APPLIED AND ENVIRONMENTAL MICROBIOLOGY, Sept. 2005, p. 4951–4959 Vol. 71, No. 9
0099-2240/05/$08.00+0 doi:10.1128/AEM.71.9.4951–4959.2005

MINIREVIEW

Use of Plant Growth-Promoting Bacteria for Biocontrol of Plant Diseases: Principles, Mechanisms of Action, and Future Prospects

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Pathogenic microorganisms affecting plant health are a major and chronic threat to food production and ecosystem stability worldwide. As agricultural production intensified over the past few decades, producers became more and more dependent on agrochemicals as a relatively reliable method of crop protection helping with economic stability of their operations. However, increasing use of chemical inputs causes several negative effects, i.e., development of pathogen resistance to the applied agents and their nontarget environmental impacts (44, 62). Furthermore, the growing cost of pesticides, particularly in less-affluent regions of the world, and consumer demand for pesticide-free food has led to a search for substitutes for these products. There are also a number of fastidious diseases for which chemical solutions are few, ineffective, or nonexistent (62). Biological control is thus being considered as an alternative or a supplemental way of reducing the use of chemicals in agriculture (44, 62, 136, 188).

There has been a large body of literature describing potential uses of plant associated bacteria as agents stimulating plant growth and managing soil and plant health (reviewed in references 63, 70, 143, 165, and 188). Plant growth-promoting bacteria (PGPB) (8) are associated with many, if not all, plant species and are commonly present in many environments. The most widely studied group of PGPB are plant growth-promoting rhizobacteria (PGPR) (82) colonizing the root surfaces and the closely adhering soil interface, the rhizosphere (82, 84). As reviewed by Kloepper et al. (84) or, more recently, by Gray and Smith (65), some of these PGPR can also enter root interior and establish endophytic populations. Many of them are able to transcend the endodermis barrier, crossing from the root cortex to the vascular system, and subsequently thrive as endophytes in stem, leaves, tubers, and other organs (10, 28, 65, 70). The extent of endophytic colonization of host plant organs and tissues reflects the ability of bacteria to selectively adapt to these specific ecological niches (65, 70). Consequently, intimate associations between bacteria and host plants can be formed (28, 70, 84) without harming the plant (70, 83, 84, 92, 191). Although, it is generally assumed that many bacterial endophyte communities are the product of a colonizing process initiated in the root zone (102, 165, 177, 188), they may also originate from other source than the rhizosphere, such as the phyllosphere, the anthosphere, or the spermosphere (70).

Despite their different ecological niches, free-living rhizobacteria and endophytic bacteria use some of the same mechanisms to promote plant growth and control phytopathogens (15, 46, 63, 70, 92, 165). The widely recognized mechanisms of biocontrol mediated by PGPB are competition for an ecological niche or a substrate, production of inhibitory allelochemicals, and induction of systemic resistance (ISR) in host plants to a broad spectrum of pathogens (15, 63, 66, 67, 97, 146) and/or abiotic stresses (reviewed in references 101 and 117). This review surveys the advances of plant-PGPB interaction research focusing on the principles and mechanisms of action of PGPB, both free-living and endophytic bacteria, and their use or potential use for the biological control of plant diseases.

COMPETITIVE ROOT COLONIZATION

Despite their potential as low-input practical agents of plant protection, application of PGPB has been hampered by inconsistent performance in field tests (167); this is usually attributed to their poor rhizosphere competence (153, 189). Rhizosphere competence of biocontrol agents comprises effective root colonization combined with the ability to survive and proliferate along growing plant roots over a considerable time period, in the presence of the indigenous microflora (95, 127, 189, 190). Given the importance of rhizosphere competence as a prerequisite of effective biological control, understanding root-microbe communication (6, 135), as affected by genetic (80, 118) and environmental (128) determinants in spatial (6) and temporal (23) contexts, will significantly contribute to improve the efficacy of these biocontrol agents.

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Competition for root niches and bacterial determinants directly involves root colonization. The root surface and surrounding rhizosphere are significant carbon sinks (143). Photosynthate allocation to this zone can be as high as 40% (34). Thus, along root surfaces there are various suitable nutrient-rich niches attracting a great diversity of microorganisms, including phytopathogens. Competition for these nutrients and niches is a fundamental mechanism by which PGPB protect plants from phytopathogens (50). PGPB reach root surfaces by active motility facilitated by flagella and are guided by chemotactic responses (41, 42, 112, 162, 171, 172). Known chemical attractants present in root exudates include organic acids, amino acids, and specific sugars (188). Some exudates can also be effective as antimicrobial agents and thus give ecological niche advantage to organisms that have adequate enzymatic machinery to detoxify them (reviewed in reference 6). The quantity and composition of chemoattractants and antimicrobials exuded by plant roots are under genetic and environmental control (6). This implies that PGPB competence highly depends either on their abilities to take advantage of a specific environment or on their abilities to adapt to changing conditions. As an example, *Azospirillum* chemotaxis is induced by sugars, amino acids, and organic acids, but the degree of chemotactic response to each of these compounds differs among strains (142). PGPB may be uniquely equipped to sense chemoattractants, e.g., rice exudates induce stronger chemotactic responses of endophytic bacteria than from non-PGPB present in the rice rhizosphere (5).

Bacterial lipopolysaccharides (LPS), in particular the O-antigen chain, can also contribute to root colonization (35). However, the importance of LPS in this colonization might be strain dependent since the O-antigenic side chain of *Pseudomonas fluorescens* WCS374 does not contribute to potato root adhesion (43), whereas the O-antigen chain of *P. fluorescens* PCL1205 is involved in tomato root colonization (35). Furthermore, the O-antigenic aspect of LPS does not contribute to rhizoplane colonization of tomato by the plant beneficial endophytic bacterium *P. fluorescens* WCS417r but, interestingly, this bacterial determinant was involved in endophytic colonization of roots (57).

It has also been recently demonstrated that the high bacterial growth rate and ability to synthesize vitamin B_1 and exude NADH dehydrogenases contribute to plant colonization by PGPB (35, 157). Another determinant of root colonization ability by bacteria is type IV pili, better known for its involvement in the adhesion of animal and human pathogenic bacteria to eukaryotic cells (69, 162, 163). The type IV pili also play a role in plant colonization by endophytic bacteria such as *Azoarcus* sp. (49, 162).

Root colonization and site-specific recombinase. Bacterial traits required for effective root colonization are subject to phase variation, a regulatory process for DNA rearrangements orchestrated by site-specific recombinase (36, 149, 174). In certain PGPB, efficient root colonization is linked to their ability to secrete a site-specific recombinase (36). Transfer of the site-specific recombinase gene from a rhizosphere-competent *P. fluorescens* into a rhizosphere-incompetent *Pseudomonas* strain enhanced its ability to colonize root tips (37).

Utilization of root exudates and root mucilage by PGPB. Since root exudates are the primary source of nutrients for rhizosphere microorganisms (143, 176), rhizosphere competence implies that PGPB are well adapted to their utilization (96). Despite the fact that sugars have often been reported as the major carbon source in exudates, the ability to use specific sugars does not play a major role in tomato root colonization (96). Similarly, although amino acids are present in root exudates, the bioavailability of amino acids alone is considered insufficient to support root tip colonization by auxotrophic mutants of *P. fluorescens* WCS365 (158). In contrast, Simons et al. (158) reported that amino acid synthesis is required for root colonization by *P. fluorescens* WCS365, indicating that amino acid prototrophy is involved in rhizosphere competence. In addition, PGPB regulate the rate of uptake of polyamines such as putrescine, spermine, and spermidine, since their high titer could retard bacterial growth and reduce their ability to competitively colonize roots (87). Root mucilage also offers a utilizable carbon source for PGPB (85) to use for the competitive colonization.

BIOCONTROL ACTIVITY MEDIATED BY THE SYNTHESIS OF ALLELOCHEMICALS

Offensive PGPB colonization and defensive retention of rhizosphere niches are enabled by production of bacterial allelochemicals, including iron-chelating siderophores, antibiotics, biocidal volatiles, lytic enzymes, and detoxification enzymes (6, 63, 166).

Competition for iron and the role of siderophores. Iron is an essential growth element for all living organisms. The scarcity of bioavailable iron in soil habitats and on plant surfaces foments a furious competition (93). Under iron-limiting conditions PGPB produce low-molecular-weight compounds called siderophores to competitively acquire ferric ion (191). Although various bacterial siderophores differ in their abilities to sequester iron, in general, they deprive pathogenic fungi of this essential element since the fungal siderophores have lower affinity (94, 122). Some PGPB strains go one step further and draw iron from heterologous siderophores produced by cohabiting microorganisms (19, 92, 94, 137, 186, 191).

Siderophore biosynthesis is generally tightly regulated by iron-sensitive Fur proteins, the global regulators GacS and GacA, the sigma factors RpoS, PvdS, and FpvI, quorum-sensing autoinducers such as *N*-acyl homoserine lactone, and site-specific recombinases (31, 141). However, some data demonstrate that none of these global regulators is involved in siderophore production. Neither GacS nor RpoS significantly affected the level of siderophores synthesized by *Enterobacter cloacae* CAL2 and UW4 (148). RpoS is not involved in the regulation of siderophore production by *Pseudomonas putida* strain WCS358 (86). In addition, GrrA/GrrS, but not GacS/GacA, are involved in siderophore synthesis regulation in *Serratia plymuthica* strain IC1270, suggesting that gene evolution occurred in the siderophore-producing bacteria (123). A myriad of environmental factors can also modulate siderophores synthesis, including pH, the level of iron and the form of iron ions, the presence of other trace elements, and an adequate supply of carbon, nitrogen, and phosphorus (52).

Antibiosis. The basis of antibiosis as a biocontrol mechanism of PGPB has become increasingly better understood over the past two decades (191). A variety of antibiotics have been

identified, including compounds such as amphisin, 2,4-diacetylphloroglucinol (DAPG), hydrogen cyanide, oomycin A, phenazine, pyoluteorin, pyrrolnitrin, tensin, tropolone, and cyclic lipopeptides produced by pseudomonads (33, 40, 114, 115, 138) and oligomycin A, kanosamine, zwittermicin A, and xanthobaccin produced by *Bacillus*, *Streptomyces*, and *Stenotrophomonas* spp. (72, 81, 103, 104, 110). Interestingly, some antibiotics produced by PGPB are finding new uses as experimental pharmaceuticals (45, 75, 192), and this group of bacteria may offer an untapped resource for compounds to deal with the alarming ascent of multidrug-resistant human pathogenic bacteria.

Regulatory cascades of these antibiotics involve GacA/GacS or GrrA/GrrS, RpoD, and RpoS, *N*-acyl homoserine lactone derivatives (15, 21, 68, 131) and positive autoregulation (17, 151). Antibiotic synthesis is tightly linked to the overall metabolic status of the cell, which in turn is dictated by nutrient availability and other environmental stimuli (167), such as major and minor minerals, type of carbon source and supply, pH, temperature, and other parameters (11, 51, 52, 61, 78, 103, 104, 124, 125). Trace elements, particularly zinc, and carbon source levels influence the genetic stability/instability of bacteria, affecting their ability to produce secondary metabolites (53). It is important to note that many strains produce pallet of secondary antimicrobial metabolites and that conditions favoring one compound may not favor another (52). Thus, the varied arsenal of biocontrol strains may enable antagonists to perform their ultimate objective of pathogen suppression under the widest range of environmental conditions. For example, in *P. fluorescens* CHA0 biosynthesis of DAPG is stimulated and pyoluteorin is repressed in the presence of glucose as a carbon source. As glucose is depleted, however, pyoluteorin becomes the more abundantly antimicrobial compound produced by this strain (52). This ensures a degree of flexibility for the antagonist when confronted with a different or a changeable environment. Biotic conditions can also influence antibiotic biosynthesis (51, 54, 68, 116, 128). For example bacterial metabolites salicylates and pyoluteorin can affect DAPG production by *P. fluorescens* CHA0 (151). Furthermore, plant growth and development also influence antiobiotic production, since biological activity of DAPG producers is not induced by the exudates of young plant roots but is induced by the exudates of older plants, which results in selective pressure against other rhizosphere microorganisms (129). Plant host genotype also plays a significant role in the disease-suppressive interaction of plant with a microbial biocontrol agent, as demonstrated by Smith et al. (160, 161).

Lytic enzyme production. A variety of microorganisms also exhibit hyperparasitic activity, attacking pathogens by excreting cell wall hydrolases (26). Chitinase produced by *S. plymuthica* C48 inhibited spore germination and germ-tube elongation in *Botrytis cinerea* (58). The ability to produce extracellular chitinases is considered crucial for *Serratia marcescens* to act as antagonist against *Sclerotium rolfsii* (121), and for *Paenibacillus* sp. strain 300 and *Streptomyces* sp. strain 385 to suppress *Fusarium oxysporum* f. sp. *cucumerinum*. It has been also demonstrated that extracellular chitinase and laminarinase synthesized by *Pseudomonas stutzeri* digest and lyse mycelia of *F. solani* (91). Although, chitinolytic activity appears less essential for PGPB such as *S. plymutica* IC14 when used to suppress *S. sclerotiorum* and *B. cinerea*, synthesis of proteases and other biocontrol traits are involved (77). The β-1,3-glucanase synthesized by *Paenibacillus* sp. strain 300 and *Streptomyces* sp. strain 385 lyse fungal cell walls of *F. oxysporum* f. sp. *cucumerinum* (159). *B. cepacia* synthesizes β-1,3-glucanase that destroys the integrity of *R. solani*, *S. rolfsii*, and *Pythium ultimum* cell walls (59). Similar to siderophores and antibiotics, regulation of lytic enzyme production (proteases and chitinases in particular) involves the GacA/GacS (30, 60, 111, 147) or GrrA/GrrS regulatory systems (123) and colony phase variation (97).

Detoxification and degradation of virulence factors. Another mechanism of biological control is the detoxification of pathogen virulence factors. For example, certain biocontrol agents are able to detoxify albicidin toxin produced by *Xanthomonas albilineans* (9, 183, 194, 195). The detoxification mechanisms include production of a protein that reversibly binds the toxin in both *Klebsiella oxytoca* (183) and *Alcaligenes denitrificans* (9), as well as an irreversible detoxification of albicidin mediated by an esterase that occurs in *Pantoea dispersa* (194, 195). Several different microorganisms, including strains of *B. cepacia* and *Ralstonia solanacearum*, can also hydrolyze fusaric acid, a phytotoxin produced by various *Fusarium* species (169, 170). More often though, pathogen toxins display a broad-spectrum activity and can suppress growth of microbial competitors, or detoxify antiobiotics produced by some biocontrol microorganisms, as a self-defense mechanism against biocontrol agents (55, 152).

Recently, it has been discovered that certain PGPB quench pathogen quorum-sensing capacity by degrading autoinducer signals, thereby blocking expression of numerous virulence genes (47, 48, 105, 106, 113, 173). Since most, if not all, bacterial plant pathogens rely upon autoinducer-mediated quorum-sensing to turn on gene cascades for their key virulence factors (e.g., cell-degrading enzymes and phytotoxins) (181), this approach holds tremendous potential for alleviating disease, even after the onset of infection, in a curative manner.

Although biocontrol activity of microorgansims involving synthesis of allelochemicals has been studied extensively with free-living rhizobacteria, similar mechanisms apply to endophytic bacteria (92), since they can also synthesize metabolites with antagonistic activity toward plant pathogens (24). For example, Castillo et al. (20) demonstrated that munumbicins, antibiotics produced by the endophytic bacterium *Streptomyces* sp. strain NRRL 30562 isolated from *Kennedia nigriscans*, can inhibit in vitro growth of phytopathogenic fungi, *P. ultimum*, and *F. oxysporum*. Subsequently, it has been reported that certain endophytic bacteria isolated from field-grown potato plants can reduce the in vitro growth of *Streptomyces scabies* and *Xanthomonas campestris* through production of siderophore and antibiotic compounds (154). Interestingly, the ability to inhibit pathogen growth by endophytic bacteria, isolated from potato tubers, decreases as the bacteria colonize the host plant's interior, suggesting that bacterial adaptation to this habitat occurs within their host and may be tissue type and tissue site specific (164). Aino et al. (1) have also reported that the endophytic *P. fluorescens* strain FPT 9601 can synthesize DAPG and deposit DAPG crystals around and in the roots of tomato, thus demonstrating that endophyte can produce antibiotics in planta.

INDIRECT PLANT GROWTH PROMOTION THROUGH INDUCED SYSTEMIC RESISTANCE

Biopriming plants with some PGPB can also provide systemic resistance against a broad spectrum of plant pathogens. Diseases of fungal, bacterial, and viral origin, and in some instances even damage caused by insects and nematodes, can be reduced after application of PGPB (79, 135, 139, 146, 165).

Induced systemic resistance. Certain bacteria trigger a phenomenon known as ISR phenotypically similar to systemic acquired resistance (SAR). SAR develops when plants successfully activate their defense mechanism in response to primary infection by a pathogen, notably when the latter induces a hypersensitive reaction through which it becomes limited in a local necrotic lesion of brown, desiccated tissue (175). As SAR, ISR is effective against different types of pathogens but differs from SAR in that the inducing PGPB does not cause visible symptoms on the host plant (175). PGPB-elicited ISR was first observed on carnation (*Dianthus caryophillus*) with reduced susceptibility to wilt caused by *Fusarium* sp. (178) and on cucumber (*Cucumis sativus*) with reduced susceptibility to foliar disease caused by *Colletotrichum orbiculare* (187). Manifestation of ISR is dependent on the combination of host plant and bacterial strain (80, 175). Most reports of PGPB-mediated ISR involve free-living rhizobacterial strains, but endophytic bacteria have also been observed to have ISR activity. For example, ISR was triggered by *P. fluorescens* EP1 against red rot caused by *Colletotrichum falcatum* on sugarcane (182), *Burkholderia phytofirmans* PsJN against *Botrytis cinerea* on grapevine (2, 3) and *Verticllium dahliae* on tomato (156), *P. denitrificans* 1-15 and *P. putida* 5-48 against *Ceratocystis fagacearum* on oak (18), *P. fluorescens* 63-28 against *F. oxysporum* f. sp. *radicis-lycopersici* on tomato (109) and *Pythium ultimum* and *F. oxysporum* f. sp. *pisi* on pea roots (12), and *Bacillus pumilus* SE34 against *F. oxysporum* f. sp. *pisi* on pea roots (13) and *F. oxysporum* f. sp. *vasinfectum* on cotton roots (29).

Determinants of ISR. The ability to act as bioprotectants via ISR has been demonstrated for both rhizobacteria and bacterial endophytes, and considerable progress has been made in elucidating the mechanisms of plant-PGPB-pathogen interaction. Several bacterial traits (i.e., flagellation and production of siderophores and lipopolysaccharides) have been proposed to trigger ISR (73, 88, 90, 175, 179), but there is no compelling evidence for an overall ISR signal produced by bacteria (67). It has recently been reported that volatile organic compounds may play a key role in this process (135, 145). For example, volatiles secreted by *B. subtilis* GBO3 and *B. amyloquefaciens* IN937a were able to activate an ISR pathway in *Arabidopsis* seedlings challenged with the soft-rot pathogen *Erwinia carotovora* subsp. *carotovora* (144). A major distinction often drawn between ISR and SAR is the dependence of the latter on the accumulation of salicylic acid (SA) (128). Some PGPB do trigger an SA-dependent signaling pathway by producing nanogram amounts of SA in the rhizosphere (38, 39). However, the majority of PGPB that activate ISR appear to do so via a SA-independent pathway involving jasmonate and ethylene signals (128, 133). ISR is associated with an increase in sensitivity to these hormones rather than an increase in their production, which might lead to the activation of a partially different set of defense genes (71, 134).

Defense mechanisms of ISR-mediated by PGPB. PGPB-triggered ISR fortifies plant cell wall strength and alters host physiology and metabolic responses, leading to an enhanced synthesis of plant defense chemicals upon challenge by pathogens and/or abiotic stress factors (117, 139). After inoculation of tomato with endophytic *P. fluorescens* WCS417r, a thickening of the outer tangential and outermost part of the radial side of the first layer of cortical cell walls occurred when epidermal or hypodermal cells were colonized (57). In *Burkholderia phytofirmans* PsJN-grapevine interaction, a host defense reaction coinciding with phenolic compound accumulation and a strengthening of cell walls in the exodermis and in several cortical cell layers was also observed during endophytic colonization of the bacterium (28). The type of bacterized plant response induced after challenge with a pathogen resulted in the formation of structural barriers, such as thickened cell wall papillae due to the deposition of callose and the accumulation of phenolic compounds at the site of pathogen attack (13, 14, 109). Biochemical or physiological changes in plants (139) include induced accumulation of pathogenesis-related proteins (PR proteins) such as PR-1, PR-2, chitinases, and some peroxidases (76, 100, 109, 126, 139, 182). However, certain PGPB do not induce PR proteins (73, 132, 139, 180) but rather increase accumulation of peroxidase, phenylalanine ammonia lyase, phytoalexins, polyphenol oxidase, and/or chalcone synthase (25, 120, 139, 178). Recent evidence indicates that induction of some of these plant defense compounds (e.g., chalcone synthase) may be triggered by the same *N*-acyl homoserine lactones that bacteria use for intraspecific signaling (99). The revelation that some PGPB genes involved in antibiotic biosynthesis (e.g., *phlD*) are highly homologous with some plant genes involved in defense (e.g., chalcone synthase) (4, 7) raises the intriguing but as yet unexplored possibility that the products of these DeVriesien-like pangens may have interspecies activity benefiting plant protection, in addition to their currently known functions.

CONCLUSIONS AND FUTURE PROSPECTS TO MAKE BETTER USE OF PGPB

Research into the mechanisms of plant growth promotion by PGPB have provided a greater understanding of the multiple facets of disease suppression by these biocontrol agents. Still, most of the focus has been on free-living rhizobacterial strains, especially to *Pseudomonas* and *Bacillus*. Much remains to be learned from nonsymbiotic endophytic bacteria that have unique associations and apparently a more pronounced growth-enhancing effect on host plants (6, 22, 29, 135).

Revelations about the mechanisms of PGPB action open new doors to design strategies for improving the efficacy of biocontrol agents (107, 108, 184). Identification of key antimicrobials produced by superior agents, such as 2,4-diacetylphloroglucinol, can be exploited for streamlining strain discovery by targeting selection of new isolates that carry relevant biosynthetic genes (193). Determination of the role of edaphic parameters favorable for disease suppression, particularly those that stimulate antibiotic production and activity, can be exploited by targeting inoculants for soils that are more likely to support biocontrol. For example, amending soils or growth substrates with minerals such as zinc or priming inoculants with

media amendments during fermentation (51, 53, 125) can be very effective. Similarly, modulation of the rhizosphere bacteria consortia can be accomplished by soil aeration, hydrogenation, and delivery of molasses, sugars and by appropriate crop rotations (reviewed in reference 188).

Identifying different mechanisms of action facilitate the combination of strains, bacteria with bacteria or bacteria with fungi, to hit pathogens with a broader spectrum of microbial weapons (32, 56, 80, 89, 98, 119, 130, 140, 150). Along this same line, biotechnology can be applied to further improve strains that have prized qualities (e.g., formulation ease, stability, or otherwise exceptionally suited to plant colonization) by creating transgenic strains that combine multiple mechanisms of action (27, 74, 168). For example, transforming the 1-aminocyclopropane-1-carboxylic acid deaminase gene, which directly stimulates plant growth by cleaving the immediate precursor of plant ethylene (64) into *P. fluorescens* CHAO, not only increases plant growth but can also increase biocontrol properties of PGPB (185). Continued work with endophytic bacteria also holds potential for developing biocontrol agents that may be self-perpetuating by colonizing hosts and being transferred to progeny much as is the case with associative nitrogen-fixing PGPB on sugarcane (16) or the nonsymbiotic endophyte bacterium *Burkholderia phytofirmans* PsJN (117, 155).

ACKNOWLEDGMENTS

This study was supported by a grant from Europôl-Agro (Reims, France). Additional support for B. Duffy was provided by the Swiss Federal Office of Agriculture (project 04.24.3.3).

REFERENCES

1. **Aino, M., Y. Maekawa, S. Mayama, and H. Kato.** 1997. Biocontrol of bacterial wilt of tomato by producing seedlings colonized with endophytic antagonistic pseudomonads, p. 120–123. *In* A. Ogoshi, K. Kobayashi, Y. Homma, F. Kodama, N. Kondo, and S. Akino (ed.), Plant growth promoting rhizobacteria: present status and future prospects. Nakanishi Printing, Sapporo, Japan.
2. **Ait Barka, E., A. Belarbi, C. Hachet, J. Nowak, and J. C. Audran.** 2000. Enhancement of in vitro growth and resistance to gray mould of *Vitis vinifera* cocultured with plant growth-promoting rhizobacteria. FEMS Microbiol. Lett. **186:**91–95.
3. **Ait Barka, E., S. Gognies, J. Nowak, J. C. Audran, and A. Belarbi.** 2002. Inhibitory effect of endophyte bacteria on *Botrytis cinerea* and its influence to promote the grapevine growth. Biol. Control. **24:**135–142.
4. **Austin, M. B., and A. J. P. Noel.** 2003. The chalcone synthase superfamily of type III polyketide synthases. Nat. Prod. Rep. **20:**79–110.
5. **Bacilio-Jiménez, M., S. Aguilar-Flores, E. Ventura-Zapata, E. Pérez-Campos, S. Bouquelet, and E. Zenteno.** 2003. Chemical characterization of root exudates from rice (*Oryza sativa*) and their effects on the chemotactic response of endophytic bacteria. Plant Soil. **249:**271–277.
6. **Bais, H. P., S. W. Park, T. L. Weir, R. M. Callaway, and J. M. Vivanco.** 2004. How plants communicate using the underground information superhighway. Trends Plant Sci. **9:**26–32.
7. **Bangera, M. G., and L. S. Thomashow.** 1999. Identification, and characterization and of gene cluster for synthesis of the polyketide antibiotic 2,4-diacetylphloroglucinol from *Pseudomonas fluorescens* Q2-87. J. Bacteriol. **181:**3155–3163.
8. **Bashan, Y., and G. Holguin.** 1998. Proposal for the division of plant growth-promoting rhizobacteria into two classifications: biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. Soil Biol. Biochem. **30:**1225–1228.
9. **Basnayake, W. V. S., and R. G. Birch.** 1995. A gene from *Alcaligenes denitrificans* that confers albicidin resistance by reversible antibiotic binding. Microbiology **141:**551–560.
10. **Bell, C. R., G. A. Dickie, W. L. G. Harvey, and J. W. Y. F. Chan.** 1995. Endophytic bacteria in grapevine. Can. J. Microbiol. **41:**46–53.
11. **Bender, C. L., V. Rangaswamy, and J. Loper.** 1999. Polyketide production by plant-associated pseudomonads. Annu. Rev. Phytopathol. **37:**175–196.
12. **Benhamou, N., R. R. Belanger, and T. C. Paulitz.** 1996. Induction of differential host responses by *Pseudomonas fluorescens* in Ri T-DNA-transformed pea roots after challenge with *Fusarium oxysporum* f. sp. *pisi* and *Pythium ultimum.* Phytopathology **86:**114–178.
13. **Benhamou, N., J. W. Kloepper, A. Quadt-Hallmann, and S. Tuzun.** 1996. Induction of defense-related ultrastructural modifications in pea root tissues inoculated with endophytic bacteria. Plant Physiol. **112:**919–929.
14. **Benhamou, N., J. W. Kloepper, and S. Tuzun.** 1998. Induction of resistance against Fusarium wilt of tomato by combination of chitosan with an endophytic bacterial strain: ultrastructure and cytochemistry of the host response. Planta **204:**153–168.
15. **Bloemberg, G. V., and B. J. J. Lugtenberg.** 2001. Molecular basis of plant growth promotion and biocontrol by rhizobacteria. Curr. Opin. Plant Biol. **4:**343–350.
16. **Boddey, R. M., S. Urquiaga, B. J. R. Alves, and V. Reis.** 2003. Endophytic nitrogen fixation in sugarcane: present knowledge and future applications. Plant Soil **252:**139–149.
17. **Brodhagen, M., M. D. Henkels, and J. E. Loper.** 2004. Positive autoregulation and signaling properties of pyoluteorin, an antibiotic produced by the biological control organism *Pseudomonas fluorescens* Pf-5. Appl. Environ. Microbiol. **70:**1758–1766.
18. **Brooks, D. S., C. F. Gonzalez, D. N. Apple, and T. H. Filer.** 1994. Evaluation of endophytic bacteria as potential biological control agents for oak wilt. Biol. Control **4:**373–381.
19. **Castignetti, D., and J. Smarelli.** 1986. Siderophores, the iron nutrition of plants, and nitrate reductase. FEBS Lett. **209:**147–151.
20. **Castillo, U. F., G. A. Strobel, E. J. Ford, W. M. Hess, H. Porter, J. B. Jensen, H. Albert, R. Robison, M. A. M. Condron, D. B. Teplow, D. Steevens, and D. Yaver.** 2002. Munumbicins, wide-spectrum antiobiotics produced by *Streptomyces* NRRL 30562, endophytic on *Kennedia nigriscans.* Microbiology **148**:2675–2685.
21. **Chancey, S. T., D. W. Wood, and L. S. Pierson.** 1999. Two-component transcriptional regulation of *N*-acyl-homoserine lactone production in *Pseudomonas aureofaciens.* Appl. Environ. Microbiol. **65:**2294–2299.
22. **Chanway, C. P., M. Shishido, J. Nairn, S. Jungwirth, J. Markham, G. Xiao, and F. B. Holl.** 2000. Endophytic colonization and field responses of hybrid spruce seedlings after inoculation with plant growth-promoting rhizobacteria. For. Ecol. Man. **133:**81–88.
23. **Chatterton, S., J. C. Sutton, and G. J. Boland.** 2004. Timing *Pseudomonas chlororaphis* applications to control *Pythium aphanidermatum*, *Pythium dissotocum*, and root rot in hydroponic peppers. Biol. Control **30:**360–373.
24. **Chen, C., E. M. Bauske, G. Musson, R. Rodriguez-Kabana, and J. W. Kloepper.** 1995. Biological control of *Fusarium* wilt on cotton by use of endophytic bacteria. Biol. Control **5:**83–91.
25. **Chen, C., R. R. Bélanger, N. Benhamou, and T. C. Paulitz.** 2000. Defense enzymes induced in cucumber roots by treatment with plant growth-promoting rhizobacteria (PGPR) and *Pythium aphanidermatum.* Physiol. Mol. Plant Pathol. **56:**13–23.
26. **Chernin, L., and I. Chet.** 2002. Microbial enzymes in biocontrol of plant pathogens and pests, p. 171–225. *In* R. G. Burns and R. P. Dick (ed.), Enzymes in the environment: activity, ecology, and applications. Marcel Dekker, New York, N.Y.
27. **Chin-A-Woeng, T. F. C., J. E. Thomas-Oates, B. J. J. Lugtenberg, and G. V. Bloemberg.** 2001. Introduction of the *phzH* gene of *Pseudomonas chlororaphis* PCL1391 extends the range of biocontrol ability of phenazine-1-carboxylic acid-producing *Pseudomonas* spp. strains. Mol. Plant-Microbe Interact. **14:**1006–1015.
28. **Compant, S., B. Reiter, A. Sessitsch, J. Nowak, C. Clément, and E. Ait Barka.** 2005. Endophytic colonization of *Vitis vinifera* L. by a plant growth-promoting bacterium, *Burkholderia* sp. strain PsJN. Appl. Environ. Microbiol. **71:**1685–1693.
29. **Conn, K. L., J. Nowak, and G. Lazarovits.** 1997. A gnotobiotic bioassay for studying interactions between potato and plant growth-promoting rhizobacteria. Can. J. Microbiol. **43:**801–808.
30. **Corbell, N., and J. E. Loper.** 1995. A global regulator of secondary metabolite production in *Pseudomonas fluorescens* Pf-5. J. Bacteriol. **177:**6230–6236.
31. **Cornelis, P., and S. Matthijs.** 2002. Diversity of siderophore-mediated iron uptake systems in fluorescent pseudomonads: not only pyoverdines. Environ. Microbiol. **4:**787–798.
32. **de Boer, M., I. van der Sluis, L. C. van Loon, and P. A. H. M. Bakker.** 1999. Combining fluorescent *Pseudomonas* spp. strains to enhance suppression of fusarium wilt of radish. Eur. J. Plant Pathol. **105:**201–210.
33. **Défago, G.** 1993. 2,4-Diacetylphloroglucinol, a promising compound in biocontrol. Plant Pathol. **42:**311–312.
34. **Degenhardt, J., J. Gershenzon, I. T. Baldwin, and A. Kessler.** 2003. Attracting friends to feast on foes: engineering terpene emission to make crop plants more attractive to herbivore enemies. Curr. Opin. Biotechnol. **14:**169–176.
35. **Dekkers, L. C., A. J. van der Bij, I. H. M. Mulders, C. C. Phoelich, R. A. R. Wentwoord, D. C. M. Glandorf, C. A. Wijffelman, and B. J. J. Lugtenberg.** 1998. Role of the O-antigen of lipopolysaccheride, and possible roles of growth rate and of NADH:ubiquinone oxidoreductase (*nuo*) in competitive

tomato root-tip colonization by *Pseudomonas fluorescens* WCS365. Mol. Plant-Microbe Interact. **11:**763–771.
36. **Dekkers, L. C., C. C. Phoelich, L. van der Fits, and B. J. J. Lugtenberg.** 1998. A site-specific recombinase is required for competitive root colonization by *Pseudomonas fluorescens* WCS365. Proc. Natl. Acad. Sci. USA **95:**7051–7056.
37. **Dekkers, L. C., I. H. Mulders, C. C. Phoelich, T. F. C. Chin-A-Woeng, A. H. Wijfjes, and B. J. J. Lugtenberg.** 2000. The *sss* colonization gene of the tomato-*Fusarium oxysporum* f. sp. *radicis-lycopersici* biocontrol strain *Pseudomonas fluorescens* WCS365 can improve root colonization of other wild-type *Pseudomonas* spp. bacteria. Mol. Plant-Microbe Interact. **13:**1177–1183.
38. **De Meyer, G., and M. Höfte.** 1997. Salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 induces resistance to leaf infection by *Botrytis cinerea* on bean. Phytopathology **87:**588–593.
39. **De Meyer, G., K. Audenaert, and M. Höfte.** 1999. *Pseudomonas aeruginosa* 7NSK2-induced systemic resistance in tobacco depends on in planta salicylic acid accumulation but is not associated with PR1a expression. Eur. J. Plant Pathol. **105:**513–517.
40. **de Souza, J. T., M. de Boer, P. de Waard, T. A. van Beek, and J. M. Raaijmakers.** 2003. Biochemical, genetic, and zoosporicidal properties of cyclic lipopeptide surfactants produced by *Pseudomonas fluorescens.* Appl. Environ. Microbiol. **69:**7161–7172.
41. **De Weert, S., H. Vermeiren, I. H. M. Mulders, I. Kuiper, N. Hendrickx, G. V. Bloemberg, J. Vanderleyden, R. de Mot, and B. J. J. Lugtenberg.** 2002. Flagella-driven chemotaxis toward exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens.* Mol. Plant-Microbe Interact. **15:**1173–1180.
42. **De Weger, L. A., C. I. M. van der Vlugt, A. H. M. Wijfjes, P. A. H. M. Bakker, B. Schippers, and B. Lugtenberg.** 1987. Flagella of a plant-growth-stimulating *Pseudomonas fluorescens* strain are required for colonization of potato roots. J. Bacteriol. **169:**2769–2773.
43. **De Weger, L. A., P. A. H. M. Bakker, B. Schippers, M. C. M. van Loosdrecht, and B. Lugtenberg.** 1989. *Pseudomonas* spp. with mutational changes in the O-antigenic side chain of their lipopolysaccharides are affected in their ability to colonize potato roots, p. 197–202. *In* B. J. J. Lugtenberg (ed.), Signal molecules in plant-microbe interactions. Springer-Verlag, Berlin, Germany.
44. **De Weger, L. A., A. J. van der Bij, L. C. Dekkers, M. Simons, C. A. Wijffelman, and B. J. J. Lugtenberg.** 1995. Colonization of the rhizosphere of crop plants by plant-beneficial pseudomonads. FEMS Microbiol. Ecol. **17:**221–228.
45. **Di Santo, R., R. Costi, M. Artico, S. Massa, G. Lampis, D. Deidda, and R. Pompei.** 1998. Pyrrolnitrin and related pyrroles endowed with antibacterial activities against *Mycobacterium tuberculosis.* Bioorg. Medicinal Chem. Lett. **8:**2931–2936.
46. **Dobbelaere, S., J. Vanderleyden, and Y. Okon.** 2003. Plant growth-promoting effects of diazotrophs in the rhizosphere. Crit. Rev. Plant Sci. **22:**107–149.
47. **Dong, Y. H., J. L. Xu, X. Z. Li, and L. H. Zhang.** 2000. AiiA, an enzyme that inactivates the acylhomoserine lactone quorum-sensing signal and attenuates the virulence of *Erwinia carotovora.* Proc. Natl. Acad. Sci. USA **97:**3526–3531.
48. **Dong, Y. H., X. F. Zhang, J. L. Xu, and L. H. Zhang.** 2004. Insecticidal *Bacillus thuringiensis* silences *Erwinia carotovora* virulence by a new form of microbial antagonism, signal interference. Appl. Environ. Microbiol. **70:**954–960.
49. **Dörr, J., T. Hurek, and B. Reinhold-Hurek.** 1998. Type IV pili are involved in plant-microbe and fungus-microbe interactions. Mol. Microbiol. **30:**7–17.
50. **Duffy, B. K.** 2001. Competition, p. 243–244. *In* O. C. Maloy and T. D. Murray (ed.), Encyclopedia of plant pathology. John Wiley & Sons, Inc., New York, N.Y.
51. **Duffy, B. K., and G. Défago.** 1997. Zinc improves biocontrol of *Fusarium* crown and root rot of tomato by *Pseudomonas fluorescens* and represses the production of pathogen metabolites inhibitory to bacterial antibiotic biosynthesis. Phytopathology **87:**1250–1257.
52. **Duffy, B. K., and G. Défago.** 1999. Environmental factors modulating antibiotic and siderophore biosynthesis by *Pseudomonas fluorescens* biocontrol strains. Appl. Environ. Microbiol. **65:**2429–2438.
53. **Duffy, B. K., and G. Défago.** 2000. Controlling instability in *gacS-gacA* regulatory genes during inoculum production of *Pseudomonas fluorescens* bicontrol strains. Appl. Environ. Microbiol. **66:**3142–3150.
54. **Duffy, B., C. Keel, and G. Défago.** 2004. Potential role of pathogen signaling in multitrophic plant-microbe interactions involved in disease protection. Appl. Environ. Microbiol. **70:**1836–1842.
55. **Duffy, B., A. Schouten, and J. M. Raaijmakers.** 2003. Pathogen self defense: mechanisms to counteract microbial antagonism. Annu. Rev. Phytopathol. **41:**501–538.
56. **Duffy, B. K., A. Simon, and D. M. Weller.** 1996. Combination of *Trichoderma koningii* with fluorescent pseudomonads for control of take-all on wheat. Phytopathology **86:**188–194.
57. **Duijff, B. J., V. Gianinazzi-Pearson, and P. Lemanceau.** 1997. Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol *Pseudomonas fluorescens* strain WCS417r. New Phytol. **135:**325–334.
58. **Frankowski, J., M. Lorito, F. Scala, R. Schmidt, G. Berg, and H. Bahl.** 2001. Purification and properties of two chitinolytic enzymes of *Serratia plymuthica* HRO-C48. Arch. Microbiol. **176:**421–426.
59. **Fridlender, M., J. Inbar, and I. Chet.** 1993. Biological control of soilborne plant pathogens by a β-1,3-glucanase-producing *Pseudomonas cepacia.* Soil Biol. Biochem. **25:**1211–1221.
60. **Gaffney, T. D., S. T. Lam, J. Ligon, K. Gates, A. Frazelle, J. Di Maio, S. Hill, S. Goodwin, N. Torkewitz, and A. M. Allshouse.** 1994. Global regulation of expression of antifungal factors by a *Pseudomonas fluorescens* biological control strain. Mol. Plant-Microbe Interact. **7:**455–463.
61. **Georgakopoulos, D. G., M. Hendson, N. J. Panopoulos, and M. N. Schroth.** 1994. Cloning of a phenazine biosynthetic locus of *Pseudomonas aureofaciens* PGS12 and analysis of its expression in vitro with the ice nucleation reporter gene. Appl. Environ. Microbiol. **60:**2931–2938.
62. **Gerhardson, B.** 2002. Biological substitutes for pesticides. Trends Biotechnol. **20:**338–343.
63. **Glick, B.** 1995. The enhancement of plant growth by free-living bacteria. Can. J. Microbiol. **41:**109–117.
64. **Glick, B. R., Penrose, D. M., and J. Li.** 1998. A model for the lowering of plant ethylene concentrations by plant growth-promoting bacteria. J. Theor. Biol. **190:**63–68.
65. **Gray, E. J., and D. L. Smith.** 2005. Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes. Soil Biol. Biochem. **37:**395–412.
66. **Haas, D., C. Blumer, and C. Keel.** 2000. Biocontrol ability of fluorescent pseudomonads genetically dissected: importance of positive feedback regulation. Curr. Opin. Biotechnol. **11:**290–297.
67. **Haas, D., C. Keel, and C. Reimmann.** 2002. Signal transduction in plant-beneficial rhizobacteria with biocontrol properties. Antonie Leeuwenhoek **81:**385–395.
68. **Haas, D., and C. Keel.** 2003. Regulation of antibiotic production in root-colonizing *Pseudomonas* spp. and relevance for biological control of plant disease. Annu. Rev. Phytopathol. **41:**117–153.
69. **Hahn, H. P.** 1997. The type-4 pilus is the major virulence-associated adhesin of *Pseudomonas aeruginosa*-a review. Gene **192:**99–108.
70. **Hallman, J., A. Quadt-Hallman, W. F. Mahafee, and J. W. Kloepper.** 1997. Bacterial endophytes in agricultural crops. Can. J. Microbiol. **43:**895–914.
71. **Hase, S., J. A. van Pelt, L. C. van Loon, and C. M. J. Pieterse.** 2003. Colonization of *Arabidopsis* roots by *Pseudomonas fluorescens* primes the plant to produce higher levels of ethylene upon pathogen infection. Physiol. Mol. Plant Pathol. **62:**219–226.
72. **Hashidoko, Y., T. Nakayama, Y. Homma, and S. Tahara.** 1999. Structure elucidation of xanthobaccin A, a new antibiotic produced from *Stenotrophomonas* sp. strain SB-K88. Tetrahedron Lett. **40:**2957–2960.
73. **Hoffland, E., C. Pieterse, L. Bik, and J. A. van Pelt.** 1995. Induced systemic resistance in radish is not associated with accumulation of pathogenesis-related proteins. Physiol. Mol. Plant Pathol. **46:**309–320.
74. **Huang, Z., R. F. Bonsall, D. V. Mavrodi, D. M. Weller, and L. S. Thomashow.** 2004. Transformation of *Pseudomonas fluorescens* with genes for biosynthesis of phenazine-1-carboxylic acid improves biocontrol of rhizoctonia root rot and in situ antibiotic production. FEMS Microbiol. Ecol. **49:**243–251.
75. **Isnansetyo, A., L. Z. Cui, K. Hiramatsu, and Y. Kamei.** 2003. Antibacterial activity of 2,4-diacetylphloroglucinol produced by *Pseudomonas* sp. AMSN isolated from a marine alga, against vancomycin-resistant *Staphylococcus aureus.* Int. J. Antimicrob. Agents **22:**545–547.
76. **Jeun, Y. C., K. S. Park, C. H. Kim, W. D. Fowler, and J. W. Kloepper.** 2004. Cytological observations of cucumber plants during induced resistance elicited by rhizobacteria. Biol. Control **29:**34–42.
77. **Kamensky, M., M. Ovadis, I. Chet, and L. Chernin.** 2003. Soil-borne strain IC14 of *Serratia plymuthica* with multiple mechanisms of antifungal activity provides biocontrol of *Botrytis cinerea* and *Sclerotinia sclerotiorum* diseases. Soil Biol. Biochem. **35:**323–331.
78. **Keel, C., C. Voisard, C. H. Berling, G. Kahr, and G. Défago.** 1989. Iron sufficiency, a prerequisite for the suppression of tobacco black root rot by *Pseudomonas fluorescens* strain CHA0 under gnotobiotic conditions. Phytopathology **79:**584–589.
79. **Kerry, B. R.** 2000. Rhizosphere interactions and the exploitation of microbial agents for the biological control of plant-parasitic nematodes. Annu. Rev. Phytopathol. **38:**423–441.
80. **Kilic-Ekici, O., and G. Y. Yuen.** 2004. Comparison of strains of *Lysobacter enzymogenes* and PGPR for induction of resistance against *Bipolaris sorokiniana* in tall fescue. Biol. Control **30:**446–455.
81. **Kim, B. S., S. S. Moon, and B. K. Hwang.** 1999. Isolation, identification and antifungal activity of a macrolide antibiotic, oligomycin A, produced by *Streptomyces libani.* Can. J. Bot. **77:**850–858.
82. **Kloepper, J. W., and M. N. Schroth.** 1978. Plant growth-promoting rhizobacteria on radishes, p. 879–882. *In* Station de pathologie vegetale et

phyto-bacteriologie (ed.), Proceedings of the 4th International Conference on Plant Pathogenic Bacteria, vol. II. Gilbert-Clarey, Tours, France.
83. **Kloepper, J. W., B. Schippers, and P. A. H. M. Bakker.** 1992. Proposed elimination of the term endorhizosphere. Phytopathology **82:**726–727.
84. **Kloepper, J. W., R. Rodriguez-Ubana, G. W. Zehnder, J. F. Murphy, E. Sikora, and C. Fernandez.** 1999. Plant root-bacterial interactions in biological control of soilborne diseases and potential extension to systemic and foliar diseases. Austral. Plant Pathol. **28:**21–26.
85. **Knee, E. M., F. C. Gong, M. Gao, M. Teplitski, A. R. Jones, A. Foxworthy, A. J. Mort, and W. D. Bauer.** 2001. Root mucilage from pea and its utilization by rhizosphere bacteria as a sole carbon source. Mol. Plant-Microbe Interact. **14:**775–784.
86. **Kojic, M., G. Degrassi, and V. Venturi.** 1999. Cloning and characterization of the *rpoS* gene from the plant growth-promoting *Pseudomonas putida* WCS358: RpoS is not involved in siderophore and homoserine lactone production. Biochim. Biophys. Acta **1489:**413–420.
87. **Kuiper, I., G. V. Bloemberg, S. Noreen, J. E. Thomas-Oates, and B. J. J. Lugtenberg.** 2001. Increased uptake of putrescine in the rhizosphere inhibits competitive root colonization by *Pseudomonas fluorescens* strain WCS365. Mol. Plant-Microbe Interact. **14:**1096–1104.
88. **Leeman, M., J. A. van Pelt, F. M. Denouden, M. Heinsbroek, P. Bakker, and B. Schippers.** 1995. Induction of systemic resistance against Fusarium wilt of radish by lipopolysaccharides of *Pseudomonas fluorescens.* Phytopathology **85:**1021–1027.
89. **Leeman, M., F. M. Denouden, J. A. VanPelt, C. Cornelissen, A. MatamalaGarros, P. A. H. M. Bakker, and B. Schippers.** 1996. Suppression of fusarium wilt of radish by co-inoculation of fluorescent *Pseudomonas* spp. and root-colonizing fungi. Eur. J. Plant Pathol. **102:**21–31.
90. **Leeman, M., E. M. Denouden, J. A. van Pelt, F. Dirkx, H. Steijl, P. Bakker, and B. Schippers.** 1996. Iron availability affects induction of systemic resistance to fusarium wilt of radish by *Pseudomonas fluorescens.* Phytopathology **86:**149–155.
91. **Lim, H. S., Y. S. Kim, and S. D. Kim.** 1991. *Pseudomonas stutzeri* YPL-1 genetic transformation and antifungal mechanism against *Fusarium solani*, an agent of plant root rot. Appl. Environ. Microbiol. **57:**510–516.
92. **Lodewyckx, C., J. Vangronsveld, F. Porteous, E. R. B. Moore, S. Taghavi, M. Mezgeay, and D. van der Lelie.** 2002. Endophytic bacteria and their potential applications. Crit. Rev. Plant Sci. **21:**583–606.
93. **Loper, J. E., and M. D. Henkels.** 1997. Availability of iron to *Pseudomonas fluorescens* in rhizosphere and bulk soil evaluated with an ice nucleation reporter gene. Appl. Environ. Microbiol. **63:**99–105.
94. **Loper, J. E., and M. D. Henkels.** 1999. Utilization of heterologous siderophores enhances levels of iron available to *Pseudomonas putida* in the rhizosphere. Appl. Environ. Microbiol. **65:**5357–5363.
95. **Lugtenberg, B. J. J., and L. C. Dekkers.** 1999. What make *Pseudomonas* bacteria rhizosphere competent? Environ. Microbiol. **1:**9–13.
96. **Lugtenberg, B. J., L. V. Kravchenko, and M. Simons.** 1999. Tomato seed and root exudate sugars: composition, utilization by *Pseudomonas* biocontrol strains, and role in rhizosphere colonization. Environ. Microbiol. **1:**439–446.
97. **Lugtenberg, B. J. J., L. Dekkers, and G. V. Bloemberg.** 2001. Molecular determinants of rhizosphere colonization by *Pseudomonas.* Annu. Rev. Phytopathol. **39:**461–490.
98. **Lutz, M. P., S. Wenger, M. Maurhofer, G. Défago, and B. Duffy.** 2004. Signaling between bacterial and fungal biocontrol agents in a strain mixture. FEMS Microbiol. Ecol. **48:**447–455.
99. **Mathesius, U., S. Mulders, M. S. Gao, M. Teplitski, G. Caetano-Anolles, B. G. Rolfe, and W. D. Bauer.** 2003. Extensive and specific responses of a eukaryote to bacterial quorum-sensing signals. Proc. Natl. Acad. Sci. USA **100:**1444–1449.
100. **Maurhofer, M., C. Hase, P. Meuwly, J. P. Metraux, and G. Défago.** 1994. Induction of systemic resistance of tobacco to tobacco necrosis virus by the root-colonizing *Pseudomonas fluorescens* strain CHA0: influence of the *gacA* gene and of pyoverdine production. Phytopathology **84:**139–146.
101. **Mayak, S., T. Tirosh, and B. R. Glick.** 2004. Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. Plant Physiol. Biochem. **42:**565–572.
102. **McInroy, J. A., and J. W. Klopper.** 1995. Population dynamics of endophytic bacteria in field-grown sweet corn and cotton. Can. J. Microbiol. **41:**895–901.
103. **Milner, J. L., S. J. Raffel, B. J. Lethbridge, and J. Handelsman.** 1995. Culture conditions that influence accumulation of zwittermicin A by *Bacillus cereus* UW85. Appl. Microbiol. Biotechnol. **43:**685–691.
104. **Milner, J. L., L. Silo-Suh, J. C. Lee, H. He, J. Clardy, and J. Handelsman.** 1996. Production of kanosamine by *Bacillus cereus* UW85. Appl. Environ. Microbiol. **62:**3061–3065.
105. **Molina, L., F. Constantinescu, C. Reimmann, B. Duffy, and G. Défago.** 2003. Degradation of pathogen quorum-sensing molecules by soil bacteria: a preventive and curative biological control mechanism. FEMS Microbiol. Ecol. **45:**71–81.
106. **Morello, J. E., E. A. Pierson, and L. S. Pierson.** 2004. Negative cross-communication among wheat rhizosphere bacteria: effect on antibiotic production by the biological control bacterium *Pseudomonas aureofaciens* 30–84. Appl. Environ. Microbiol. **70:**3103–3109.
107. **Morrissey, J. P., J. M. Dow, G. L. Mark, and F. O'Gara.** 2004. Are microbes at the root of a solution to world food production? EMBO Rep. **5:**922–926.
108. **Morrissey, J. P., U. F. Walsh, A. O'Donnell, Y. Moënne-Loccoz, and F. O'Gara.** 2002. Exploitation of genetically modified inoculants for industrial ecology applications. Antonie Leeuwenhoek **81:**599–606.
109. **M'Piga, P., R. R. Belanger, T. C. Paulitz, and N. Benhamou.** 1997. Increased resistance to *Fusarium oxysporum* f. sp. *radicis-lycopersici* in tomato plants treated with the endophytic bacterium *Pseudomonas fluorescens* strain 63-28. Physiol. Mol. Plant Pathol. **50:**301–320.
110. **Nakayama, T., Y. Homma, Y. Hashidoko, J. Mizutani, and S. Tahara.** 1999. Possible role of xanthobaccins produced by *Stenotrophomonas* sp. strain SB-K88 in suppression of sugar beet damping-off disease. Appl. Environ. Microbiol. **65:**4334–4339.
111. **Natsch, A., C. Keel, H. A. Pfirter, D. Hass, and G. Défago.** 1994. Contribution of the global regulator gene *gacA* to persistence and dissemination of *Pseudomonas fluorescens* biocontrol strain CHA0 introduced into soil microcosms. Appl. Environ. Microbiol. **60:**2553–2560.
112. **Nelson, E. B.** 2004. Microbial dynamics and interactions in the spermosphere. Annu. Rev. Phytopathol. **42:**271–309.
113. **Newton, J. A., and R. G. Fray.** 2004. Integration of environmental and host-derived signals with quorum sensing during plant-microbe interactions. Cell. Microbiol. **6:**213–224.
114. **Nielsen, T. H., D. Sørensen, C. Tobiasen, J. B. Andersen, C. Christeophersen, M. Givskov, and J. Sørensen.** 2002. Antibiotic and biosurfactant properties of cyclic lipopeptides produced by fluorescent *Pseudomonas* spp. from the sugar beet rhizosphere. Appl. Environ. Microbiol. **68:**3416–3423.
115. **Nielsen, T. H., and J. Sørensen.** 2003. Production of cyclic lipopeptides by *Pseudomonas fluorescens* strains in bulk soil and in the sugar beet rhizosphere. Appl. Environ. Microbiol. **69:**861–868.
116. **Notz, R., M. Maurhofer, U. Schnider-Keel, B. Duffy, D. Haas, and G. Défago.** 2001. Biotic factors affecting expression of the 2,4-diacetylphloroglucinol biosynthesis gene *phlA* in *Pseudomonas fluorescens* biocontrol strain CHA0 in the rhizosphere. Phytopathology **91:**873–881.
117. **Nowak, J., and V. Shulaev.** 2003. Priming for transplant stress resistance in in vitro propagation. In Vitro Cell. Dev. Biol.-Plant. **39:**107–124.
118. **Okubara, P. A., J. P. Kornoely, and B. B. Landa.** 2004. Rhizosphere colonization of hexaploid wheat by *Pseudomonas fluorescens* strains Q8rl-96 and Q2-87 is cultivar-variable and associated with changes in gross root morphology. Biol. Control. **30:**392–403.
119. **Olivain, C., C. Alabouvette, and C. Steinberg.** 2004. Production of a mixed inoculum of *Fusarium oxysporum* Fo47 and *Pseudomonas fluorescens* C7 to control *Fusarium* diseases. Biol. Sci. Technol. **14:**227–238.
120. **Ongena, M., F. Daayf, P. Jacques, P. Thonart, N. Benhamou, T. C. Paulitz, and R. R. Bélanger.** 2000. Systemic induction of phytoalexins in cucumber in response to treatments with fluorescent pseudomonads. Plant Pathol. **49:**523–530.
121. **Ordentlich, A., Y. Elad, and I. Chet.** 1988. The role of chitinase of *Serratia marcescens* in biocontrol of *Sclerotium rolfsii.* Phytopathology **78:**84–88.
122. **O'Sullivan, D. J., and F. O'Gara.** 1992. Traits of fluorescent *Pseudomonas* spp. involved in suppression of plant root pathogens. Microbiol. Rev. **56:**662–676.
123. **Ovadis, M., X. Liu, S. Gavriel, Z. Ismailov, I. Chet, and L. Chernin.** 2004. The global regulator genes from biocontrol strain *Serratia plymuthica* IC1270: cloning, sequencing, and functional studies. J. Bacteriol. **186:**4986–4993.
124. **Ownley, B. H., D. M. Weller, and L. S. Thomashow.** 1992. Influence of in situ and in vitro pH on suppression of *Gaeumannomyces graminis var. tritici* by *Pseudomonas fluorescens* 2–79. Phytopathology **82:**178–184.
125. **Ownley, B. H., B. K. Duffy, and D. M. Weller.** 2003. Identification and manipulation of soil properties to improve the biological control performance of phenazine-producing *Pseudomonas fluorescens.* Appl. Environ. Microbiol. **69:**3333–3343.
126. **Park, K. S., and J. W. Kloepper.** 2000. Activation of PR-1a promoter by rhizobacteria which induce systemic resistance in tobacco against *Pseudomonas syringae* pv. *tabaci.* Biol. Control **18:**2–9.
127. **Parke, J. L.** 1991. Root colonization by indigenous and introduced microorganisms, p. 33–42. *In* D. L. Keister and P. B. Gregan (ed.), The rhizosphere and plant growth. Kluwer Academic Publishers, Dordrecht, The Netherlands.
128. **Pettersson, M., and E. Bååth.** 2004. Effects of the properties of the bacterial community on pH adaptation during recolonization of a humus soil. Soil Biol. Biochem. **36:**1383–1388.
129. **Picard, C., F. Di Cello, M. Ventura, R. Fani, and A. Guckert.** 2000. Frequency and biodiversity of 2,4-diacetylphloroglucinol-producing bacteria isolated from the maize rhizosphere at different stages of plant growth. **66:**948–955.
130. **Pierson, E. A., D. W. Wood, J. A. Cannon, F. M. Blachere, and L. S. Pierson.** 1998. Interpopulation signaling via *N*-acyl-homoserine lactones among bacteria in the wheat rhizosphere. Mol. Plant-Microbe Interact. **11:**1078–1084.
131. **Pierson, L. S., D. W. Wood, and E. A. Pierson.** 1998. Homoserine lactone-

mediated gene regulation in plant-associated bacteria. Annu. Rev. Phytopathol. **36:**207–225.
132. **Pieterse, C. M. J., S. C. M. van Wees, E. Hoffland, J. A. van Pelt, and L. C. van Loon.** 1996. Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. Plant Cell **8:**1225–1237.
133. **Pieterse, C. M. J., S. C. M. van Wees, J. A. van Pelt, M. Knoester, R. Laan, H. Gerrits, P. J. Weisbeek, and L. C. van Loon.** 1998. A novel signaling pathway controlling induced systemic resistance in *Arabidopsis.* Plant Cell **10:**1571–1580.
134. **Pieterse, C. M. J., and L. C. van Loon.** 1999. Salicylic acid-independent plant defense pathways. Trends Plant Sci. **4:**52–58.
135. **Ping, L., and W. Boland.** 2004. Signals from the underground: bacterial volatiles promote growth in *Arabidopsis.* Trends Plant Sci. **9:**263–269.
136. **Postma, J., M. Montanari, and P. H. J. F. van den Boogert.** 2003. Microbial enrichment to enhance the disease suppressive activity of compost. Eur. J. Soil Biol. **39:**157–163.
137. **Raaijmakers, J. M., I. Vandersluis, M. Koster, P. A. H. M. Bakker, P. J. Weisbeek, and B. Schippers.** 1995. Utilization of heterologous siderophores and rhizosphere competence of fluorescent *Pseudomonas* spp. Can. J. Microbiol. **41:**126–135.
138. **Raaijmakers, J. M., M. Vlami, and J. T. de Souza.** 2002. Antibiotic production by bacterial biocontrol agents. Antonie Leeuwenhoek **81:**537–547.
139. **Ramamoorthy, V., R. Viswanathan, T. Raguchander, V. Prakasam, and R. Smaiyappan.** 2001. Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. Crop Prot. **20:**1–11.
140. **Raupach, G. S., and J. W. Kloepper.** 1998. Mixtures of plant growth-promoting rhizobacteria enhance biological control of multiple cucumber pathogens. Phytopathology **88:**1158–1164.
141. **Ravel, J., and P. Cornelis.** 2003. Genomics of pyoverdine-mediated iron uptake in pseudomonads. Trends Microbiol. **11:**195–200.
142. **Reinhold, B., T. Hurek, and I. Fendrik.** 1985. Strain-specific chemotaxis of *Azospirillum* spp. J. Bacteriol. **162:**190–195.
143. **Rovira, A. D.** 1965. Interactions between plant roots and soil microorganisms. Annu. Rev. Microbiol. **19:**241–266.
144. **Ryan, P. R., E. Delhaize, and D. L. Jones.** 2001. Function and mechanism of organic anion exudation from plant roots. Annu. Rev. Plant Physiol. Plant Mol. Biol. **52:**527–560.
145. **Ryu, C.-M., M. A. Farag, C. H. Hu, M. S. Reddy, J. W. Kloepper, and P. W. Paré.** 2004. Bacterial volatiles induce systemic resistance in *Arabidopsis.* Plant Physiol. **134:**1017–1026.
146. **Ryu, C. M., J. F. Murphy, K. S. Mysore, and J. W. Kloepper.** 2004. Plant growth-promoting rhizobacterial systemically protect *Arabidopsis thaliana* against *Cucumber mosaic virus* by a salicylic acid and NPR1-independent and jasmonic acid-dependent signaling pathway. The Plant J. **39:**381–392.
147. **Sacherer, P., G. Défago, and D. Hass.** 1994. Extracellular protease and phospholipase C are controlled by the global regulatory gene *gacA* in the biocontrol strain *Pseudomonas fluorescens* CHA0. FEMS Microbiol. Lett. **116:**155–160.
148. **Saleh, S. S., and B. R. Glick.** 2001. Involvement of gacS and rpoS in enhancement of the plant growth promoting capabilities of *Enterobacter cloacae* CAL2 and UW4. Can. J. Microbiol. **47:**698–705.
149. **Sánchez-Contreras, M., M. Martín, M. Villacieros, F. O'Gara, I. Bonilla, and R. Rivilla.** 2002. Phenotypic selection and phase variation occur during alfalfa root colonization by *Pseudomonas fluorescens* F113. Appl. Environ. Microbiol. **184:**1587–1596.
150. **Schisler, D. A., P. J. Slininger, and R. J. Bothast.** 1997. Effects of antagonist cell concentration and two-strain mixtures on biological control of *Fusarium* dry rot of potatoes. Phytopathology **87:**177–183.
151. **Schnider-Keel, U., A. Seematter, M. Maurhofer, C. Blumer, B. Duffy, C. Gigot-Bonnefoy, C. Reimmann, R. Notz, G. Défago, D. Haas, and C. Keel.** 2000. Autoinduction of 2,4-diacetylphloroglucinol biosynthesis in the biocontrol agent *Pseudomonas fluorescens* CHA0 and repression by the bacterial metabolites salicylate and pyoluteorin. J. Bacteriol. **182:**1215–1225.
152. **Schouten, A., G. van der Berg, V. Edel-Hermann, C. Steinberg, N. Gautheron, C. Alabouvette, C. H. de Vos, P. Lemanceau, and J. M. Raaijmakers.** 2004. Defense responses of *Fusarium oxysporum* to 2,4-diacetylphloroglucinol, a broad-spectrum antibiotic produced by *Pseudomonas fluorescens.* Mol. Plant-Microbe Interact. **17:**1201–1211.
153. **Schroth, M. N., and J. G. Hancock.** 1981. Selected topics in biological control. Annu. Rev. Microbiol. **35:**453–476.
154. **Sessitsch, A., B. Reiter, and G. Berg.** 2004. Endophytic bacterial communities of field-grown potato plants and their plant growth-promoting and antagonistic abilities. Can. J. Microbiol. **50:**239–249.
155. **Sessitsch, A., T. Coenye, A. V. Sturz, P. Vandamme, E. Ait Barka, J. F. Salles, J. D. van Elsas, D. Faure, B. Reiter, B. R. Glick, G. Wang-Pruski, and J. Nowak.** 2005. *Burkholderia phytofirmans* sp. nov., a novel plant-associated bacterium with plant beneficial properties. Int. J. Syst. Evol. Microbiol. **55:**1187–1192.
156. **Sharma, V. K., and J. Nowak.** 1998. Enhancement of verticillium wilt resistance in tomato transplants by in vitro coculture of seedlings with a plant growth-promoting rhizobacterium (*Pseudomonas* sp. strain PsJN). Can. J. Microbiol. **44**:528–536.
157. **Simons, M., A. J. van der Bij, L. A. de Weger, C. A. Wijffelman, and B. J. Lugtenberg.** 1996. Gnotobiotic system for studying rhizosphere colonization by plant growth-promoting *Pseudomonas* bacteria. Mol. Plant-Microbe Interact. **9:**600–607.
158. **Simons, M., H. P. Permentier, L. A. de Weger, C. A. Wijffelman, and B. J. J. Lugtenberg.** 1997. Amino acid synthesis is necessary for tomato root colonization by *Pseudomonas fluorescens* strain WCS365. Mol. Plant-Microbe Interact. **10:**102–106.
159. **Singh, P. P., Y. C. Shin, C. S. Park, and Y. R. Chung.** 1999. Biological control of *Fusarium* wilt of cucumber by chitinolytic bacteria. Phytopathology **89:**92–99.
160. **Smith, K. P., and R. M. Goodman.** 1999. Host variation for interactions with beneficial plant-associated microbes. Annu. Rev. Phytopathol. **37:**473–491.
161. **Smith, K. P., J. Handelsman, and R. M. Goodman.** 1999. Genetic basis in plants for interactions with disease-suppressive bacteria. Proc. Natl. Acad. Sci. USA **96:**4786–4790.
162. **Steenhoudt, O., and J. Vanderleyden.** 2000. *Azospirillum*, a free-living nitrogen-fixing bacterium closely associated with grasses: genetic, biochemical and ecological aspects. FEMS Microbiol. Rev. **24:**487–506.
163. **Strom, M. S., and S. Lory.** 1993. Structure-function and biogenesis of the type IV pili. Annu. Rev. Microbiol. **30**:565–596.
164. **Sturz, A. V., B. R. Christie, B. G. Matheson, W. J. Arsenault, and N. A. Buchanan.** 1999. Endophytic bacterial communities in the epiderm of potato tubers and their potential to improve resistance to soil-borne plant pathogens. Plant Pathol. **48:**360–369.
165. **Sturz, A. V., B. R. Christie, and J. Nowak.** 2000. Bacterial endophytes: potential role in developing sustainable systems of crop production. Crit. Rev. Plant Sci. **19:**1–30.
166. **Sturz, A. V., and B. R. Christie.** 2003. Beneficial microbial allelopathies in the root zone: the management of soil quality and plant disease with rhizobacteria. Soil Tillage Res. **72:**107–123.
167. **Thomashow, L. S.** 1996. Biological control of plant root pathogens. Curr. Opin. Biotechnol. **7:**343–347.
168. **Timms-Wilson, T. M., R. J. Ellis, A. Renwick, D. J. Rhodes, D. V. Mavrodi, D. M. Weller, L. S. Thomashow, and M. J. Bailey.** 2000. Chromosomal insertion of phenazine-1-carboxylic acid biosynthetic pathway enhances efficacy of damping-off disease control by *Pseudomonas fluorescens.* Mol. Plant-Microbe Interact. **13:**1293–1300.
169. **Toyoda, H., H. Hashimoto, R. Utsumi, H. Kobayashi, and S. Ouchi.** 1988. Detoxification of fusaric acid by a fusaric acid-resistant mutant of *Pseudomonas solanacearum* and its application to biological control of fusarium wilt of tomato. Phytopathology **78:**1307–1311.
170. **Toyoda, H., and R. Utsumi.** January 1991. Method for the prevention of *Fusarium* diseases and microorganisms used for the same. U.S. patent 4,988,586.
171. **Turnbull, G. A., J. A. W. Morgan, J. M. Whipps, and J. R. Saunders.** 2001. The role of motility in the in vitro attachment of *Pseudomonas putida* PaW8 to wheat roots. FEMS Microbiol. Ecol. **35:**57–65.
172. **Turnbull, G. A., J. A. W. Morgan, J. M. Whipps, and J. R. Saunders.** 2001. The role of bacterial motility in the survival and spread of *Pseudomonas fluorescens* in soil and in the attachment and colonization of wheat roots. FEMS Microbiol. Ecol. **36:**21–31.
173. **Uroz, S., C. D'Angelo-Picard, A. Carlier, M. Elasri, C. Sicot, A. Petit, P. Oger, D. Faure, and Y. Dessaux.** 2003. Novel bacteria degrading *N*-acylhomoserine lactones and their use as quenchers of quorum-sensing-regulated functions of plant-pathogenic bacteria. Microbiology **149:**1981–1989.
174. **Van der Broek, D., T. F. C. Chin-A-Woeng, K. Eijkemans, I. H. M. Mulders, G. V. Bloemberg, and B. J. J. Lugtenberg.** 2003. Biocontrol traits of *Pseudomonas* spp. are regulated by phase variation. Mol. Plant-Microbe Interact. **16:**1003–1012.
175. **Van Loon, L. C., P. A. H. M. Bakker, and C. M. J. Pieterse.** 1998. Systemic resistance induced by rhizosphere bacteria. Annu. Rev. Phytopathol. **36:**453–483.
176. **Van Overbeek, L. S., and J. D. Van Elsas.** 1995. Root exudates-induced promoter activity in *Pseudomonas fluorescens* mutants in the wheat rhizosphere. Appl. Environ. Microbiol. **61:**890–898.
177. **Van Peer, R., H. L. M. Punte, L. A. de Weger, and B. Schippers.** 1990. Characterization of root surface and endorhizosphere pseudomonads in relation to their colonization of roots. Appl. Environ. Microbiol. **56:**2462–2470.
178. **Van Peer, R., G. J. Niemann, and B. Schippers.** 1991. Induced resistance and phytoalexin accumulation in biological control of *Fusarium* wilt of carnation by *Pseudomonas* sp. strain WCS417r. Phytopathology **81:**728–734.
179. **van Wees, S., C. Pieterse, A. Trijssenaar, Y. Van't Westende, F. Hartog, and L. C. van Loon.** 1997. Differential induction of systemic resistance in *Arabidopsis* by biocontrol bacteria. Mol. Plant-Microbe Interact. **10:**716–724.
180. **van Wees, S. C. M., M. Luijendijk, I. Smoorenburg, L. C. van Loon, and C. M. J. Pieterse.** 1999. Rhizobacteria-mediated induced systemic resistance (ISR) in *Arabidopsis* is not associated with a direct effect on expres-

sion of known defense-related genes but stimulates the expression of the jasmonate-inducible gene *Atvsp* upon challenge. Plant Mol. Biol. **41:**537–549.
181. **von Bodman, S. B., W. D. Bauer, and D. L. Coplin.** 2003. Quorum sensing in plant-pathogenic bacteria. Annu. Rev. Phytopathol. **41:**455–482.
182. **Viswanathan, R., and R. Samiyappan.** 1999. Induction of systemic resistance by plant growth-promoting rhizobacteria against red rot disease caused by *Colletotrichum falcatum* went in sugarcane, p. 24–39. *In* Proceedings of the Sugar Technology Association of India, vol. 61. Sugar Technology Association, New Delhi, India.
183. **Walker, M. J., R. G. Birch, and J. M. Pemberton.** 1988. Cloning and characterization of an albicidin resistance gene from *Klebsiella oxytoca.* Mol. Microbiol. **2:**443–454.
184. **Walsh, U. F., Morrissey, J. P., and F. O'Gara.** 2001. *Pseudomonas* for biocontrol of phytopathogens: from functional genomics to commercial exploitation. Curr. Opin. Biotechnol. **12:**289–295.
185. **Wang, C., E. Knill, B. R. Glick, and G. Défago.** 2000. Effect of transferring 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase genes into *Pseudomonas fluorescens* strain CHA0 and its *gacA* derivative CHA96 on their growth-promoting and disease-suppressive capacities. Can. J. Microbiol. **46:**898–907.
186. **Wang, Y., H. N. Brown, D. E. Crowley, and P. J. Szaniszlo.** 1993. Evidence for direct utilization of a siderophore, ferrioxamine B in axenically grown cucumber. Plant Cell Environ. **16:**579–585.
187. **Wei, L., J. W. Kloepper, and S. Tuzun.** 1991. Induction of systemic resistance of cucumber to *Colletotrichum orbiculare* by select strains of plant growth-promoting rhizobacteria. Phytopathology **81:**1508–1512.
188. **Welbaum, G., A. V. Sturz, Z. Dong, and J. Nowak.** 2004. Fertilizing soil microorganisms to improve productivity of agroecosystems. Crit. Rev. Plant Sci. **23:**175–193.
189. **Weller, D. M.** 1988. Biological control of soilborne plant pathogens in the rhizosphere with bacteria. Annu. Rev. Phytopathol. **26:**379–407.
190. **Whipps, J. M.** 1997. Developments in the biological control of soil-borne plant pathogens. Adv. Bot. Res. **26:**1–133.
191. **Whipps, J. M.** 2001. Microbial interactions and biocontrol in the rhizosphere. J. Exp. Bot. **52:**487–511.
192. **Yamaki, M., M. Miwa, K. Ishiguro, and S. Takagi.** 1994. Antimicrobial activity of naturally occurring and synthetic phloroglucinols against *Staphylococcus aureus.* Phytother. Res. **8:**112–114.
193. **Zala, M., C. Gyawali, B. Duffy, K. Keel, and G. Défago.** 1999. Application of phloroglucinol (PHL) production as a phenotypic marker for selecting better biocontrol bacteria. Phytopathology **89:**88–89.
194. **Zhang, L., and R. G. Birch.** 1996. Biocontrol of sugar cane leaf scald disease by an isolate of *Pantoea dispersa* which detoxifies albicidin phytotoxins. Lett. Appl. Microbiol. **22:**132–136.
195. **Zhang, L., and R. G. Birch.** 1997. The gene for albicidin detoxification from *Pantoea dispersa* encodes an esterase and attenuates pathogenicity of *Xanthomonas albilineans* to sugarcane. Proc. Natl. Acad. Sci. USA **94:**9984–9989.