Lysinibacillus fusiformis M5 induces increased complexity in *Bacillus subtilis* 168 colony biofilms via hypoxanthine.

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Abstract

In recent years, biofilms have become a central subject of research in the fields of microbiology, medicine, agriculture, or systems biology amongst others. The sociomicrobiology of multispecies biofilms, however, is still poorly understood. Here, we report a screening system that allowed us to identify soil bacteria, which induce architectural changes in biofilm colonies when cocultured with B. subtilis We identified the soil bacterium Lysinibacillus fusiformis M5 as inducer of wrinkle-formation in B. subtilis colonies mediated by a diffusible signaling molecule. This compound was isolated by bioassay-guided chromatographic fractionation. The elicitor was identified to be the purine hypoxanthine using mass spectrometry and nuclear magnetic resonance (NMR) spectroscopy. We show that the induction of wrinkle formation by hypoxanthine is not dependent on signal recognition by the histidine kinases KinA, KinB, KinC, and KinD, which are generally involved in phosphorylation of the master regulator Spo0A. Likewise, we show that hypoxanthine signaling does not induce the expression of biofilm-matrix related operons epsA-O and tasA-sipW-tapA Finally, we demonstrate that the purine permease PbuO, but not PbuG, is necessary for

hypoxanthine to induce an increase in wrinkle formation of B. subtilis biofilm colonies. Our results suggest that hypoxanthine-stimulated wrinkle development is not due to a direct induction of biofilm-related gene expression, but rather caused by the excess of hypoxanthine within B. subtilis cells, which may lead to cell stress and death.Importance Biofilms are a bacterial lifestyle with high relevance regarding diverse human activities. Biofilms can be favorable, for instance in crop protection. In nature, biofilms are commonly found as multispecies communities displaying complex social behaviors and characteristics. The study of interspecies interactions will thus lead to a better understanding and use of biofilms as they occur outside laboratory conditions. Here, we present a screening method suitable for the identification of multispecies interactions, and showcase L. fusiformis as a soil bacterium that is able to live alongside B. subtilis and modify the architecture of its biofilms.

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Leibniz-HKI-Authors

Robert Barnett

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Sebastian Götze

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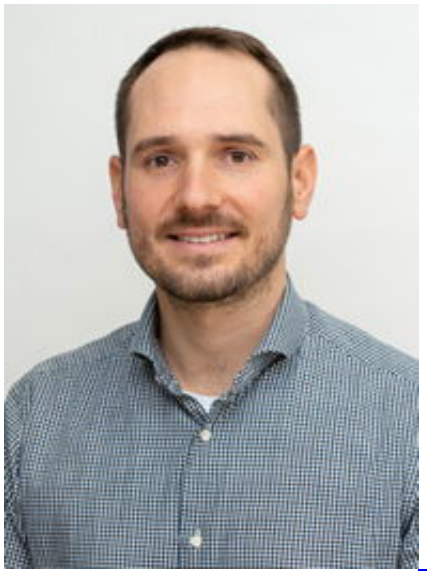

Pierre Stallforth

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