Eur J Plant Pathol (2008) 122:395–401
DOI 10.1007/s10658-008-9306-1

Germination of *Fusarium oxysporum* in root exudates from tomato plants challenged with different *Fusarium oxysporum* strains

Siegrid Steinkellner · Roswitha Mammerler · Horst Vierheilig

Received: 1 August 2007 / Accepted: 6 March 2008 / Published online: 3 April 2008

Abstract The response of microconidia from pathogenic and non-pathogenic *Fusarium oxysporum* to root exudates from tomato plants inoculated with different pathogenic and non-pathogenic *F. oxysporum* strains was studied. Root exudates from non-inoculated tomatoes highly stimulated the microconidial germination of the two tomato pathogens, *F. oxysporum* f.sp. *lycopersici* strain *Fol* 007 and *F. oxysporum* f.sp. *radicis-lycopersici* strain *Forl* 101587. In root exudates from tomato plants challenged with the pathogen *Fol* 007 the microconidial germination of *Fol* 007 was increased, whereas in root exudates from plants challenged with *Forl* 101587 the microconidial germination of *Fol* 007 was reduced. Root exudates of tomato plants challenged with the non-pathogenic unspecific *F. oxysporum* strain *Fo* 135 and the biocontrol strain *Fo* 47 clearly reduced microconidial germination of the pathogenic strain *Forl* 101587. Moreover, the microconidial germination rate of the biocontrol strain *Fo* 47 was increased in the presence of root exudates of tomato plants challenged with the tomato wilt pathogen *Fol* 007. These results indicate that pathogenic and non-pathogenic *F. oxysporum* strains alter the root exudation of tomato plants differently and consequently the fungal propagation of pathogenic and non-pathogenic *F. oxysporum* strains in the rhizosphere is affected differently.

Keywords Microconidial germination · Fusarium wilt · Fusarium root rot · Plant–fungus interaction · Root exudates · Response

S. Steinkellner (✉) · R. Mammerler · H. Vierheilig
Department of Applied Plant Sciences and Plant Biotechnology, Institute of Plant Protection,
University of Natural Resources and Applied Life Sciences,
Peter-Jordan-Strasse 82,
1190 Vienna, Austria
e-mail: siegrid.steinkellner@boku.ac.at

H. Vierheilig
Departamento de Microbiología,
Estación Experimental de Zaidín, CSIC,
E-18008 Apdo. 419, Granada, Spain

Introduction

Fusarium oxysporum is an abundant saprophyte in soil and organic matter and occurs worldwide in the rhizosphere of many plant species. The fungus has numerous specialized forms known as formae speciales (f.sp.) that infect a range of host plants causing diseases such as vascular wilt, corm rot, root rot or damping-off (Armstrong and Armstrong 1981). Two formae speciales of this fungus are known to affect tomato, a crop plant of great economic importance. *Fusarium oxysporum* f.sp. *lycopersici (Fol)* is the cause of a severe wilt disease, whereas *F. oxysporum* f.sp. *radicis-lycopersici* (*Forl*) causes crown and root rot (Jones 1991).

Apart from their role as plant pathogens several strains of *F. oxysporum* are known to control *Fusarium* diseases (Fravel et al. 2003) and are

involved in the suppressiveness of soils (Alabouvette 1990). Non-pathogenic strains are present in the rhizosphere soil and colonise plant roots, but seem not to invade the vascular system (Olivain and Alabouvette 1997, 1999). The mechanisms by which non-pathogenic *F. oxysporum* strains antagonize pathogenic strains and the biochemical responses of the plant are only partially understood (Olivain and Alabouvette 1997). Biocontrol strains, such as strain *Fo* 47, an antagonist of *F. oxysporum* f.sp. *lycopersici*, have been suggested to have several modes of action: competition for nutrients, competition for infection sites on the root surface, activation of the plant's defence and an effect on the germination of chlamydospores of the pathogen (Alabouvette et al. 2006; Fravel et al. 2003; Olivain et al. 2006).

Although extensive studies have been performed on the biology of *F. oxysporum*, strains and the colonization process of *F. oxysporum* strains is well explored (Olivain and Alabouvette 1997; 1999; Lagopodi et al. 2002; Olivain et al. 2006), the role of root exudates, primary signals in fungus–plant interactions in the rhizosphere, still remains mostly unclear. Root exudates are supposed to play a key role in determining the positive or negative outcome of an interaction in the rhizosphere (recently reviewed by Bertin et al. 2003; Bais et al. 2006) and contain predominantly sugars, amino acids and organic acids which are known as general germination stimuli of spores (Nelson 1991). As shown by Lugtenberg et al. (1999) and Kravchenko et al. (2003), at different growth stages tomato roots exude varying amounts of sugars and organic acids. Interestingly, depending on plant age, the effect of tomato root exudates on spore germination of the tomato pathogen *F. oxysporum* also varies (Steinkellner et al. 2005). However, the signals affecting spore germination of *F. oxysporum* are still not clearly identified.

The signals affecting spore germination of the tomato pathogen *F. oxysporum* seem not to be host-specific, since a similar pattern of microconidial germination was found in the presence of root exudates from the host plant tomato and several non-host plants, such as sweet pepper, bean, barley, tobacco and cucumber (Steinkellner et al. 2005). However, there are indications for a certain *F. oxysporum*-strain specific effect of compounds found in tomato root exudates. In a recent study it was reported that the germination rate of several *F. oxysporum* strains is affected differently by tomato root exudates (Steinkellner et al. 2005). Moreover, studying the spore germination of a *Forl* strain and a biocontrol strain of *F. oxysporum* in tomato root exudates and two of its major known compounds, glucose and citric acid, Bolwerk et al. (2005) found a higher stimulation for the biocontrol strain than for the pathogenic strain.

In several studies it has been shown that root colonisation by symbiotic arbuscular–mycorrhizal fungi alters the root exudation pattern and thus the effect of the exudates on soil-inhabiting microbes (Lioussanne et al. 2003; Pinior et al. 1999; Sood 2003). Pinior et al. (1999) reported that root exudates from mycorrhizal plants affect the hyphal growth of arbuscular mycorrhizal fungi differently, compared to root exudates from non-mycorrhizal plants. Recently, Scheffknecht et al. (2006, 2007) reported that root colonisation by an arbuscular–mycorrhizal fungus also affects the microconidial germination of the tomato pathogen *F. oxysporum*.

Besides the effects of mycorrhiza, Kamilova et al. (2006) reported changes in the composition of organic acids and sugars in tomato root exudates due to the presence of a *Forl* strain. However, it is not yet known if, and how, root exudates from tomato plants inoculated with *F. oxysporum* influence the microconidial germination of *F. oxysporum*.

In the present study we tested whether the inoculation of tomato with *F. oxysporum* alters the effect of tomato root exudates on the microconidial germination of *F. oxysporum*. In order to detect *F. oxysporum* strain-specific alterations of the root exudation pattern, the effect of exudates from tomato plants inoculated with pathogenic and non-pathogenic *F. oxysporum* strains on the microconidial germination of pathogenic and non-pathogenic *F. oxysporum* strains was tested.

Materials and methods

Fusarium culture

All *Fusarium* strains were stored as conidial suspensions in 30% glycerol at −80°C, regularly transferred to a growth medium and cultivated at 24°C in darkness. The two pathogens, *F. oxysporum* f.sp. *lycopersici* strain *Fol* 007 (provided by B.J. Cornelissen, University

of Amsterdam, The Netherlands) and *F. oxysporum* f.sp. *radicis-lycopersici* strain *Forl* 101587 (purchased from Centraalbureau voor Schimmelcultures, The Netherlands), the biocontrol strain *F. oxysporum* strain *Fo* 47 (provided by C. Steinberg, INRA/Université de Bourgogne, Dijon, France) and the unspecific non-pathogenic *F. oxysporum* strain *Fo* 135 (provided by M. Lemmens, IFA Tulln, Austria) were cultivated on Czapek Dox medium (Duchefa Biochemie, Haarlem, The Netherlands). Under sterile conditions, fungal culture plates (2 to 3 weeks old) were flooded with sterile distilled water (SDW) and the suspension obtained was filtered through three layers of filter paper (fleece filters, 20–150 μm pore diam; Laporte Ges.m.b.H., Wels, Austria) to separate the microconidia from the mycelium. The conidial concentration was determined using a haemocytometer and adjusted to a final concentration of 1×10^7 microconidia ml^{-1}.

Plant material

Seeds of tomato (*Solanum lycopersicum* cv. Micro Tom) were surface-sterilised with household bleach (3.8% NaOCl) for 5 min, rinsed four times in sterile double-distilled water and sown in pots containing steam-sterilised perlite (Granuperl S 3-6, Knauf Perlite GmbH, Vienna, Austria). Sixteen days after seeding (first true leaf unfolded), the plantlets were removed by gently washing the perlite off the roots with tap water. Thereafter the roots were dipped in a microconidial suspension (1×10^7 microconidia ml^{-1}) of *Fol* 007, *Forl* 101587, *Fo* 47 and *Fo* 135, respectively, for 5 min. Non-inoculated plants treated in the same way as inoculated plants and dipped in water were used as the control. Each treatment consisted of 20 plantlets. Each plantlet was transplanted in a plastic pot (volume 630 ml) containing moist, sterilised perlite. Perlite was chosen because it is frequently used in soilless tomato production (Hochmuth and Hochmuth 2003) and can easily be washed off the roots. The transplanted plants were cultivated for a further 24 days and watered with a nutrient solution (Steinkellner et al. 2005) throughout the experiments. All the experiments were performed in a plant growth chamber (York International) at 24°C with a photoperiod of 16 h light/8 h dark (photosynthetically-active irradiation 296 μmol m^{-2} s^{-1}).

Collection of root exudates

For root exudate collection, heavily infested plants with a wilting appearance were excluded to eliminate the effects of potential decomposition products. After the total growth period of 40 days plants were removed by gently washing the perlite off the roots with tap water. For each treatment, three batches consisting of five to seven plants were placed in a beaker (volume 100 ml) containing sterile distilled water, such that the roots were completely submerged. The plants were placed in a plant growth chamber for 24 h at 24°C, and thereafter removed from the beaker. Subsequently, the root system was separated from the shoot and the fresh weight of the root and shoot was determined. Additionally, all plants were examined for disease development by eye. Based on preliminary experience (Stevenson et al. 1995; Pinior et al. 1999; Steinkellner et al. 2005) the volume of each exudate obtained was adjusted with sterilised water to 20 ml g^{-1} root fresh weight. The exudates were passed through 0.22 μm sterile filters (Steriflip, Millipore, Bedford, USA) and stored at −20°C for further investigation.

Germination experiments

The microconidial germination in the presence of root exudates collected from non-inoculated tomato plants and plants inoculated with different *F. oxysporum* strains (two pathogenic, one biocontrol and one unspecific strain) was tested. Czapek Dox broth was used as a positive control and SDW alone as a negative control.

The germination assay was performed in sterile culture plates (24 wells, Greiner bio-one, Nr. 662160, Frickenhausen, Germany). Aliquots of 500 μl of root exudate were mixed with 100 μl of microconidial suspension and incubated at 24°C in the dark while shaking at 200 rpm. After 20 h, lactophenol cotton blue was added and the microconidial germination was determined microscopically by counting 200 microconidia/well. A microconidium was considered germinated if the germ tube length was at least as long as the spore. The germination experiments were performed with at least two exudate batches originating from different tomato plants and with three replicates each time.

Statistical analysis

Analysis of variance was performed after a variance check by the Levene's test. Mean values were compared using Fisher's least significant difference (LSD=0.05). All analyses were performed using Statgraphics Plus version 5.0 (Statpoint, Inc., Herndon, VA, USA).

Results

All plants inoculated with *Fol* 007 showed a characteristic discolouration of the vessels within the lower part of the stem and all plants inoculated with *Forl* 101587 showed characteristic brownish lesions on the root system. The plants inoculated with the non-pathogenic strains (*Fo* 47, *Fo* 135) and the non-inoculated plants had no visible disease symptoms (Table 1). The plants inoculated with *Fol* 007 and *Fo* 47 had a significantly lower root fresh weight than the other treatments. The shoot fresh weight significantly increased after inoculation with the unspecific strain *Fo* 135.

The highest microconidial germination of the root rot pathogen strain *Forl* 101587 compared to the water control was observed in root exudates from plants inoculated with *Forl* 101587 (72.1%) and *Fol* 007 (62.8%) and from non-inoculated plants (66.9%) (Fig. 1a). Compared to the root exudates from non-inoculated plants, germination rates were significantly lower in root exudates from plants inoculated with *Fo* 135 and *Fo* 47 at 43.9% and 52.3%, respectively.

In all root exudates microconidial germination of *Fol* 007 was significantly higher than in water (32.1%) and lower than in Czapek Dox broth (90.1%) (Fig. 1b). The highest stimulating effect was found in root exudates collected from tomato plants inoculated with *Fol* 007 (71.9%). Exudates from plants inoculated with the biocontrol strain *Fo* 47 (50.8%) and the unspecific strain *Fo* 135 (56.6%) showed a similar effect to exudates from non-inoculated plants (control, 56.1%). Exudates from plants inoculated with strain *Forl* 101587 resulted in reduced microconidial germination (47.8%) compared to exudates from non-inoculated control plants.

Strain *Fo* 135 microconidia were clearly less disposed to germinate in water (14.6%) and in Czapek Dox broth (48.9%) (Fig. 1c) compared to *Fol* 007 and *Forl* 101587 microconidia. Compared to the water control, the germination rate was always enhanced by root exudates; however only root exudates collected from tomato plants inoculated with *Fo* 47 (19.0%) showed a significantly different effect compared to exudates from non-inoculated control plants (25.7%).

Compared to the water control, microconidial germination of the biocontrol strain *Fo* 47 was less affected by root exudates (Fig. 1d). The exudates from non-inoculated control plants and the exudates from strain *Fo* 47-inoculated plants resulted in similar germination rates to the water control (20.9%, 18.8% and 16.1%, respectively). Except with root exudates from *Fol* 007-treated plants, no significant difference was found between exudates from non-inoculated control plants and exudates from inoculated plants.

Discussion

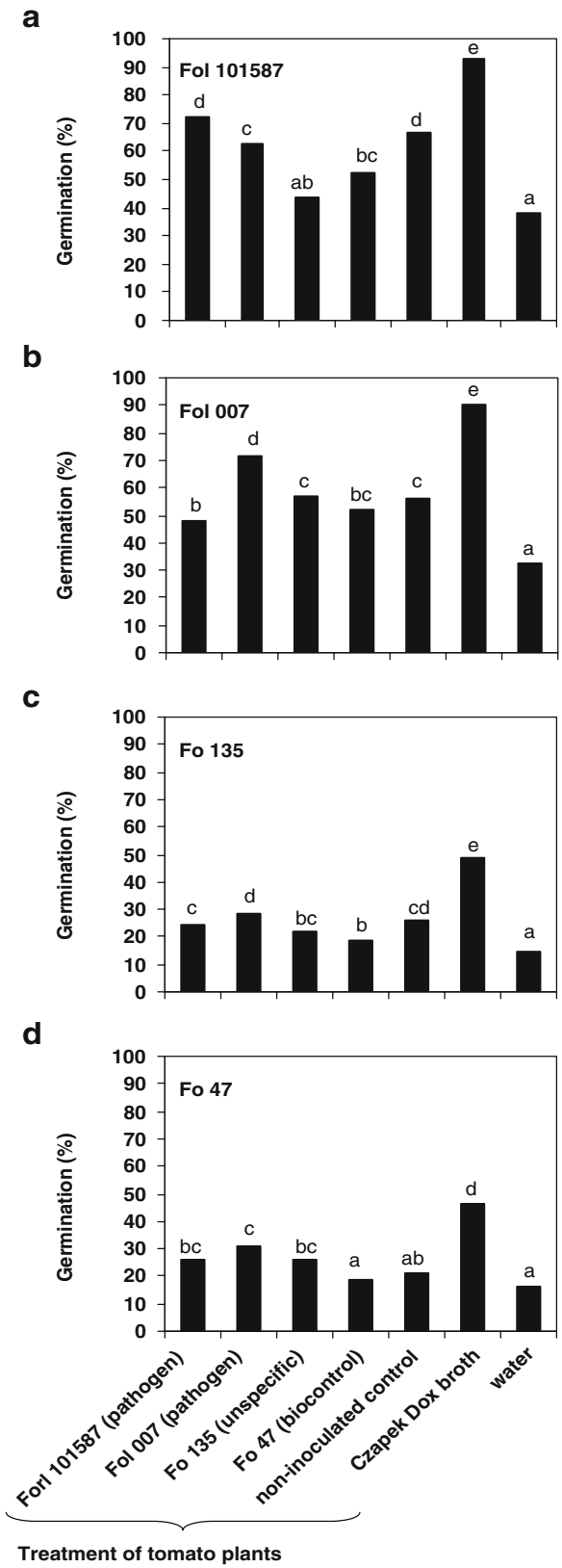
Tomato root exudates almost always stimulated the microconidial germination of the two tomato pathogens *Fol* 007 and *Forl* 101587, confirming previous findings showing that tomato root exudates stimulate the microconidial germination of tomato-pathogenic *F. oxysporum* strains (Steinkellner et al. 2005).

In the present study the germination of *Fol* 007 was four to five fold compared to the water control, in

Table 1 Influence of *F. oxysporum* strains on plant weight and disease symptoms

Treatment	Root fresh weight (g/plant)	Shoot fresh weight (g/plant)	Disease incidence (%)	Diseases symptoms
Forl 101587	0.58a*	4.28b*	100	Small brown spots on roots
Fol 007	0.35b	3.68b	100	Vascular discolouration of lower stem (1–2 cm)
Fo 135	0.52a	5.53a	–	–
Fo 47	0.39b	4.04b	–	–
Non-inoculated plants	0.53a	4.17b	–	–

*$P<0.01$, means of data followed by different letters are significantly different according to Fisher's least significant difference test



◀ **Fig. 1** Microconidial germination of **a** the tomato root rot pathogen *Forl* 101587, **b** the tomato wilt pathogen Fol 007, **c** the unspecific strain Fo 35 and **d** the biocontrol strain Fo 47 in root exudates from tomato plants inoculated with different *F. oxysporum* strains (*Forl* 101587, *Fol* 007, *Fo* 135, *Fo* 47) and non-inoculated control plants, in Czapek Dox broth and water. Results are given as mean values. *Bars with different letters* are significantly different according to Fisher's least significant difference test ($P<0.001$)

contrast to previous results when it was only double (Steinkellner et al. 2005). This may be due to high variation in microconidial germination in the water control reported in previous studies (Scheffknecht et al. 2006, 2007). In all our studies with *Fol* 007 (Steinkellner et al. 2005; Scheffknecht et al. 2006, 2007) a highly standardised experimental set-up was used for fungal cultures of the same age, the same spore preparation and concentration, the same type of microplates, the same water treatment (distilled and autoclaved), the same growth chamber and temperature for the germination assay, the water control values varied. Thus, the observed variation must be attributed to the biological variation of the fungal material which is not uncommon for living organisms. Differences in the response of *Fusarium* spp. to the same control medium have also been reported by others (Ruan et al. 1995; Steinberg et al. 1999).

In our study, challenging plants with the tomato wilt pathogen *Fol* 007 resulted in a further stimulation of *Fol* 007 microconidial germination compared to the non-inoculated control. However, in the presence of root exudates from tomato plants challenged with the root rot pathogen *Forl* 101587, the microconidial germination of *Fol* 007 was reduced. This indicates that in the plant–*Fol* 007 interaction, the pathogen alters the root exudation to its own advantage, whereas the pathogenic competitor, *Forl* 101587, impairs the germination conditions for the tomato wilt pathogen *Fol* 007.

Our data are in contrast to He et al. (2001), who reported no effect of root exudates of *Asparagus officinalis*, on spore germination of *F. oxysporum* f.sp. *asparagi,* regardless of whether *A. officinalis* was challenged by the pathogen or not. However, recently, it has been shown that fungi in the rhizosphere can alter the exudation pattern of plant roots and thus can affect microconidial germination of *F. oxysporum.* Root exudates of tomato, barley, maize, papaya, cucumber and many more plants, colonized by the

arbuscular-mycorrhizal fungus *Glomus mosseae*, exhibited a different effect on the microconidial germination of *Fol* 007 than root exudates from non-mycorrhizal plants (Scheffknecht et al. 2006, 2007). This indicates that alterations of the root exudation pattern due to fungi are fungus-specific. This hypothesis also seems to be confirmed when looking at our data with *Forl* 101587.

Microconidial germination of *Forl* 101587 in the presence of root exudates of tomato plants challenged with *Fol* 007 or *Forl* 101587 was similar to that in the presence of root exudates from non-inoculated control plants. Apparently, *Forl* 101587 is not able to improve the conditions for its own germination, whereas the presence of *Fol* 007 does not affect the microconidial germination of *Forl* 101587. In contrast, root exudates of tomato plants challenged with the non-pathogenic unspecific strain *Fo* 135 and the biocontrol strain *Fo* 47 clearly reduced microconidial germination of the root rot pathogen *Forl* 101587. Thus, the presence of these two non-pathogenic strains could possibly reduce the infection by *Forl* 101587 via a decreased microconidial germination of this pathogen. A decrease in symptom development of plants challenged with an incompatible *F. oxysporum* strain and thereafter inoculated with a pathogenic strain has been described for several *F. oxysporum*–plant interactions (Matta 1989; Larkin and Fravel 1999). The fact that microconidial germination of the biocontrol strain *Fo* 47 was increased in the presence of root exudates of tomato plants challenged with the tomato wilt pathogen *Fol* 007 indicates that plants challenged with a pathogen can promote potential pathogen antagonists.

In conclusion, our results indicate that the pathogenic *Fusarium* strains *Fol* 007 and *Forl* 101587 and the non-pathogenic *Fusarium* strains *Fo* 135 and *Fo* 47 trigger different responses in tomato plants that consequently influence fungal propagation in the rhizosphere differently. However, further studies are needed to characterise the signalling compounds in tomato root exudates involved in the tomato–*F. oxysporum* interaction.

References

Alabouvette, C. (1990). Biological control of Fusarium wilt pathogens in suppressive soils. In D. Hornby (Ed.) *Biological control of plant pathogens* (pp. 27–43). Wallingford: CAB.

Alabouvette, C., Olivain, C., & Steinberg, C. (2006). Biological control of plant diseases: The European situation. *European Journal of Plant Pathology*, *114*, 329–341.

Armstrong, G. M., & Armstrong, J. K. (1981). Formae speciales and races of *Fusarium oxysporum* causing wilt diseases. In P. E. Nelson, T. A. Toussoun, & R. J. Cook (Eds.) *Fusarium: Diseases, biology and taxonomy* (pp. 392–399). University Park: The Pennsylvania State University Press.

Bais, H. P., Weir, T. L., Perry, L. G., Gilroy, S., & Vivanco, J. M. (2006). The role of root exudates in rhizosphere interactions with plants and other organisms. *Annual Review of Plant Biology*, *57*, 233–266.

Bertin, C., Yang, X., & Weston, L. A. (2003). The role of root exudates and allelochemicals in the rhizosphere. *Plant and Soil*, *256*, 67–83.

Bolwerk, A., Lagopodi, A. L., Lugtenberg, B. J. J., & Bloemberg, G. V. (2005). Visualization of interactions between a pathogenic and a beneficial Fusarium strain during biocontrol of tomato foot and root rot. *Molecular Plant Microbe Interactions*, *18*, 710–721.

Fravel, D., Olivain, C., & Alabouvette, C. (2003). *Fusarium oxysporum* and its biocontrol. *New Phytologist*, *157*, 493–502.

He, C., Hsiang, T., & Wolyn, D. J. (2001). Activation of defence responces to *Fusarium* infection in *Asparagus densiflorus*. *European Journal of Plant Pathology*, *107*, 473–483.

Hochmuth, G. J., & Hochmuth, R. (2003). Keys to successful tomato and cucumber production in perlite media. Factsheet HS927. Department of Horticultural Sciences, Florida cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. Retrieved June 30, 2007, from http://edis.ifas.ufl.edu/HS169.

Jones, J. P. (1991). Fusarium wilt. In J. B. Jones, R. E. Stall, & T. A. Zitter (Eds.) *Compendium of tomato diseases*. St. Paul, Minnesota: APS.

Kamilova, F., Kravchenko, L. V., Shaposhnikov, A. I., Makarova, N., & Lugtenberg, B. (2006). Effects of the tomato pathogen *Fusarium oxysporum* f.sp. *radicis-lycopersici* and the biocontrol bacterium *Pseudomonas fluorescens* WCS365 on the composition of organic acids and sugars in tomato root exudates. *Molecular Plant Microbe Interactions*, *19*, 1121–1126.

Kravchenko, L. V., Azarova, T. S., Leonova-Erko, E. I., Shaposhnikov, A. I., Makarova, N. M., & Tikhonovich, I. A. (2003). Root exudates of tomato plants and their effect on the growth and antifungal activity of *Pseudomonas* strains. *Microbiology*, *72*, 37–41.

Lagopodi, A. L., Ram, A. F. J., Lamers, G. E. M., Punt, P. J., Van den Hondel, C. A. M., Lugtenberg, B. J. J., et al. (2002). Novel aspects of tomato root colonization and infection by *Fusarium oxysporum* f.sp. *radicis-lycopersici* revealed by confocal laser scanning microscopic analysis using the green fluorescent protein as a marker. *Molecular Plant Microbe Interactions*, *15*, 172–179.

Larkin, R. P., & Fravel, D. R. (1999). Mechanisms of action and dose–response relationships governing biological

control of *Fusarium* wilt by nonpathogenic *Fusarium* spp. *Phytopathology*, *89*, 1152–1161.

Lioussanne, L., Jolicoeur, M., & St-Arnaud, M. (2003). Effects of the alteration of tomato root exudation by *Glomus intraradices* colonization on *Phytophthora parasitica* var. *nicotianae* zoospores. In: Proceedings of the Fourth International Conference on Mycorrhizae, Aug. 10–15, Montreal/Canada, p. 291.

Lugtenberg, B. J. J., Kravchenko, L. V., & Simons, M. (1999). Tomato seed and root exudate sugars: Composition, utilization by *Pseudomonas* biocontrol strains and role in the rhizosphere colonization. *Environmental Microbiology*, *1*, 439–446.

Matta, A. (1989). Induced resistance to fusarium wilt diseases. In E. C. Tjamos, & C. H. Beckman (Eds.) *Vascular wilt diseases of plants—Basic studies and control* (pp. 175–196). NATO ASI Series, Berlin: Springer.

Nelson, E. B. (1991). Exudate molecules initiating fungal responses to seed and roots. In D. L. Keister, & P.B. Cregan (Eds.) *The rhizosphere and plant growth* (pp. 197–209). Dordrecht: Kluwer Academic Publishers.

Olivain, C., & Alabouvette, C. (1997). Colonization of tomato root by a non-pathogenic strain of *Fusarium*. *New Phytologist*, *137*, 481–494.

Olivain, C., & Alabouvette, C. (1999). Process of tomato root colonization by a pathogenic strain of *Fusarium oxysporum* f.sp. *lycopersici* in comparison with a non-pathogenic strain. *New Phytologist*, *141*, 497–510.

Olivain, C., Humbert, C., Nahalkova, J., Fatehi, J., L'Haridon, F., & Alabouvette, C. (2006). Colonization of tomato root by pathogenic and nonpathogenic *Fusarium oxysporum* strains inoculated together and separately into the soil. *Applied and Environmental Microbiology*, *72*, 1523–1531.

Pinior, A., Wyss, U., Piché, Y., & Vierheilig, H. (1999). Plants colonized by AM fungi regulate further root colonization by AM fungi through altered root exudation. *Canadian Journal of Botany*, *77*, 891–897.

Ruan, Y., Kotraiah, V., & Straney, D. C. (1995). Flavonoids stimulate spore germination in *Fusarium solani* pathogenic on legumes in a manner sensitive to inhibitors of cAMP-dependent protein kinase. *Molecular Plant Microbe Interactions*, *8*, 929–938.

Scheffknecht, S., Mammerler, R., Steinkellner, S., & Vierheilig, H. (2006). Root exudates of mycorrhizal tomato plants exhibit a different effect on microconidia germination of *Fusarium oxysporum* f.sp. *lycopersici* than root exudates from non-mycorrhizal tomato plants. *Mycorrhiza*, *16*, 365–370.

Scheffknecht, S., St-Arnaud, M., Khaosaad, T., Steinkellner, S., & Vierheilig, H. (2007). An altered root exudation pattern through mycorrhization affecting microconidia germination of the highly specialized tomato pathogen *Fusarium oxysporum* f.sp. *lycopersici* (Fol) is not tomato specific but also occurs in Fol non-host plants. *Canadian Journal of Botany*, *85*, 347–351.

Sood, S. G. (2003). Chemotactic response of plant-growth-promoting bacteria towards roots of vesicular–arbuscular mycorrhizal tomato plants. *FEMS Microbiology Ecology*, *45*, 219–227.

Steinberg, C., Whipps, J. M., Wood, D., Fenlon, J., & Alabouvette, C. (1999). Mycelial development of *Fusarium oxysporum* in the vicinity of tomato roots. *Mycological Research*, *103*, 769–778.

Steinkellner, S., Mammerler, R., & Vierheilig, H. (2005). Microconidia germination of the tomato pathogen *Fusarium oxysporum* in the presence of root exudates. *Journal of Plant Interactions*, *1*, 23–30.

Stevenson, P. C., Padgham, D. E., & Haware, M. P. (1995). Root exudates associated with resistance of four chickpea cultivars (*Cicer arietinum*) to two races of *Fusarium oxysporum* f.sp. *ciceri*. *Plant Pathology*, *44*, 686–694.