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1 **Landmark Papers: No. 7**

2

3 **Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J. & Rey, A.. 2003. Exchange**  
4 **of greenhouse gases between soil and atmosphere: interactions of soil physical factors and**  
5 **biological processes. European Journal of Soil Science, 54, 779–791.**

6

7 Commentary on the impact of Smith et al. (2003): by G. Guggenberger, B. Ludwig & M. Menon

8

9

10 **Introduction**

11 Smith et al. (2003) published their review on the interactions of soil physical factors and  
12 biological processes controlling the exchange of greenhouse gases between soil and atmosphere  
13 at a time when global change was already considered to be one of the most important challenges  
14 of mankind (IPCC, 2001). In the Climate Change 2014 Synthesis Report (IPCC, 2014) a global  
15 warming of 0.7°C between 1951 and 2010 was reported and further warming and long-lasting  
16 changes in all components of the climate systems forecasted. Smith K.A. et al. (2003) and later  
17 Smith P. et al. (2008) emphasized that about one third of CH<sub>4</sub> and two thirds of N<sub>2</sub>O emitted  
18 globally to the atmosphere per year derive from soil processes, while soil is considered a small  
19 CO<sub>2</sub> sink, which may change with increasing warming (Crowther et al., 2016). This is reason  
20 enough to analyse the processes that lead to this net emission of gases to the atmosphere. While  
21 biological processes produce or consume these greenhouse gases, the size of the fluxes is  
22 strongly controlled by soil physical factors. However, the controlling factors on the interaction  
23 between the controlling physical factors and biological processes in the exchange of greenhouse  
24 gases between the soil and atmosphere had not been widely considered. Keith Smith and his  
25 co-authors were pioneering in this field (e.g. Smith, 1980; Ball et al., 1997a, Ball et al., 1997b;

26 Conen et al., 2000; Dobbie & Smith, 2001), which finally led to the review of Smith et al.  
27 (2003).

28

29 Controlling factors for CO<sub>2</sub> emissions

30 Smith et al. (2003) summarized that the release of CO<sub>2</sub> by aerobic respiration can be described  
31 by a non-linear function of temperature over a wide range of water contents. The link between  
32 microbial processes and physical factors, in addition to availability of substrate and chemical  
33 factors (e.g. soil pH), is of substantial importance because of the direct and indirect effects of  
34 physical factors on the production of CO<sub>2</sub> by microorganisms and roots. The non-linear  
35 response of CO<sub>2</sub> as a function of temperature has been confirmed in several recent studies (e.g.  
36 Schaufler et al., 2010). The factors affected by water content that were discussed by Smith et  
37 al. (2003) are also now well established; water is important for gas diffusivity (Ball, 2013) and  
38 substrate supply to soil microorganisms (Schindlbacher et al., 2004). Notably, Schaufler et al.  
39 (2010) reported that maximum CO<sub>2</sub> emissions from European soils under different land uses  
40 occur at intermediate soil moisture, which accords well with the summarizing synthesis by  
41 Smith et al. (2003).

42 Smith et al. (2003) reported a marked scatter of Q<sub>10</sub> values for CO<sub>2</sub> emissions and pointed  
43 out the need for standardization and accurate interpretation of temperature responses of the  
44 soil's CO<sub>2</sub> emissions at greater depths. They emphasized that for accurate determinations and  
45 interpretations of Q<sub>10</sub> values, diurnal temperature changes, thermal conductivities and thermal  
46 diffusivities of the soil need to be considered in greater detail in future studies. In fact, a later  
47 study by Pavelka et al. (2007) also addressed this important issue and recommended  
48 measurement of soil temperature at a very shallow soil depth to determine useable values of  
49 Q<sub>10</sub>, and suggested a procedure to standardize Q<sub>10</sub> values for soil temperatures measured at  
50 different depths.

51

52 Controlling factors for N<sub>2</sub>O emissions

53 For N<sub>2</sub>O, Smith et al. (2003) focused on the important microbiological processes of nitrification  
54 of ammonium and denitrification of nitrate in soil, and the governing processes for the  
55 respective rates. In particular, they elucidated soil conditions, e.g. structure, wetness, O<sub>2</sub> content  
56 of pores and soil depth, being responsible for the release of N<sub>2</sub>O to the atmosphere or further  
57 reduction to N<sub>2</sub>. Nitrate ammonification and nitrifier denitrification as additional processes  
58 leading to the formation of N<sub>2</sub>O have been discussed since in greater detail by Baggs & Phillipot  
59 (2010) and Smith (2017). The merit of the review by Smith et al. (2003) lies again in the  
60 important emphasis of the link between microbial processes and physical factors in addition to  
61 other factors, such as substrate availability and chemical factors such as soil pH (e.g. Weslien  
62 et al., 2009). This link is crucial for an understanding and prognosis of N<sub>2</sub>O emissions.

63 Smith et al. (2003) emphasized that the anaerobic volume is affected by increases in the  
64 water-filled pore space (WFPS), where an increase in WFPS may also result in an exponential  
65 increase in N<sub>2</sub>O emissions. There is still some controversy about which physical soil property  
66 is most useful for estimating N<sub>2</sub>O emissions; for example the ratio of gas diffusivity within the  
67 soil to that in free air, the degree of aggregation and compaction, matric potential, WFPS and  
68 volumetric water content (for a discussion see Ball, 2013 and Smith, 2017). Smith et al. (2003)  
69 indicated that N<sub>2</sub>O emissions also increase markedly with temperature. They attributed this to  
70 increases in the anaerobic volume fraction. An increase in temperature results in an increase in  
71 the size of the anaerobic zones because of increased respiration, which causes larger gradients  
72 in O<sub>2</sub>. In addition, increased temperatures are also likely to lead to increased rates of  
73 denitrification per unit anaerobic volume. Both increases then favour a dramatic increase in  
74 N<sub>2</sub>O emissions. In fact, the concept of anaerobic zones is a key feature of the process-based  
75 DNDC (denitrification-decomposition) model, for which there are several versions for different  
76 land uses. This model has a kinetic scheme for the anaerobic volumetric fraction (an ‘anaerobic  
77 balloon’) that is implemented to calculate the anaerobic fraction of soil in a given soil layer in

78 relation to O<sub>2</sub> diffusion and the respiratory activity of soil micro-organisms and roots (for a  
79 summary of the DNDC model see Gilhespy et al., 2014). Overall, there is no doubt that soil  
80 temperature and soil moisture are important for explaining much of the temporal variation in  
81 N<sub>2</sub>O emissions within a site (e.g. Pilegaard et al. 2006).

82

83 Controlling factors for CH<sub>4</sub> emissions

84 For CH<sub>4</sub> production and transport, Smith et al. (2003) reported that ebullition and diffusion  
85 through the aerenchyma of rice and plants in natural wetlands contribute substantially to the  
86 emission of CH<sub>4</sub> and that the proportion of the emissions taking place by each pathway varies  
87 seasonally.. The oxidation of atmospheric CH<sub>4</sub> to CO<sub>2</sub> is controlled by gas diffusivity, whereas  
88 the effect of temperature is small (Smith et al., 2003). Ball (2013) suggested that the control of  
89 gas diffusivity on the oxidation of CH<sub>4</sub> might not hold for all sites and that the effect of pH,  
90 moisture, temperature, and nitrogen and type of organic matter and content might be  
91 pronounced. The role of nitrogen as a regulatory factor of CH<sub>4</sub> oxidation has been addressed in  
92 detail by Bodelier & Laanbroek (2004), who discussed the inhibiting role of additions of  
93 nitrogenous fertilizer. The effect of WFPS on CH<sub>4</sub> oxidation may be seen as a hump-shaped  
94 function where the optimum oxidation occurs at 20–50% WFPS. At smaller water contents,  
95 desiccation stress and at larger water contents diffusion limitation might be inhibiting CH<sub>4</sub>  
96 oxidation (Dunfield, 2007). Thus, moist, well-aerated soil favours CH<sub>4</sub> oxidation and CO<sub>2</sub>  
97 exchange (Ball, 2013).

98

99 Soil structure, microbial communities and greenhouse gas emissions

100 Smith et al. (2003) emphasized that although the greenhouse gases are produced by microbial  
101 processes, the size of their fluxes between soil and atmosphere depends largely on soil physical  
102 factors. The transport of gases within the soil and the gas exchange between soil and atmosphere  
103 is a function of gas diffusivity, which depends on the air-filled porosity or, inversely, with the

104 WFPS. Most soils develop a three-dimensional architecture with pedogenesis, which is  
105 characterized by the aggregate size distribution. The distribution of aggregates largely controls  
106 almost every process in soil. This refers to the air-filled porosity or WFPS at a given matric  
107 potential (Ball, 2013) as well as to the distribution of microbial populations in soil (Nunan et  
108 al., 2003). Therefore, soil structure controls the habitat of the actors involved in the production  
109 of greenhouse gases and determines the diffusion of O<sub>2</sub> and dissolved organic matter (DOM) to  
110 fuel aerobic microbes. Consequently, inter- and intra-aggregate pore space needs to be  
111 considered. Sey et al. (2008) compared the greenhouse gas emissions from various aggregate  
112 size classes (<0.25 mm, 0.25–2 mm and 2–6 mm) and from 2-mm sieved bulk soil at different  
113 WFPS (20, 40, 80 and 80%). They found that denitrification was responsible for 95% of N<sub>2</sub>O  
114 emissions in microaggregates, whereas nitrification was responsible for 97–99% of N<sub>2</sub>O  
115 production in macroaggregates. This inferred that diffusion of O<sub>2</sub> was largely inhibited in  
116 microaggregates when the WFPS was 80%, whereas macroaggregates maintained aerobic  
117 conditions.

118         The interrelations between soil structure and greenhouse gas emissions can be readily  
119 investigated when the natural soil structure and size distribution of aggregates are disrupted due  
120 to external forces (e.g. compaction), which in turn can alter the pore size distribution and  
121 hydraulic properties (Menon et al., 2015). Beare et al. (2009) showed that the production of  
122 N<sub>2</sub>O was 67 times greater in compacted than uncompacted soil at field moisture contents, and  
123 they demonstrated the effect of soil moisture on emissions of N<sub>2</sub>O and CO<sub>2</sub>. Deurer et al. (2012)  
124 reported enhanced carbon sequestration under the wheel tracks, probably because of reduced  
125 microbial decomposition of organic matter. Bessou et al. (2010) also found that compacted soil  
126 had smaller emissions of CO<sub>2</sub>, but at the same time larger N<sub>2</sub>O emissions by inducing anoxic  
127 conditions favourable for denitrification activity.

128         Experiments with compacted soil also help to elucidate the relation between microbial  
129 communities and greenhouse gas emissions depending on soil physical factors. So Nadian et

130 al. (1998) reported a significant decline in vesicular-arbuscular mycorrhizal fungi biomass at  
131 higher bulk density, and Peacock et al. (2001) found a significant reduction in microbial  
132 biomass for heavy traffic treatments. Schnurr-Pütz et al. (2006) observed that fungi, in  
133 particular, are negatively affected by soil compaction, whereas denitrifiers and methanogens  
134 appear to be more prominent. From that, the links between soil physical properties and  
135 greenhouse gas emissions can be conceptualized as in Fig. 1.

136

137 New developments in linking soil physical factors to biological processes

138 In their landmark paper on the interactions of soil physical factors and biological processes,  
139 Smith et al. (2003) focus on gas diffusivity, which affects soil aeration and the capacity of the  
140 soil microbial community to produce or consume CO<sub>2</sub>, N<sub>2</sub>O and CH<sub>4</sub>. The concept of hotspots  
141 and hot moments (Kuzyakov & Blagodatskaya, 2015) adds the supply of the organic substrates,  
142 which is also linked partly to soil physical factors. Transport of the labile OM sources to the  
143 microbial community occurs largely through biotic activities such as the release of root  
144 exudates (Jones et al. 2004) and the detritus of soil animals (Schrader et al. 2007), but also as  
145 DOM leached from the O and A horizons (Qualls & Haines 1992). Translocation of DOM to  
146 the subsoil depends strongly on the flow paths in soil and on soil structure and precipitation  
147 events (Leinemann et al. 2016). Because DOM is mainly translocated in the inter-aggregate  
148 pore space of the soil, it is retained on aggregate surfaces, which are enriched in OM (Amelung  
149 et al. 2002), thus creating a hotspot. At the same time, the inter-aggregate pore space usually  
150 enables good aeration, leading to the release of CO<sub>2</sub> with microbial decomposition of the  
151 substrate. In otherwise aerobic soil, strong microenvironments may exist that are important  
152 sources of N<sub>2</sub>O and CH<sub>4</sub> (Keiluweit et al. 2016). Hotspots of denitrification and methanogenesis  
153 in the intra-aggregate pore space results from slow diffusion of O<sub>2</sub>, whereas in the rhizosphere  
154 this is caused by the inflow of very available OM from root exudation (Henry et al. 2008). This,  
155 once again, emphasizes the complex interplay of soil physical factors and biological processes

156 in the production of greenhouse gases in soil and their exchange between soil and atmosphere  
157 (Smith et al. 2003).

158

159 Methodological progress

160 The landmark paper of Smith et al. (2003) on these interactions also triggered substantially the  
161 methodological development with respect to the visualization of pores of different size, to  
162 measurement of microbial activity and the resulting O<sub>2</sub> and CO<sub>2</sub> partial pressures at small  
163 scales, and the development of physical and biophysical models. In the last decade much  
164 progress in the understanding of soil structure and the associated pore-space architecture has  
165 been? gained by X-ray computed tomography (CT), which enables an in-situ and real-time 3-  
166 D mapping at scales of a few microns. Measured properties include porosity, pore-size  
167 distribution, tortuosity and topology (Naveed et al. 2013; Vogel et al. 2010). Peth et al. (2014)  
168 showed that synchrotron-based X-ray CT in combination with osmium staining is not only  
169 suitable for describing soil structure, but also for identifying the location of organic matter in  
170 soil, e.g. in the intra-aggregate pore space. Neutron radiography emerged as a useful method to  
171 map the water distribution within soil and its temporal changes (Oswald et al. 2008; Carminati  
172 et al. 2010), whereas the 2-D distribution of oxygen concentration can be analysed by  
173 fluorescence imaging with planar optodes (Blossfeld et al. 2011). Rudolph-Mohr et al. (2017)  
174 emphasized the great potential of combining neutron radiography with fluorescence imaging  
175 to investigate the effect of different soil moisture conditions on the oxygen patterns in soil. Such  
176 analyses may provide important input parameters for geometry-based mechanistic models.

177 Keith Smith also pioneered modelling of microbial respiration and denitrification at the  
178 aggregate scale by systematically incorporating factors such as oxygen supply and nitrogen  
179 concentration (Smith, 1980). Ebrahimi & Or (2015, 2016) have built on that and developed a  
180 3-D pore-scale model that simulates the aerobic and anaerobic microbial communities within  
181 aggregates together with rates of production of N<sub>2</sub>O and CO<sub>2</sub> along the aggregate radius. This



182 model considers substrate and oxygen diffusion processes and is integrated with individual cell-  
183 based models that link soil physical processes with microbial community dynamics. Ebrahimi  
184 & Or (2016) upscaled this modelling framework to quantify depth-resolved rates of production  
185 of CO<sub>2</sub> and N<sub>2</sub>O depending on small-scale environmental conditions. In a very recent model,  
186 this approach was used to quantify methane production in thawing permafrost soil, based on  
187 the microbial activity dynamics in pore networks with? consideration of transport dynamics and  
188 physiological aspects of the cells (Ebrahimi & Orr, 2017).

189

## 190 **Conclusions**

191 Smith and co-authors expressed hope that their review would demonstrate the key roles played  
192 by soil physical factors in controlling the biological processes responsible for the exchange of  
193 greenhouse gases between soil and atmosphere. Indeed, the authors convincingly built a bridge  
194 between soil physics and soil biology. From this landmark publication and some other  
195 manuscripts, soil biophysics has developed as an emerging field within the soil sciences. Inter-  
196 and intra-aggregate pore architecture is decisive in the control of the availability of O<sub>2</sub> and  
197 organic substrates to microorganisms. It is thus of utmost importance not only for the  
198 production of the different greenhouse gases, but also for organic matter stabilization and biotic  
199 redox processes associated with mineral weathering and mineral transformation. The effect of  
200 biota on soil physical factors has also received increasing interest recently. This concerns, for  
201 example, the formation of aggregates by living and dead organic agents, which affects soil  
202 structure and associated pore architecture, or the rhizosphere, where water uptake by the roots  
203 strongly modifies the WFPS. Novel instrumental and modelling approaches will allow an  
204 understanding of the multiple interactions between soil physical and biotic processes in soil in  
205 relation to soil functioning and ecosystem services. This is only possible by crossing the  
206 boundaries in soils science, which is what this landmark paper emphasized.

207

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333 **Figure**

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335 Figure 1. Conceptual model on the link between soil physical properties and greenhouse gas  
336 emission depending on soil compaction (Menon and Blaud, unpublished). Soil compaction  
337 leads to changes in soil structure (e.g. porosity), which will affect the flow of air and water,  
338 and thereby create a more anaerobic environment in soil. This may lead to a shift in the  
339 relative abundance and functions of the microbial population, shown here as effects on the  
340 C and N cycles. Abundance of nitrifiers and aerobic degraders are given by dashed lines and  
341 abundance of denitrifiers and methanogens are given by solid lines.

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