

Plant–microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture

Gabriele Berg

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Abstract Plant-associated microorganisms fulfill important functions for plant growth and health. Direct plant growth promotion by microbes is based on improved nutrient acquisition and hormonal stimulation. Diverse mechanisms are involved in the suppression of plant pathogens, which is often indirectly connected with plant growth. Whereas members of the bacterial genera *Azospirillum* and *Rhizobium* are well-studied examples for plant growth promotion, *Bacillus*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, and *Streptomyces* and the fungal genera *Ampelomyces*, *Coniothyrium*, and *Trichoderma* are model organisms to demonstrate influence on plant health. Based on these beneficial plant–microbe interactions, it is possible to develop microbial inoculants for use in agricultural biotechnology. Dependent on their mode of action and effects, these products can be used as biofertilizers, plant strengtheners, phytostimulators, and biopesticides. There is a strong growing market for microbial inoculants worldwide with an annual growth rate of approximately 10%. The use of genomic technologies leads to products with more predictable and consistent effects. The future success of the biological control industry will benefit from interdisciplinary research, e.g., on mass production, formulation, interactions, and signaling with the environment, as well as on innovative business management, product marketing, and education. Altogether, the use of microorganisms and the exploitation of beneficial plant–microbe interactions offer promising and environmentally friendly strategies for conventional and organic agriculture worldwide.

Keywords Plant-associated microorganisms · Biocontrol · Antagonist · Plant strengthener · Biofertilizers · Biopesticide

Introduction

One of the major challenges for the twenty-first century will be an environmentally sound and sustainable crop production. An enhanced production is necessary to provide sufficient food for the increasing human population, renewable energy, as well as basic compounds in industrial processes. Current production methods in agriculture, e.g., the improper use of chemical pesticides and fertilizers, create a long list of environmental and health problems (Gunnell et al. 2007; Leach and Mumford 2008). Furthermore, emerging, re-emerging, and endemic plant pathogens continue to challenge our ability to safeguard plant growth and health worldwide (Miller et al. 2009). Altogether, there is a growing demand for sound and ecologically compatible strategies in agriculture. Plant biotechnology contributed to the development of numerous new crop varieties with enhanced disease resistance, greater drought and salt tolerance, and better nutritional value. Unfortunately, the beneficial plant–microbe interaction was often ignored in breeding strategies although plant-associated microorganisms fulfill important ecosystem functions for plants and soils (reviewed in Smith et al. 1999). This includes the effects of plant-associated microorganisms on plant health and growth; they enhance stress tolerance, provide disease resistance, aid nutrient availability and uptake and promote biodiversity (Lugtenberg et al. 2002; Morrissey et al. 2004). Furthermore, plant-associated microbial communities show, due to specific secondary metabolism and morphology, a certain degree of specificity for each plant species (reviewed in Berg and Smalla 2009).

G. Berg (✉)
Environmental Biotechnology, Graz University of Technology,
Petersgasse 12,
8010 Graz, Austria
e-mail: Gabriele.Berg@tugraz.at

This knowledge has yet to be exploited in agricultural biotechnology.

However, over the past 150 years, research repeatedly demonstrated that bacteria and fungi have an intimate interaction with their host plants and are able to promote plant growth as well as to suppress plant pathogens (Whipps 2001; Thakore 2006; Ehlers 2006). All plant-associated microenvironments, especially the rhizosphere, are colonized in high abundances by microbes (Berg et al. 2005b). When testing microbial isolates from plant-associated habitats, between 1% and 35% showed antagonistic capacity to inhibit the growth of pathogens in vitro (Berg et al. 2002, 2006). The proportion of isolates which express plant growth-promoting traits is much higher in general and was found up to two thirds of the cultivable population (Cattelan et al. 1999; Furnkranz et al. 2009). In general, there are two possibilities to influence the antagonistic/plant growth-promoting potential: (1) by managing the indigenous microbial potential, e.g., by the introduction of organic or inorganic amendments (Hallmann et al. 1999; Conn and Lazarovits 2000), and (2) by applying autochthonous microorganisms as biocontrol or plant growth-promoting agents (PGPAs; Emmert and Handelsman 1999; Whipps 2001; Weller et al. 2002; Compant et al. 2005; Weller 2007). Furthermore, diverse microbial inoculants are already on the market and, in recent years, the popularity of microbial inoculants increased substantially, as extensive and systematic research has enhanced their effectiveness and consistency (Thakore 2006). Recent surveys of both conventional and organic growers indicate an interest in using microbial inoculants, suggesting that the market potential of biocontrol products will increase in coming years (McSpadden Gardener and Fravel 2002).

Plant growth promotion can be achieved by the direct interaction between beneficial microbes and their host plant and also indirectly due to their antagonistic activity against plant pathogens (Fig. 1). In this review, plant growth promotion achieved on both ways was considered. The current status of research, commercial development, and application of microbial inoculants to promote plant growth was described. In comparison with chemical/synthesized pesticides and fertilizers, microbial inoculants have several advantages: they (1) are more safe, (2) show reduced environmental damage and potentially smaller risk to human health, (3) show much more targeted activity, (4) are effective in small quantities, (5) multiply themselves but are controlled by the plant as well as by the indigenous microbial populations, (6) decompose more quickly than conventional chemical pesticides, (7) resistance development is reduced due to several mechanisms, and (8) can be also used in conventional or integrated pest management systems.

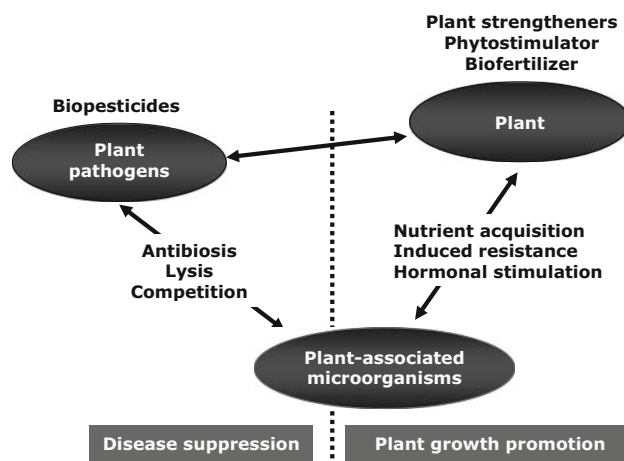


Fig. 1 Plant–microbe interactions promoting plant growth and health: mode of action and potential use in biotechnological applications

Mechanisms of plant growth promotion by microorganisms

Diverse mechanisms are involved in plant–microbe interaction (Whipps 2001; Compant et al. 2005). In many cases of individual beneficial plant–microbe interactions, several mechanisms are involved (Berg et al. 2002; Haas and Defago 2005; Muller et al. 2009). *Ad planta*, direct mechanisms of plant growth promotion are difficult to differentiate from disease suppression. In addition, the importance on a specific mechanism can vary within different pathosystems (Chet and Chermine 2002). However, for all successful plant–microbe interactions, the competence to colonize plant habitats is important (Lugtenberg et al. 2002; Kamilova et al. 2005). Steps of colonization include recognition, adherence, invasion (only endophytes and pathogens), colonization and growth, and several strategies to establish interactions. Plant roots initiate crosstalk with soil microbes by producing signals that are recognized by the microbes, which in turn produce signals that initiate colonization (Bais et al. 2006). To participate and react in this crosstalk, motile organisms are preferred (Lugtenberg et al. 2002). Moreover, there is growing appreciation that the intensity, duration, and outcome of plant–microbe interactions are significantly influenced by the conformation of adherent microbial populations (Danhorn and Fuqua 2004). Examples for successful colonization of the rhizosphere of two biological control agents (BCAs) belonging to the genus *Pseudomonas* are shown in Fig. 2. The three-dimensional reconstruction of a cross-section of an area densely colonized allowed the detection of endophytic growth by *Pseudomonas trivialis* RE*1-1-14 (Fig. 2c).

In the processes of plant growth, phytohormones, e.g., production of indole-3-acetic acid (IAA), ethylene, cytokinins, and gibberellins, play an important role. These

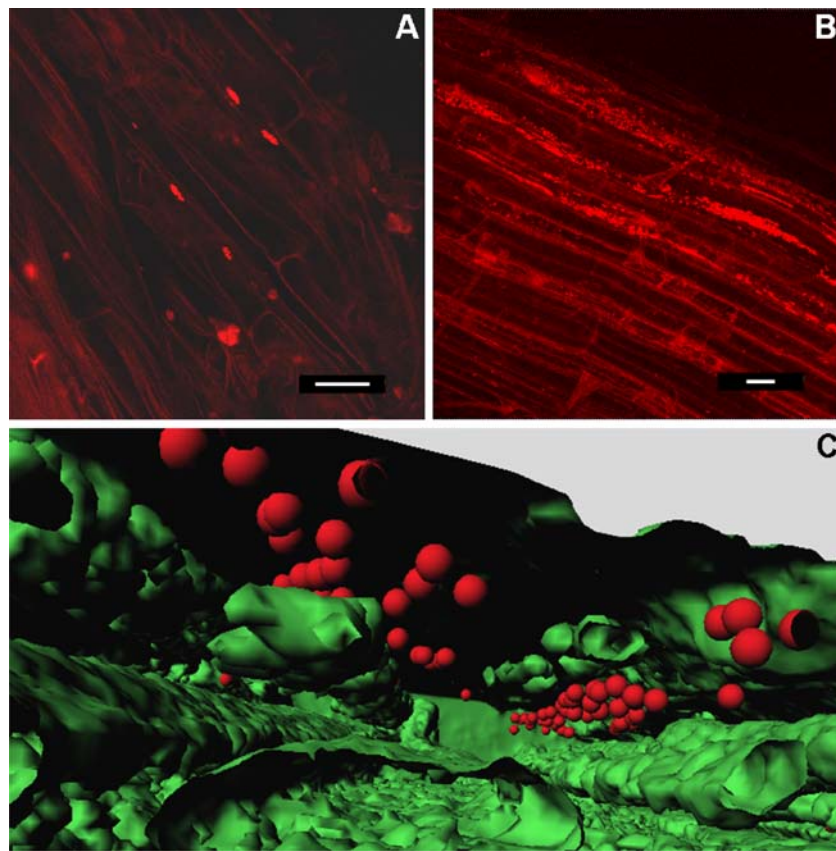


Fig. 2 Confocal laser scanning microscopy of 3-week-old sugar beet roots colonized by DsRed2-labeled bacteria: **a** *P. fluorescens* L13-6-12 and **b** *P. trivialis* RE*1-1-14. **c** Three-dimensional reconstruction of a cross-section of an area densely colonized by *P. trivialis* RE*1-1-14

with Imaris® 6.0 (Bitplane AG, Zürich, Switzerland) clearly shows that the bacterial cells also colonized endophytic parts of the sugar beet root. The pictures were prepared by Christin Zachow and Massimiliano Cardinale (Graz)

hormones can be synthesized by the plant themselves and also by their associated microorganisms. Furthermore, plant-associated bacteria can influence the hormonal balance of the plant. Ethylene is an important example to show that the balance is most important for the effect of hormones: at low levels, it can promote plant growth in several plant species including *Arabidopsis thaliana*, while it is normally considered as an inhibitor of plant growth and known as a senescence hormone (Pierik et al. 2006). Interestingly, bacteria are able to reduce the ethylene level by the following way. The compound 1-aminocyclopropane-1-carboxylic acid (ACC) is a precursor of ethylene in plants. As ACC deaminase-producing bacteria are able to degrade this substance, the uptake by and the level in the root is reduced. Thus, these bacteria can increase root growth by lowering the endogenous ACC levels (Glick 2005). Due to the fact that ethylene has also been established as a stress hormone, ACC deaminase-producing bacteria have an additional potential to protect plants against biotic and abiotic stress (reviewed in Saleem et al. 2007). Another example to explain the intimate plant–microbe interaction regarding phytohormones is the root-associated bacterium

Serratia plymuthica HRO-C48 in which IAA production is surprisingly negatively regulated by quorum sensing (QS) (Müller et al. 2009). On the other side, low amounts of IAA induced resistance in the plant (Hartmann et al. 2004). While IAA is involved in many bacteria–plant signaling (Spaepen et al. 2007), an important role of auxin signaling for plant growth promotion was also shown for *Trichoderma* spp. (Contreras-Cornejo et al. 2009). Besides these mechanisms, improved nutrient acquisition is involved in direct growth promotion. Plant-associated microorganisms can supply macronutrients and micronutrients. The most prominent example is bacterial nitrogen fixation. The symbiosis between rhizobia and its legume host plants is an important example for plant growth-promoting rhizobacteria (PGPR). Bacteria of this group metabolize root exudates (carbohydrates) and in turn provide nitrogen to the plant for amino acid synthesis. The ability to fix nitrogen also occurs in free-living bacteria like *Azospirillum*, *Burkholderia*, and *Stenotrophomonas* (Dobbela et al. 2003). Another nutrient is sulfate, which can be provided to the plant via oxidation by bacteria (Banerjee and Yesmin 2002). Bacteria may contribute to plant nutrition

by liberating phosphorous from organic compounds such as phytates and thus indirectly promote plant growth (Unno et al. 2005). *Azospirillum* treatment resulted in enhancement of root growth and activities (e.g., acidification of the root surroundings) that increases phosphorous and other macroelements and microelements uptake (Dobbelaere and Okon 2007). Mineral supply is also involved in plant growth promotion and includes synthesis of siderophores and siderophore uptake systems (Katiyar and Goel 2004). Poorly soluble inorganic nutrients can be made available through the solubilization of bacterial siderophores and the secretion of organic acids. Recently, de Werra et al. (2009) showed that the ability of *Pseudomonas fluorescens* CHA0 to acidify its environment and to solubilize mineral phosphate is strongly dependent on its ability to produce gluconic acid. Furthermore, the study provides new evidence for a close association of gluconic acid metabolism with antagonistic activity against plant pathogens.

Microbial antagonism include (1) the inhibition of microbial growth by diffusible antibiotics and volatile organic compounds (VOCs), toxins, and biosurfactants [antibiosis], (2) competition for colonization sites and nutrients, (3) competition for minerals, e.g., for iron through production of siderophores or efficient siderophore uptake systems, (4) degradation of pathogenicity factors of the pathogen such as toxins, and (5) parasitism that may involve production of extracellular cell wall-degrading enzymes such as chitinases and β -1,3-glucanase (reviewed in Whipps 2001; Wheatley 2002; Compant et al. 2005; Haas and D efago 2005; Raaijmakers et al. 2006). Plant-associated bacteria can reduce the activity of pathogenic microorganisms not only through microbial antagonisms, but also by activating the plant to better defend itself, a phenomenon termed “induced systemic resistance” (ISR; Conrath et al. 2002; Van Loon 2007). However, sometimes, the mechanism of ISR elicited by PGPR overlaps partly with that of pathogen-induced systemic acquired resistance (SAR). Both ISR and SAR represent a state of enhanced basal persistence of the plant that depends on the signaling compounds jasmonic acid and salicylic acid (Van Loon 2007). Pathogens are differently sensitive to the resistance activated by these signaling pathways. These interactions are highly specific on each component: the host plant, the pathogen, as well as the PGPR strain. They recognize each other by chemical signaling: root exudates as well as microbial metabolites can have this function. The mechanisms of ISR include (1) developmental—escape: linked to growth promotion, (2) physiological—tolerance: reduced symptom expression, (3) environmental: associated with microbial antagonisms in the rhizosphere, and (4) biochemical—resistance: induction of cell wall reinforcement, induction of phytoalexins, induction of pathogenesis-related proteins, and “priming” of defense responses (resistance).

The plant–microbe interaction has mutual effects and affects both partners. For example, plants commonly react to root colonization by microbes by increasing the release of exudates (Phillips et al. 2004) or they produce several compounds that mimic QS signals that influence the bacterial communities (Bauer and Mathesius 2004). Kamilova et al. (2006) showed that the pathogen *Fusarium oxysporum* as well as the biocontrol bacterium *P. fluorescens* WCS365 influences the composition of organic acids and sugars in tomato root exudates. Plant-associated microorganisms have been shown to activate plant host defense when the symbiotic interaction becomes unproductive (Parniske et al. 1991). In conclusion, there is a high individuality of the plant–microbe interaction. PGPR that elicit ISR in one plant species may not do so in another, again indicating specificity in the interaction between rhizobacteria and plants. Substances involved in ISR are partly the same with those involved in microbial antagonisms: siderophores, antibiotics, *N*-acyl-homoserine lactones, VOCs (e.g., 2,3-butandiol). Whereas some PGPR activate defense-related gene expression, other examples appear to act solely through priming of effective resistance mechanisms, as reflected by earlier and stronger defense reaction once infection occurs.

There are several model organisms for plant growth promotion which are well-studied in their mode of action and regulation in detail. These comprise members of the bacterial genera *Azospirillum* (Okon 1994; Cass an and Garc ia Salamone 2008), *Bacillus* (Jacobsen et al. 2004), *Pseudomonas* (Haas and D efago 2005; Loper et al. 2007), *Rhizobium* (Long 2001), *Serratia* (De Vleeschauwer and H ofte 2007), *Stenotrophomonas* (Ryan et al. 2009), and *Streptomyces* (Schrey and Tarkka 2008) and the fungal genera *Ampelomyces*, *Coniothyrium*, and *Trichoderma* (Harman et al. 2004).

Using molecular techniques, it is possible to identify new factors involved in plant–microbe interaction (Berg and Smalla 2009). For example, assessing a genomic library of *P. fluorescens* B16, pyrroloquinoline quinone (PQQ) biosynthetic genes were identified as being responsible for plant growth promotion in this strain; results suggested that PQQ acts as an antioxidant in plants (Choi et al. 2008). Furthermore, the research can result in new targets and plant protection strategies.

Products and bottlenecks for controlled use of microorganisms in agriculture

Microbial inoculants can be divided into different categories. The latter depends on the official rules in the respective country. In the US, the products have to be registered by the United States Environmental Protection

Agency, while in Europe, common EU rules are responsible (see <http://www.rebeca.de>). From a scientific point of view, we can differentiate between (1) biofertilizers, (2) plant strengtheners, (3) phytostimulators, and (4) biopesticides (Lugtenberg et al. 2002). While the first three categories are based on PGPAs, biopesticides contain BCAs. Examples for all product categories are listed in Table 1. A new but, maybe in the future, growing category is flavor-stimulating agents, which enhance fruit flavor like *Methylobacterium* in strawberry (Zabetakis 1997). In general, microbial inoculants are available as liquid-based formulations, water-dispersible granules, or wettable powders or pellets.

There are several hurdles to be surmounted before innovative biocontrol studies can be transformed to practical strategies. First, there are technical problems in the mass production of microbes (upscaling). In addition, formulation into products with a long shelf-life is sometimes rather problematic for gram-negative than for spore-producing gram-positive bacteria. However, during the last years, a lot of progress has been seen for *Azospirillum* as well as for *Pseudomonas* isolates. A big obstacle is the registration procedure, which is often expensive and time-consuming (Ehlers 2006); especially, the costs of registration are the principal obstacles to the development of new products (Guillon 2008).

Another challenge is that plant-associated bacteria especially those from the rhizosphere play an emerging role as opportunistic human pathogens (Berg et al. 2005a). Examples are antagonistic species of the genera *Burkholderia*, *Enterobacter*, *Herbaspirillum*, *Ochrobactrum*, *Pseudomonas*, *Serratia*, *Staphylococcus*, and *Stenotrophomonas* that are root-associated bacteria that can enter interactions with plant and human hosts (Parke and Gurian-Sherman 2001; Ribbeck-Busch et al. 2005; Egamberdieva et al. 2008). Mechanisms involved in the interaction between antagonistic plant-associated bacteria and their host plants are similar to those responsible for the pathogenicity of bacteria to humans (Rahme et al. 1995; reviewed in Berg et al. 2005a). The mechanisms of interaction with potential eukaryotic hosts are species-specific and strain-specific (Berg et al. 2002). To avoid the use of potential human pathogens in biological plant protection, it is necessary to evaluate the risk of each potential BCA.

It is important to exclude potential pathogenic bacteria in the early step of product development. There are several criteria which allow for fast first evaluation, e.g., (1) growth at 37°C, (2) grouping in risk groups above one (<http://www.dsmz.de>), or (3) toxic effect in pathogenicity assays such as the *Caenorhabditis elegans* assay (Zachow et al. 2009b). Otherwise, more research and toxicological data are necessary to accurately evaluate the risk. However, in studies assessing the risk for the environment, only negligible short-term

effects were reported (Winding et al. 2004; Castro-Sowinski et al. 2007; Scherwinski et al. 2008; Jäderlund et al. 2008).

Market for microbial inoculants

In 2004, the global market for biocontrol was valued at about \$588 million (Bolckmans 2008). This was divided into 43.5% of sales in North American Free Trade Agreement countries (including Mexico), 20.7% in Europe, 12.2% in Asia, 11.2% in Oceania (including Australia), 8.3% in Latin America (excluding Mexico), and 3.9% in Africa. Strains of *Bacillus thuringiensis*, *Bacillus subtilis*, and *P. fluorescens* belong to the most important microbials. While *B. thuringiensis* is used to control most of the economically important insect pests, including American bollworm, *Heliothis* sp., *Earias* spp., *Spodoptera* sp., and *Plutella* sp., *B. subtilis* and *P. fluorescens* are used to control bacterial as well as fungal pathogens. The majority of commercialized BCAs has a broad host range and finds its application in rice, maize, tomato, and numerous other commercial crops. Between 1985 and 2004, the biocontrol market in the EU doubled, although the percentage of the main BCA of the market, *B. thuringiensis*, fell from 95% to 25%. Future growth in biopesticide sales is expected to be strongly tied to growth in organic production. The current annual growth rate of 9–10% in biopesticide sales is expected to stabilize at about 5%. In addition, in developing countries, there is a great potential for the use of microbial inoculants. The market is also benefiting from consumer demand for organic products (Thakore 2006). The EU has also removed a number of chemical products from the approved pesticide list with further reductions expected during the forecast period. Detailed data about the market and forecasts are available in different commercial studies. Furthermore, a detailed report about nitrogen-fixing bacteria as biofertilizers, for which the market is also growing, was published by Bhattacharjee et al. (2008).

Future prospects and challenges

Microbial inoculants, which can fulfill diverse functions in plants, lead to promising solutions for a sustainable, environmentally friendly agriculture. While inoculants for plant growth promotion and biocontrol already exist, in the future, stress-protecting agents (stress conditions like those generated by salinity, drought, waterlogging, heavy metals, and pathogenicity) will be of emerging importance not only due to climate change. Furthermore, to improve food quality by microbials is an important task. For all kinds of inoculants, microbial mixtures as multitasking inoculants are one alternative to overcome inconsistent *in vivo* effects.

Table 1 Representatives of microbial inoculants

Microorganisms	Name of the product	Plants, pathogens, or pathosystems	Company
<i>Ampelomyces quisqualis</i> M-10	AQ10 Biofungicide	Powdery mildew on apples, cucurbits, grapes, ornamentals, strawberries, and tomatoes	Ecogen
<i>Azospirillum</i> spp.	Biopromoter	Paddy, millets, oilseeds, fruits, vegetables, sugarcane, banana	Manidharma Biotech
<i>Bacillus subtilis</i> FZB24	FZB24 li, TB, WG RhizoPlus	Potatoes, vegetables, ornamentals, strawberries, bulbs, turf, and woods	AbiTep
<i>Bacillus subtilis</i> strain GB03	Kodiak	Growth promotion; <i>Rhizoctonia</i> and <i>Fusarium</i> spp.	(Gustafson); Bayer CropScience
<i>Bacillus pumilus</i> GB34	YieldShield	Soil-borne fungal pathogens	(Gustafson); Bayer CropScience
<i>Bacillus subtilis</i> QST716	Serenade	Tobacco, tomato, lettuce, spinach	AgraQuest
<i>Bacillus subtilis</i> GB03, other <i>B. subtilis</i> , <i>B. licheniformis</i> , and <i>B. megaterium</i>	Companion	<i>Rhizoctonia</i> , <i>Pythium</i> , <i>Fusarium</i> , and <i>Phytophthora</i>	Growth Products
<i>Bradyrhizobium japonicum</i>	Soil implant+	Soy bean	Nitragin
<i>Coniothyrium minitans</i>	Contans WG, Intercept WG	<i>Sclerotinia sclerotiorum</i> , <i>S. minor</i>	Prophyta Biologischer Pflanzenschutz
<i>Delftia acidovorans</i>	BioBoost	Canola	Brett-Young Seeds Limited
<i>Paecilomyces lilacinus</i>	Bioact WG	Nematodes	Prophyta Biologischer Pflanzenschutz
<i>Phlebiopsis gigantea</i>	Rotex	<i>Heterobasidium annosum</i>	E~nema Biologischer Pflanzenschutz
<i>Pseudomonas chlororaphis</i>	Cedomon	Leaf stripe, net blotch, <i>Fusarium</i> sp., sot blotch, leaf spot, etc. on barley and oats	BioAgri AB
<i>Pseudomonas fluorescens</i> A506	BlightBan A506	Frost damage, <i>Erwinia amylovora</i> , and russet-inducing bacteria on almond, apple, peach, pear, etc.	NuFarm
<i>Pseudomonas trivialis</i> 3Re-27	Salavida	Lettuce	Sourcon Padena
<i>Pseudomonas</i> spp.	Proradix	<i>Rhizoctonia solani</i>	Sourcon Padena
<i>Serratia plymuthcia</i> HRO-C48	RhizoStar	Strawberries, oilseed rape	Prophyta Biologischer Pflanzenschutz
<i>Streptomyces griseoviridis</i> K61	Mycostop	<i>Phomopsis</i> spp., <i>Botrytis</i> spp., <i>Pythium</i> spp., <i>Phytophthora</i> spp.	Kemira Agro Oy
<i>Trichoderma harzianum</i> T22	RootShield, PlantShield T22, Planter box	<i>Pythium</i> spp., <i>Rhizoctonia solani</i> , <i>Fusarium</i> spp.	Bioworks

Using molecular technologies and exploiting new bio-resources, new efficient BCAs can be detected. For examples, endophytes with a specific intimate interaction are promising bioresources (Ryan et al. 2008). In addition, naturally occurring antagonists on noncrop plants from natural vegetation are of interest. First investigations show this high potential for microorganisms associated with mosses (Opelt et al. 2007) or with the natural vegetation of Tenerife (Zachow et al. 2009a).

Another interesting point is the molecular analysis of the mode of interaction with the host plant as well as with pathogens including its regulation, e.g., by “-omics” technologies. These results help to stabilize the effect or

can result in new targets for the inoculants. In addition, it is necessary to study the ecological behavior of microbes and the interaction with other eukaryotes. The possibility of such interactions must be considered in risk assessment studies before commercializing. Extensive research is also required to improve the scale-up and bioprocess development for microbial inoculants. Further optimization is required for fermentation and formulation processes. The lack of such improved protocols is among the reasons why many promising microbes, especially gram-negatives, are still not included in practical approaches. The recent progresses achieved with genomic technologies will certainly help to optimize these

processes. Beyond these technical questions, it is also necessary to revise the legislative processes to efficiently commercialize microbial inoculants. In this context, new and standardized methods have to be established for appropriate risk evaluation of microbial inoculants. Clearly, the future success of the industry producing microbial inoculants will depend on innovative business management, product marketing, extension education, and progress in research. The field of plant growth will contribute substantially to making the twenty-first century the age of biotechnology by the development of innovative biological strategies in agriculture.

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