SJSS
SPANISH JOURNAL OF SOIL SCIENCE

Soil “biofilms”: “Bioclusters” would be a much better descriptor

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Received: 12.09.2020 | **Revised:** 05.02.2021 | **Accepted:** 05.02.2021

Comment

Over the last few years, a steadily increasing number of articles have advocated the use of the expression “soil biofilm” to describe the spatial distribution of bacteria, archaea, and their associated exopolymers in soils (e.g., Redmile-Gordon et al. 2014; Kuzyakov and Blagodatskaya 2015; Castorena et al. 2016; Volk et al. 2016; Lerch et al. 2017; Coyte et al. 2017; Carrel et al. 2018; Wilpiszeski et al. 2019; Cai et al. 2019, 2020; Wu et al. 2019; Aufrecht et al. 2019). This usage of a term that previously had not been common at all in the soil science literature has been criticized on the grounds that the concept of a film could be misleading (e.g., Baveye and Darnault 2017; Baveye 2020). The purpose of the present comment is to provide one additional argument in that sense, and more importantly to propose an alternative terminology, which has less of a chance to lead researchers astray.

That soil scientists would find this label of “biofilm” appealing is not entirely surprising. Over the last 4 decades, researchers in a wide array of disciplines have documented the existence of “biofilms” in the systems with which they were dealing (e.g., in water distribution networks, on teeth, in the gut of animals, or on solid surfaces immersed in rivers, lakes, or oceans), and they have extensively studied their characteristics and dynamics (e.g., Block 1992; Block et al. 1993; Flemming and Wingender 2010; Boltz et al. 2017; Flemming and Wuertz 2019). Early on, biofilms were thought to cover surfaces or interfaces uniformly, hence the reference made to the notion of “film.” However, it has since become obvious that in many instances, for a variety of reasons (e.g., hydrodynamics, predation), biofilms are more likely to be patchy than to cover surfaces or interfaces entirely, with no consensus existing at the moment on a minimum size necessary for a group of cells and their surrounding EPS to be labelled as a biofilm (Flemming and Wuertz 2019). Realisation of the fact that, in many situations, the label of “film” was no longer suitable prompted occasionally heated debates, in particular at meetings around the world of so-called “Biofilms club”, during which researchers discussed back and forth about whether or not a transition to another descriptor would be desirable. Eventually, the weight of tradition and a concern about continuity with older literature prevailed, with the upshot that the term “biofilm” continues to be used to this day in many disciplines, a major exception being in the field of dentistry, where researchers and practitioners continue steadfastly to refer to “plaque” instead of biofilm (see, e.g., discussion in Flemming et al. 2021).

DOI: 10.3232/SJSS.2021.V11.N1.01

In the context of soils, the adoption of the term "biofilm" to refer to groups of bacteria, archaea, and their associated exopolymers would present the advantage of establishing an apparent connection with a huge body of literature on the topic outside soil science. From that perspective, various authors (e.g., Kuzyakov and Blagodatskaya 2015) have not hesitated to transfer to soils some of the observations made in other contexts, such as in water distribution networks, where sessile bacteria are routinely observed to adsorb to the inner surfaces of pipes, form colonies, and eventually evolve into true biofilm structures. The problem with assuming that this information is pertinent in soils is that, as pointed out by Baveye and Darnault (2017) and Baveye (2020), biofilms are seldom observed in soils, except in rare circumstances. In the wealth of visual information that has accumulated since the 1950s about the spatial distribution of bacteria and archaea in soils and in fine-textured sand columns (e.g., Clark 1951; Jones and Griffiths 1964; Vandevivere and Baveye 1992b,c; White et al. 1994; DeLeo et al. 1997; Nunan et al. 2001; Li et al. 2003, 2004; Eickhorst and Tipkötter 2008; Raynaud and Nunan 2014; Watteau and Villemin 2018; Baveye et al. 2018; Juyal et al. 2018, 2019, 2020), including at the interfaces between soil and plant roots (e.g., Danhorn and Fuqua 2007; Cardinale 2014; Schmidt et al. 2018), nothing that even vaguely looks like a film, patchy or not, has ever been reported, except in the case of artefactual bacterial growth outside sand columns (e.g., Vandevivere and Baveye 1992a) or when working with porous materials made up of very coarse particles (e.g., 500 µm glass beads). In actual soils, what one finds as a rule are very small, isolated groups of cells sheathed in partially degraded organic matter, extracellular polymeric substances (EPS), and often fine-textured mineral particles (e.g., Foster 1988; Watteau and Villemin 2018).

This last point needs to be emphasized, because it constitutes a clear difference between typical groups of cells in soils, and biofilms found, e.g., in water distribution systems or on teeth. Among the soil minerals of particular significance in that context, clay particles have surfaces that are generally very reactive chemically (e.g., in terms of cation exchange, complexation of metals and trace elements, and sorption of hydrophobic compounds). Based on studies of the adsorption of bacteria to clays and of the co-flocculation of microorganisms and clays in suspensions (e.g., Filip 1973, 1979; Marshall 1980; Stotsky 1985), one would expect that the frequent presence of these minerals in bacterial and archaeal sheaths in soils should in principle have a significant effect on the availability of nutrients to cells, on their growth kinetics, and possibly also on their protection against protozoan predators. This effect, also potentially occurring with fungi (e.g., Davids et al. 2017), is too often ignored, and should be the object of far more research than is the case at the moment, research that one might fear could be hindered if the perspective afforded by "soil biofilms" becomes dominant.

In this general context, it seems questionable at best to promote and try to establish as a new standard, the use of the concept of "soil biofilm". Very little would seem to be gained practically by calling "biofilm" something that, in soils, does not look or behave at all like a film. Even the common argument that adoption of the biofilm terminology enables us to use various tools (e.g., computer models), developed to describe biofilms, is weak, since mathematically identical models can be obtained without adopting the biofilm perspective (Baveye and Valocchi 1989).

Based on this conclusion, I suggested earlier (Baveye 2020) a number of alternative terminologies that would be suitable to describe the spatial distribution of soil bacteria or archaea. A first criterion to be met by these alternatives is that they should not lead to ambiguity. For this reason, the term of "aggregate", which Moshynets and Spiers (2016) recommend as a broader concept including biofilms, would not be ideal in the soil context, since it has been used historically to describe a completely different type of structure: assemblages of soil particles, bound together by organic matter and fungal hyphae (e.g., Vos et al. 2013). The term is also used in connection with either natural or engineered nanoparticles that are occasionally present in soils, in which case it implicitly assumes that a physical aggregation process is operational. The process of physical aggregation does not necessarily fit well with the process of "failure to separate after replication" that arguably accounts better for why bacterial or archaeal cells stick together in soil microenvironments. A second criterion that any new terminology should fulfil is that it should not assume more about the spatial distribution of microorganisms than what we know. Aside from the potentially misleading notion that bacterial or archaeal cells form films when they do not, we should also not assume that local groups of cells have any kind of conformational regularity, a feature that some modelers have associated with the concept of bacterial "microcolony" (e.g., Molz et al. 1986; Baveye and Valocchi 1989). This being said, to facilitate communication, it would be good to have a concise terminology that is less cumbersome than "groups of cells occupying specific microenvironments", one of the possible expressions mentioned by Baveye (2020). A likely candidate that would be vastly more attractive is "clusters", which has already been used so far by several researchers (Van Veen et al. 1994; Pachepsky et al. 2006; Flemming and Wuertz 2019) and could be accompanied by various qualifiers ("cell clusters", "bacterial clusters", archaeal clusters", or "microbial clusters"). To rival in catchiness with the word "biofilm", one could coin the word "biocluster", which does not seem to have been used in that context before, has definite appeal, and meets the criteria set above. In virtually all respects, "soil bioclusters" is preferable to "soil biofilms" and will help to establish the much-needed research on microbial processes in soils on a solid conceptual foundation, free from unwarranted assumptions.

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