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Microbial interactions and biocontrol in the rhizosphere

John M. Whipps[1]

Plant Pathology and Microbiology Department, Horticulture Research International, Wellesbourne, Warwick CV35 9EF, UK

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Abstract

The loss of organic material from the roots provides the energy for the development of active microbial populations in the rhizosphere around the root. Generally, saproptrophs or biotrophs such as mycorrhizal fungi grow in the rhizosphere in response to this carbon loss, but plant pathogens may also develop and infect a susceptible host, resulting in disease. This review examines the microbial interactions that can take place in the rhizosphere and that are involved in biological disease control. The interactions of bacteria used as biocontrol agents of bacterial and fungal plant pathogens, and fungi used as biocontrol agents of protozoan, bacterial and fungal plant pathogens are considered. Whenever possible, modes of action involved in each type of interaction are assessed with particular emphasis on antibiosis, competition, parasitism, and induced resistance. The significance of plant growth promotion and rhizosphere competence in biocontrol is also considered. Multiple microbial interactions involving bacteria and fungi in the rhizosphere are shown to provide enhanced biocontrol in many cases in comparison with biocontrol agents used singly. The extreme complexity of interactions that can occur in the rhizosphere is highlighted and some potential areas for future research in this area are discussed briefly.

Key words: Bacteria, biocontrol, fungi, roots, soil.

Introduction

As seeds germinate and roots grow through the soil the loss of organic material provides the driving force for the development of active microbial populations around the root, known as the rhizosphere effect (Whipps, 1990; Morgan and Whipps, 2001). Although the stimulation in microbial activity is a general phenomenon largely involving saprotrophs, specific groups of symbionts may be selectively enhanced. For example, mutualistic biotrophic symbioses may develop between *Rhizobia* and legumes, and mycorrhizal fungi may interact with their plant hosts. However, antagonistic symbioses between pathogens and roots can also form resulting in disease. The microbial interactions taking place in the spermosphere and rhizosphere associated with disease development and especially biocontrol of these diseases form the background of this review.

Interest in biological control has increased recently fuelled by public concerns over the use of chemicals in the environment in general, and the need to find alternatives to the use of chemicals for disease control. The key to achieving successful, reproducible biological control is the gradual appreciation that knowledge of the ecological interactions taking place in soil and root environments is required to predict the conditions under which biocontrol can be achieved (Deacon, 1994; Whipps, 1997*a*) and, indeed, may be part of the reason why more biocontrol agents are reaching the market-place (Fravel, 1999; Whipps and Lumsden, 2001; Whipps and Davies, 2000). This type of work requires a study not only of any potential biocontrol agent *per se* but also its interactions with the crop, the natural resident microbiota and the environment as well. In this regard, it is well known that some soils are naturally suppressive to some soil-borne plant pathogens such as *Fusarium oxysporum* Schlect.: Fr. Emend. Snyder & Hansen, *Gaeumannomyces graminis* (Sacc.) v. Arx & Oliver, *Pythium* and *Phytophthora* species and this suppression relates to both physicochemical and microbiological features of the soil (Whipps,

[1] Fax: +44 1789 470552. E-mail: john.whipps@hri.ac.uk

1997*a*). Importantly, a soil that is suppressive to one pathogen is not necessarily suppressive to another, and so specificity in the soil–plant–microbe interactions for disease suppression exists. Modern methods for analysing microbial community structures may prove particularly valuable to help define the key organisms or groups of organisms responsible for such natural suppression as well as for monitoring the spread and impact of introduction of specific biocontrol agents or other management practices on natural microbial populations (Duineveld *et al*., 1998; Natsch *et al*., 1998; Abassi *et al*., 1999; Buyer *et al*., 1999; Gamo and Shoji, 1999; Mazzola, 1999; Shiomi *et al*., 1999; Tiedje *et al*., 1999; Smit *et al*., 1999; Postma *et al*., 2000). Significantly, disease suppression can also be achieved by manipulation of the physicochemical and microbiological environment through management practices such as the use of soil amendments, crop rotations, use of fumigants or soil solarization. However, at present, greatest interest resides with the development and application of specific biocontrol agents for the control of diseases on seeds and roots and the interaction of these with pathogens and hosts, and will form the focus of this paper. There have been numerous reviews in recent years on this topic (see Whipps, 1997*a*, *b*, *c*; Punja, 1997; van Loon, 1997; Burges, 1998; Boland and Kuykendall, 1998; Harman and Kubicek, 1998; Funck Jensen and Lumsden, 1999; Hoitink and Boehm, 1999; Mathre *et al*., 1999, and references therein) and so only selected recent examples, illustrating key features of biocontrol on seeds and roots, particularly the different modes of action, will be discussed whenever possible. Modes of action include: inhibition of the pathogen by antimicrobial compounds (antibiosis); competition for iron through production of siderophores; competition for colonization sites and nutrients supplied by seeds and roots; induction of plant resistance mechanisms; inactivation of pathogen germination factors present in seed or root exudates; degradation of pathogenicity factors of the pathogen such as toxins; parasitism that may involve production of extracellular cell wall-degrading enzymes, for example, chitinase and β-1,3 glucanase that can lyse pathogen cell walls (Keel and Défago, 1997; Whipps, 1997*a*). None of the mechanisms are necessarily mutually exclusive and frequently several modes of action are exhibited by a single biocontrol agent. Indeed, for some biocontrol agents, different mechanisms or combinations of mechanisms may be involved in the suppression of different plant diseases.

Bacteria–bacterial pathogen interactions

In the last few years there have been relatively few studies of bacteria applied to seeds and roots for the purpose of controlling bacterial diseases. One example, is the application of non-pathogenic strains of *Streptomyces* to control scab of potato (*Solanum tuberosum* L.) caused by *Streptomyces scabies* (Thaxter) Waksman and Henrici (Ryan and Kinkel, 1997; Neeno-Eckwall and Schottel, 1999). Here biocontrol may operate through antibiosis or competition for space or nutrients in the rhizosphere. In contrast, *Pseudomonas fluorescens* (Trevisan) Migula F113 was shown to control the soft rot potato pathogen *Erwinia carotovora* subsp. *atroseptica* (van Hall) Dye by production of the antibiotic 2,4-diacetylphloroglucinol (DAPG) and, through use of co-inoculation experiments with mutants lacking DAPG production, that competition was not a feature of biocontrol in this system (Cronin *et al*., 1997). Some evidence was also obtained that siderophore production by *P. fluorescens* F113 may play a role in biocontrol of potato soft rot under iron-limiting conditions, but DAPG appears to be the major biocontrol determinant. *Pseudomonas* species may also control crown gall disease in many dicotyledonous plants caused by *Agrobacterium tumefaciens* (Smith & Townsend) Conn (Khmel *et al*., 1998). However, the classic, and still commercially successful, bacterial-based biocontrol system is the use of non-pathogenic *Agrobacterium* strains to control *Agrobacterium tumefaciens*. Long-term molecular and ecological studies of this control system have identified how the biocontrol works and have also allowed potential problems associated with its use in the field to be overcome. The most widely used non-pathogenic *Agrobacterium* strain K84 produces a highly specific antibiotic agrocin 84, which is encoded by plasmid pAgK84. Inundative inoculation of *Agrobacterium* strain K84 to roots by dipping in cell suspensions prior to exposure to the pathogen effectively controls those strains of pathogen susceptible to agrocin 84. However, because there is a risk that plasmid pAgK84 could be transferred to pathogenic strains and reduce effectiveness of control (Vicedo *et al*., 1996; Stockwell *et al*., 1996; López-López *et al*., 1999), a transfer deletion mutant of K84, K1026 has been constructed (Jones *et al*., 1988). Strain K1026 is as efficient as K84 in biocontrol of both strains susceptible to agrocin 84 and those resistant to agrocin 84 (Jones and Kerr, 1989; Vicedo *et al*., 1993) and so, clearly, production of agrocin 84 is not the only mechanism of biocontrol. Production of other antibiotics such as agrocin 434 or ALS 84 may play a part (Peñalver *et al*., 1994; McClure *et al*., 1998), but the ability to survive and compete on roots may also be important. Studies where pathogenic cells were co-inoculated with K84 or K1026 resulted in survival of the pathogen on roots up to 8 months later, although no symptoms were present, providing evidence that the non-pathogenic strains prevented disease expression rather than killing pathogen cells directly (Peñalver and Lopez, 1999; Johnson and DiLeone, 1999).

Bacteria–fungal pathogen interactions

The volume of literature in this area continues to increase at a rapid rate, stimulated by the increasing ease with which molecular techniques can be applied to answer questions concerning distribution, and occurrence and relative importance of specific modes of action. Some examples of the different types of bacteria-fungal pathogen interactions examined in the spermosphere and rhizosphere in just the last three years are given in Table 1. Although a range of different bacterial genera and species have been studied, the overwhelming number of papers have involved the use of *Pseudomonas* species. Clearly, *Pseudomonas* species must have activity but it begs the question as to the features that make this genus so effective and the choice of so many workers. Pseudomonads are characteristically fast growing, easy to culture and manipulate genetically in the laboratory, and are able to utilize a range of easily metabolizable organic compounds, making them amenable to experimentation. But, in addition, they are common rhizosphere organisms and must be adapted to life in the rhizosphere to a large extent (deWeger *et al*., 1995; Marilley and Aragno, 1999). Having appropriate ecological rhizosphere competence may be a key feature for reproducible biological control activity in the spermosphere and rhizosphere. This criterion is already widely appreciated for many fungal biocontrol agents (see later). A few specific examples of the modes of action involved with bacterial biocontrol of fungal pathogens in the rhizosphere and spermosphere are given below.

Antibiosis

There are numerous reports of the production of antifungal metabolites (excluding metal chelators and enzymes) produced by bacteria *in vitro* that may also have activity *in vivo*. These include ammonia, butyrolactones, 2,4-diacetylphloroglucinol (Ph1), HCN, kanosamine, Oligomycin A, Oomycin A, phenazine-1-carboxylic acid (PCA), pyoluterin (Plt), pyrrolnitrin (Pln), viscosinamide, xanthobaccin, and zwittermycin A as well as several other uncharacterized moieties (Milner *et al*., 1996; Keel and Défago, 1997; Whipps, 1997*a*; Nielson *et al*., 1998; Kang *et al*., 1998; Kim *et al*., 1999; Thrane *et al*., 1999; Nakayama *et al*., 1999). To demonstrate a role for antibiotics in biocontrol, mutants lacking production of antibiotics or over-producing mutants have been used (Bonsall *et al*., 1997; Chin-A-Woeng *et al*., 1998; Nowak-Thompson *et al*., 1999). Alternatively, the use of reporter genes or probes to demonstrate production of antibiotics in the rhizosphere is becoming more commonplace (Kraus and Loper, 1995; Raaijmakers *et al*., 1997; Chin-A-Woeng *et al*., 1998). Indeed, isolation and characterization of genes or gene clusters responsible for antibiotic production has now been achieved (Kraus and Loper, 1995; Bangera and Thomashow, 1996; Hammer *et al*., 1997; Kang *et al*., 1998; Nowak-Thompson *et al*., 1999). Significantly, both Phl and PCA have been isolated from the rhizosphere of wheat following introduction of biocontrol strains of *Pseudomonas* (Thomashow *et al*., 1990; Bonsall *et al*., 1997; Raaijmakers *et al*., 1999), finally confirming that such antibiotics are produced *in vivo*. Further, Ph1 production in the rhizosphere of wheat was strongly related to the density of the bacterial population present and the ability to colonize roots (Raaijmakers *et al*., 1999). PCA from *Pseudomonas aureofaciens* Kluyver Tx-1 has even been used as a direct field treatment for the control of dollar spot (*Sclerotinia homeocarpa* F. T. Bennett) on creeping bentgrass (*Agrostis palustris* Hudson) (Powell *et al*., 2000).

Antibiotic production by bacteria, particularly pseudomonads, seems to be closely regulated by a two-component system involving an environmental sensor (presumably a membrane protein) and a cytoplasmic response factor (Keel and Défago, 1997). Mutation in either gene has similar multiple effects on antibiotic production. For example, *P. fluorescens* Pf-5 with a mutation in the *apdA* sensor gene lost the ability to produce HCN, Plt and Pln (Hrabak and Willis, 1992; Corbell and Loper, 1995) and *P. fluorescens* CHA0 with a defect in the *gacA* response gene lost the ability to produce Phl, Plt and HCN as well as protease and phospholipase C (Laville *et al*., 1992; Sacherer *et al*., 1994). However, the environmental signals that control the two-component system are unknown. Interestingly, the *gacA* gene is required for biocontrol activity in *P. fluorescens* CHA0 in the rhizosphere of dicotyledous plants, but not in those of the Gramineae (Schmidli-Sacherer *et al*., 1997), although the mechanisms are unclear.

Other two-component signalling phenomena may also be involved in PCA production by pseudomonads on roots. *Pseudomonas aureofaciens* 30-84 is a biocontrol agent of take-all disease of wheat (*Triticium aestivum* L.) caused by *Gaeumannomyces graminis* var. *tritici* Walker and operates through inhibiting growth of the pathogen by production of PCA (Pierson III and Pierson, 1996). In this system, pathogen growth on the root increases root exudation and this results in an increase in the population of *P. aureofaciens* 30-84 and other bacteria in the infection zone. Consequently, there is an increase in the level of the signal molecule N-acyl-L-homoserine lactone (HSL) produced at low levels constitutively by the *phzI* gene, in the rhizosphere which is sufficient to switch on the PCA synthesis pathway in *P. aureofaciens* 30-84 controlled by the *phzR* gene. The resulting PCA production inhibits further growth of the pathogen. This explains why *P. aureofaciens* 30-84 does not reduce the number of infection sites on the roots, but inhibits secondary growth

Table 1. *Recent examples of bacteria applied to seeds or roots providing biocontrol of fungal plant pathogens*

Bacteria	Fungal pathogen	Plant	Environment	Reference
Actinoplanes spp.	*Pythium ultimum*	Table beet	Soil	Khan *et al*., 1997
Bacillus spp.	*Rhizoctonia solani*; *Gaeumannaomyces graminis* var. *tritici*	Wheat	Soil	Ryder *et al*., 1999
Bacillus subtilis GB03	*Fusarium oxysporum* f. sp. *ciceris*	Chickpea	Sterile soil	Hervás *et al*., 1998
B. subtilis BACT-D	*Pythium aphanidermatum*	Tomato	Soil	Utkhede *et al*., 1999
Burkholderia cepacia A3R	*Fusarium graminearum*	Wheat	Soil	Huang and Wong, 1998
B. cepacia PHQM 100	*Fusarium* spp.	Maize	Soil	Hebbar *et al*., 1998
	Pythium spp.	Maize	Soil	Hebbar *et al*., 1998
Comamonas acidovorans HF42	*Magnaporthe poae*	Kentucky bluegrass	Soil	Thompson *et al*., 1998
Enterobacter sp. BF14	*Magnaporthe poae*	Kentucky bluegrass	Soil	Thompson *et al*., 1998
Paenibacillus sp. 300	*Fusarium oxysporum* f. sp. *cucumerinum*	Cucumber	Soil-less mix	Singh *et al*., 1999
Pseudomonas spp.	*Fusarium oxysporum* f. sp. *radicis-lycopersici*	Tomato	Rockwool	Sharifi-Tehrani *et al*., 1998
Pseudomomas aureofaciens AB244	*Pythium ultimum*	Tomato	Soil-less mix	Warren and Bennett, 1999
P. aureofaciens 63-28	*P. aphanidermatum*	Cucumber	Vermiculite	Chen *et al*., 1998
Pseudomonas chlororaphis MA342	*Drechslera graminea*	Barley	Soil	Johnsson *et al*., 1998
	D. teres	Barley	Soil	Johnsson *et al*., 1998
	D. avenae	Oats	Soil	Johnsson *et al*., 1998
	Ustilago avenae	Oats	Soil	Johnsson *et al*., 1998
	U. hordei	Barley	Soil	Johnsson *et al*., 1998
	Tilletia caries	Wheat	Soil	Johnsson *et al*., 1998
P. chlororaphis PCL 1391	*Fusarium oxysporum* f. sp. *radicis-lycopersici*	Tomato	Soil	Chin-A-Woeng *et al*., 1998
P. chlororaphis RD31-3A	*Fusarium* spp.	Douglas fir	Seed	Hoefnagels and Linderman, 1999
Pseudomonas corrugata 13	*Pythium aphanidermatum*	Cucumber	Vermiculite	Chen *et al*., 1998
Pseudomonas fluorescens	*Fusarium oxysporum* f. sp. *raphani*	Radish	Soil/sand	de Boer *et al*., 1999
P. fluorescens WCS417	*F. oxysporum* f. sp. *raphani*	Radish	Rockwool	Duijff *et al*., 1998
P. fluorescens WCS358	*F. oxysporum* f. sp. *lini*	Flax	Nutrient solution	Duijff *et al*., 1999
P. fluorescens Q8r1-96	*Gaeumannomyces graminis*	Wheat	Soil	Raaijmakers and Weller, 1998
P. fluorescens BTP7	*Pythium aphanidermatum*	Cucumber	Vermiculite	Ongena *et al*., 1999
P. fluorescens VO61	*Pythium ultimum*	*Lotus corniculatus*	Soil mix	Bagnasco *et al*., 1998
	Rhizoctonia solani	Rice	Soil	Vidhyasekaran and Muthamilan, 1999
Pseudomonas putida	*Fusarium oxysporum* f. sp. *raphani*	Radish	Soil/sand	de Boer *et al*., 1999
P. putida BTP1	*Pythium aphanidermatum*	Cucumber	Vermiculite	Ongena *et al*., 1999
Serratia plymuthica	*Pythium ultimum*	Cucumber	Peat-perlite-vermiculite	Benhamou *et al*., 2000
Stenotrophomonas maltophilia C3	*Rhizoctonia solani*	Tall fescue	Soil mix	Giesler and Yuen, 1998
Streptomyces sp. 385	*Fusarium oxysporum* f. sp. *cucumerinum*	Cucumber	Soil-less mix	Singh *et al*., 1999

of the pathogen. Significantly, HSL from other members of the rhizosphere microbial community can contribute to PCA production in *P. aureofaciens* 30-84 raising the question of the significance of interpopulation signalling on biocontrol and perhaps the enhanced performance of certain strains of bacteria when introduced with mixtures of other bacterial biocontrol strains (Pierson and Weller, 1994). In addition, antibiotic production in *Pseudomonas* spp. may be further controlled by the activity of housekeeping sigma factors encoded by *rpoS* or *rpoD* genes (Sarniguet *et al*., 1995; Schnider *et al*., 1995), illustrating the complexity of these regulatory systems.

Interestingly, signalling between pathogenic fungi and potential biocontrol bacteria has also been detected. In one case, trehalose derived from *Pythium debaryanum* Hesse up-regulated genes in its biocontrol strain *Pseudomonas fluorescens* ATCC 17400 (Gaballa *et al*., 1997) and yet in another example *Pythium ultimum* Trow caused a down-regulation of five gene clusters of *P. fluorescens* F113 which provides biocontrol of this pathogen in the rhizosphere of sugar beet (*Beta vulgaris* L.) (Fedi *et al*., 1997). These findings may be of considerable significance for bacterial–fungal interactions in general and has major implications for the control of gene expression in complex microbial communities.

Competition for iron

Although competition between bacteria and fungal plant pathogens for space or nutrients has been known to exist as a biocontrol mechanism for many years (see Whipps, 1997*a*, for references) the greatest interest recently has involved competition for iron. Under iron-limiting conditions, bacteria produce a range of iron chelating compounds or siderophores which have a very high affinity for ferric iron. These bacterial iron chelators are thought to sequester the limited supply of iron available in the rhizosphere making it unavailable to pathogenic fungi, thereby restricting their growth (O'Sullivan and O'Gara, 1992; Loper and Henkels, 1999). Recent studies have clearly shown that the iron nutrition of the plant influences the rhizosphere microbial community structure (Yang and Crowley, 2000). Iron competition in pseudomonads has been intensively studied and the role of the pyoverdine siderophore produced by many *Pseudomonas* species has been clearly demonstrated in the control of *Pythium* and *Fusarium* species, either by comparing the effects of purified pyoverdine with synthetic iron chelators or through the use of pyoverdine minus mutants (Loper and Buyer, 1991; Duijff *et al*., 1993). Pseudomonads also produce two other siderophores, pyochelin and its precursor salicylic acid, and pyochelin is thought to contribute to the protection of tomato plants from *Pythium* by *Pseudomonas aeruginosa* (Schroeter) Migula 7NSK2 (Buysens *et al*., 1996). However, siderophores are not always implicated in disease control by pseudomonads (Schmidli-Sacherer *et al*., 1997; Ongena *et al*., 1999). The dynamics of iron competition in the rhizosphere are often complex. For example, some siderophores can only be used by the bacteria that produce them (Ongena *et al*., 1999), whereas others can be used by many different bacteria (Loper and Henkels, 1999). Different environmental factors can also influence the quantity of siderophores produced (Duffy and Défago, 1999). There is also the further complication that pyoverdine and salicylate may act as elicitors for inducing systemic resistance against pathogens in some plants (Métraux *et al*., 1990; Leeman *et al*., 1996*b*).

Parasitism and production of extracellular enzymes

The ability of bacteria, especially actinomycetes, to parasitize and degrade spores of fungal plant pathogens is well established (El-Tarabily *et al*., 1997). Assuming that nutrients pass from the plant pathogen to bacteria, and that fungal growth is inhibited, the spectrum of parasitism could range from simple attachment of cells to hyphae, as with the *Enterobacter cloacae* (Jordan) Hormaeche & Edwards–*Pythium ultimum* interaction (Nelson *et al*., 1986) to complete lysis and degradation of hyphae as found with the *Arthrobacter–Pythium debaryanum* interaction (Mitchell and Hurwitz, 1965). If fungal cells are lysed and cell walls are degraded then it is generally assumed that cell wall-degrading enzymes produced by the bacteria are responsible, even though antibiotics may be produced at the same time. Considerable effort has gone into identifying cell wall-degrading enzymes produced by biocontrol strains of bacteria even though relatively little direct evidence for their presence and activity in the rhizosphere has been obtained. For example, biocontrol of *Phytophthora cinnamomi* Rands root rot of *Banksia grandis* Willd. was obtained using a cellulase-producing isolate of *Micromonospora carbonacea* Luedemann & Brodsky (El-Tarabily *et al*., 1996) and control of *Phytophthora fragariae* var. *rubi* Hickman causing raspberry root rot was suppressed by the application of actinomycete isolates that were selected for the production of β-1,3-, β-1,4- and β-1,6-glucanases (Valois *et al*., 1996). Chitinolytic enzymes produced by both *Bacillus cereus* Frankland and *Pantoea* (*Enterobacter*) *agglomerans* (Beijerinck) Gavini *et al*. also appear to be involved in biocontrol of *Rhizoctonia solani* Kühn (Chernin *et al*., 1995, 1997; Pleban *et al*., 1997). Tn*5* mutants of *E. agglomerans* (Beijerinck) Gavini *et al*. deficient in chitinolytic activity were unable to protect cotton (*Gossypium barbardense* L.) and expression of the *chiA* gene for endochitinase in *Escherichia coli* (Migula) Castellani & Chalmers allowed the transformed strain

to inhibit *R. solani* on cotton seedlings. Similar techniques involving Tn*5* insertion mutants and subsequent complementation demonstrated that biocontrol of *Pythium ultimum* in the rhizosphere of sugar beet by *Stenotrophomonas maltophila* (Hugh) Palleroni & Bradbury W81 was due to the production of extracellular protease (Dunne *et al*., 1997).

Induced resistance

Perhaps the greatest growth area in biocontrol in the last few years has been concerned with induced resistance defined as 'the process of active resistance dependent on the host plant's physical or chemical barriers, activated by biotic or abiotic agents (inducing agents)' (Kloepper *et al*., 1992). This has come about through the synergistic interaction of microbiologists, plant pathologists and plant scientists armed with an appropriate battery of molecular tools. The effect had previously often been overlooked through inadequate techniques or controls as well as the biocontrol agent exhibiting other modes of action at the same time. Most work has focused on the systemic resistance induced by non-pathogenic rhizosphere-colonizing *Bacillus* and *Pseudomonas* species in systems where the inducing bacteria and the challenging pathogen remained spatially separate for the duration of the experiment, and no direct interaction between the bacteria and pathogen was possible (Sticher *et al*., 1997; van Loon, 1997). Such split root or spatial root inoculation experiments were used to demonstrate the phenomenon in radish (*Raphanus sativus* L.) and *Arabidopsis* against *Fusarium oxysporum* (Leeman *et al*., 1996*a*; van Wees *et al*., 1997) and in cucumber (*Cucumis sativus* L.) against *Pythium aphanidermatum* (Edson) Fitzp. (Chen *et al*., 1998). Various combinations of timing and position have indicated that induced resistance also occurs in carnation (*Dianthus caryophyllus* L.) (van Peer *et al*., 1991), tobacco (*Nicotiana tabacum* L.) (Maurhaufer *et al*., 1994) and tomato (*Lycopersicon esculentum* Mill.) (Duijff *et al*., 1997). Bacteria differ in ability to induce resistance, with some being active on some plant species and not others; variation in inducibility also exists within plant species (van Loon, 1997). The full range of inducing moieties produced by bacteria is probably not yet known, but lipopolysaccharides (Leeman *et al*., 1995) and siderophores (Métraux *et al*., 1990; Leeman *et al*., 1996*b*) are clearly indicated.

The definition of induced resistance suggested by Kloepper *et al*. covered both biotic and abiotic inducers (Kloepper *et al*., 1992). Although the phenotypic effects of root inoculation with bacteria may be similar to treatment with abiotic agents or micro-organisms that cause localized damage, the biochemical and mechanistic changes appear to be subtly different. This has resulted in the term induced systemic resistance (ISR) for bacterially-induced resistance and systemic acquired resistance for the other forms (Pieterse *et al*., 1996). The major differences are that pathogenesis-related (PR) proteins such as chitinases, β-1,3-glucanases, proteinase inhibitors and one or two other rarer types, are not universally associated with bacterially induced resistance (Hoffland *et al*., 1995) and salicylic acid (a known inducer of SAR) is not always involved in expression of ISR, but this is dependent on bacterial strain and host plant involved (Pieterse *et al*., 1996; de Meyer *et al*., 1999; Chen *et al*., 1999). Ethylene responsiveness may also be required at the site of inoculation of the inducing bacteria for ISR to occur (Knoester *et al*., 1999).

Changes that have been observed in plant roots exhibiting ISR include: (1) strengthening of epidermal and cortical cell walls and deposition of newly formed barriers beyond infection sites including callose, lignin and phenolics (Benhamou *et al*., 1996*a*, *b*, *c*, 2000; Duijff *et al*., 1997; Jetiyanon *et al*., 1997; M'Piga *et al*., 1997); (2) increased levels of enzymes such as chitinase, peroxidase, polyphenol oxidase, and phenylalanine ammonia lyase (M'Piga *et al*., 1997; Chen *et al*., 2000); (3) enhanced phytoalexin production (van Peer *et al*., 1991; Ongena *et al*., 1999); (4) enhanced expression of stress-related genes (Timmusk and Wagner, 1999). However, not all of these biochemical changes are found in all bacterial–plant combinations (Steijl *et al*., 1999). Similarly, the ability of bacteria to colonize the internal tissue of the roots has been considered to be an important feature in many of the bacterial–root interactions involving ISR, but is not a constant feature of them all (Steijl *et al*., 1999).

Plant growth-promoting rhizobacteria (PGPR)

The concept of PGPR is now well established (Bashan, 1998; Shishido and Chanway, 1999) and so some consideration of the relationship of PGPRs to biocontrol is worthwhile. PGPR increase plant growth indirectly either by the suppression of well-known diseases caused by major pathogens or by reducing the deleterious effects of minor pathogens (micro-organisms which reduce plant growth but without obvious symptoms). Most of the bacteria discussed so far in this review fall into this category of PGPR. Alternatively, PGPR may increase plant growth in other ways, for example, by associative N_2 fixation (Hong *et al*., 1991), solubilizing nutrients such as P (Whitelaw, 2000), promoting mycorrhizal function (Garbaye, 1994), regulating ethylene production in roots (Glick, 1995), releasing phytohormones (Arshad and Frankenberger, 1991; Beyeler *et al*., 1999), and decreasing heavy metal toxicity (Burd *et al*., 1998). It has been suggested that the two groups should be reclassified into biocontrol plant growth-promoting bacteria (biocontrol PGPB) and PGPB (Bashan and Holguin, 1998). To date

this proposal does not seem to have been widely accepted, but it does highlight the need to consider the full ecological interactions taking place following application of bacteria to seeds and roots that lead to plant growth promotion. It is also important to remember that deleterious rhizobacteria that inhibit plant growth are also known (Nehl *et al*., 1996) which can influence such interactions.

Irrespective of mode of action, a key feature of all PGPR is that they all colonize roots to some extent. In some cases this may involve specific attachment through, for example, pili, as with the attachment of *Pseudomonas fluorescens* 2-79 to the surface of wheat roots (Vesper, 1987). However, such specific attachment does not seem to be an absolute requirement for colonization (de Weger *et al*., 1995). Colonization may involve simply root surface development but, endophytic colonization of the root is also known, and the degree of endophytic colonization depends on bacterial strain and plant type. Endophytic growth in roots has been recorded with the PGPR *Bacillus polymyxa* (Prazmowski) Macé Pw-ZR and *Pseudomonas fluorescens* Sm3-RN on spruce (*Picea glauca*×*P. engelmannii*) (Shishido *et al*., 1999), with the biocontrol strains of *Bacillus* sp. L324-92R_{12} and *P. fluorescens* 2-79RN_{10} on wheat (Kim *et al*., 1997) and with several that induce resistance such as *Bacillus pumilus* Meyer & Gottheil SE34 and *P. fluorescens* 63-28 on pea (*Pisum sativum* L.) (Benhamou *et al*., 1996*a*, *b*; M'Piga *et al*., 1997), *P. fluorescens* CHA0 on tobacco (Troxler *et al*., 1997) and *P. fluorescens* WCS417r on tomato (Duijff *et al*., 1997). Large scale differences in spread within the plant may occur. Some, such as *B. polymyxa* Pw-2B, *P. fluorescens* SM3-RN, *Bacillus* sp. L324-92R_{12}, and *P. fluorescens* 2-79RN_{10} spread from roots to aerial plant parts whereas others may not (Kim *et al*., 1997). Small scale differences are also known. For example, both *B. pumilus* SE34 and *P. fluorescens* 63-28 grow on the root surface and intercellarly in pea roots (Benhamou *et al*., 1996*a*, *b*; M'Piga *et al*., 1997) whereas surface growth, inter- and intra-cellular growth occurred with *P. fluorescens* WCS417r in tomato and *P. fluorescens* CHA0 in tobacco (Duijff *et al*., 1997; Troxler *et al*., 1997). These endophytic bacteria may be in a particularly advantageous ecological position in that they may be able to grow and compete on the root surface, but also may be capable of developing within the root, relatively protected from the competitive and high-stress environment of the soil. Indeed, many seeds, roots and tubers are normally colonized by endophytic bacteria (McInroy and Kloepper, 1995; Sturz *et al*., 1999). Any plant resistance encountered must be minimal, although, in many cases, sufficient to allow ISR to develop. The localized signalling between plant and bacteria within the root environment deserves further study. Certainly, use of mutants and promoter probe techniques are beginning to identify genes in bacteria that are important in colonization and these are often related to nutrient uptake (Bayliss *et al*., 1997; Roberts *et al*., 2000). Such nutrient uptake genes may also play a role in biocontrol by aiding the uptake and metabolism of nutrients that stimulate germination of pathogen propagules (Maloney *et al*., 1994).

The ability to colonize seeds is also an important feature for many bacterial biocontrol agents. *Pseudomonas chlororaphis* (Guignard & Sauvngeau) Bergey *et al*. MA342 is applied to cereal seeds to control many seed and soil-borne pathogens (Table 1) and has been found to colonize specific areas of the seed coat (Tombolini *et al*., 1999). After inoculation, the bacteria were found under the seed glume (or husk), but after planting they were found to colonize the glume cells epiphytically. Bacterial aggregates were also found in the grooves formed by the base of the coleoptile and the scutellum, and near the embryo but never within it. In this case, the biocontrol bacteria co-located with the seed-borne pathogen *Drechslera teres* (Sacc.) Shoemaker providing biocontrol through the production of fungitoxic compounds. The spermosphere competence of this bacterium allowed biocontrol to take place. Microcolony or microaggregate production by bacteria has also been found on the grooves or cracks on the outer seed coat of sugar beet and cotton (*Gossypium hirsutum* L.) (Fukui *et al*., 1994; Hood *et al*., 1998) perhaps reflecting areas of increased nutrient availability or environmental protection.

Fungal–protozoan interactions

The soil-borne protozoan *Plasmodiophora brassicae* Woronin is an ecologically obligate biotroph of brassicas causing clubroot disease which is characterized by proliferation of galls on infected roots. From a large-scale screening exercise, two isolates of the root-colonizing fungus *Heteroconium chaetospira* (Grove) Ellis were found to suppress clubroot on chinese cabbage (*Brassica campestris* L.) in non-sterile soil (Narisawa *et al*., 1998). Hyphal growth occurred in the inner parts of the cortical tissues and into the root tips without causing any external symptoms on the plant and there was no sign of infection by *P. brassicae*. Further studies demonstrated that *H. chaetospira* infected epidermal cells from appressoria via infection pegs and, subsequently, intracellular hyphal growth occurred (Narisawa *et al*., 2000). However, the actual mechanism of the disease control observed in the field was unclear. *Heteroconium chaetospira* appears to form a mutualistic symbiosis with *B. campestris* in terms of disease control which is of interest as the Brassicacae family is largely non-mycorrhizal. In addition, *H. chaetospira* was found to colonize the roots of

plants from eight families and may have a wide host range (Narisawa *et al*., 2000). Its ability to control diseases in these other plant families and the mechanisms involved deserves further study.

Fungal–bacterial pathogen interactions

In the last few years there have been no clear examples of fungi used to control bacterial plant pathogens in the rhizosphere or spermosphere. The reasons for this are unclear but could perhaps indicate an area that deserves further research in the future.

Fungal–fungal pathogen interactions

Interactions between biocontrol fungi and fungal plant pathogens continue to be the focus of a large number of researchers, on a par with work on bacterial–fungal plant pathogen interactions described earlier. However, there is an extra dimension in the quality of the interactions between fungi as biocontrol fungi have much greater potential than bacteria to grow and spread through soil and in the rhizosphere through possession of hyphal growth. Some recent examples of fungal–fungal interaction concerning biocontrol in the rhizosphere and spermosphere are given in Table 2. There are a variety of fungal species and isolates that have been examined as biocontrol agents but *Trichoderma* species clearly dominate, perhaps reflecting their ease of growth and wide host range (Whipps and Lumsden, 2001). There has been an upsurge in interest in non-pathogenic *Pythium* species, particularly *P. oligandrum* Drechsler where additional modes of action have been determined recently, and a continued interest in well-established saprotrophic antagonists such as non-pathogenic *Fusarium* species, non-pathogenic binucleate *Rhizoctonia* isolates and *Phialophora* species, as well as mutualistic symbionts including mycorrhizal fungi such as *Glomus intraradices* Schenk & Smith. At least one novel biocontrol agent, *Cladorrhinum foecundissimum* Saccardo & Mardial, has been described. Numerous others are listed elsewhere (Whipps, 1997*a*). The most common pathogen targets are *Pythium* species, *Fusarium* species and *Rhizoctonia solani* reflecting their world-wide importance and perhaps their relative ease of control under protected cropping systems, although numerous other pathogens have been examined. Significantly, relatively few of the examples given in Table 2 involve studies in non-sterile soil or field conditions, with most carried out in soil-less conditions reflecting the need to keep the complexity of the system to a minimum in order to achieve reproducible control. Some specific examples of the modes of action found to occur in the rhizosphere and spermosphere during interactions between fungi and fungal plant pathogens are given below.

Competition

There have been relatively few studies on competition for nutrients, space or infection sites between fungi in the rhizosphere and spermosphere recently. Competition for carbon, nitrogen and iron has been shown to be a mechanism associated with biocontrol or suppression of *Fusarium* wilt in several systems by non-pathogenic *Fusarium* and *Trichoderma* species (Mandeel and Baker, 1991; Couteadier, 1992; Sivan and Chet, 1989) and competition for thiamine as a significant process in the control of *Gaeumannomyces graminis* var. *tritici* by a sterile red fungus in the rhizosphere of wheat (Shankar *et al*., 1994). Many studies have shown a relationship between increased colonization of the rhizosphere by a non-pathogen, associated subsequently, with disease suppression. This is well established for non-pathogenic strains of *Fusarium oxysporum* controlling pathogenic *F. oxysporum* on a variety of crop plants (Eparvier and Alabouvette, 1994; Postma and Rattink, 1991), hypovirulent or non-pathogenic binucleate strains of *Rhizoctonia* species to control pathogenic isolates of *R. solani* (Herr, 1995) and several fungi including *Phialophora* species, *Gaeumannomyces graminis* var. *graminis* and *Idriella bolleyi* (Sprague) von Arx as well as several non-sporulating fungi, to control *G. graminis* var. *tritici* (Deacon, 1974; Wong and Southwell, 1980; Kirk and Deacon, 1987; Shivanna *et al*., 1996). As just one example, *I. bolleyi* exploits the naturally senescing cortical cells of cereal roots during the early stages of the crop and outcompetes *G. graminis* var. *tritici* for infection sites and nutrients. Rapid production of spores, which are then carried down the root by water, continue the root colonization process and this is suggested to be a key feature in the establishment of the biocontrol agent on the root (Lascaris and Deacon, 1994; Allan *et al*., 1992; Douglas and Deacon, 1994).

Mycorrhizal fungi are also strong candidates for providing biocontrol through competition for space by virtue of their ecologically obligate association with roots. Ectomycorrhizal fungi because of their physical sheathing morphology may well occupy normal pathogen infection sites. Strangely, little work has been carried out to demonstrate this mechanism since it was first suggested (Marx, 1972) with most biocontrol interest focused on antibiotic production and induced resistance (Perrin, 1990; Duschesne, 1994). Similarly, arbuscular mycorrhizas also have potential to occupy space and infection sites on roots, but evidence suggests that biocontrol provided by arbuscular mycorrhizas relates more to induced resistance, improved plant growth and changes in root morphology rather than competition *per se* (Cordier *et al*., 1996; Norman *et al*., 1996; Mark and Cassells, 1996).

Table 2. *Recent examples of fungal–fungal interactions examined in the spermosphere and rhizosphere associated with biological disease control*

Antagonist	Pathogen	Host plant	Medium	Reference
Cladorrhinum foecundissimum	*Pythium ultimum*	Eggplant, pepper	Soil-less potting mix	Lewis and Larkin, 1998
	Rhizoctonia solani	Eggplant, pepper	Soil-less potting mix	Lewis and Larkin, 1998
Fusarium spp. (CS-1, CS-20, Fo47) (non-pathogenic)	*Fusarium oxysporum* f. sp. *lycopersici*	Tomato	Soil-less potting mix	Larkin and Fravel, 1999
	F. oxysporum f. sp. *niveum*	Watermelon	Soil-less potting mix	Larkin and Fravel, 1999
Fusarium oxysporum Fo47 (non-pathogenic)	*F. oxysporum* f. sp. *lycopersici*	Tomato	Soil and rockwool	Fuchs *et al*., 1999
Fusarium oxysporum (non-pathogenic)	*F. oxysporum* f. sp. *lycopersici*	Tomato	Soil-less potting mix	Larkin and Fravel, 1998
Fusarium solani (non-pathogenic)	*F. oxysporum* f. sp. *lycopersici*	Tomato	Soil-less potting mix	Larkin and Fravel, 1998
Glomus intraradices	*F. oxysporum* f. sp. *dianthi*	Carnation	Clay	St Arnaud *et al*., 1997
Idriella bolleyi	*Bipolaris sorokiniana*	Barley	Soil	Duczek, 1997
Penicillium oxalicum	*F. oxysporum* f. sp. *lycopersici*	Tomato	Peat/soil	de Cal *et al*., 1999
Phialophora sp. I-52	*Gaeumannomyces gramminis* var. *tritici*	Wheat	Soil	Mathre *et al*., 1998
Pythium acanthophoron	*Fusarium culmorum*	Barley	Sand	Davanlou *et al*., 1999
Pythium mycoparasiticum	*Fusarium culmorum*	Barley	Sand	Davanlou *et al*., 1999
Pythium oligandrum	*Fusarium culmorum*	Barley	Sand	Davanlou *et al*., 1999
	Pythium spp.	Cucumber	Hydroponic system	Wulff *et al*., 1998
	Pythium spp.	Sugar beet	Soil	McQuilken *et al*., 1998
	P. ultimum	Sugar beet	Soil-based compost	Holmes *et al*., 1998
	Verticillium dahliae	Pepper	Potting mix	Al-Rawahi and Hancock, 1998
Pythium periplocum	*Fusarium culmorum*	Barley	Sand	Davanlou *et al*., 1999
Rhizoctonia solani (binucleate, non-pathogenic)	*Phytophthora parasitica* var. *nicotianae*	Tobacco	Soil-less mix	Cartwright and Spurr, 1998
	Rhizoctonia solani	Cabbage	Soil	Ross *et al*., 1998
	R. solani; *Pythium ultimum*	Pepper	Potting mix	Harris and Adkins, 1999
Talaromyces flavus	*Verticillium dahliae*	Eggplant	Soil-less potting mix	Engelkes *et al*., 1997
Trichoderma hamatum TRI-4	*Rhizoctonia solani*	Eggplant	Soil-less potitng mix	Lewis *et al*., 1998
Trichoderma harzianum 2413	*Phytophthora capsici*	Pepper	Peat-sand mix	Ahmed *et al*., 1999
T. harzianum T-22	*Pyrenophora triticis-repentis*	Wheat	Soil	da Luz *et al*., 1998
T. harzianum T-1	*Pythium ultimum*	Bean	Soil	Woo *et al*., 1999
	Rhizoctonia solani	Bean	Soil	Woo *et al*., 1999
T. harzianum 1295-22	*R. solani*	Creeping bent grass	Peat	Lo *et al*., 1998
T. harzianum Th-87	*R. solani*	Eggplant	Soil-less potting mix	Lewis *et al*., 1998
T. harzianum BAFC 742	*Sclerotinia sclerotiorum*	Soybean	Soil	Menendez and Godeas, 1998
Trichoderma longibrachiatum CECT 2606	*Pythium ultimum*	Cucumber	Potting mix	Migheli *et al*., 1998
Trichoderma viride WT-6	*Rhizoctonia solani*	Eggplant	Soil-less potting mix	Lewis *et al*., 1998
Trichoderma (*Gliocladium*) *virens* GL-21	*Pythium ultimum*	Cucumber	Potting mix	Koch, 1999
	Rhizoctonia solani	Pea	Potting mix	Koch, 1999
T. virens GL-1, GL-21, GL-23	*R. solani*	Eggplant	Soil-less potting mix	Lewis *et al*., 1998
T. virens GL-3	*Fusarium graminearum; Pythium arrhenomanes; P. ultimum*	Maize	Soil	Mao *et al*., 1997

Antibiosis

Although production of antibiotics by fungi involved in biocontrol is a well-documented phenomenon (Howell, 1998; Sivasithamparam and Ghisalberti, 1998), there is little recent work clearly demonstrating production of antibiotics by fungi in the rhizosphere and spermosphere. Unlike the situation with biocontrol bacteria, there appear to be no detailed studies in biocontrol fungi of genes coding for antibiotic synthesis. Mutants with raised or decreased production of antibiotics are either natural spontaneous ones or generated by UV or chemical mutagenesis, with inherent problems of pleiotropic gene effects, rather than targeted gene disruption (Howell and Stipanovic, 1995; Graeme-Cook and Faull, 1991; Wilhite *et al*., 1994; Fravel and Roberts, 1991). Consequently, clear identification and understanding of the role of antibiotics in disease control lags far behind that in bacteria and needs to be addressed.

Antibiotic production by fungi exhibiting biocontrol activity has most commonly been reported for isolates of *Trichoderma*/*Gliocladium* (Howell, 1998) and *Talaromyces flavus* (Klöcker) Stolk & Samson (Kim *et al*., 1990; Fravel and Roberts, 1991) although in the last few years antibiotics have been at least partially characterized in *Chaetomium globosum* (Kunze) (Di Pietro *et al*., 1992). *Minimedusa polyspora* (J. W. Hotson) Weresub & Le Clair (Beale and Pitt, 1995) and *Verticillium biguttatum* Gams (Morris *et al*., 1995). Of particular interest are those studies where antibiotic production has a definite link to biocontrol. For example, *Trichoderma* (*Gliocladium*) *virens* (J. Miller, Giddens & Foster) von Arx comprises P and Q group strains, based on their antibiotic profiles (Howell, 1999). Strains of P group produce the antibiotic gliovirin which is active against *Pythium ultimum* but not against *Rhizoctonia solani* AG-4. Strains of the Q group produce the antibiotic gliotoxin which is very active against *R. solani* but less so against *P. ultimum*. In seedling bioassay tests, strains of the P group are more effective biocontrol agents of damping-off on cotton caused by *Pythium*, while those from the Q group are more effective as biocontrol agents of damping-off incited by *R. solani* (Howell, 1991; Howell *et al*., 1993). Thus there is strong circumstantial evidence for a role for antibiotics in biocontrol in this experimental system. This has been confirmed in a zinnia–*Pythium* system where *T. virens* G-20 incorporated into soil and potting mix resulted in disease suppression clearly associated with maximum accumulation of gliotoxin in the medium (Lumsden and Locke, 1989; Lumsden *et al*., 1992*a*, *b*). Gliotoxin minus mutants displayed only 54% of the *Pythium* disease suppressive activity in zinnia compared with the wild-type (Wilhite *et al*., 1994). Gliotoxin production by *Trichoderma* is also thought to be responsible for cytoplasmic leakage from *R. solani* observed directly on membranes in potting mix (Harris and Lumsden, 1997).

Production of hydrogen peroxide in the rhizosphere, catalysed by glucose oxidase from *Talaromyces flavus* is thought to be responsible for the biocontrol of *Verticillium* wilt caused by *Verticillium dahliae* Kleb. on eggplant (*Solanum tuberosum* L.) (Stosz *et al*., 1996). Purified glucose oxidase significantly reduced the growth rate of *V. dahliae* in the presence, but not the absence, of eggplant roots, suggesting that a supply of glucose from the roots was of major importance (Fravel and Roberts, 1991). Further, a single-spored variant, Tf-l-np, which produced 2% of the level of glucose oxidase activity of the wild-type did not control *Verticillium* wilt on eggplant in non-sterile field soil in a glasshouse experiment, whilst the wild-type provided significant control (Fravel and Roberts, 1991). Glucose oxidase also suppressed growth of *V. dahliae in vitro* and killed microsclerotia of *V. dahliae in vitro* and in soil.

Induced resistance

As with bacteria described earlier, the ability of fungi to induce resistance in plants and provide biocontrol has gradually been receiving more attention in the last few years. A considerable number of fungi previously described to provide biocontrol by mechanisms such as competition, antibiosis, mycoparasitism or direct growth promotion are now thought to provide control, at least in part, by this mechanism. These include saprotrophs such as non-pathogenic *Fusarium* isolates (Hervás *et al*., 1995; Larkin *et al*., 1996; Postma and Luttikholt, 1996; Fuchs *et al*., 1997, 1999; Duijff *et al*., 1998; Larkin and Fravel, 1999), *Trichoderma* species (Yedidia *et al*., 1999), *Pythium oligandrum* (Benhamou *et al*., 1997; Rey *et al*., 1998), non-pathogenic binucleate *Rhizoctonia* isolates (Poromarto *et al*., 1998; Xue *et al*., 1998; Jabaji-Hare *et al*., 1999), and *Penicillium oxalicum* Currie & Thom (de Cal *et al*., 1997) as well as mutualistic biotrophs such as mycorrhizal fungi (Volpin *et al*., 1995; Dugassa *et al*., 1996; Morandi, 1996; St Arnaud *et al*., 1997).

However, not all these studies used the strict criterion of spatial separation between application of the biocontrol fungus and the challenging pathogen to define induced resistance. Indeed, some simply measured changes in enzymes, PR-proteins or cell wall characteristics found to be induced in plants through SAR (described earlier) without involvement of a pathogen at all (Volpin *et al*., 1995; Morandi, 1996; Yedidia *et al*., 1999; Rey *et al*., 1998). Certainly with some mycorrhizal fungi it has been questioned whether the biochemical responses similar to induced resistance found following infection are of sufficient magnitude or quality, or too transient, to provide disease control (Dumas-Gaudot *et al*., 1996; Morandi, 1996; Mohr *et al*., 1998). Indeed,

during some mycorrhizal syntheses there is little or no induced resistance response detected (Mohr *et al*., 1998). However, spatial or temporal separation experiments have indicated that increased levels of chitinases, β-1,3 glucanases, β-1,4 glucosidase, PR-1 protein, and peroxidase as well as cell wall appositions and phenolics may be associated with induced resistance due to fungi (Benhamou *et al*., 1997; Fuchs *et al*., 1997; Duijff *et al*., 1998; Xue *et al*., 1998; Jabaji-Hare *et al*., 1999). Nevertheless, more work is needed to identify the biochemical changes taking place in a larger number of fungal–plant combinations as not all these biochemical markers were found to be important in each system examined. Further, there appear to be differences in the quality of the induced resistance found between bacteria and on fungi on the same plant. For example, the suppression of *Fusarium* wilt (*F. oxysporum* f. sp. *lycopersici*) (Sacc.) Snyder & Hansen on tomato by *Pseudomonas fluorescens* WCS417r did not involve production of PR-1 protein and chitinases whereas that induced by *F. oxysporum* Fo47 did (Duijff *et al*., 1998). Again more work in this area is required to determine the extent of differences in induced resistance produced by bacteria and fungi.

The elicitors responsible for inducing resistance are not known in detail. *Trichoderma* species produce a 22 kDa xylanase that, when injected in plant tissues, will induce plant defence responses including K^+, H^+ and Ca^{2+} channelling, PR protein synthesis, ethylene biosynthesis, and glycosylation and fatty acylation of phytosterols (Bailey and Lumsden, 1998). However, whether such a system is active in roots exposed to *Trichoderma* is not known. Pectic oligogalacturonides released after hydrolysis by a non-pathogenic binucleate *Rhizoctonia* isolate may act as elicitors of defence responses in bean (*Phaseolus vulgaris* L.) (Jabaji-Hare *et al*., 1999).

Dose–response experiments involving non-pathogenic *Fusarium* species to control *F. oxysporum* on tomato have indicated that induced resistance is not an all or nothing response (Larkin and Fravel, 1999). By varying the level of inoculum of the inducing strain and the pathogenic isolate in soil, it was shown that some non-pathogenic isolates such as *Fusarium* CS-20 controlled *Fusarium* wilt effectively with antagonist levels of only 100 chlamydospores g^{-1} of soil (cgs) with pathogen densities of up to 10^5 cgs. In contrast, isolate Fo47 was effective only at antagonist densities of 10^4–10^5 cgs, regardless of pathogen density. Subsequent mathematical modelling provided evidence that CS-20 control was largely through induced resistance whereas Fo47 was active primarily through competition for nutrients (Larkin and Fravel, 1999). Similar dose–response effects were found with non-pathogenic isolate of *F. oxysporum* f. sp. *ciceris* (Padw.) Matuo & Sato and non-pathogenic isolates of *F. oxysporum* to control wilt of chickpea (*Cicer arietinum* L.) caused by pathogenic *F. oxysporum* f. sp. *ciceris* (Hervás *et al*., 1995). However, in addition, the plant genotype also seemed to influence the degree of resistance induced.

Mycoparasitism

There is a huge literature on the ability of fungi to parasitize spores, sclerotia, hyphae, and other fungal structures and many of these observations are linked with biocontrol (Jeffries and Young, 1994; van den Boogert and Deacon, 1994; Madsen and de Neergaard, 1999; Mischke, 1998; Al-Rawahi and Hancock, 1998; Davanlou *et al*., 1999). However, most of the microscopical observations concerning mycoparasitism have come from *in vitro* studies or sterile systems (Benhamou and Chet, 1996, 1997; Inbar *et al*., 1996; Cartwright *et al*., 1997; Benhamou *et al*., 1999; Davanlou *et al*., 1999) and examples clearly demonstrating mycoparasitism in the rhizosphere or spermosphere are rare (Lo *et al*., 1998). However, indirect population dynamic studies showed that mycelium of *Rhizoctonia solani* in the rhizosphere of potato was a prerequisite for development of the mycoparasite *Verticillium biguttatum* (van den Boogert and Velvis, 1992) and rhizosphere competence was strongly related to biocontrol in mycoparasite isolates of *Trichoderma* species (Sivan and Harman, 1991; Peterbauer *et al*., 1996; Thrane *et al*., 1997; Harman and Björkman, 1998).

The process involved in mycoparasitism may consist of sensing the host, followed by directed growth, contact, recognition, attachment, penetration, and exit. Although not all these features occur in every fungal–fungal interaction, the key factor is nutrient transfer from host to mycoparasite. Directed growth of hyphae of *Trichoderma* to hyphae of *Rhizoctonia solani* prior to penetration has often been observed (Chet *et al*., 1981) and the presence of host sclerotia have been shown to stimulate germination of conidia of *Coniothyrium minitans* Campbell (Whipps *et al*., 1991) and *Sporidesmium sclerotivorum* Uecker, Adams & Ayers (Mischke *et al*., 1995; Mischke and Adams, 1996). However, the factors involved in controlling directed growth in these systems have not been fully characterized. Similarly, the factors controlling recognition and binding between fungal host and parasite are not yet clear. This process may involve hydrophobic interactions or interactions between complementary molecules present on the surface of both the host and the mycoparasite such as between lectins and carbohydrates. With *Trichoderma*, there is good evidence of lectin production by both parasite and host *Corticum* (*Sclerotium*) *rolfsii* Curzi and involvement of lectins in the differentiation of mycoparasitism-related structures (Inbar and Chet, 1994; Neethling and Nevalainen, 1995). Recently, both hydrophobic characteristics and surface carbohydrate moieties

have been investigated in the mycoparasite *C. minitans* as a prerequisite to examining the interaction with its host *Sclerotinia sclerotiorum* (Lib.) de Bary (Smith *et al.*, 1998, 1999). Little is known of the signalling pathways following recognition of the host. However, preliminary evidence in *Trichoderma harzianum* indicates that the signal is transduced by heterotrimeric G proteins and mediated by cAMP (Omero *et al.*, 1999).

As penetration or cell wall degradation are frequently observed during mycoparasitism, great emphasis has been placed on characterizing and cloning the extracellular enzymes such as β-1,3 glucanases, chitinases, cellulases, and proteases produced by fungal biocontrol strains (Haran *et al.*, 1996*a*; Peterbauer *et al.*, 1996; Archambault *et al.*, 1998; Deane *et al.*, 1998; Vázquez-Garcidueñas *et al.*, 1998). By manipulating their activity through construction of 'overproducing' mutants, enzyme-negative mutants or even transgenic plants expressing the enzyme, a role for their production in biocontrol has been implied. Several fungi have been examined in this way including *Talaromyces flavus* (Madi *et al.*, 1997), but this type of work has essentially focused on *Trichoderma* species. For example, a series of transformants of *T. longibrachiatum* Rifai were constructed with extra copies of *egl1* gene encoding the production of β-1,4 endoglucanase (Migheli *et al.*, 1998). When applied to cucumber seeds sown in *Pythium ultimum*-infested soil, the transformants with inducible or constitutive expression of *egl1* were generally more suppressive than the wild type strain. In this case, it was suggested that *P. ultimum* was controlled through the action of β-1,4 glucanase degrading the cellulose of the cell wall of the pathogen. Similarly, transformants of *T. harzianum*, overproducing proteinase encoded by *prb1*, provided up to a 5-fold increase in control of damping-off in cotton caused by *Rhizoctonia solani* (Flores *et al.*, 1996). Interestingly, the best protection was provided by a strain which produced only an intermediate level of proteinase activity and it was suggested that very high levels of proteinase production might cause degradation of other enzymes which are important in the mycoparasitic process (Flores *et al.*, 1996). In this regard, chitinases have received the greatest attention in mycoparasitism. Numerous studies have been made of β-*N*-acetylhexosaminidase (EC 3.2.1.52) (which splits the chitin polymer into *N*-acetylglucosamine monomers in an exo-manner), endochitinase (EC 3.2.1.14) (which cleaves randomly at internal sites over the entire length of the chitin microfibril) and chitin 1,4-β-chitobiosidase (exochitinases or chitobiosidases) (which releases diacetylchitobiose in a stepwise fashion such that no monosaccharides or oligosaccharides are formed) (Haran *et al.*, 1996*a*; Schickler *et al.*, 1998; Lorito, 1998). For example, transformants of *T. harzianum* CECT 2413 that over-expressed on 33 kDa endochitinase (chit33) were more effective in inhibiting the growth of *Rhizoctonia solani in vitro* compared with the wild type (Limón *et al.*, 1999).

The combination of chitinases as well as other cell wall-degrading enzymes differ between species and strains (Lorito, 1998) and chitinases are differently expressed during mycoparasitism (Haran *et al.*, 1996*b*; Mach *et al.*, 1999; Zeilinger *et al.*, 1999). For example, an *N*-acetylhexosaminidase (CHIT 102) was the first to be induced in *T. harzianum* T-Y, but as early as 12 h after contact with its host *Sclerotium rolfsii*, its activity diminished, while that of another *N*-acetylhexosaminidase increased (Haran *et al.* 1996*b*). In contrast, when *Rhizoctonia solani* was the host, CHIT 102 was stimulated along with three endochitinases within 12 h following contact but, as the interaction proceeded, CHIT 102 activity decreased and that of the endochitinases increased (Haran *et al.*, 1996*b*). In *T.* (*atroviride*) *harzianum* P1, expression of endochitinase *ech42* occurred before contact with the host *R. solani* when a *N*-acetylhexosaminidase *nag1* was not induced until after contact (Zeilinger *et al.*, 1999). Degradation products of the cell wall were considered to act as inducers of these enzymes in this host–pathogen system. Interestingly, when examining *T. harzianum* P1 interaction with *Botrytis cinerea* Pers., *ech42* gene transcription was found to be triggered by physiological stress reflecting carbon source depletion rather than the presence of chitin as the inducer (Mach *et al.*, 1999). Significantly, *ech42* minus mutants did not reduce biocontrol activity against *Pythium ultimum* or *S. rolfsii* and appeared to enhance activity against *R. solani*, suggesting that expression of this gene in *T. harzianum* P1 was not directly important for the biocontrol of these fungi (Woo *et al.*, 1999; Carsolio *et al.*, 1999). In contrast, activity against *B. cinerea* was impaired, clearly indicating that the mechanism involved in antagonistic interactions with *T. harzianum* P1 differs with host, and is unlikely to depend solely on the production of a single cell wall-degrading enzyme. Indeed, evidence from studies involving combinations of purified cell wall-degrading enzymes and antibiotics from *Trichoderma* species support this idea (Lorito, 1998; Schirmbock *et al.*, 1994).

The final evidence for a role for cell wall-degrading enzymes in biocontrol involves the expression of fungal genes in transgenic plants. For example, an endochitinase from *Trichoderma harzianum* has been transformed into tobacco and potato and the transgenic plants showed a high level of resistance to a broad spectrum of diseases (Lorito, 1998). Similarly, transgenic apple trees expressing an endochitinase from *T. harzianum* also exhibited increased resistance to apple scab caused by *Venturia inaequalis* (Cooke) Winter, although plant growth was reduced (Bolar *et al.*, 2000). The potential consequently exists to combine different enzymes in transgenic plants to obtain synergistic biocontrol and

these experiments are underway (Lorito, 1998; Bolar *et al*., 2000).

One feature often overlooked with mycoparasitism is that it may not always be confined to control of plant pathogens. A mycoparasite may also have the potential to attack beneficial fungi such as those forming mycorrhiza. For example, *T. harzianum* T-203 was shown to attack mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices* in an axenic system (Rousseau *et al*., 1996). However, in a soil-based system, *G. intraradices* was unaffected by the presence of *T. harzianum* T3a. Indeed *T. harzianum* appeared to be suppressed through nutrient competition (Green *et al*., 1999). In contrast, in a different *in vitro* system, soluble material obtained from *G. intraradices* mycelium stimulated conidial germination of *T. harzianum*, but not that of the pathogen *F. oxysporum* f. sp. *chrysanthemi* G. M. & J. K. Armstrong & Littrell (Filion *et al*., 1999). These results may reflect the different isolates of fungi and plants used, and the experimental systems applied, but they clearly demonstrate the complexity of the interactions that can occur in the rhizosphere.

Plant growth promotion and rhizosphere competence

The terminology associated with biocontrol in the rhizosphere and with soil–plant–microbe interactions has gradually become more complex through the use of a range of descriptive rather than mechanistic terms such as plant growth promotion and rhizosphere competence. Much like the situation with PGPR, many saprotrophic fungi, particularly certain isolates of *Trichoderma* species, can provide plant growth promotion in the absence of any major pathogens (Whipps, 1997*a*; Inbar *et al*., 1994). In many cases these studies are restricted to simple observations of improved plant growth with no indication of the possible mechanisms involved, although there are exceptions. For example, *Trichoderma harzianum* 1295–27 was shown to solubilize phosphate and micronutrients that could be made available to provide plant growth (Altomare *et al*., 1999). This situation is compounded by the fact that many proven fungal biocontrol agents including some *Trichoderma* species, binucleate *Rhizoctonia* isolates and *Pythium oligandrum* can provide improved plant growth in the absence of pathogens (Chang *et al*., 1986; Windham *et al*., 1986; Shivanna *et al*., 1996; Wulff *et al*., 1998; Harris, 1999). Further, colonization of the surface of the seeds or roots or behaviour as endophytes has frequently been seen to be a desirable trait for biocontrol activity (Kleifeld and Chet, 1992; Harman and Bjôrkman, 1998) and although there is a clear relationship between rhizosphere colonization and biocontrol activity with some isolates of biocontrol fungi such as *Trichoderma* species, non-pathogenic Fusaria, *P. oligandrum*, *Verticillium biguttatum*, and *Talaromyces flavus* (Ahmad and Baker, 1988; Couteadier *et al*., 1993; van den Boogert and Velvis, 1992; Al-Rawahi and Hancock, 1997; Lo *et al*., 1996; Tjamos and Fravel, 1997; Nagtzaam and Bollen, 1997; Björkman *et al*., 1998), this is not always the case. Indeed transient plant growth inhibition following application of some biocontrol agents to seeds or roots is known (Wulff *et al*., 1998; Bailey and Lumsden, 1998). Consequently, it is important to appreciate that just because a microorganism can grow in the rhizosphere or spermosphere, it may not automatically provide biocontrol or plant growth promotion. Similarly, the converse is true. A proven biocontrol agent of a soil-borne plant pathogen may not always be capable of colonizing the rhizosphere or providing plant growth promotion.

The situation is much clearer with mycorrhizal fungi where, through ecologically mutualistic symbiosis with the plant, the major feature involves improving plant nutritional status, perhaps water balance and thus plant growth. Biocontrol of plant pathogens is generally viewed as a secondary role (Hooker *et al*., 1994). Interestingly, a non-mycorrhizal endophytic fungus *Piriformospora indica* Verma, Varma, Kost, Rexer and Franken has recently been shown to promote growth of a range of plant species (Varma *et al*., 1999) and it would be valuable to understand the mechanisms of action.

The factors controlling rhizosphere competence are unclear. It has been suggested that ability to produce cellulases and thus utilize substrates available in the rhizosphere may be an important feature (Baker, 1991). However, UV mutants of *Trichoderma harzianum* lacking cellulase production were found to have enhanced rhizosphere competence whereas two cellulase overproducers were found not to colonize the rhizosphere of bean plants (Melo *et al*., 1997). In a different system, both pathogenic and non-pathogenic *Fusarium oxysporum* populations exhibited their own characteristic growth and development features, as well as nutritional competence, which were not related to the ability to grow in the rhizosphere or to infect roots of tomato (Steinberg *et al*., 1999*a*, *b*). Factors controlling rhizosphere competence deserve further study.

Multiple microbial interactions

The majority of interactions considered so far concern a single pathogen and a single biocontrol agent in the rhizosphere. However, one way of improving biocontrol in the rhizosphere may be to add mixtures or combinations of biocontrol agents, particularly if they exhibit different or complementary modes of action or abilities to colonize root microsites. Such multiple interactions are the normal situation in the rhizosphere. Numerous

permutations have been considered, including combinations of different bacteria, fungi and both bacteria and fungi. For example, a seed application of a combination of three PGPR, *Bacillus pumilus* Meyer & Gotheil, *Bacillus subtilis* (Ehrenberg) Cohn and *Curtobacterium flaccumfaciens* (Hedges) Collins & Jones provided greater control of several pathogens on cucumber (*Cucumis sativa* L.) than when any were inoculated singly (Raupach and Kloepper, 1998), combinations of *Paenibacillus* sp. and a *Streptomyces* sp. suppressed *Fusarium* wilt of cucumber better than when either was used alone (Singh *et al*., 1999) and a combination of *Pseudomonas fluorescens* and *Stenotrophomonas maltophila* improved protection of sugar beet against *Pythium*-mediated damping-off in comparison with either applied individually (Dunne *et al*., 1998). Combinations of fungi and bacteria have also been shown to provide enhanced biocontrol. For instance, *Trichoderma koningii* Oud. combined with either *Pseudomonas chlororaphis* 30–84 or *P. fluorescens* Q2-87 provided greater suppression of take-all of wheat than *T. koningii* alone (Duffy *et al*., 1996), *Trichoderma* (*Gliocladium*) *virens* GL-3 combined with *Burkholderia cepacia* (Burkholder) Yabunchi *et al*. provided stands of pepper (*Capsicum annuum* L.) greater protection than either antagonist used alone in the presence of a mixture of up to four soil-borne pathogens (Mao *et al*., 1998) and non-pathogenic *Fusarium oxysporum* Fo47 combined with *Pseudomonas putida* WCS358 provided better suppression of *Fusarium* wilt of flax (*Linum usitassimum* L.) caused by *F. oxysporum* f. sp. *lini* (Bolley) Snyder & Hansen than either alone (Duijff *et al*., 1999). In the latter study, a high population density of Fo47 was important for disease control in general. Only when Fo47 was present at low population density was enhanced activity of the combination seen. Enhanced plant growth promotion has also been recorded in the absence of pathogens by applications of combinations of bacterial or fungal plant growth promoting microorganisms. For example, *Trichoderma aureoviride* Rifai inoculated with the arbuscular mycorrhizal fungus *Glomus intraradices* enhanced growth of *Citrus reshni* more than the *G. intraradices* used alone (Camprubi *et al*., 1995).

However, it is important when considering the use of mixtures or combinations of strains that no member of the mixture is inhibitory to another or interferes excessively with the existing, normal and non-pathogenic microbiota associated with the roots. Certainly there are examples of combinations of different bacteria or fungi providing no better or, in some cases, worse plant growth promotion or biocontrol than the isolates used singly (Chiarini *et al*., 1998; Larkin and Fravel, 1998; de Boer *et al*., 1999). Similarly, a combination of *Bacillus subtilis* and non-pathogenic *Fusarium oxysporum* did not provide control of *Fusarium* wilt of chickpea (*F. oxysporumi* f. sp. *ciceris*) whereas either applied alone did (Hervás *et al*., 1998). Several biocontrol agents including isolates of *Pseudomonas*, *Gliocladium* and *Trichoderma* species have been shown to have little or no adverse effect on establishment and function of arbuscular mycorrhizas (Paulitz and Linderman, 1989, 1991; Calvet *et al*., 1989; Edwards *et al*., 1998) although there are reports of adverse effects of some isolates of *Trichoderma* and *Streptomyces griseoviridis* Anderson *et al*. on arbuscular mycorrhiza formation (Wyss *et al*., 1992; McAllister *et al*., 1994). Clearly, the complex interactions that can take place in the rhizosphere between biocontrol agents and the indigenous microbiota needs to be considered during development of commercial microbial products.

Conclusions and future considerations

This review has focused on recent research concerning interactions between biocontrol agents and pathogens in the rhizosphere and a large number of differing types of interaction operating through a variety of modes of action have been identified. Greatest interest recently has concerned the phenomenon of induced resistance as the molecular tools for its study became available and more work in this area is clearly justified. Several other areas requiring further work have been highlighted in the text, and in addition, there are a few other topics that could develop further in the future. For example, the concept of breeding plants to improve the effectiveness of biocontrol agents or plant growth promoting microbes appears to be a novel approach (Smith *et al*., 1997; Smith and Goodman, 1999). This idea has been tested using mathematical modelling systems whereby the relative influence of host plant, pathogen and biocontrol agent could be partitioned (Smith *et al*., 1997). A tomato pathogen (*Pythium* species) and biocontrol agent (*Bacillus cereus* Frankland & Frankland UW85) combination was the experimental system used but could easily be adapted to other plant–microbe combinations to extend these studies further. Statistical procedures have also been devised using other systems which allow separation of direct growth promotion effects of a biocontrol agent from that effect obtained by disease control, using data from factorial experiments in which biocontrol agents were applied in the presence or absence of pathogens (Larkin and Fravel, 1999; Ryder *et al*., 1999). Mathematical modelling has also been used to predict the behaviour of epidemics of soil-borne pathogens in populations of plants, in the presence of a biocontrol agent, based on a simple, single plant system (Bailey and Gilligan, 1997). These examples indicate the potential of modelling approaches in general for predicting the outcome of interactions in the rhizosphere.

Integration of biological and chemical control systems may also be an approach that receives more attention in

the future. If pesticide tolerant isolates of biocontrol agents could be used to reduce the application of pesticides then an environmental benefit would ensue. Thus, combined treatment of rosemary (*Rosemarinus officinalis* L.) with the biocontrol agent *Laetisaria arvalis* Burdsall and an experimental fungicide CGA 173506 at one-half the recommended rate reduced *Rhizoctonia* disease more than treatment with either fungus or fungicide alone (Conway *et al*., 1997). Several other combinations of biocontrol agents and pesticides have been tested and others are under development (Harris and Nelson, 1999; Budge and Whipps, 2001).

Another area that has been largely neglected is the role of soil fauna in the interaction between biocontrol agents and plant pathogens in the rhizosphere. Often soil fauna are studied in isolation from microorganisms and the significance of this is only just beginning to be appreciated. For instance, sclerotia of *Sclerotinia sclerotiorium* which had been grazed by the larvae of the fungus gnat *Bradysia coprophila* Lintner were degraded rapidly in soil infested with *Trichoderma hamatum* (Bon.) Bain (Gracia-Garza *et al*., 1997). Larval damage altered the sclerotia both physically and chemically, enhancing the activity of *T. hamatum*. In other studies, both collembolans and mites were shown to transmit conidia of the mycoparasite *Coniothyrium minitans* between sclerotia of *S. sclerotiorum* in soil (Williams *et al*., 1998*a*, *b*).

Finally, perhaps the greatest interest in the future lies with the application of modern molecular techniques and their integration with conventional experimental procedures to understand and utilize soil–plant–microbe interactions. The significance of these techniques has already been described with the monitoring of biocontrol agents and their impact on microbial populations, in the construction of *Agrobacterium radiobacter* K1026, and in understanding the modes of action of biocontrol agents, particularly with induced resistance in plants. Further, much effort has gone into developing transgenic bacteria and fungi expressing genes that provide enhanced biocontrol activity, and in transgenic plants expressing genes that provide disease resistance, while also allowing a greater understanding of the mechanisms operating in the rhizosphere. With environmental concerns and existing legislation, it remains to be seen whether transgenic micro-organisms and plants for disease control become universally accepted both as research tools and as commercial products.

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