

## **Fungal Highways : Ecological Bases and Implications**

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*Supervisors : Daniel Job, Prof. Pilar Junier (Laboratory of microbiology, University of Neuchâtel)*

Bacterial dispersal in most soils is greatly limited because of insufficient water for moving. Moreover, as bacteria cannot fly, they cannot cross air-filled pores in soil. This is why bacterial activity in soils is probably limited by the encounters between bacteria and their substrate. The hindered dispersal of soil bacteria could also be involved in the maintenance of the huge prokaryotic diversity in this environment. However, bacteria can migrate along fungal mycelia and reach the substrate otherwise inaccessible. Consequently, this mechanism of “fungal highway” promotes bacterial dispersal in water unsaturated porous media like soils. In this study, three questions are asked about fungal highways: (i) is there a fungal benefit in the interaction?; (ii) how fungal highways promote flagellated bacteria in soil water conditions?; (iii) how the water regime impacts fungal highways?

In chapter 2, different strains of bacteria and fungi are co-inoculated in a Petri dish and the interaction is observed. Results show a widespread ability of flagellated bacteria to migrate on different fungal networks. Fungal highways drastically increase the dispersal of these bacteria in this agar medium. This phenomenon can be explained by purely physical considerations since glass fibers are also efficient dispersal networks for the same bacteria. However, the behavior of *Morchella esculenta* changed in the presence of bacteria.

Actually, sclerotia formation pattern by *M. esculenta* suggests that bacteria can be used as a nutrient pool by the fungus. A large body of experiments (ranging from bacterial population monitoring to stable isotope probing) shows that bacteria are indeed consumed by the fungus. More precisely, bacteria are dispersed, bred, harvested and finally stored by *M. esculenta*. This work thus provides the first example of farming by a fungus in a very sophisticated strategy allowing the fungus to invest in the bacterial pool when the environment is rich and to harvest this pool when the conditions are getting poor.

Chapter 4 tries to unravel the following question: why being flagellated in a waterdepleted environment? Actually, recent studies suggest that, most of the time, flagellar motility is impossible in soil water conditions because the water film is too thin for swimming. However many soil bacteria are flagellated although flagella are energetically costly. This section demonstrates that flagellar motility is not beneficial in term of dispersal and fitness in soil water conditions. However being flagellated allows bacteria to use fungal highways and to disperse much faster than without flagella. Consequently fungal highways make flagellar motility beneficial in term of dispersal and fitness even in water conditions where flagellar motility is otherwise impossible. This section thus provides a new and strong explanation for the maintenance of costly flagella in soil. Moreover these results suggest a dynamic and structured model of bacterial dispersal and ecology in soil.

In the last chapter, the sensitivity of fungal highways to water conditions is investigated. If bacteria really migrate within the liquid film surrounding the hyphae, the dispersal rate on fungal highways should be influenced by water conditions in the medium. Results from chapter 5 suggest that the “efficiency of fungal highways” indeed depends on water unsaturation. It first confirms that bacteria can cross an air-filled pore or a glass beads layer thanks to fungal highways. Besides it shows that the degree of evaporation in the medium strongly impacts the speed of bacterial migration along fungal highways.

This work first sheds light on questions in the literature concerning fungal highways (e.g., the requirement of flagellar motility, the influence of water or the directionality of the bacterial migration). Secondly the bacterial farming by *M. esculenta* provides a surprising example of benefit that fungi can gain from this interaction. Thirdly, as fungal highways allow a rapid and constant dispersal of flagellated bacteria, they explain the maintenance of costly flagella in water unsaturated environments like soils. Consequently this work improves the understanding of fungal highways but most of all suggests many evolutionary bases and consequences of fungal highways for soil bacteria and fungi.