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Chapter 5
Control of Biotic and Abiotic Stresses in Cultivated Plants by the Use of Biostimulant Microorganisms

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1 Introduction

Nowadays, agriculture is increasingly focused on the quality of products and on the environmental, hygienic and sanitary aspects. Therefore, agricultural practices are moving toward a sustainable management of the agricultural crops, in order to ensure quantitative and qualitative product properties. In this context, the main objective of agriculture is to suggest techniques and technologies able to guarantee environmental, human and animal protection. In the agri-food sector, the European Community approved numerous legislative dispositions (e.g. Reg. 1095/07 e 33/2008) and has recently indicated the new objectives of scientific and technological research in the agricultural sector (Horizon Program 2020). Crop management is actually carried out by chemical products that ensure an efficacious plant protection but often interfere with the other biological components of the environment, determining irreversible imbalances. In addition, these products can cause serious risks for consumer's health as a consequence of the residues in food products. From this scenario, it emerges the need of a gradual decline in the use of chemical tools in agriculture and specifically in the control of plant diseases. During the last decade, the studies on alternative environmental friendly technologies have received a strong impulse and have proposed a wide range of options, including agronomical, physical and biological control means (Verma et al. 2007; Shoresh et al. 2010; Bharti et al. 2013; Yeoh et al. 2013). Recently, it was growing the idea that the plants have enormous self-defence potentiality, and this would allow a natural disease control with positive effects on environmental and human health safeguard (Hogekamp and Küster 2013; Estrada et al. 2013; Wu et al. 2013).

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The studies on the biochemical mechanisms associated to systemic resistance in plants could allow individuating new control strategies against plant pathogens and parasites, based on the exploitation of the natural mechanisms of plant defence. This type of resistance mechanism, already documented by Ross (1961), is known as "systemic acquired resistance" (SAR); it is effective against a wide range of pathogens and its action differs in relation to the inducer agent.

2 Systemic Acquired Resistance and SAR Second Messengers

Systemic acquired resistance (SAR) against pathogens is associated with the expression of pathogenesis-related (PR) genes that are considered molecular markers of SAR (Van Loon and Van Strien 1999). The activation of PR genes is in turn mediated by endogenous salicylic acid (SA) as molecule involved in signal transduction. The first step is the activation of calcium channels in plasmalemma, mediated by G proteins (pathogen protein) (Legendré et al. 1992). The increase of cytoplasmatic calcium concentration stimulates the superoxide anion production (O_2^-), a reactive oxygen species (ROS) (Schwacke and Hager 1992). The O_2^- released into the apoplast is dismutated in H_2O_2 naturally or by the action of the enzyme family of superoxide dismutase (SODs) (Buonaurio et al. 1987; Scandalios 1993). Then, the H_2O_2 can be in turn reduced to water and molecular oxygen by enzymatic and nonenzymatic plant antioxidant defences, such as catalase (CATs) (Scandalios et al. 1997) and ascorbate peroxidase (APXs) (Asada 1992), ascorbic acid, tocopherols, flavonoids and anthocyanins (Dixon and Paiva 1995; Noctor and Foyer 1998). The radical (OH^-), a strong oxidant, is obtained from H_2O_2, by Hebert–Weiss and Fenton's reactions, completing the reaction chain that is known as oxidative "burst" (Bolwell et al. 1999). Among ROS, H_2O_2 plays a predominant and diversified role in the events which lead to induction of resistance and to the transduction of the molecular signal of defence gene activation (Van Breusegem et al. 2001).

The main messengers of SAR are salicylic acid (SA), jasmonic acid (JA), ethylene (C_2H_2) and nitric oxide (NO) (Fragnière et al. 2011). An excessive ROS production may cause negative effects on the plant cells. The antioxidant systems control the cellular ROS concentration to avoid their potential toxicity. CATs and peroxidases (POXs) are the most important enzymes which allow removing H_2O_2. Because SAR is a normal answer in plant defence, it can be artificially induced by pathogen pre-inoculations or using chemical inducers of acquired resistance (Kuć 1982), such as beta-aminobutyric acid (Cohen 2002), benzothiadiazole (Ryals et al. 1996) and 2,6-dicloisonicotinic acid (Kauss et al. 1992). It is known that SA-induced resistance to viruses in tobacco and *Arabidopsis thaliana* is mediated in part by a pathway that appears to involve signals transduced through changes in ROS (Singh et al. 2004). Indeed, SA impedes electron flow through the respiratory electron transport chain and enhances ROS levels in the mitochondria (Mayers et al. 2005). SA-induced resistance to *Tobacco mosaic virus* (TMV) is altered in transgenic tobacco plants with altered levels of alternative oxidase (AOX), an enzyme that negatively regulates mitochondrial ROS levels (Gilliland et al. 2003). In *Arabidopsis thaliana*, as in tobacco, SA treatments inhibited the systemic movement of *Cucumber mosaic virus* (CMV). In addition, in squash SA-induced resistance to CMV and this was most likely due to inhibition of viral cell-to-cell movement. This means that the mechanisms of SA-induced resistance may differ markedly between host species (Mayers et al. 2005) and they are very poorly known.

3 Biostimulant Microorganisms and Their Importance in Sustainable Agriculture

Some microorganisms and the molecules they produce are able to biocontrol plant pathogens by inducing SAR and thus can be defined as biocontrol microorganisms (BCMs) (Vargas et al. 2008; Shoresh et al. 2010; Amaresan et al. 2012). Current biocontrol studies have confirmed the effectiveness of *Bacillus* spp., *Trichoderma* spp. and *Glomus* spp. in the plant protection not only against a wide range of pathogens fungi (Avis et al. 2008; Akrami et al. 2011; Hernández-Suárez et al. 2011) but also against bacteria (Avis et al. 2008; Segarra et al. 2009; Berić et al. 2012) and viruses (Wang et al. 2009; Luo et al. 2010; Wang et al. 2011; Elsharkawy et al. 2012), likely due to the induction of plant resistance mechanisms similar to SAR, hypersensitive response (HR) and induced systematic resistance (ISR) (Kaewchai et al. 2009). On the other hand, some fungal BCMs are able to promote plant growth and development, so acting as plant growth-promoting microorganisms (PGPMs), that in turn determines a higher tolerance of the plants against abiotic stresses, such as drought and salinity.

Both BCMs and PGPMs can be defined as "biostimulant microorganisms", able to foster plant growth and defence against pathogens throughout the crop life cycle, from seed germination to plant maturity. The study of the biochemical and molecular mechanisms involved in host–pathogen–antagonist interaction is essential for understanding the dynamics of infectious processes and can be useful for developing new strategies for the control of plant pathogens. At the same time, innovative methodologies and practices aimed to increase plant tolerance against abiotic stresses are required in sustainable agriculture.

The borderline between BCMs and PGPMs is not well defined. Indeed, BCMs, whose main action is to prevent or inhibit the growth of pathogens by SAR, exercise "indirect" benefits on plant growth by antibiosis based on the production of hydrolytic enzymes or inhibiting substances. These indirect effects have been clarified only in part, and even less is known regarding the "direct" effects of BCMs on the improvement of plant growth through production of siderophores and phytochelatins, which chelate metals and make them available to the roots. The most interesting PGPMs are those able to colonise the rhizosphere. This latter is particularly rich in nutrients and supports a microbial population that can exert positive effects on the physiological state of the roots, on the absorption of nutrients and on plant tolerance to environmental stresses. A particular attention should be given to endomycorrhizal (*Glomus* spp.) and rhizosphere (*Trichoderma* spp.) coloniser, that could allow plants to achieve optimum yields.

The SAR represents a valid opportunity in plant natural protection. Therefore, the research activities should be oriented to the use of BCMs as inducers of SAR in agronomically important species against some of their most severe pathogens. Among BCMs, the most used in sustainable agriculture practices belong to *Bacillus* spp., *Trichoderma* spp. and *Glomus* spp. (Djonović et al. 2007; Samolski et al. 2009; Ambrico and Trupo 2011; Dichio et al. 2012; Bonneau et al. 2013; Li et al. 2013). Research data accumulated in the past few years have produced a completely novel understanding of the way by which bacteria and fungi interact not only with other microbes but also with plants and soil components. This has opened an avenue of new applications, in both agriculture and biotechnology that exploit the ability of biostimulant microorganisms to change plant metabolism and resistance to biotic and abiotic stresses (Woo et al. 2006).

4 *Bacillus*, *Trichoderma* and *Glomus spp.*

The bacteria belonging to *Bacillus* spp. are ubiquitous microorganisms, present in the soil and in the phylloplane, and they are also able to live as endophytes. They have been studied for their antagonistic activity and induction of plant resistance against stresses. In the last years, endophyte isolates of *B. subtilis* (ET-1), able to control several diseases caused by leaf and soil pathogens, have been identified (Felici et al. 2008; Ambrico et al. 2010; Ambrico and Trupo 2011). Many *Bacillus* isolates can promote plant vegetative development by producing several extracellular substances, so acting as plant growth-promoting microorganisms (PGPMs).

Trichoderma spp. and *Glomus* spp. are some of the most abundant fungi found in many soil types, able to colonise plant roots and plant debris (Harman et al. 2004). They are agriculturally and industrially important, being the major source of many commercial biostimulants and biofungicides. These fungi are rarely causes of plant diseases (Gams and Bissett 1998). On the contrary, many *Trichoderma* and *Glomus* species (e.g. *T. harzianum, T. viride, G. intraradices*) are strong BCMs against bacteria, fungi and nematodes, and for this reason more than 60 % of all registered biostimulants used for plant disease control are *Trichoderma*- and/or *Glomus*-based (Verma et al. 2007; Shoresh et al. 2010; Bharti et al. 2013; Estrada et al. 2013). Many studies considered the use of proteomic and functional genomic analysis in the attempt to obtain a complete picture of the changes that occur in the expressions of fungus, plant and pathogen when they interact each other, especially when an increase in disease resistance is generated (Grinyer et al. 2005; Woo et al. 2006; Yeoh et al. 2013; Leung et al. 2013). However, the mechanisms of the interaction *Trichoderma-/Glomus*-plant pathogen are very complex and includes not only the mycoparasitism but also competition for nutrients, release of extracellular hydrolytic enzymes, antagonism against nematodes, colonisation of rhizosphere and phyllosphere, production of secondary metabolites that are toxic to plant pathogens, promotion of plant growth and root development and induction of systemic resistance against different pathogens (Harman et al. 2004; Mathivanan et al. 2008; Dutta and Podile 2010; Estrada et al. 2013).

The saprophytic fungi belonging to *Trichoderma* spp. can grow along the entire length of the root system along which it establishes a barrier against pathogen attack (Harman et al. 2004). Overall morphology and metabolism of plant inoculated with *Trichoderma harzianum* showed an increase in root growth and cell wall suberification in the exoderm and endoderm (Sofo et al. 2011, 2012) and the induction of the synthesis of antimicrobial phenolic compounds (Mathivanan et al. 2008). Furthermore, the cloning and functional characterization of a gene (*Sm1*) from *Trichoderma virens* that codes for a cerato-platanin has more recently allowed the identification of a novel proteinaceous nonenzymatic elicitor that triggers SAR in plants (Djonović et al. 2007). *Trichoderma* spp. are also important for their ability to synthesise peptaibols, a family of peptides with antibiotic function characterised by short chain lengths (<20 residues), C-terminal alcohol residues and high levels of nonstandard amino acids (Whitmore and Wallace 2004). Their antibiotic function arises from their membrane-insertion and pore-forming abilities, and it has been shown that peptaibols produced by *Trichoderma pseudokoningii* can induce programmed cell death in plant fungal pathogens (Shi et al. 2012).

The endomycorrhizal fungi belonging to *Glomus* spp. form a hyphal network that can obtain and transport nutrients, propagate the association and interconnect plants (Newman 1988). The production of plant-external hyphae varies according to the species and isolates of *Glomus*, can be influenced by soil properties and is an important determinant of mutualistic effectiveness (Kogel et al. 2006). The mycorrhization of plants by *Glomus* makes possible an enduring protection of cultivated plants against pathogens and a better use of nutrients, so improving plant tolerance to the diseases and to abiotic stresses and increasing plant productivity and quality in degraded soils (Datnoff et al. 1995; Augé 2001; Estrada et al. 2013).

It was recently discovered that plant mycorrhization with *Glomus* and soil colonisation by *Trichoderma* enhanced plant growth, in terms of total biomass and root development, by about 20 % and 30 %, respectively (Sofo et al. 2010). *Trichoderma harzianum* strain T-22 enhances root growth in both herbaceous (Fig. 5.1) and tree species (Fig. 5.2).

The ability of all these PGPMs in modulating plant defence mechanisms by the activation of the hypersensitive response (HR) and the induced systemic resistance (ISR) was demonstrated, but the details of this PGPM-plant molecular dialogue are poorly known, and many defensive compounds are likely to exist but remain to be identified. It seems that both SAR and ISR are intertwined molecularly and that a key role in plant defence mechanisms is played by molecules with signal functions, such as phytohormones (Vallad and Goodman 2004; Krouk et al. 2011). Moreover, the crosstalk between the different plant hormones, whose levels change after plant inoculation with PGPMs, results in synergetic or antagonistic interactions that play crucial roles in response of plants to abiotic stress, such as drought, salinity and

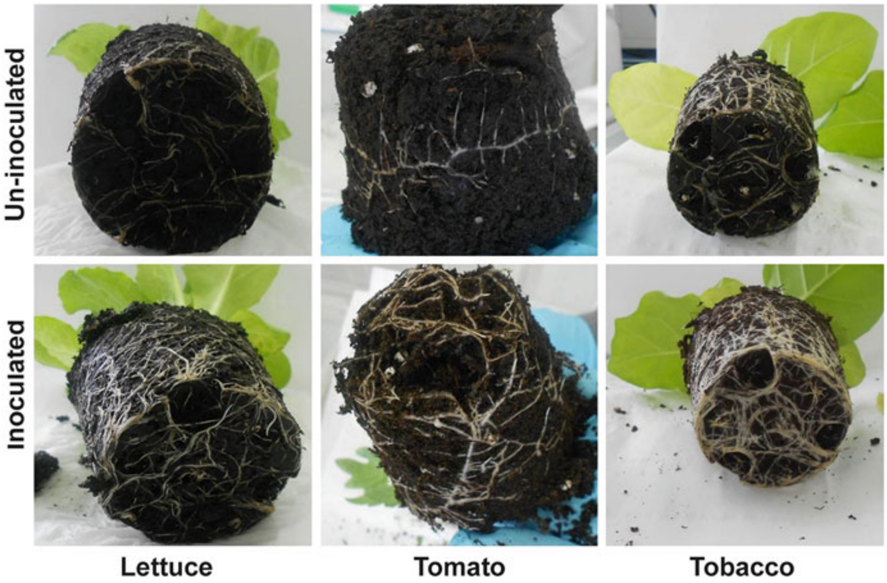

Fig. 5.1 Root growth in lettuce, tomato and tobacco seedlings observed after 25, 21 and 20 days, respectively, from the inoculation with *Trichoderma harzianum* strain T-22 (*below*) and in uninoculated controls (*above*)

toxic metals (Baroni et al. 2004; Peleg and Blumwald 2011). Thus, plant hormones play central roles in the ability of plants to adapt changing environments by mediating growth, development, nutrient allocation and source/sink transitions. Recently, the changes in phytohormone levels, particularly auxins and cytokinins have been demonstrated to be one of the direct mechanism by which *Trichoderma harzianum* promotes plant growth (Sofo et al. 2011). On this basis, the differences between BCMs and PGPMs seem to be increasingly blurred and their mechanisms of action appear to be overlapped.

5 Case Studies and Applications with Biostimulant Microorganisms

In BCM-inoculated plants, important physiological and biochemical parameters should be considered to individuate the degree of response against the pathogens under study. Notably, the integrity and functional status of the photosynthetic machinery, the assimilation, respiration and transport process and the mechanisms of photo-inhibition and photo-oxidation are of key importance in this kind of researches. Moreover, in the same plant systems, qRT-PCR-based gene transcripts analyses should be carried out to identify genes important for SAR induction, such as

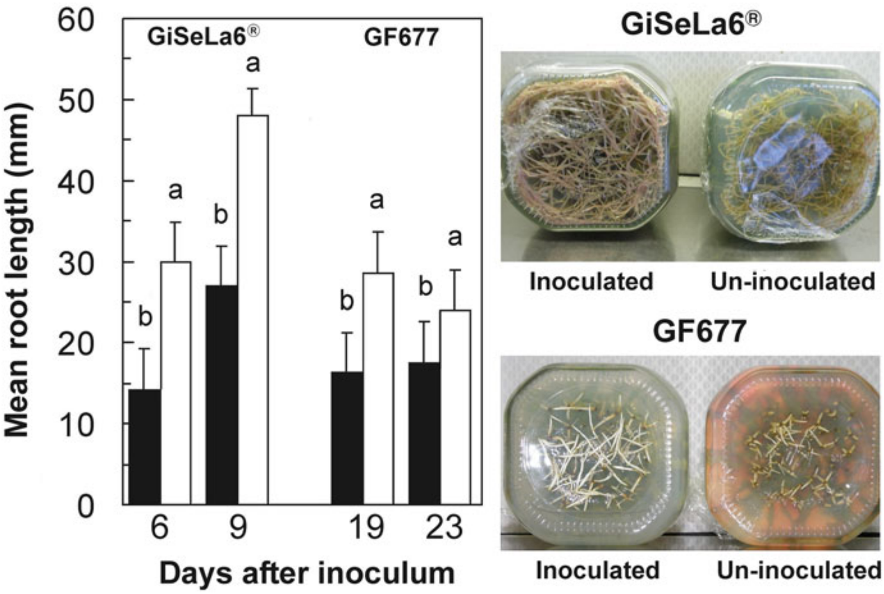

Fig. 5.2 (*On the left*) Mean root length (± standard error, $n = 100$) in in vitro cultured GiSeLa6® (cherry) and GF677 (peach) rootstocks inoculated with *Trichoderma harzianum* strain T-22 (*white columns*) and in uninoculated controls (*black columns*). For each treatment, mean values followed by a different lower-cased letter are significantly different at $P < 0.05$ according to Fisher's LSD test. (*On the right*) Root growth of GiSeLa6® and GF677 rootstocks inoculated with *Trichoderma harzianum* strain T-22 and in uninoculated controls observed after 9 days from inoculation. The medium was agarised Murashige and Skoog medium without vitamins and supplemented with indole-3-butyric acid

those associated with ROS (e.g. coding for SODs, CAT, POXs, etc.), PR proteins and peptides (e.g. chitinases, glucanases, ceratoplatanins, peptaibols, phytoalexins), phenylpropanoid (e.g. phenylalanine lyase, chalcone synthase) and phytohormones synthesis. Time course transcriptional analyses has to be performed in accordance to the progression of the infection and appearance of phenotypic and biochemical markers of damage. Genes known to be involved into metabolic processes underlying the plant–pathogen–antagonist interactions or the tolerance against abiotic stresses should be retrieved from public gene and EST databases. If not present in public databases, target genes from each plant species investigated can be amplified and cloned using sequence information from model species.

In plants subjected to different types of abiotic stress, comparative proteomics experiments should be carried out to identify specific proteins involved in plant resistance against pathogens, drought, salinity and other stresses. For this analysis, 2D-electrophoretic cells, protein fractionation and isoelectric focusing techniques and MALDI-TOF MS are commonly used. Accurate microscopic analyses should be carried out through electron (SEM and ESEM), epifluorescence and light microscopes in order to ascertain BCMs/PGPMs persistence and evaluate their colonisation. Finally, comparative proteomics experiments are of primary importance to identify specific proteins involved in the common response (overlapping) against biotic and abiotic stresses.

6 Conclusions and Future Perspective

From an environmental point of view, the use of biostimulant microorganisms is an agronomic practice able to preserve natural resources and, due to reduced use of pesticides and fertilisers, to maintain soil fertility and safeguard human health.

The studies on biostimulant microorganisms can allow to discover new formulation of bioactive compounds. At the same time, the application of this innovative knowledge will foster the use of biostimulant microorganisms in agriculture, with evident benefits on soil fertility, natural resources saving, food safety and human health. In this way, biostimulant microorganisms can act on the plants through different pathways to improve crop vigour, yields and quality, increasing plant tolerance and recovery from biotic and abiotic stresses. This could ameliorate plant physiological status, facilitate nutrient assimilation, translocation and use and improve plant water balance, so increasing plant survival in the absence of pesticides and with a reduced chemical fertilisation. Furthermore, the antiviral effects of these biostimulant microorganisms and the associated biochemical and molecular mechanisms implicated are still scarcely known and could be of key importance in the biological pest control. Finally, the identification of elicitor-like substances produced by the studied BCMs and involved in defence responses against pathogens will be an important applied research field in the next future.

References

Akrami M, Golzary H, Ahmadzadeh M (2011) Evaluation of different combinations of *Trichoderma* species for controlling *Fusarium* rot of lentil. Afr J Biotechnol 10(14):2653–2658

Amaresan N, Jayakumar V, Kumar K, Thajuddin N (2012) Isolation and characterization of plant growth promoting endophytic bacteria and their effect on tomato (*Lycopersicon esculentum*) and chilli (*Capsicum annuum*) seedling growth. Ann Microbiol 62(2):805–810

Ambrico A, Trupo M (2011) Evaluation of the antifungal activity of morphologically distinct colonies of *Bacillus subtilis* strain ET-1. J Plant Pathol 93(4):S4.25–S4.62

Ambrico A, Trupo M, Lopez L (2010) Identification and characterization of *Bacillus subtilis* ET-1, a strain with antifungal activity against fruit rot pathogens. J Plant Pathol 92(4):S4.72

Asada K (1992) Ascorbate peroxidase - a hydrogen peroxide scavenging enzyme in plants. Physiol Plant 85:235–241

Augé RM (2001) Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhizae 11:3–42

Avis T, Gravel V, Antoun H, Tweddel RJ (2008) Multifaceted beneficial effects of rhizosphere microorganisms on plant health and productivity. Soil Biol Biochem 40:1733–1740

Baroni F, Boscaglia A, Di Lella LA, Protano G, Riccobono F (2004) Arsenic in soil and vegetation of contaminated areas in southern Tuscany (Italy). J Geochem Explor 81:1–14

Berić T, Kojić M, Stanković S, Topisirović L, Degrassi G, Myers M, Venturi V, Fira D (2012) Antimicrobial activity of *Bacillus* sp. natural isolates and their potential use in the biocontrol of phytopathogenic bacteria. Food Technol Biotechnol 50(1):25–31

Bharti N, Baghel S, Barnawal D, Yadav A, Kalra A (2013) The greater effectiveness of Glomus mosseae and Glomus intraradices in improving productivity, oil content and tolerance of salt-stressed menthol mint (*Mentha arvensis*). J Sci Food Agric 93:2154–2161

Bolwell GP, Blee KA, Butt VS, Davies DR, Gardner SL, Gerrish C, Minibayeva F, Rowntree EG, Wojtaszek P (1999) Recent advances in understanding the origin of the apoplastic oxidative burst in plant cells. Free Rad Res 31:S137–S145

Bonneau L, Huguet S, Wipf D, Pauly N, Truong HN (2013) Combined phosphate and nitrogen limitation generates a nutrient stress transcriptome favorable for arbuscular mycorrhizal symbiosis in *Medicago truncatula*. New Phytol 199:188–202

Buonaurio R, Torro DG, Monatlbini P (1987) Soluble superoxide dismutase (SOD) in susceptible and resistant host-parasite complexes of *Phaseolus vulgari*s and *Uromyces phaseoli*. Physiol Pathol 31:173–184

Cohen YR (2002) β-Aminobutyric acid-induced resistance against plant pathogens. Plant Dis 86(5):448–457

Datnoff LE, Nemec S, Pernezny K (1995) Biological control of *Fusarium crown* and root rot of tomato in Florida using *Trichoderma harzianum* and *Glomus intraradices*. Biol Control 5: 427–431

Dichio B, Tataranni G, Bardas GA, Mavrodimos C, Katis N, Ipsilantis I, Xylogiannis V (2012) Production of micropropagated and mycorrhisated myrobolan 29C rootstock. Acta Hort (ISHS) 966:67–70

Dixon RA, Paiva NL (1995) Stress-induced phenylpropanoid metabolism. Plant Cell 7: 1085–1097

Djonović S, Vargas WA, Kolomiets MV, Horndeski M, Wiest A, Kenerley CM (2007) A proteinaceous elicitor Sm1 from the beneficial fungus *Trichoderma virens* is required for induced systemic resistance in maize. Plant Physiol 145:875–889

Dutta S, Podile AR (2010) Plant growth promoting rhizobacteria (PGPR): the bugs to debug the root zone. Crit Rev Microbiol 36(3):232–244

Elsharkawy MM, Shimizu M, Takahashi H, Hyakumachi M (2012) The plant growth-promoting fungus *Fusarium equiseti* and the arbuscular mycorrhizal fungus *Glomus mosseae* induce systemic resistance against *Cucumber mosaic virus* in cucumber plants. Plant Soil 361:397–409

Estrada B, Barea JM, Aroca R, Ruiz-Lozano JM (2013) A native Glomus intraradices strain from a Mediterranean saline area exhibits salt tolerance and enhanced symbiotic efficiency with maize plants under salt stress conditions. Plant Soil 366:339–349

Felici C, Vettori L, Toffanin A, Nuti M (2008) Development of a strain-specific genomic marker for monitoring a *Bacillus subtilis* biocontrol strain in the rhizosphere of tomato. FEMS Microbiol Ecol 65:289–298

Fragnière C, Serrano M, Abou-Mansour E, Métraux JP, L'Haridon F (2011) Salicylic acid and its location in response to biotic and abiotic stress. FEBS Lett 585(12):1847–1852

Gams W, Bissett J (1998) Morphology and identification of *Trichoderma*. In: Kubicek CP, Harman GE (eds) *Trichoderma* and *Gliocladium*, basic biology, taxonomy, and genetics vol 1. Taylor and Francis, London, pp 3–34

Gilliland A, Singh DP, Hayward JM, Moore CA, Murphy AM, York CJ, Slator J, Carr JP (2003) Genetic modification of alternative respiration has differential effects on antimycin A-induced versus salicylic acid-induced resistance to *Tobacco mosaic virus*. Plant Physiol 132: 1518–1528

Grinyer J, Hunt S, McKay M, Herbert BR, Nevalainen H (2005) Proteomic response of the biological control fungus *Trichoderma atroviride* to growth on the cell walls of *Rhizoctonia solani*. Curr Genet 47(6):381–388

Harman GE, Lorito M, Lynch JM (2004) Uses of *Trichoderma* spp. to alleviate or remediate soil and water pollution. In: Laskin AI, Bennett JW, Gadd GM (eds) Advances in Applied Microbiology, vol 56. Elsevier Academic Press, San Diego, CA, USA, pp 313–330

Hernández-Suárez M, Hernández-Castillo FD, Gallegos-Morales G, Lira-Saldivar RH, Rodríguez-Herrera R, Aguilar CN (2011) Biocontrol of soil fungi in tomato with microencapsulates containing *Bacillus subtilis*. Am J Agri & Biol Sci 6(2):189–195

Hogekamp C, Küster H (2013) A roadmap of cell-type specific gene expression during sequential stages of the arbuscular mycorrhiza symbiosis. BMC Genomics 14:306

Kaewchai S, Soytong K, Hyde KD (2009) Mycofungicides and fungal biofertilizers. Fungal Divers 38:25–50

Kauss H, Krause K, Jeblick W (1992) Methyl jasmonate conditions parsley suspension cells for increased elicitation of phenylpropanoid defense responses. Biochem Biophys Res Commun 189:304–308

Kogel KH, Franken P, Huckelhoven R (2006) Endophyte or parasite-what decides? Curr Opin Plant Biol 9:358–363

Krouk G, Ruffel S, Gutiérrez RA, Gojon A, Crawford NM, Coruzzi GM, Lacombe B (2011) A framework integrating plant growth with hormones and nutrients. Trends Plant Sci 16(4): 178–182

Kuć J (1982) Induced immunity to plant disease. BioScience 32:854–860

Legendré L, Heinstein PF, Low PS (1992) Evidence for participation of GTP-binding proteins in elicitation of the rapid oxidative burst in cultured soybean cells. J Biol Chem 267:20140–20147

Leung HM, Leung AO, Ye ZH, Cheung KC, Yung KK (2013) Mixed arbuscular mycorrhizal (AM) fungal application to improve growth and arsenic accumulation of *Pteris vittata* (As hyperaccumulator) grown in As-contaminated soil. Chemosphere S0045-6535((13):00718–2

Li T, Hu YJ, Hao ZP, Li H, Chen BD (2013) Aquaporin genes *GintAQPF1* and *GintAQPF2* from *Glomus intraradices* contribute to plant drought tolerance. Plant Signal Behav 8:e24030

Luo Y, Zhang DD, Dong XW, Zhao PB, Chen LL, Song XY, Wang XJ, Chen XL, Shi M, Zhang YZ (2010) Antimicrobial peptaibols induce defense responses and systemic resistance in tobacco against *Tobacco mosaic virus*. FEMS Microbiol Lett 313:120–126

Mathivanan N, Prabavathy VR, Vijayanandraj VR (2008) The effect of fungal secondary metabolites on bacterial and fungal pathogens. In: Karlovsky P (ed) Secondary metabolites in soil ecology. Soil biology, vol 14. Springer, Berlin, pp 129–140

Mayers CN, Lee KC, Moore CA, Wong SM, Carr JP (2005) Salicylic acid-induced resistance to *Cucumber mosaic virus* in squash and *Arabidopsis thaliana*: contrasting mechanisms of induction and antiviral action. Mol Plant Microbe Interact 18(5):428–434

Newman EI (1988) Mycorrhizal links between plants: their functioning and ecological significance. Adv Ecol Res 18:243–270

Noctor G, Foyer CH (1998) Ascorbate and glutathione: keeping active oxygen under control. Annu Rev Plant Physiol Plant Mol Biol 49:249–279

Peleg Z, Blumwald E (2011) Hormone balance and abiotic stress tolerance in crop plants. Curr Opin Plant Biol 14:290–295

Ross AF (1961) Systemic acquired resistance induced by localized virus infections in plants. Virology 14:340–358

Ryals JA, Neuenschwande UH, Willits MG, Molina A, Steiner HY, Hunt MD (1996) Systemic acquired resistance. Plant Cell 8:1809–1819

Samolski I, de Luis A, Vizcaino JA, Monte E, Suarez MB (2009) Gene expression analysis of the biocontrol fungus *Trichoderma harzianum* in the presence of tomato plants, chitin, or glucose using a high-density oligonucleotide microarray. BMC Microbiol 9:217–231

Scandalios JG (1993) Oxygen stress and superoxide dismutase. Plant Physiol 101:7–12

Scandalios JG, Guan L, Polidoros AN (1997) Catalases in plants: gene structure, properties, regulation, and expression. In: Scandalios JG (ed) Oxidative stress and the molecular biology of antioxidant defenses. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY, pp 343–406

Schwacke R, Hager A (1992) Fungal elicitors induce a transient release of active oxygen species from cultured spruce cells that is dependent on Ca^{2+} and protein-kinase activity. Planta 187:136–141

Segarra G, Van der Ent S, Trillas I, Pieterse CMJ (2009) MYB72, a node of convergence in induced systemic resistance triggered by a fungal and a bacterial beneficial microbe. Plant Biol 11:90–96

Shi M, Chen L, Wang XW, Zhang T, Zhao PB, Song XY, Sun CY, Chen XL, Zhou BC, Zhang YZ (2012) Antimicrobial peptaibols from *Trichoderma pseudokoningii* induce programmed cell death in plant fungal pathogens. Microbiology 158(1):166–175

Shoresh M, Harman GE, Mastouri F (2010) Induced systemic resistance and plant responses to fungal biocontrol agents. Annu Rev Phytopathol 48:21–43

Singh DP, Moore CA, Gilliland A, Carr JP (2004) Activation of multiple anti-viral defence mechanisms by salicylic acid. Mol Plant Pathol 5:57–63

Sofo A, Milella L, Tataranni G (2010) Effects of *Trichoderma harzianum* strain T-22 on the growth of two *Prunus* rootstocks during the rooting phase. J Hortic Sci Biotechnol 85:497–502

Sofo A, Scopa A, Manfra M, De Nisco M, Tenore G, Trisi J, Di Fiori R, Novellino E (2011) *Trichoderma harzianum* strain T-22 induces changes in phytohormone levels in cherry rootstocks (*Prunus cerasus* X *P. canescens*). Plant Growth Regul 65:421–425

Sofo A, Tataranni G, Di Chio B, Xiloyannis C, Scopa A (2012) Direct effects of *Trichoderma harzianum* strain T22 on micropropagated GiSeLa6® (*Prunus* pp) rootstocks. Env Exp Bot 76:33–38

Vallad GE, Goodman RM (2004) Systemic acquired resistance and induced systemic resistance in conventional agriculture. Crop Sci 44:1920–1934

Van Breusegem F, Vranová E, Dat JF, Inzé D (2001) The role of active oxygen species in plant signal transduction. Plant Sci 161:05–414

Van Loon LC, Van Strien EA (1999) The families of pathogenesis-related proteins, their activities, and comparative analysis of PR-1 type proteins. Physiol Mol Plant Pathol 55:85–97

Vargas WA, Djonović S, Sukno SA, Kenerley CM (2008) Dimerization controls the activity of fungal elicitors that trigger systemic resistance in plants. J Biol Chem 283:19804–19815

Verma M, Brar SK, Tyagi RD, Surampalli RY, Valéro JR (2007) Antagonistic fungi, *Trichoderma* spp.: panoply of biological control. Biochem Eng J 37:1–20

Wang S, Wu H, Qiao J, Ma L, Liu J, Xia Y, Gao X (2009) Molecular mechanism of plant growth promotion and induced systemic resistance to *Tobacco mosaic virus* by *Bacillus* spp. J Microbiol Biotechnol 19(10):1250–1258

Wang S, Wu H, Zhan J, Xia Y, Gao S, Wang W, Xue P, Gao X (2011) The role of synergistic action and molecular mechanism in the effect of genetically engineered strain *Bacillus subtilis* OKBHF in enhancing tomato growth and *Cucumber mosaic virus* resistance. BioControl 56: 113–121

Whitmore L, Wallace BA (2004) The peptaibol database: a database for sequences and structures of naturally occurring peptaibols. Nucl Acids Res 32(1):D593–D594

Woo SL, Scala F, Ruocco M, Lorito M (2006) The molecular biology of the interactions between *Trichoderma* spp., phytopathogenic fungi, and plants. Am Phytopathol Soc 96(2):181–185

Wu Q, Bai L, Liu W, Li Y, Lu C, Li Y, Fu K, Yu C, Chen J (2013) Construction of a *Streptomyces lydicus* A01 transformant with a chit42 gene from *Trichoderma harzianum* P1 and evaluation of its biocontrol activity against *Botrytis cinerea*. J Microbiol 51:166–173

Yeoh KA, Othman A, Meon S, Abdullah F, Ho CL (2013) Sequence analysis and gene expression of putative oil palm chitinase and chitinase-like proteins in response to colonization of *Ganoderma boninense* and *Trichoderma harzianum*. Mol Biol Rep 40:147–158