

REVIEW ARTICLE

Swarming motility in plant-associated bacteria

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Summary Plant-associated environments harbor a huge number of diverse bacteria that compete and/or cooperate for the occupation of the most nutrient-rich ecological niches. Motility, a common trait among bacteria, has long been assumed to provide a survival advantage to skilful bacteria in invading these environments. Bacterial surface motility, such as swarming, a flagella-driven type of surface movement, although mostly observed and studied on agar substrates, is emerging as a major trait involved in many functions of plant-associated bacteria in regard to their ability to colonize and spread on their host. In this review, we address some novel swarming motility strategies, which enable bacteria to colonize, disperse and compete in plant surfaces.

Additional keywords: Competition, cooperation, fungi

Introduction

Plants harbor epiphytic or endophytic communities of bacteria that colonize almost all tissues (roots, leaves, stems, vascular tissues, seeds and fruit). In general, plant-associated prokaryotes can be grouped based on the nature of their interaction with host into commensal, mutualistic, and pathogenic; mutualistic, when it is beneficial for both organisms, commensal, when one organism benefits and the other is not affected and pathogenic, when only the microbe benefits at the expense of the host or host damage. Mutualistic and commensal bacteria in association with plants are either so-called ectophytes or endophytes, if their location is outside or within plant tissues, respectively (Mentes *et al.*, 2013; Berg *et al.*, 2015).

Bacteria move from one location to another in natural niches and this movement is referred as motility. Plant colonization is a complex process and motility of bacteria in soil and/or on plant surfaces is a basic com-

ponent of this process. Bacterial motility has been classified into discrete types, based on structural surface appendages or internal structures involved, and bacterial species may employ more than one type for translocation and colonization (Jarrell and McBride, 2008). Most bacteria are able to swim in aquatic environments powered by rotating flagella. This type of motility is referred as swimming motility. However, a range of different mechanisms have evolved that facilitate movement and spreading on a variety of surfaces (Jarrell and McBride, 2008). Swimming motility is considered to be an individual bacterial behavior (Jarrell and McBride, 2008; Harshey, 2003; Kearns, 2010). Surface movement can depend on the presence of flagella (i.e., swarming), the extension and retraction of type IV pili (i.e., twitching motility), the involvement of rearrangements in the shape of the cell that generate standing waves, the secretion of material from the poles, and localized focal adhesion complexes between cells and the substrate (i.e., gliding), or “passive” surface translocation where the expansive force of cell proliferation moves cells at the periphery of a cell mass (i.e., sliding).

Swarming is a multicellular movement of flagellated bacteria over solid surfaces and this trait is displayed by dozens of bacterial species under laboratory conditions.

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Such a mode of motility allows bacteria to escape local stresses, translocate to a better nutritional environment and efficiently invade host tissue (Harshey, 2003). Thus, we can infer that swarming motility must be an important mean for overriding surface impediments and claiming more space in the bacteria's natural habitat. However, despite the benefits, this trait is energy expensive and is dependent on surface wetness. The loss of motility may be considered as another adaptive strategy of bacteria to cope with harsh environmental conditions.

Swarming regulatory mechanisms and strategies are diverse among the different bacteria species and have recently been reviewed (Harshey, 2003; Kearns, 2010; Partridge and Harshey, 2013; Harshey and Partridge, 2015). In plant-associated bacteria the ability to swarm can play an important role in colonization of interior and exterior surfaces of plants, in biofilm formation and in virulence or protective functions (Xu *et al.*, 2012). In this review, we focus on highlighting the recently emerging novel tactics of plant-associated swarming bacteria to occupy, disperse and duel and/or cooperate on plant surfaces.

Swarming bacteria dispersed over fungi

While numerous studies have been focused on identifying bacterial genes involved in root colonization, limited attention was given to the involvement of fungi in facilitating migration of bacteria (Hannula *et al.*, 2011). Soils are heterogeneous particulate systems exhibiting chemical heterogeneity. In the majority of soils, the patchiness and thickness of the liquid films restrict the dispersal of individual cells or populations. Flagellum-driven swimming requires bacterial cells to be fully immersed in liquid while swarming is restricted to a narrow range of wet conditions (Partridge and Harshey, 2013; Partridge and Harshey, 2015). Thus, flagellated bacteria would be expected to swim or to swarm under certain soil saturation levels. Recent

studies demonstrated that displacement of *Bradyrhizobium japonicum* is achieved in 80% saturated soil (Covelli *et al.*, 2013) while *Pseudomonas fluorescens* strain X (Kremmydas *et al.*, 2013) displayed a fast movement in 50% saturated soil (Fig. 1). Movement of bacteria in bulk unsaturated soils or rhizosphere, conditions that limit the dispersal of microbes due to environments of low water potential or discontinuous water films, may not be achievable without additional aid. Several lines of evidence suggested that mycelia may also provide the appropriate conditions for motile bacteria migration in unsaturated soils. First, the abundance of fungi which is ranging from 100 to 700 mgr per g of soil, the extensive network of growing mycelia which according to estimates sum up to 20.000 km per m³ of soil (Simon *et al.*, 2015). Second, their ability to colonize both water-saturated and air-filled voids between soil particles (Wösten, 2001). Third, flagellated bacterial strains could move along the hyphal surface (Kohlmeier *et al.*, 2005). The role of fungi in facilitating the dispersal of bacteria was further substantiated in a recent work, where it was shown that fungal mycelia facilitate the spread of motile bacte-

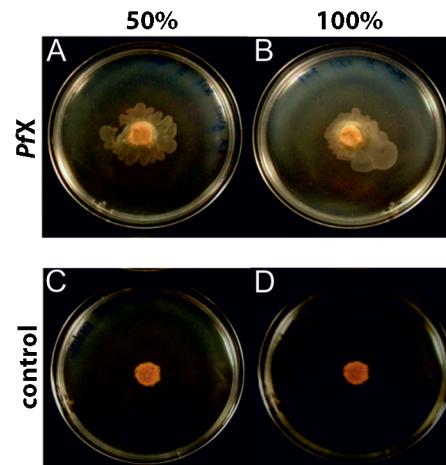


Figure 1. Motility of *Pseudomonas fluorescens* strain X in 100% and 50% saturated soil.

The soil tablets included in solid (0.5% agar) Nutrient Agar (NA) medium were inoculated with 3 µl of bacteria in the center of each tablet and growth was recorded at the NA–soil interfaces after incubation for 20 h.

ria in the soil, acting as highways for motile bacteria (Nazir et al., 2010). In a recent study, this concept was further extended; the authors using the bacterium *Paenibacillus vortex* have shown that *P. vortex* swarms can transport conidia of the *Aspergillus fumigatus* over long distances. Inoculation of *A. fumigatus* conidia near to an artificial air revealed that the fungi grown across the gap, permitting a successful cross of *P. vortex*, suggesting a role for swarming and/or flagella in this mutually facilitating migration process (Ingham et al., 2011).

Dispersal along fungal hyphae appears to be a widespread trait of swarming bacteria (Bravo et al., 2013; Furuno et al., 2012; Pion et al., 2013; Simon et al., 2015). *In vitro* studies have shown that migration along mycelium surface facilitated the bacterial degradation of organic soil pollutants (Banitz et al., 2013) and the migration of *Burkholderia terrae* BS001 along mycelium surface (Warmink et al., 2011). Shiga toxin-producing *Escherichia coli* was found to spread over several food-related fungi (Lee et al., 2013). Enhanced colonization of rhizosphere by saprotrophic fungi stimulated root surface colonization by indigenous rhizosphere inhabiting bio-control bacteria (de Boer et al., 2014).

Bacterial swarms recruit cargo bacteria or facilitate the migration of fellow swarmers

Swarming offers a competitive advantage to some bacteria in invading some plant habitats (Barak et al., 2009). However, co-swarmering or transporting other bacterial species may expand the abilities of the partners in occupying and exploiting new territories. This combination of properties is well illustrated by recent studies at laboratory conditions. A non-swarmering gentamycin resistant *Burkholderia cepacia* (cargo bacterium) allowed the gentamycin-sensitive proficient-swarmering *Pseudomonas aeruginosa* to swarm and colonize a gentamycin-containing area of the plate, dispersing both bacteria (Venturi et al., 2010). Moreover, it

has been shown that an ampicillin-sensitive *Paenibacillus vortex* was capable to swarm and colonize an ampicillin plate using non-motile ampicillin resistant *Escherichia coli* as a cargo organism; one species provides an enzyme that detoxifies the antibiotic (a sessile cargo bacterium carrying a resistance gene), while the other (*P. vortex*) moves itself and transports the cargo bacterium (Finkelstein et al., 2015). Fast-swarmering *Myxococcus xanthus* strains cooperated with slower isolates, allowing the latter to keep pace with faster strains in mixed groups (Kraemer and Velicer, 2014).

Whether these cooperative phenomena between swarming bacteria may occur in natural habitats is not clear. However, *in situ* experiments have provided evidence that non-motile bacteria may behave as hitch-hikers and thus are able to move along fungal hyphae only with the aid of other motile bacteria acting as 'community migrators' (Simon et al., 2015). Cooperation among non-competitive swarming bacterial strains provide a mechanism for mixing, thus it would be predicted that they may form mixed strains biofilm (Reichenbach et al., 2007). The ability of three species (an antibiotic-producing *Pseudomonas aeruginosa* strain P1, a resistant *Raoultella ornithinolytica* strain R1 and a sensitive *Brevibacillus borstelensis* strain S1) to establish biofilms (Narisawa et al., 2008), and the recent demonstration that kin but not identical swarming *B. subtilis* strains were able to co-exist in biofilms formed in *Arabidopsis thaliana* roots (Stefanic et al., 2015), suggested that co-swarmering but non-competitive bacterial strains may lead to the establishment of an non-transitive competitive network in natural habitat.

Interspecies communication affecting swarming motility

In most environmental niches, multiple bacterial species coexist as dynamic communities. Bacteria have developed intercellular signaling to adapt and survive in natural environments and to detect each other as

they colonize different surfaces (Park, 2003). Many bacteria secrete small diffusible as quorum sensing (QS) signaling molecules such as acyl-homoserine lactones (AHLs) (Rajput *et al.*, 2015) or volatile signal molecules such as terpenoids, alkenes, aldehydes (Piechulla and Degenhardt, 2014), thus mediating different types of cell-to-cell communication among physically separated microorganisms (Schmidt *et al.*, 2015).

AHLs are commonly synthesized by members of the LuxI family of proteins and are sensed by members of the LuxR family of transcriptional regulators (Daniels *et al.*, 2004). Above threshold concentrations which is dependent by the cell population density (quorum sense signals), AHLs are involved in the activation of expression of certain genes which confer the ability to the bacterium to migrate in a wide range of ecological niches.

The complexity of AHL signal molecules (QS signals) produced by bacteria are limited, thus there is considerable opportunity for cross talk among bacteria, as in most environmental niches, multiple bacterial species coexist as dynamic communities. Gantner and colleagues, using a reporter engineered *Pseudomonas putida* strain on plant surfaces, showed that some AHL signals were able to travel relatively long distances (up to 78 mm) but was most commonly detected only a few micrometers away from the producing strain (Gantner *et al.*, 2006). This was referred to as the cell-to-cell calling distance. Culturable rhizosphere bacteria of wheat also produced signal that could inhibit QS in *P. chlororaphis (aureofaciens)* via mechanisms that remain uncharacterized (Morello *et al.*, 2004).

The ability of QS signals to influence QS regulated networks is an important mechanism in modulating the QS-controlled surface motility of physically separated bacteria. This conjecture was elegantly demonstrated in recent studies where it was shown that bacterial epiphytes produced signals capable of interfering with the QS system of *Pseudomonas syringae* pv. *syringae* (Pss) affected its swarming motility (Dulla *et al.*, 2009). The plant epiphytic

pathogenic bacterium Pss grows and survives on leaf surfaces, invades into the leaf tissue and contributes to brown spot disease, thus the assessment of lesion formation was considered as sensitive marker of its motility behavior; non-motile bacteria were less virulent (Haefele and Lindow, 1987). In this respect, proficiency in swarming motility on plant surface has been categorized as a virulence factors.

QS suppresses swarming in Pss and QS-deficient hyperswarmer strains invade leaves more readily than wild-type strains, thereby causing a higher incidence of brown spot lesions on bean, suggesting that swarming motility of Pss strongly contributes to its ability to invade leaves and incite disease on the leaves (Quinones *et al.*, 2005). Nonmotile mutants of Pss are less able to survive desiccation stresses on leaves, apparently because they cannot access protected sites in or on the leaf surface (Quinones *et al.*, 2004). Microarray analysis of Pss gene expression during growth in epiphytic versus apoplastic sites, revealed that genes involved in motility were relatively expressed at higher levels when bacteria are located in former site, suggesting that bacteria are requiring active motility for relocation on leaves surface compared to a the apoplast where these traits were less expressed (Yu *et al.*, 2013). Co-inoculation of wild type Pss along with selected AHLs-producing epiphytic bacteria which produced large amounts of AHLs identical to those produced by Pss, decreased mobility Pss B728a on the leaf surface caused by inappropriate induction of Pss B728a QS system, resulting in less invasion into the tissue (Dulla *et al.*, 2009). Similarly, premature induction of *Xylella fastidiosa* by its QS diffusible signal factor which however was produced by the transgenic host plant enforced the pathogen to prematurely adopt a suite of phenotypes that would restrict its ability to move in the plant. Diffusible signal factor is also produced by other beneficial endophytic bacteria such as *Stenotrophomonas maltiphila* (Fouhy *et al.*, 2007; Zhu *et al.*, 2012), thus it may represent an alternative to inhibit the migration of *X. fastidiosa*.

Volatile organic compounds (VOCs) produced by plant-associated bacteria are involved in their interaction with plant associated microorganisms as well as with host plants, providing a new source of compounds with antibiotic and plant growth-promoting activities. Rhizobacterial VOCs have been shown to inhibit microbial plant pathogens, induce systemic resistance in plants and trigger plant growth promotion (Bitas et al., 2013). Volatiles emitted by *Serratia plymuthica* decreased the cell-to-cell communication quorum-sensing (QS) network mediated by AHLs produced in several plant pathogenic and plant-beneficial bacteria (Chernin et al., 2011).

The ability of bacterial volatiles signals to influence motility of physically separated bacteria demonstrated in a recent study, where the authors presented data showing that volatiles produced by bouquet of phylogenetically different bacterial isolates (*Collimonas pratensis*, *S. plymuthica*, *Paenibacillus* sp. and *Pedobacter* sp.) affected the expression of genes involved in *P. fluorescens* motility (Garbeva et al., 2014). Recent studies further substantiated swarming motility among the traits influenced by VOCs. Co-inoculation experiments of physically separated *P. vortex* and the non-motile plant pathogen *Xanthomonas perforans* revealed a massively spread of both bacteria on the plates (Hagai et al., 2014). The influence of diffusible and/or volatile signals on mobilization of *X. perforans* appears also to occur in planta; fluorescence-stained *X. perforans* spotted on a leaf surface seems to swarm towards the distantly located *P. vortex* (Hagai et al., 2014). Modulation of swarming motility by interspecies or cross- kingdom signaling appears a quite common phenomenon among bacteria. Volatiles emitted by *B. subtilis* 168 to modulate the swarming motility of an array of bacterial species including *E. coli* (Kim et al., 2013). Several *Xanthomonas* species affected *Paenibacillus vortex*, *Paenibacillus dendritiformis* and *Proteus mirabilis* surface motility through volatiles (Hagai et al., 2014). Volatile metabolites such as farnesol produced by *Candida albicans* re-

duce the swarming motility of *Pseudomonas aeruginosa* (McAlester et al., 2008).

Swarmers dueling

Plant surfaces are the habitat to a complex and competitive microbiota. The root surface and surrounding rhizosphere are significant carbon sinks which is produced by the plant (Compañt et al., 2005). Thus, along root surfaces, there are various suitable nutrient-rich niches attracting a great diversity of microorganisms, including phytopathogens (Nelson et al., 2004). Competition for these nutrients and niches is a fundamental mechanism by which biological control agents such as biocontrol bacteria protect plants from phytopathogens. Thus proficiency in surface motility can provide a competitive advantage to the invading bacterial populations over other swarming or non-swarming microorganisms that are colonizing similar plant niches and either intercept and/or kill the opponents or merge with them.

In vitro studies using converging swarming colonies between less or more phylogenetically related bacteria revealed the presence of a complex social behavior pattern ranging from discriminatory aggression, by forming a boundary between the two advancing swarms, to cooperating merging of the two swarms. This phenomenon provided evidence that there is a general tendency for discrimination of self and non-self between phylogenetically unrelated interacting swarms, and have been studied in the soil bacterium *Myxococcus xantus* (Vos and Velicer, 2009; Rendueles et al., 2015), *Burkholderia pseudomallei* (Ngamdee et al., 2015), the pathogen *Proteus mirabilis* (Gibbs et al., 2008; Alteri et al., 2013; Wenren et al., 2013) and in *B. subtilis* (Stefanic et al., 2015).

Different strains of the soil inhabiting bacterium *B. subtilis*, isolated from 1-cm³ soil samples, examined on swarm plates in pairwise combinations were found to form either distinct boundaries (phylogenetically unrelated, nonkin strains) or the swarms merge (phylogenetically related, kin strains).

Interestingly, the nonkin bacteria competed with each other and only one was able to colonize plant roots. The possible lack of alive cells in many swarm boundaries and the competition for root surface colonization between nonkin strains may suggest that antagonistic mechanisms preventing coexistence of nonkin *B. subtilis* on roots (Stefanic *et al.*, 2015). On the other hand, the kin strains demonstrated the ability to merge on agar substrate and *in situ* - colonization of the same root surface suggests that co-swarming on root surface is taking place which permitted the formation of mixed biofilms. In contrast, genetically identical strains (*siblings*) of *Paenibacillus dendritiformis* swarming colonies mutually inhibit growth through secretion of a toxic protein termed sibling lethal factor (Slf) (Be'er *et al.*, 2009; Be'er *et al.*, 2010). Slf is produced in an isolated, nutrient-starved colony. This protein is not toxic for other phylogenetically related bacteria such as *B. subtilis*. However Slf is produced along with subtilisin, a biosurfactant, in swarming colonies and not in immobile isolated colonies; thus, we suggest that the Slf represents a new class of toxins that are most effective for regulating swarming interspecies competition.

Proteus mirabilis is capable of movement on solid surfaces by swarming motility. Swarms of independent *P. mirabilis* isolates can recognize each other as nonkin and establish a visible boundary where they meet. In contrast, genetically identical swarms merge (Gibbs *et al.*, 2003; Alteri *et al.*, 2013). In an elegant study, Alteri and coworkers have shown that in *P. mirabilis* upon initiation of swarming differentiation, the type VI secretion system (T6SS) apparatus is assembled and appears to fire when opposing swarms meet by injecting the toxin into the cytosol of the rival strain. The Dienes line represents a zone of dead bacteria of the less dominant strain. The dominant strain infiltrates deeply beyond the boundary of the two swarms and continues to assemble and discharge the T6SS (Alteri *et al.*, 2013; Sarris *et al.*, 2013).

The T6SSs are prevalent and conserved among plant pathogenic and plant bene-

ficial Gram-negative bacteria (Loper *et al.*, 2012; Sarris *et al.*, 2013). By now multiple cases have been described where T6SS-harboring plant associated bacteria are able to duel and outcompete competitor bacterial cells. For example, the plant beneficial *Pseudomonas protegens* strains were competed under cell contact-promoting conditions against *P. putida*, a bacterium that inhabits similar environments, whereas those lacking *tge2*, a type VI effector resembling glycoside hydrolase protein, were 6-fold less fit compared with the wild-type (Whitney *et al.*, 2003). Hemolysin-coregulated protein (Hcp) function is also required for *P. syringae* pv. *tomato* DC3000 antibacterial activity against other Gram-negative bacteria, yeast and amoeba during contact on a solid surface (Haapalainen *et al.*, 2012).

In a recent study, the competitive advantage of plant associated bacteria harboring T6SS in dueling with other bacteria in planta has been illustrated (Ma *et al.*, 2014). The authors presented data showing that *Agrobacterium tumefaciens* (a Gram-negative soil inhabiting bacterium that causes crown gall in infected plants) T6SS is important in interspecies completion with the soil bacterium *P. aeruginosa*. When *A. tumefaciens* and *P. aeruginosa* duels *in vitro* under cell contact-promoting conditions, the former was efficiently outcompeted. The competitive advantage of *P. aeruginosa* included a T6SS-mediated counterattack. However, co-infection experiments conducted in tobacco plants revealed that the outcome of the duel was reverted within the plant habitat.

Pseudomonas fluorescens strain MFE01, under cell contact-promoting conditions, outcompete *E. coli*, *P. aeruginosa* PA14, *P. fluorescens* Pf0-1 and *P. fluorescens* MFE1032, whereas a MFE01 Δ hcp2 and MFE01 Δ hcp1 mutants demonstrated a significant loss in their ability to reduce prey cell population (Decoin *et al.*, 2014; Decoin *et al.*, 2015). The bacterial killing capacity of MFE01 against *E. coli* cells was neutralized by the constitutive expression of a T6SS-mediated-injected immunity cognate protein from *Serratia marcescens*. MFE01 was also able to outcompete the

competitor under swarming conditions possibly through the combined action of secreted Hcps; Hcp1 could reduce the motility of prey cells and the killing conducted by Hcp2 (Decoin *et al.*, 2015). The capacity of MFE01 to duel and kill other bacteria was also tested in physiological relevant environments, coinfection of potato tuber with a mixture of MFE01 and *Pectobacterium atrosepticum* protected efficiently potatoes against soft-rot symptoms caused by *P. atrosepticum* whereas MFE01Δhcp2 was unable to confer protection (Decoin *et al.*, 2014). However, *P. atrosepticum* harbor the T6SS and excretes Hcps (Mattinen *et al.*, 2008), thus it will be of interest to examine the dueling of this bacterium with MFE01 *in vitro* on plates.

Because T6SS is dependent on cell-to-cell contact, it would seem beneficial for bacteria exhibiting multicellular behavior to employ the T6SS to discriminate and kill competitors rather than indiscriminately secrete bactericidal agents when competing for resources in their natural habitats. Plant beneficial swarming bacteria harboring T6SS may encounter each other or competitor pathogenic bacteria when are migrating on plant surface or rhizosphere, thus among the traits of a biocontrol bacterium may be its efficient T6SS against a wide range of competitor bacteria thereby indirectly supporting the protection for the plant.

A recent study in our laboratory has shown that *Pseudomonas fluorescens* strain X (*Pf. X*) displayed a killing aggression against prokaryotic and eukaryotic competitors on agar substrate. The *Pf. X*, a nonpathogenic rhizobacterium, was isolated from the rhizosphere of sugar been (Georgakopoulos *et al.*, 2002). This strain harbors a gene cluster coding for a cyclic lipopeptide surfactant similar to masetolide A, which is important for swarming motility and T6SS core component genes (Venieraki *et al.*, unpublished observations). *Pf. X* forms discrete boundaries between neighboring swarms on an agar substrate with different competitor pathogenic and beneficial *Pseudomonas* strains, the boundary demarcation is occupied by killed bacteria and a one-sided invasion by

the dominant *Pf. X* swarm within the swarm of the opponents (Fig. 2). To quantify the killing, competition assays were conducted between *Pf. X* and the other *Pseudomonas* sp. For example, wild-type *Pf. X* killed *Pseudomonas* strain P21 by at least 5-logs when plated together on agar to permit swarming or non-swarming conditions and co-cultured for 20 h (unpublished data).

Although strain *Pf. X* clearly exhibited antagonism against *Fusarium* sp., *Botrytis* sp. and *Rhizoctonia solani* on 1.5% agar nutrient plates (Fig. 3), all fungi ended up occupying more than 90% of the plate surface area. In contrast, mycelium spreading of fungi was safely hampered when co-cultivated with the surface-motile *Pf. X* (Fig. 3). Once the *Pf. X* colony started to expand, contact between the spreading bacterial front and the fungus was achieved within a few hours. In some cases, a boundary line was observed and the advancing *Pf. X* swarm colonies moved along the hyphae. The trapped fungus was no longer viable as judged by its failure to resume mycelium growth when transfer to a new nutrient plate or in liquid culture.

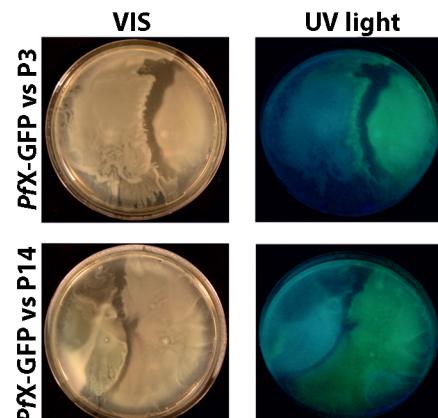


Figure 2. Warfare between swarming *Pseudomonas fluorescens* strain X (green) GFP-tagged and *Pseudomonas* sp. strain P3 and P14 (bluish).

Pseudomonas fluorescens strain X-GFP was cultured in pairs with *Pseudomonas* sp. strain P3 or P14 on swarming agar plates. The boundary formed between the different strains is referred as Dienes line. Note the presence of *Pseudomonas fluorescens* strain X-GFP (green) within the swarms of the rival strains.

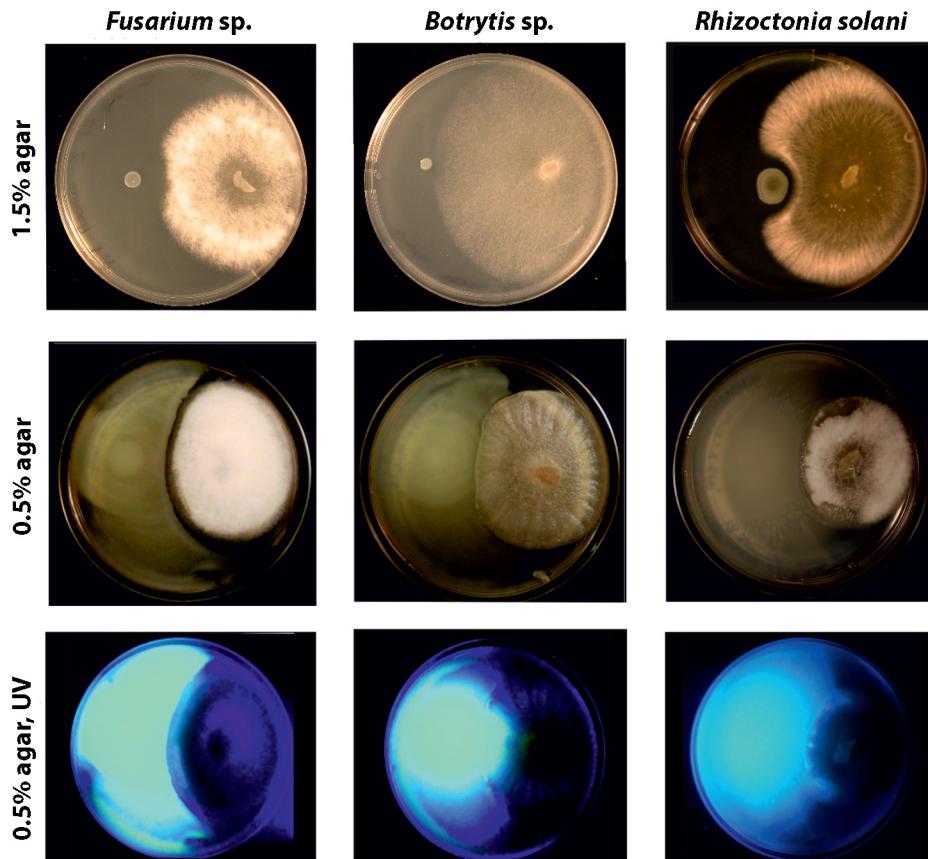


Figure 3. Antifungal properties of swarming (0.5% agar) and non-swarming (1.5% agar) of *Pseudomonas fluorescens* strain X against *Fusarium* sp., *Botrytis* sp. and *Rhizoctonia solani*.

Conclusions

This review has focused on recent research concerning bacterial surface motility as a trait that provides a survival advantage to competitive environments. Furthermore, it is stressing the point that flagella- or type IV pili-driven surface motility appears to provide a competitive advantage to plant pathogenic or biocontrol bacteria for colonization of plant tissues. These motility modalities may be harnessed for beneficial tasks through novel and ecologically safe strategies. Aiming at plant growth and health future challenges should therefore concentrate in exploring the genetic basis of these phenomena placing emphasis on

biocontrol bacteria, to discover appropriate partners for the fungus-driven bacterial dispersal and resolve the importance of microbially produced volatiles in plant protection.

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Received: 13 December 2015; Accepted: 7 January 2016

ΑΡΘΡΟ ΑΝΑΣΚΟΠΗΣΗΣ

Η ομαδική κινητικότητα των βακτηρίων στις επιφάνειες των φυτών

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Περίληψη Το φυτά φιλοξενούν πλήθος βακτηριακών ειδών τα οποία ανταγωνίζονται ή/και συνεργάζονται για την εγκατάστασή τους στο πλέον κατάλληλο, κατά περίπτωση, οικολογικό ενδιαίτημα. Η κινητικότητα, ένα κοινό χαρακτηριστικό των βακτηρίων, εικάζεται ότι παρέχει στους βακτηριακούς πληθυσμούς πλεονεκτήματα επιβίωσης, έναντι άλλων μη-κινητικών, όσον αφορά την εγκατάστασή τους σε ανταγωνιστικά περιβάλλοντα. Η ομαδική κινητικότητα των βακτηρίων σε επιφάνειες (swarming), τύπος κινητικότητας που οφείλεται στην ύπαρξη μαστιγίων, αν και έχει παρατηρηθεί και μελετηθεί σε τεχνητά θρεπτικά υποστρώματα, φαίνεται να αποτελεί βασικό λειτουργικό χαρακτηριστικό των βακτηρίων των φυτών αναφορικά με την ικανότητά τους να αποκινούν και να εξαπλώνονται στον ξενιστή τους. Στο άρθρο αυτό, παραθέτουμε ορισμένες νέες στρατηγικές ομαδικής κινητικότητας των βακτηρίων οι οποίες τους παρέχουν τη δυνατότητα αποκισμού, εξάπλωσης και διαχείρισης της ανταγωνιστικής ικανότητας τους στις επιφάνειες των φυτών.

Hellenic Plant Protection Journal 9: 16-27, 2016
