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COMMENTARY

Syntrophy in microbial fuel cells

Jan Dolfing

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Syntrophy has a pivotal role in the microbial degradation of organic compounds in methanogenic ecosystems (McInerney *et al.*, 2009). Methanogenic degradation of organic compounds is a sequential process: a series of organisms is involved in the various conversion steps of these compounds into methane and carbon dioxide (Dolfing, 1988). Typically, the product of one conversion step is the substrate for the next organism in the chain; each organism lives off the waste product(s) of its predecessor. Their defining characteristic as it relates to syntrophy is that in many of these associations the producer is critically dependent on the activities of the consumer (Schink and Stams, 2006): degradation of short chain volatile fatty acids like propionate and butyrate is only sustainable if the electrons produced in the process are removed by other organisms (Dolfing, 2013). This concept was first put forward by Bryant *et al.* (1967) who famously invoked thermodynamics to rationalize their observation that ethanol degradation could only sustain growth of an ethanol degrader if the hydrogen produced in the process is removed by a hydrogenotrophic methanogen. Since then we have learned that interspecies hydrogen transfer is not the only mechanism to facilitate syntrophy: interspecies formate transfer and direct interspecies electron transfer (DIET) are distinct alternatives to the classical pathway (Stams and Plugge, 2009; Summers *et al.*, 2010). Obviously, the very core value of syntrophy—the *critical* interdependency between producer and consumer—has not been challenged by this changing perspective. That is, until recently. Earlier this year Kimura and Okabe (2013) reported that *Geobacter sulfurreducens* PCA can oxidize acetate in what the authors labelled 'a syntrophic cooperation' with *Hydrogenophaga* sp. strain AR20 in conjunction with an electrode as the final electron acceptor. However, close reading of their paper reveals that *G. sulfurreducens* PCA does not require the presence and activity of strain AR20 to perform this feat: in pure culture *G. sulfurreducens* PCA can also oxidize acetate in conjunction with an electrode as the final electron acceptor; the organism can grow on this reaction, as expected (Bond and Lovley, 2003). Thus *G. sulfurreducens* PCA does not critically depend on its partner, and the association between the two organisms is therefore not syntrophic. For the co-culture to be syntrophic, it would require that *G. sulfurreducens* ceases to be an electrogen, or more precisely ceases to be able to use electrodes as electron acceptor. The data put forward by Kimura and Okabe (2013) provide no evidence that this indeed the case, though they do indicate that *G. sulfurreducens* PCA benefits from the presence of *Hydrogenophaga* sp. strain AR20. It will be interesting to see to what extent the anode potential modulates the interactions between these two electrogens, and it is tempting to speculate that applying the 'optimal' electrode potential may coax the co-culture into syntrophy.

Morris *et al.* (2013) recently noted that in the literature on anaerobic ecosystems syntrophy is traditionally described in detailed mechanistic terms, making explanations of the concept rather wordy. They therefore propose to define syntrophy as 'obligately mutualistic metabolism'. This definition indeed covers the very core value of syntrophy highlighted above—the critical interdependency between producer and consumer—but will not alleviate the need to highlight the (thermodynamic) rational behind this interdependency in anaerobic ecosystems. Interestingly, the host–bacterial mutualism in the human intestine (Bäckhed *et al.*, 2005) and area of much current research (for a recent review, see for example Sommer and Bäckhed, 2013) also seems to fall within the realm of syntrophy.

It is to be expected that the recent eye-openers on DIET and DIET-based syntrophic growth (Summers *et al.*, 2010; Shrestha *et al.*, 2013) will not only lead to more exciting work on this mechanism but will also give new impetus to the traditionally more biochemical and thermodynamical-oriented research on syntrophy via interspecies hydrogen and formate transfer (Stams and Plugge, 2009; Sieber *et al.*, 2012). Surprisingly, little is known about the kinetics behind syntrophic interactions and the interplay between kinetics and thermodynamics (Dolfing and Tiedje, 1986; Dwyer *et al.*, 1988; Stams *et al.*, 2006). Microbial fuel cells are promising tools to tackle those issues, but traditional chemostat studies offer perspective as well, not only for studies on syntrophy but also for studies on other types of interactions like those between acetogenesis and methanogenesis (Lever, 2012; Oren, 2012). Given the long running times needed to obtain comprehensive data sets with chemostat

systems, it seems prudent to start such studies with some modelling work to delineate at which dilution rates insightful results can be expected (Xu *et al.*, 2011; Dolfing and Xu, 2012).

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J Dolfing is at School of Civil Engineering and Geosciences, Newcastle University, Newcastle, UK
E-mail: jan.dolfing@ncl.ac.uk

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