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Biocontrol of aerial plant diseases in agriculture and horticulture: current approaches and future prospects

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Until recently, the majority of research on the biological control of aerial plant diseases was focused on control of bacterial pathogens. Such research led to the commercialization of the biocontrol agent *Pseudomonas fluorescens* A506, as BlightBan A506™, for control of fire blight of pear. In contrast, chemical fungicides typically have provided adequate control of most foliar fungal pathogens. However, fungicide resistance problems, concerns regarding pesticide residues and revocation of registration of certain widely used fungicides have led to increased activity in the development of biocontrol agents of foliar fungal pathogens. Much of this activity has centered around the use of *Trichoderma* spp and *Gliocladium* spp to control *Botrytis cinerea* on grape and strawberry. The biocontrol agent *Trichoderma harzianum* T39 is commercially available in Israel, as Trichodex™, for control of grey mold in grapes and may soon be registered for use in the US. Also targeted primarily against a foliar disease of grapes, in this case powdery mildew caused by *Uncinula necator*, is the biocontrol agent *Ampelomyces quisqualis* AQ10, marketed as AQ^{10} ™ biofungicide. Another promising development in the area of foliar disease control, though one which is not yet commercialized, is the use of rhizobacteria as seed treatments to induce systemic resistance in the host plant, a strategy which can protect the plant against a range of bacterial and fungal pathogens.

Keywords: biological control; foliar disease; fungi; bacteria; mycoparasite

Current approaches to biological control on aerial plant surfaces

Biological approaches for the control of pathogens on aerial surfaces have been reviewed extensively over the past 20 years [2,3,5,11,20,38,42]. During this period, most approaches employed for the biological control of diseases of aerial plant surfaces have concentrated on the use of a single, empirically-selected biocontrol agent to antagonize a single pathogen. Indeed, this approach has led to the successful development of some commercial biocontrol products, including Trichodex™, AQ^{10} ™, and BlightBan™ A506. Recently, however, several novel approaches have been developed which may lead to the more rapid integration of commercial biocontrol products into sustainable agricultural and horticultural practices. These novel approaches include: (i) mixtures of biocontrol agents; (ii) integrated biological control strategies; (iii) rhizobacterial-mediated systemic induced resistance; and (iv) integration of biological and chemical agents. In this review, both currently used and novel approaches to the biological control of fungal and bacterial pathogens of aerial plant surfaces will be discussed.

Fungal pathogens

The availability of several relatively effective fungicides for use against the majority of foliar fungal pathogens has meant that research efforts to develop biocontrol agents for these pathogens have been minimal compared to those invested in the biocontrol of soilborne fungal pathogens. However, the now frequent occurrence of fungicide resistance, for example to the benzimidazoles and dicarboximides, has necessitated the development of alternate control strategies, particularly for pathogens such as *Botrytis cinerea* and the powdery mildews *Uncinula necator* and *Sphaerotheca fuliginea*. The recent introduction of the A2 mating type of *Phytophthora infestans*, which is resistant to the fungicide metalaxyl, is a major threat to the US potato and tomato production; hence, this pathogen too is now the target for development of alternate biocontrol strategies. Resistance problems, concerns about fungicide residues on produce, and the revocation of registration of certain pesticides are creating strong interest in biocontrol of foliar fungal pathogens.

The pathogen *B. cinerea* causes the disease grey mold which is a serious economic problem on a number of field crops, such as grape, and greenhouse crops, such as tomato and potted plants. Biological approaches to the control of the necrotrophic pathogen *B. cinerea* have been directed toward the inhibition of infection, or alternatively the suppression of sporulation and dissemination. Conidia of *B. cinerea* typically require exogenous nutrients during germination and germ tube elongation; hence, these pathogens are subject to competition for these nutrients with the indigenous saprophytic microbial community on foliar surfaces [6,7]. Foliar applications of both saprophytic bacteria and yeasts have been reported to have some effect in reducing infection by *B. cinerea* [15,37]. Suppression of sporulation of *B. cinerea* has been effectively achieved through foliar applications of the saprophytic fungi *Trichoderma* spp, *Penicillium* spp, and *Gliocladium roseum* in various hosts, including strawberry [43–46], grape [12,23,29,35],

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and cucumber [16]. Field use of these biocontrol agents is not limited to spray application, since conidia of *G. roseum* can also be disseminated by bees [36,45]. In some cases, these biocontrol agents have been effectively integrated with chemical fungicides to provide disease suppression with fewer fungicide applications than the conventional spray regime [12–14,16].

The apparent success in control of grey mold, in particular with *Trichoderma* spp and *G. roseum*, suggests that there is potential for the development of commercial biocontrol agents of *B. cinerea*. The biocontrol agent Trichodex™ 25WP, based on *Trichoderma harzianum* isolate T39, is now commercially available in several countries for control of *B. cinerea* on grape [12,29,35]. Although Trichodex™ is not yet commercially available in the US, the US Environmental Protection Agency approved an Experimental Use Permit to Abbott Laboratories (Illinois, USA) in 1996 for the use of Trichodex™ to control grey mold on wine grapes, table grapes and strawberries. *T. harzianum* 1295-22 (KRL-AG2), which is commercially available as Bio-Trek™ 22G and T22™ hopper box (BioWorks, New York, USA) for control of soilborne pathogens, is also being tested for control of grey mold on grapes in New York State [23]. An example of a novel approach to the biocontrol of *B. cinerea* is the development of the product GREYGOLD™, which consists of a mixture of the fungi *Trichoderma hamatum* and *Rhodotorula glutinis* and the bacterium *Bacillus megaterium* (Schading R, Eden Bioscience, Poulsbo, WA, USA, personal communication).

Spores of the biotrophic powdery mildews, such as *U. necator* and *S. fuliginea*, typically do not require exogenous nutrients during germination, precluding the use of nutrient competition as a biocontrol strategy as used against *B. cinerea*. Further, host penetration occurs within a short period following germination, limiting the use of antibiotic-producing antagonists to suppress germination. For these reasons, biological approaches for the control of biotrophic fungal pathogens to date have been directed primarily toward the suppression of pathogen sporulation and dissemination using mycoparasites. Biocontrol of powdery mildews on various plant hosts has been achieved using the mycoparasites *Ampelomyces quisqualis* [18,19,21,22,25,41]; *Stephanoascus flocculosus* [26]; and *Verticillium lecanii* [49]. The mycoparasite *A. quisqualis* isolate M-10 was recently released in the US as the product AQ^{10}™ (Ecogen, Langhorne, Pennsylvania, USA) for control of powdery mildew of grape caused by *U. necator*. This biocontrol agent has been used with some success to control powdery mildew of grape in California [22] and New York [18,19] vineyards, but was not successful in the control of *S. fuliginea* on muskmelon [34]. One limitation of this biocontrol agent may be the requirement of high relative humidities for spore germination, which could account for the superior efficacy of AQ^{10} in the moist coastal vineyards of California compared to those in the drier Central Valley [22].

Rusts and downy mildews are economically significant pathogens on some crops. The pathogens causing foliar rusts and downy mildews are also biotrophs; hence, once again mycoparasitism is an approach which has had some success, at least experimentally. Sporulation and dissemination of rusts have been suppressed using the mycoparasite *V. lecanii* [51]. Additionally some success has been achieved using foliar applications of antibiotic-producing bacilli [4,10] or pseudomonads [30] to reduce spore germination. While there have been few reports on the use of foliar applications of either antagonistic bacteria or mycoparasites for the control of downy mildews, *V. lecanii* has been reported to parasitize *Peronospora parasitica* [24].

In the future, systemic acquired resistance (SAR) may prove to be one of the most effective biological approaches to the control of the biotrophic pathogens causing powdery mildews, rusts, and downy mildews. The effectiveness of foliar applications of antagonistic bacteria or mycoparasitic fungi to inhibit germination or sporulation is limited by the development of biotrophic pathogens in the interior of the leaf tissue. In contrast, chemicals or biologicals which cause physiological changes in the host plant that result in SAR are not limited by this constraint. Stem injections of sporangiospores of the tobacco blue mold pathogen *Peronospora tabacina* provided significant SAR-mediated protection against subsequent infection of tobacco by *P. tabacina* [48]. While stem injections may be impractical on a commercial scale, SAR may also be induced by seed treatment with certain strains of rhizobacteria. Although rhizobacterial strains have already been selected which induce SAR in cucumber to the foliar fungal pathogen *Colletotrichum orbiculare* [50], no strains have yet been found which induce SAR against the powdery mildew pathogen *S. fuliginea*.

Bacterial pathogens

Bacterial diseases of agricultural and horticultural crops have traditionally been controlled through the use of antibiotics or copper bactericides and plant resistance. The advent of streptomycin resistance in populations of *Erwinia amylovora*, which causes fire blight of apple and pear, and copper resistance in populations of pathogens such as *Xanthomonas campestris* pathovar *vesicatoria*, which causes bacterial spot of tomato, has prompted the development of novel biocontrol strategies. The first biocontrol agent of a bacterial pathogen of aerial plant surfaces, *Pseudomonas fluorescens* A506, marketed as BlightBan™ A506 (Plant Health Technologies, Idaho, USA), was released in 1996 for the control of fire blight and frost injury in apple and pear [28,32]. *P. fluorescens* A506 appears to prevent blossom colonization by *E. amylovora* by prior utilization of nutrients or other resources associated with the blossom [54]. This means that the biocontrol agent must be applied to blossoms prior to the arrival of immigrant *E. amylovora*. This can be achieved either by spray application [29,32] or by dissemination with honey bees [47]. Certain *Pantoea agglomerans* (syn. *Erwinia herbicola*) strains are also effective against *E. amylovora* [17,28,55], and a recent novel approach is the use of mixtures of *P. fluorescens* A506 with *P. agglomerans* (*E. herbicola*) strain C9-1 [39]. Both *P. fluorescens* A506 and a streptomycin-resistant derivative of *P. agglomerans* (*E. herbicola*) C9-1 can be integrated with the antibiotic streptomycin in an orchard spray program [40].

Although research on biological control of other foliar bacterial pathogens has lagged behind the development of biocontrol agents for fire blight, the increasing prevalence of resistance to copper among pathovars of *Pseudomonas syringae* and *Xanthomonas campestris* will certainly prompt greater activity in this area. Biocontrol of bacterial speck of tomato, caused by *Pseudomonas syringae* pv. *tomato*, can be achieved using either naturally occurring saprophytic bacteria [8,52], or nonpathogenic mutant strains of the pathogen [9,31]. The product BlightBan™ A506 has provided significant reductions in bacterial speck severity under field conditions [52,53], although it is not yet recommended for this disease. Biocontrol of bacterial spot of tomato, caused by *X. c.* pv. *vesicatoria*, can also be achieved with naturally occurring saprophytic bacteria. The biocontrol agent *P. syringae* Cit7 has provided significant reductions in severity of both bacterial speck and spot of tomato under field conditions at various locations (Wilson, unpublished). Nonpathogenic *hrp*-minus mutants of *X. c.* pv. *vesicatoria* are also being investigated for control of bacterial spot and may prove to be superior to nonpathogenic saprophytes (Wilson, unpublished).

Systemic acquired resistance may also be valuable for control of foliar bacterial diseases. In this case, the inducing agent may be applied as a seed treatment or as a foliar 'immunization'. Biological control through SAR, achieved by seed bacterization with rhizobacteria, has been observed with *P. syringae* pv. *lachrymans* in cucumber [33], *P. syringae* pv. *phaseolicola* in bean [1], and *P. syringae* pv. *tomato* in tomato [53]. Foliar 'immunization' has been achieved by the introduction of nonpathogenic or incompatible *X. campestris* strains into the leaf tissue through hydathodes or stomates, using a polysilicone (Silwet™) surfactant, to provide protection against black rot of cabbage, caused by *X. campestris* pv. *campestris* [27]. Perhaps the greatest potential for control of bacterial diseases, however, lies with the integration of foliar antagonists and rhizobacterial-mediated SAR [53]. Recent field trials in Alabama and Florida have both demonstrated additive effects in the control of bacterial speck of tomato through the combination of seed/root application of SAR-inducing rhizobacteria and weekly foliar applications of the biocontrol agent *P. syringae* Cit7 (Wilson, unpublished). Alternatively the integration of foliar antagonists with the new SAR chemicals such CGA-245704 (Novartis, Basel, Switzerland) which have no direct antibacterial activity may also be possible.

Future prospects

The next few years will likely see more applications of biocontrol agents in agriculture, with particular emphasis on the use of Gram-positive bacteria, which have superior capacities for survival in formulated products. This trend is already evident in the widespread use of *Bacillus subtilis* GB03 and GB07 as seed treatments on a large proportion of the cotton planted in the US for control of late season Rhizoctonia root-rot. However, in areas where there are no other disease control alternatives available, and in which economic losses are considerable, such as bacterial spot of fresh-market tomato, the development of Gram-negative organisms for use as a foliar application will probably occur, necessitating the development of alternative formulation or distribution strategies.

The use of an integrated biological control (IBC) strategy [53], in which several tactics are employed to combat the same pathogen, is a promising approach to improve the level of disease control or the consistency of the biological treatment. The future combination of foliar biologicals with seed/root-applied SAR-inducing rhizobacteria is probable in the tomato transplant industry in which the rhizobacteria can be incorporated into the media mix and the foliar biological can be inoculated through the overhead irrigation, thereby producing a transplant which is already colonized and protected by the biocontrol agents.

The use of mixtures of organisms on the same plant organ (eg seed or foliage) will likely become more commonplace. This approach may lead to a wider spectrum of activity of the biological treatment or an increase in either the efficacy or consistency of the biological treatment. However, one cannot assume that all mixtures will lead to an improvement of these traits. While synergistic mixtures can be selected empirically through factorial experiments, it would be desirable to see the development of approaches for the strategic selection of synergistic mixtures.

In conclusion, the concerted effort of academic, federal and private sector scientists should lead to the development of effective and consistent biocontrol of aerial plant diseases based on an IBC strategy or on strain mixtures; whether such approaches/products are economically viable, however, is another question.

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