SYMBIOTIC PLANT–MICROBE INTERACTIONS: STRESS PROTECTION, PLANT GROWTH PROMOTION, AND BIOCONTROL BY *STENOTROPHOMONAS*

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1. Introduction

The genus *Stenotrophomonas* is phylogenetically placed in the γ-subclass of *Proteobacteria* (Moore et al., 1997). The genus was first described with the type species *Stenotrophomonas maltophilia* (Palleroni and Bradbury, 1993), previously called *Pseudomonas maltophilia* (Hugh and Ryschenko, 1961) and later changed to *Xanthomonas maltophilia* (Swings et al., 1983). Actually, the genus comprises eight validly described species: *S. maltophilia*, *S. nitritireducens* (Finkmann et al., 2000), *S. rhizophila* (Wolf et al., 2002), *S. acidaminophila* (Assih et al., 2002), *S. koreensis* (Yang et al., 2006), *S. terrae*, *S. humi* (Heylen et al., 2007), and *S. chelatiphaga* (Kaparullina et al., 2009). However, pheno- and genotypic studies revealed much more differentiation at species level (Ryan et al., 2009). Only two species, *S. maltophilia* and *S. rhizophila* (Wolf et al., 2002), show a strong association with plant hosts. In comparison with *S. maltophilia*, the defining phenotypic characteristics of *S. rhizophila* are: growth at 4°C and no growth at 40°C; the utilization of xylose as a carbon source; higher osmotic tolerance (<5% NaCl [w/v]); and the absence of lipase and β-glucosidase production (Wolf et al., 2002). Both species produce osmoprotective substances (Roder et al., 2005). These are compounds compatible at very high internal concentrations with cellular functions, e.g., DNA replication, DNA–protein interactions, and cellular metabolism; they regulate the osmotic balance and are effective stabilizers of enzymes (Welsh, 2000). A molecular protocol was developed for the differentiation of the two *Stenotrophomonas* species. It targets specifically the *ggpS* gene responsible for glucosylglycerol (GG) synthesis because this marker occurs only in *S. rhizophila*

strains and was absent from all *S. maltophilia* isolates (Ribbeck-Busch et al., 2005). As a further genetic marker the *smeD* gene was used, which is part of the operon coding for the multi-drug efflux pump SmeDEF only occurring in *S. maltophilia* (Alonso and Martinez, 2000).

The great heterogeneity in physiological parameters among *S. maltophilia* strains has already been shown by Van den Mooter and Swings (1990), and also by Palleroni and Bradbury (1993) in the type description of *S. maltophilia*. Heterogeneity has been confirmed by genotypic studies (Gerner-Smidt et al., 1995; Chatelut et al., 1995; Nesme et al., 1995; Hauben et al., 1999; Berg et al., 1999).

2. Occurrence of *Stenotrophomonas* on/in Plants

S. maltophilia and *S. rhizophila* are typical plant-associated microorganisms. Their main reservoir is the rhizosphere of plants (Juhnke and Des Jardins, 1989; Berg et al., 1996). The rhizosphere is defined as the layer of soil influenced by root metabolism. In comparison to root-free soil, the rhizosphere forms a nutrient-rich niche for microorganisms as a result of exudation of organic compounds (Sørensen, 1997). Additionally, this microenvironment is described as "microbial hot-spot" where diverse interactions between organisms, beneficial as well as pathogenic, take place (Whipps, 2001). *S. maltophilia* is reported to be associated with a long list of plant species, which includes all branches of plant phylogeny. Examples are potato *Solanum tuberosum* L. (Garbeva et al., 2001), oilseed rape *Brassica napus* L. (Berg et al., 1996), rice *Oryza sativa* (Sun et al., 2008), sweet flag *Acorus calmus* L. (Marecik et al., 2008), tropical orchids like *Paphiopedilum appletonianum* and *Pholidota articulata* (Tsavkelova et al., 2007), coffee *Coffea arabica* L. (Vega et al., 2005), grape-vine *Vitis vinifera* (Prieto et al., 2007), poplar *Populus* spp. L. (Taghavi et al., 2009), and marram grass *Ammophila arenaria* (L.) Link (De Boer et al., 2001). In many studies, *Stenotrophomonas* was reported as dominant member of the plant-associated bacterial community. The proportion of *S. maltophilia* in the cultivable fraction of bacteria was estimated up to 38% for *Graminaceae* (Juhnke and Des Jardins, 1989) and up to 48% for *Brassicaceae* (Berg et al., 1996). Using cultivation-independent methods, the dominance of *Stenotrophomonas* was confirmed, e.g., for rice plants (Sun et al., 2008). They were also found on bryophytes, which are the phylogenetically oldest land plants (Opelt et al., 2007). Although the rhizosphere seems to be a preferred habitat, strains of *S. maltophilia* are also found in other microenvironments such as phyllospheres (Krimm et al., 2005; Schreiber et al., 2005). Recently, *Stenotrophomonas* strains were isolated from extraordinary plant-associated habitats such as root nodules of herbaceous legumes (Kan et al., 2007) or the plant pathogenic fungus *Fusarium oxysporum* (Minerdi et al., 2008) and arbuscular mycorhizal fungal spores (Bharadwaj et al., 2008). Interestingly, they are also a member of the lichen symbiosis, where they fulfill the function of nitrogen fixation (Liba et al., 2006). It has been assumed that many *S. maltophilia* strains associated with the rhizosphere are also capable to fix inorganic nitrogen promoting growth of the host plants. *S. maltophilia* has not only been isolated from typical terrestrial and

aquatic environments (Minkwitz and Berg, 2001) but also from the extreme environment of a soda lake (Denton and Kerr, 1998). Altogether, *S. maltophilia* was found in a wide variety of environments and geographical regions, and occupies diverse ecological niches including hospitals and medical equipments (Denton and Kerr, 1998).

The second species, *S. rhizophila*, was first described in 2002; since that time, it was also reported from diverse plant species and microenvironments. In contrast to *S. maltophilia*, strains of this species were exclusively found on plants. Possibly, in the older studies on plant-associated bacteria *S. rhizophila* strains were wrongly identified as *S. maltophilia*. In an extensive study, clinical and environmental *Stenotrophomonas* strains from several countries were distinguished according to the protocol of Ribbeck-Busch et al. (2005): none of the clinical strains (>100) was identified as *S. rhizophila* (Berg, 2005, unpublished). Another important criterion, which points to the intimate interaction of *Stenotrophomonas* with plants, is their endophytic occurrence. Both *Stenotrophomonas* species are able to live in the endosphere of plants (Garbeva et al., 2001; Krechel et al., 2002; Vega et al., 2005; Hallmann and Berg, 2006; Sun et al., 2008; Taghavi et al., 2009).

3. Plant–Microbe Interaction

Bacteria showing beneficial interaction with plants comprise the group of plant growth-promoting bacteria (PGPB), which influence plant growth by producing phytohormones or by enhancing the availability of nutrients. Moreover, such strains may induce systemic resistance in plants and may act as antagonistic bacteria for pathogens (Kloepper, 1992; Whipps, 2001). Antagonists are naturally occurring organisms with traits, which enable them to interfere with pathogen growth, survival, infection, or plant attack (Chernin and Chet, 2002). Mechanisms responsible for antagonistic activity include: (i) inhibition of pathogens by antibiotics, toxins, and biosurfactants (antibiosis), (ii) competition for colonization sites and nutrients, (iii) competition for minerals, e.g., for iron through production of siderophores or efficient siderophore-uptake systems, (iv) degradation of pathogenicity factors of the pathogen such as toxins, and (v) parasitism that may involve production of extracellular cell wall-degrading enzymes such as chitinases and β-1,3 glucanase (Bloemberg and Lugtenberg, 2001; Whipps, 2001; Raaijmakers et al., 2008). Furthermore, the importance to recognize and adhere to plant roots for all plant-associated bacteria is corroborated by many studies.

An early step in the establishment of a plant–bacterium interaction is attachment of cells to plant roots, in which, for example, fimbriae and cell-surface proteins are involved (Lugtenberg et al., 2001). For the colonization of plant roots, flagella, O-antigen of lipopolysaccharides (LPS), the growth rate, and the ability to grow on root exudates are important (Lugtenberg and Dekkers, 1999; Lugtenberg et al., 2001). Other factors that contribute to rhizosphere fitness include the ability to use seed and root exudates as carbon sources or, more in

general, ecological and nutritional versatility. Which of these factors are already described for *Stenotrophomonas*? An overview about the possible mode of interaction of *Stenotrophomonas* cells with their plant hosts is given in Fig. 1.

Antagonistic mechanisms are reported, especially for *S. maltophilia*. In vitro, the majority of *Stenotrophomonas* isolates show an antagonistic activity toward plant pathogenic fungi (Minkwitz and Berg, 2001). New antifungal antibiotics with strain-specific occurrence were discovered: maltophilin (Jacobi et al., 1996) and xanthobaccins (Nakayama et al., 1999b). A gene encoding a potential pathogenicity factor – the zonula occludens toxin – could be detected, but only in several clinical *Stenotrophomonas* strains (Hagemann et al., 2006). It was earlier described that *S. maltophilia* produces not only antibiotics but also plant-associated as well as clinical strains, which are also highly resistant to several antibiotics (Berg et al., 1999; Alonso and Martinez, 1997). The rhizosphere is an environment, where a lot of bacteria possess antibiotic resistances and preferential horizontal gene transfer occurs to submit the encoding gene cluster (Berg et al., 2005).

These resistances can protect microorganisms against antibiotics produced by other microbial colonizers or against toxic metabolites produced by the plant hosts themselves. Some antibiotic resistance determinants have been carefully analyzed, including aminoglycosides inactivating enzymes (Lambert et al., 1999; Li et al., 2003), β-lactamases (Kataoka et al., 2003), and multidrug (MDR) efflux pumps like SmeABC (Li et al., 2002) or SmeDEF (Alonso and Martinez, 2000, 2001; Vila and Martínez, 2008). The first complete genome sequence of the clinical

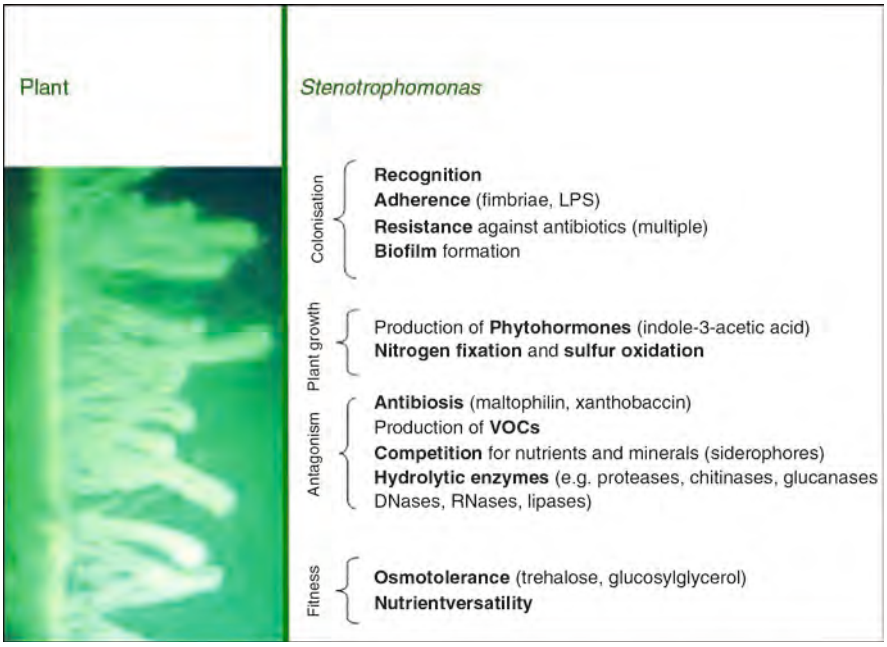


Figure 1. Mode of interaction of *Stenotrophomonas* with plant hosts.

isolate *S. maltophilia* K279a confirms the remarkable capacity for drug and heavy metal resistance (Crossman et al., 2008). In addition to a number of genes conferring resistance to antimicrobial drugs of different classes via alternative mechanisms, nine resistance-nodulation-division (RND)-type putative antimicrobial efflux systems are present. *Stenotrophomonas* strains are also known for their extraordinary high hydrolytic potential. They produce diverse proteases, chitinases, glucanases, DNases, RNases, lipases, and laccases (Debette, 1991; Berg et al., 1996; Dunne et al., 2000; Galai et al., 2008). However, the precise roles of these enzymes in the antagonistic activity of *Stenotrophomonas* remain to be elucidated. Furthermore, *Stenotrophomonas* cells synthesize siderophores, possess siderophore-uptake systems, and are able to take up or scavenge efficiently siderophores from other microorganisms (Jurkevitch et al., 1992). Besides the excretion of soluble antibiotics and enzymes also volatile organic compounds (VOCs) produced by bacteria like *Stenotrophomonas* can inhibit growth of pathogenic fungi (Wheatley, 2002). Furthermore, VOCs may serve as inter- and intraorganismic communication signals in general (Stotzky and Schenk, 1976; Wheatley, 2002). Recently, it has been shown that the VOCs of *S. maltophilia* and *S. rhizophila* inhibit mycelial growth of the soil-borne pathogen *Rhizoctonia solani* to more than 90% in dual culture tests. Out of a vast diversity of VOCs produced by *S. rhizophila*, two, namely dodecanal and β-phenylethanol, could be identified by GC-MS (Kai et al., 2007). Beta-phenylethanol is a typical floral fragrance compound, which exerts its antimicrobial effects by inhibition of macromolecule synthesis and by altering the permeability of the plasma membrane and sugar and amino acid transport processes (Ingram and Buttke, 1984).

In addition, synthesis of compatible solutes by bacteria contributes to survival under changing osmotic conditions, which occur in the rhizosphere (Miller and Wood, 1996). Hiltner (1904) described the phenomenon, designated as the "rhizosphere effect," that in rhizospheres, in comparison to bulk soil, the biomass and activity of microorganisms is enhanced as a result of the exudation of compounds. A long list of diverse substances, such as organic acids, sugars, amino acids, vitamins, and polymeric carbohydrates, is known to be released by plant roots (Bais et al., 2006). However, the nutrient content is not constant and the different amounts of nutrients lead to changing osmolarities in the rhizosphere (Miller and Wood, 1996). The two type strains of *Stenotrophomonas* species, *S. maltophilia* strain DSM 50170 and *S. rhizophila* strain DSM 14405 produce different compatible solutes. *S. maltophilia* accumulated trehalose as the only osmolyte, whereas *S. rhizophila* was shown to produce glucosylglycerol (GG) in addition to trehalose. As expected, the different spectrum and amounts of compatible solutes in these two strains led to differences in terms of their salt tolerance. The human-associated *S. maltophilia* was able to grow in media containing up to 3% NaCl (w/v). In contrast, *S. rhizophila* can be propagated in salinities up to 5% NaCl (w/v). The genes for trehalose and GG synthesis can be used to differentiate the two species (Ribbeck-Busch et al., 2005). Moreover, the molecular basis for GG synthesis was revealed in *S. rhizophila*. This strain possesses a new type of GG-synthesis enzyme, which combines the two-step biosynthesis

employing GG-phosphate synthase and GG-phosphate phosphatase on a single enzyme (Hagemann et al., 2008).

It is common in many bacteria that genes encoding factors involved in interaction are regulated in a cell density-dependent manner. Many plant-associated bacteria produce *N*-acyl homoserine lactones as cell–cell signaling molecules (Berg et al., 2002). In contrast, *S. maltophilia* uses a signaling system mediated by a diffusible signal molecule (DSF) (Fouhy et al., 2007). The latter authors described that DSF activity controls resistance to several antibiotics, aggregative and biofilm behavior, and virulence in a nematode model.

Interestingly, using a genomic approach to analyze endophytic bacteria of poplar and their plant–microbe interaction, Taghavi and coauthors (2009) found none of the well-known genes known for positive interaction (e.g., phytohormone biosynthesis, ethylene degradation) in an endophytic strain of *S. maltophilia*. Additional new insights into the interaction of *Stenotrophomonas* with eukaryotes resulted from the genome sequencing of the clinical *S. maltophilia* K279a strain (Crossman et al., 2008). Many genes encoding for drug resistance, secretion systems of type I, II (*sec*), IV, and V (autotransporter), as well as the twin arginine secretion systems genes are present in the K279a genome. Furthermore, this genome harbors genes for extracellular enzymes such as nonhemolytic phospholipase C, enzymes of the phospholipase D family, DNase, gelatinase, hemolysin, lipases, proteinase K, and proteases. The genome comparison confirmed also the high similarity of the human pathogen *S. maltophilia* to the phytopathogen *X. campestris*. However, in contrast to the closely related genus *Xanthomonas*, no phytopathogenic capacity of *Stenotrophomonas* is known (Palleroni and Bradbury, 1993).

4. Plant Growth Promotion and Biocontrol by *Stenotrophomonas* Treatment

Stenotrophomonas species have an important ecological role in the element cycle in nature (Ikemoto et al., 1980). The biotechnological importance of *S. maltophilia* is partly due to their potential plant growth-promoting effects and application in biological control of fungal diseases in plants. An overview about the use of *Stenotrophomas* strains in biocontrol and plant growth promotion is given in Table 1.

The influence of *Stenotrophomonas* treatment on in vitro plant growth is shown in Fig. 2.

Plant growth promotion was also observed in the highly salinated soils of Uzbekistan, where statistically significant promoting effects of strain DSM 14405 treatments were observed for wheat, tomato, lettuce, sweet pepper, melon, celery, and carrot (Egamberdiyeva, 2008, unpublished results). These treatments resulted in higher germination rates as well as in longer shoots and roots. For example, in tomato the germination rate was 180% and the growth of the shoot was 120% and root was 142% in comparison to the values found for the untreated control. Furthermore, up to 100 mM NaCl in the soil, there is no influence of salt on the survival of *S. rhizophila* in

Table 1. Examples of applications of *Stenotrophomonas maltophilia* and *S. rhizophila* in biocontrol and plant growth promotion.

No.	Strain	Pathosystem: pathogen and/or plant species	Reference
1.	*S. maltophilia*	Soil-borne pathogens	Elad et al. (1987)
2.	*S. maltophilia*	Rhizoctonia damping-off in bark compost media	Kwok et al. (1987)
3.	*S. maltophilia* 3089	*Verticillium dahliae* – oilseed rape	Berg et al. (1994)
4.	Chitinolytic *S. maltophilia*	Summer patch disease of turf grass	Kobayashi et al. (1995)
5.	*Stenotrophomonas* sp. strain SB-K88	Sugar beet damping-off disease	Nakayama et al. (1999)
6.	*S. maltophilia* mutant with overproduction of an extracellular serine protease	Biological control of *Pythium ultimum*	Dunne et al. (2000)
7.	*S. maltophilia* PD3533	Potato – *Ralstonia solanacearum* race 3 biovar 2	Messiha et al. (2007)
8.	Endophytic *S. maltophilia* R551-3	Poplar	Taghavi et al. (2009)

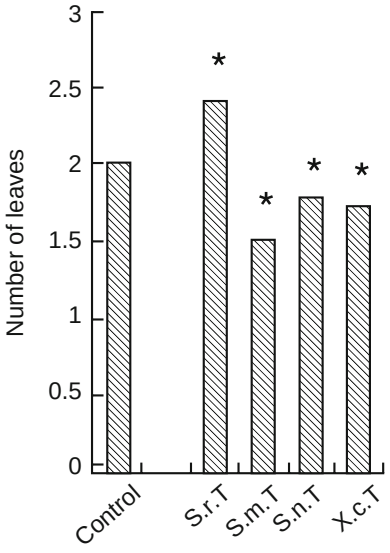


Figure 2. Influence of the treatment of strawberry seedlings with *Stenotrophomonas rhizophila* DSM 14405^T (S.r.T), *S. maltophilia* DSM 50170^T (S.m.T), *S. nitritireducens* DSM 12575^T (S.n.T), and *Xanthomonas campestris* DSM 3586^T on the number of leaves. Control: untreated seedlings. Significant differences are indicated by asterisks. (Adapted from Suckstorff and Berg, 2003.)

the rhizosphere of cucumber and tomato (Egamberdiyeva, unpublished results). In comparison to literature (see Table 1), the plant-promoting effect of *Stenotrophomonas* treatment is much higher under salt stress conditions than in nonsaline soil. Also under in vitro conditions, salt stress has an important influence on the antagonistic activity of *Stenotrophomonas*. Salt stress significantly enhanced the antagonistic activity against phytopathogenic fungi such as *Rhizoctonia solani* and *Verticillium dahliae* (Berg, unpublished); the molecular mechanisms behind this phenomenon have to be analyzed.

5. The Ambivalent Role of *Stenotrophomonas* as Opportunistic Pathogen

In the last two decades, *S. maltophilia* has also become important as a nosocomial multidrug-resistant pathogen associated with significant case to fatality ratios in certain patient populations, particularly in those who are severely debilitated or immunosuppressed (for a review see Denton and Kerr, 1998). *S. maltophilia* is the third most common nosocomial nonfermenting gram-negative bacterium (Sader and Jones, 2005). A study of intensive care patients in the USA found that 4.3% of almost 75,000 Gram-negative infections studied were caused by *S. maltophilia* (Lockhart et al., 2007). *S. maltophilia* is also involved in polymicrobial infections as may occur in wounds, abscesses, and the cystic fibrosis lung (Ryan et al., 2008; Sibley et al., 2008).

6. Possible Applications in Biotechnology

Due to their diverse capabilities, *Stenotrophomonas* is an interesting candidate for many biotechnological applications. Strains are used to biologically control plant diseases or enhance plant growth (see Table 1). The high hydrolytic potential is used to breakdown natural and man-made pollutants applied in bioremediation and phytoremediation strategies (Barac et al., 2004). Furthermore, *Stenotrophomonas* is used for the production of biomolecules of economic value, e.g., enzymes and compatible solutes (Roder et al., 2005).

Opportunistic pathogens cannot be used for field trials and other direct applications. However, *S. rhizophila* is not known as a human pathogen. Strains of *S. rhizophila*, which very often live endophytically, are promising candidates for biocontrol and stress protection on plants.

7. Summary

The genus *Stenotrophomonas* comprises at least ten species of which the most predominant ones on plants are *S. maltophilia* and *S. rhizophila*. Strains of both species are able to colonize more or less in all the microenvironments of plants but

have a preference for the rhizosphere. They show beneficial interactions with their plant hosts, since they are able to promote plant growth as well as plant health. The mechanisms involved in this interaction are discussed. *Stenotrophomonas* strains are able to live under salt stress due to the production of compatible solutes. This observation explains their use in salinated soils, where they may protect plants against diseases and possibly also against salt stress. Strains of *S. maltophilia* are known for their ambivalent behavior. On the one hand, they exhibit an extraordinary range of capabilities that includes detrimental effects as opportunistic multidrug-resistant human pathogens, whereas on the other hand, they can exert beneficial effects such as biocontrol of plant diseases. In this chapter, the importance of symbiotic bacteria in the genus *Stenotrophomonas* for plants as well as benefits and problems is discussed.

8. Outlook

Further insights into the diversity in adaptation and metabolic capabilities will be provided by comparative genomic analysis in the future. The genome sequence of the clinical isolate *S. maltophilia* K279a has recently been published (Crossman et al., 2008). Additionally, the genome sequences of the endophytic strain *S. maltophilia* R551-3 (http://genome.jgi-psf.org/finished_microbes/stema/stema.home.html) and of a marine *S. maltophilia* SKA14 (https://research.venterinstitute.org/moore) will be finished soon. The genome sequences of isolates of different origin will lead to a better understanding of the mechanisms of adaptation and evolution of this fascinating group of organisms, ranging from understanding of medical consequences to environmental applications.

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