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Complementary cooperation between two syntrophic bacteria in pesticide degradation

Chie Katsuyama [a], Shinji Nakaoka [b,c], Yasuhiro Takeuchi [a], Kanako Tago [d], Masahito Hayatsu [d], Kenji Kato [a,e,*]

[a] *Department of Environment and Energy System, Graduate School of Science and Technology, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan*
[b] *JST ERATO Aihara Complexity Modelling Project, The University of Tokyo, 4-6-1 Komaba, Meguro-ku, Tokyo 153-8505, Japan*
[c] *Graduate School of Mathematical Sciences, The University of Tokyo, 3-8-1 Komaba, Meguro-ku, Tokyo 153-8914, Japan*
[d] *Department of Environmental Science for Human Life, Faculty of Agriculture, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan*
[e] *Department of Geosciences, Faculty of Science, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan*

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ABSTRACT

Interactions between microbial species, including competition and mutualism, influence the abundance and distribution of the related species. For example, metabolic cooperation among multiple bacteria plays a major role in the maintenance of consortia. This study aims to clarify how two bacterial species coexist in a syntrophic association involving the degradation of the pesticide fenitrothion. To elucidate essential mechanisms for maintaining a syntrophic association, we employed a mathematical model based on an experimental study, because experiment cannot elucidate various conditions for two bacterial coexistence. We isolated fenitrothion-degrading *Sphingomonas* sp. TFEE and its metabolite of 3-methyl-4-nitrophenol (3M4N)-degrading *Burkholderia* sp. MN1 from a fenitrothion-treated soil microcosm. Neither bacterium can completely degrade fenitrothion alone, but they can utilize the second intermediate, methylhydroquinone (MHQ). *Burkholderia* sp. MN1 excretes a portion of MHQ during the degradation of 3M4N, from which *Sphingomonas* sp. TFEE carries out degradation to obtain carbon and energy. Based on experimental findings, we developed mathematical models that represent the syntrophic association involving the two bacteria. We found that the two bacteria are characterized by the mutualistic degradation of fenitrothion. Dynamics of two bacteria are determined by the degree of cooperation between two bacteria (i.e., supply of 3M4N by *Sphingomonas* sp. TFEE and excretion of MHQ by *Burkholderia* sp. MN1) and the initial population sizes. The syntrophic association mediates the coexistence of the two bacteria under the possibility of resource competition for MHQ, and robustly facilitates the maintenance of ecosystem function in terms of degrading xenobiotics. Thus, the mathematical analysis and numerical computations based on the experiment indicate the key mechanisms for coexistence of *Sphingomonas* sp. TFEE and *Burkholderia* sp. MN1 in syntrophic association involving fenitrothion degradation.

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1. Introduction

Bacteria distribute everywhere on the Earth, and their biomass is estimated to be equal to or even exceed that of plants (Whitman et al., 1998). In a given system, bacteria exist at a high density, and the community comprises numerous clones (species) and various functional groups (Torsvik et al., 2002; Torsvik and Øvreås, 2002; Gans et al., 2005). Metabolically related bacterial populations occur within a given space. Indeed, some bacterial populations correlate strongly with each other in the expression of function (e.g., Overmann and Schubert, 2002); such an association is regarded as a microbial consortium. The microbial consortia, thus being a fundamental component of an ecosystem, may demarcate biodiversity and ecosystem function.

One of the mechanisms for maintaining microbial consortia is syntrophic association: a process whereby two or more microorganisms cooperate to degrade a substrate or substrates that neither can degrade alone (Madigan et al., 2000; Keller and Surette, 2006). Under the syntrophic association, the fitness of each partner positively depends on the fitness of the other. These microorganisms depend on one another for metabolic products or maintenance of chemically permissive conditions. Syntrophic association have been demonstrated in several ecosystems, for example, interspecies hydrogen transfer in methanogenic

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[*] Corresponding author at: Department of Geosciences, Faculty of Science, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan.
Tel./fax: +81 54 238 4950.
E-mail address: skkato@ipc.shizuoka.ac.jp (K. Kato).

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degradation (Schink, 1997; Hattori, 2008), archaean–bacterium partnerships that link methane oxidation and sulfate-reduction (Valentine, 2002) or denitrification (Raghoebarsing et al., 2006), and xenobiotic degradation (Dejonghe et al., 2003; Smith et al., 2005).

The advantage of studying a xenobiotic-degrading consortium as a model for investigating the role of syntrophic association in microbial communities is that the number of species associated with the degradation of a xenobiotic is relatively small compared with the number involved in degrading a natural organic compound in a given environment. The exposure of soil microbes to xenobiotics commonly leads to a functional shift in the ecosystem associated with the replacement of the dominant bacterial species by those with different traits that confer the ability to degrade the introduced xenobiotics. Thus the introduction of xenobiotics may develop the novel interactions between bacterial species. We are therefore able to establish a simple environment in which to study syntrophic association. It is often the case that more than two species are synergistically involved in the degradation of a xenobiotics by syntrophic association or cross-feeding in a xenobiotic-degrading consortium (Dejonghe et al., 2003; Smith et al., 2005). Although a diverse range of studies have investigated xenobiotics-degrading consortia where syntrophic associations play an important role (Alonso et al., 1997; Dejonghe et al., 2003; Smith et al., 2005), our current understanding of microbial consortia is limited to descriptions of the members and their inherent functions. The manner of the interaction required to maintain a syntrophic association of two or more species in a given metabolic sequence has yet to be elucidated.

In case of intraspecies interaction, various theories have been presented to address the question of how cross-feeding, which is very similar to syntrophic association though it is not necessarily mutualism, evolves in microbial communities. Pfeiffer and Bonhoeffer (2004) showed how stable polymorphisms are maintained by cross-feeding as a consequence of optimization principles. Doebeli (2002) proposed a theory that explains how cross-feeding polymorphisms can emerge from a monomorphism, based on a framework of adaptive dynamics. Many experimental studies have investigated the adaptive diversification of *Escherichia coli* populations (Rosenzweig et al., 1994; Friesen et al., 2004). Rainey and Rainey (2003) showed empirically the evolution of cooperation in bacterial communities via a diversification of morphology. Such cooperative activity might determine the diversity of species in a community. Although these previous studies clearly demonstrate the feasibility of cross-feeding in microbial communities as a consequence of evolution, the emergence and maintenance mechanism of syntrophic association in a microbial consortium has yet to be fully investigated. In case of interspecies interaction, it was shown by mathematical modeling that excretion of intermediate substrate facilitates commensal interactions which enable competitive species to coexist (Bratbak and Thisstad, 1985; Zissi and Lyberatos, 2001; Miki and Yamamura, 2005). The mechanism of mutualistic interspecies interaction to sustain coexistence is scarcely elucidated from the stand point of population dynamics of bacteria constituting a syntrophic association.

In this paper, we report mathematical solution on the sustainable mechanism of the smallest subset of an obligately syntrophic bacterial consortium, consisting of two bacteria: *Sphingomonas* sp. TFEE and *Burkholderia* sp. MN1. These bacteria were isolated from soil microcosms treated with the pesticide fenitrothion [O,O-dimethyl O-(4-nitro-m-tolyl) phosphorothioate]. Although fenitrothion was completely degraded by these bacteria, neither is capable of degrading fenitrothion alone. If syntrophic association of two bacteria occur in the fenitrothion-treated soil, they were able to grow on the intermediate products. It is not practical to carry out long-term experiments of fenitrothion degradation repeatedly and to examine various combinations of conditions. Thus, to compensate those difficulties of experimental microbiology, mathematical analysis is employed to understand the sustainable mechanisms using a representative example of syntrophic association taken from the experiment.

We developed mathematical models that represent the manner of interaction in the syntrophic association of the two bacteria. The intermediate methylhydroquinone (MHQ) is a common resource for *Sphingomonas* sp. TFEE and *Burkholderia* sp. MN1, suggesting the occurrence of exploitative competition for MHQ between these bacteria. The competitive exclusion principle states that a single limiting resource can support only a single competitor (Armstrong and McGehee, 1980; Smith and Waltman, 1994; Grover, 1997). It is notable that *Burkholderia* sp. MN1 excretes MHQ to the surrounding environment. Our study addresses the question of how a syntrophic association mediates the coexistence of two phylogenetically distant bacteria in a given soil under the possibility of exploitative competition for MHQ.

2. Experimental results

2.1. Isolation of the fenitrothion-degrading bacterium TFEE and the 3M4N-degrading bacterium MN1 from soil

Repeated applications of fenitrothion to soil microcosms led to the development of fenitrothion-degrading microbial populations. The number of fenitrothion-degrading bacteria increased from day 42, amounting to 1.2×10^7 colony-forming units (CFU) g^{-1} of dry soil at day 396 (Fig. 1). We successfully isolated predominant two degraders from the treated soil directly. The first degrader, a fenitrothion-degrading bacterium, was designated TFEE. The second degrader, a 3-methyl-4-nitrophenol (3M4N)-degrading bacterium, was designated MN1. The 16S rRNA gene sequence showed TFEE and MN1 was preliminarily identified to be the genera *Sphingomonas* and *Burkholderia*, respectively.

2.2. Degradation of fenitrothion and its metabolites

Both *Sphingomonas* sp. TFEE and *Burkholderia* sp. MN1 lacked the complete pathway of fenitrothion degradation. *Sphingomonas* sp. TFEE degraded fenitrothion to produce an almost stoichiometric amount of 3M4N. However, it did not degrade 3M4N. Thus

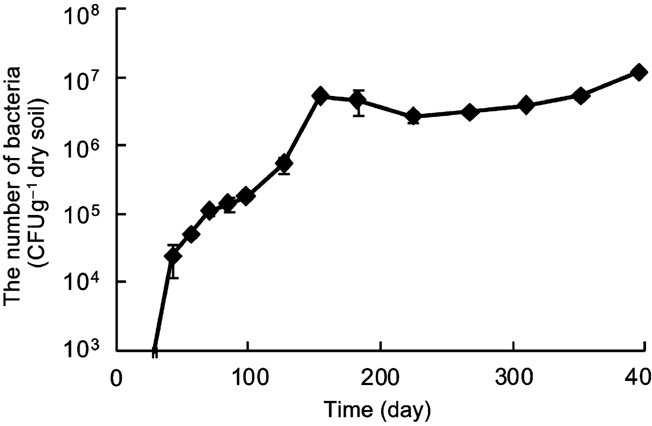

Fig. 1. The number of fenitrothion-degrading bacteria (i.e., *Sphingomonas* sp. TFEE) in the soil microcosm. The data points show the means based on data from triplicate measurements. The initial number of *Sphingomonas* sp. TFEE was below the detection limit (10^3 cells g^{-1}).

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