasitic activity of the pathogen and the level of disease incidence or severity. Roget *et al.* (1999) found that all soils have some potential for disease suppressiveness and thus disease suppression is not an absolute characteristic but a continuum from highly suppressive soils to poorly suppressive (i.e. conducive) soils. This means that theoretically soils could all be ranked according to their level of suppressiveness. However, such a ranking should also consider the type of suppressiveness in order to evaluate its usefulness across diseases, crops, soil types and environments.

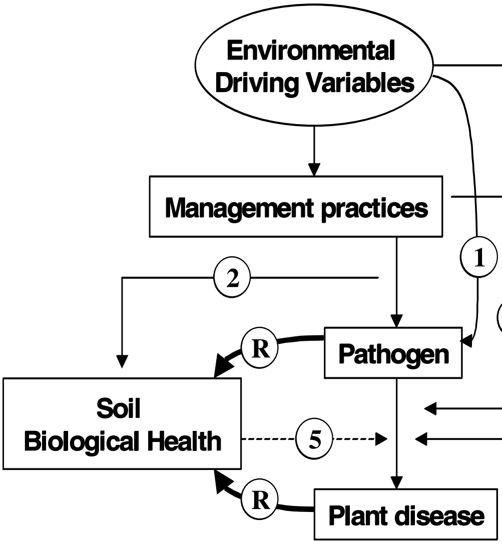

Figure 5 A conceptual scheme showing the various influencing factors in considering the relevance of plant pathogens (R) to evaluate soil biological fertility (based on reports by Neate 1994, Roper and Gupta 1995, Roget 1995, Hornby and Bateman 1997, Gupta and Neate 1999, Herdina *et al.* 2001). 1- environmental variables affecting the pathogen, effect of summer rainfall on take-all fungus inoculum (Roget 2001); 2 - management effects on general soil biological health independent of pathogen, might even be conflicting, direct drill benefits on microbial activity but negative for rhizoctonia bare patch; 3 - environmental changes affecting host response to disease; 4 - management effects that influence host response to disease, effects of fertiliser type (Smiley and Cook 1973), plant variety, tillage method etc. and 5 - biological factors that influence the host response to disease incidence; predation induced reduction in disease incidence and disease suppressiveness through improvements in plant nutrient availability (Gupta *et al.* 1999, Lemanceau *et al.* 2000).

For the disease suppression known as ‘general suppression’, the inhibition of pathogenic populations is related to either the activity of the total microflora or diverse microbial-faunal interactions. The ‘specific suppression phenomenon’ has been attributed to the activity of specific microbial groups (antagonists). Some abiotic factors of soil such as pH and clay content have also been attributed to certain types of disease suppressiveness e.g. fusarium wilts (Lemanceau *et al.* 2000). Disease suppression especially of root diseases is most evident in highly fertile soils.

'General antagonism' (Cook and Baker 1983) has generally been associated with soil fertility. Suppression in such situations is evident as a continuum, the levels being determined by soil fertility and often related to cropping history. Therefore, the interpretation of pathogen assays as indicators of soil biological fertility needs to consider the level of disease suppressiveness of a particular soil and farming system.

8. CONCLUSIONS

Soil-borne plant pathogens affect biological fertility directly and indirectly. Directly, they affect the efficiency of roots to acquire water and nutrients. Indirectly, the reduction in plant biomass resulting from root disease leads to reduced input of the quality and quantity of organic matter that eventually enters the soil. A complex set of organisms, both beneficial and deleterious (including pathogens), is active in soil especially in the rhizosphere region. The environmental conditions, both physical and chemical, determine the balance in their activities that affect soil fertility and plant growth. Management options to enhance soil biological fertility therefore need to consider these interactions and their outcomes both in the bulk and rhizosphere region.

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