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Introduction

Smith et al. (2003) published their review on the interactions of soil physical factors and biological processes controlling the exchange of greenhouse gases between soil and atmosphere at a time when global change was already considered to be one of the most important challenges of mankind (IPCC, 2001). In the Climate Change 2014 Synthesis Report (IPCC, 2014) a global warming of 0.7°C between 1951 and 2010 was reported and further warming and long-lasting changes in all components of the climate systems forecasted. Smith K.A. et al. (2003) and later Smith P. et al. (2008) emphasized that about one third of CH$_4$ and two thirds of N$_2$O emitted globally to the atmosphere per year derive from soil processes, while soil is considered a small CO$_2$ sink, which may change with increasing warming (Crowther et al., 2016). This is reason enough to analyse the processes that lead to this net emission of gases to the atmosphere. While biological processes produce or consume these greenhouse gases, the size of the fluxes is strongly controlled by soil physical factors. However, the controlling factors on the interaction between the controlling physical factors and biological processes in the exchange of greenhouse gases between the soil and atmosphere had not been widely considered. Keith Smith and his co-authors were pioneering in this field (e.g. Smith, 1980; Ball et al., 1997a, Ball et al., 1997b;
Conen et al., 2000; Dobbie & Smith, 2001), which finally led to the review of Smith et al. (2003).

Controlling factors for CO₂ emissions

Smith et al. (2003) summarized that the release of CO₂ by aerobic respiration can be described by a non-linear function of temperature over a wide range of water contents. The link between microbial processes and physical factors, in addition to availability of substrate and chemical factors (e.g. soil pH), is of substantial importance because of the direct and indirect effects of physical factors on the production of CO₂ by microorganisms and roots. The non-linear response of CO₂ as a function of temperature has been confirmed in several recent studies (e.g. Schaufler et al., 2010). The factors affected by water content that were discussed by Smith et al. (2003) are also now well established; water is important for gas diffusivity (Ball, 2013) and substrate supply to soil microorganisms (Schindlbacher et al., 2004). Notably, Schaufler et al. (2010) reported that maximum CO₂ emissions from European soils under different land uses occur at intermediate soil moisture, which accords well with the summarizing synthesis by Smith et al. (2003).

Smith et al. (2003) reported a marked scatter of Q₁₀ values for CO₂ emissions and pointed out the need for standardization and accurate interpretation of temperature responses of the soil’s CO₂ emissions at greater depths. They emphasized that for accurate determinations and interpretations of Q₁₀ values, diurnal temperature changes, thermal conductivities and thermal diffusivities of the soil need to be considered in greater detail in future studies. In fact, a later study by Pavelka et al. (2007) also addressed this important issue and recommended measurement of soil temperature at a very shallow soil depth to determine useable values of Q₁₀, and suggested a procedure to standardize Q₁₀ values for soil temperatures measured at different depths.
Controlling factors for N$_2$O emissions

For N$_2$O, Smith et al. (2003) focused on the important microbiological processes of nitrification of ammonium and denitrification of nitrate in soil, and the governing processes for the respective rates. In particular, they elucidated soil conditions, e.g. structure, wetness, O$_2$ content of pores and soil depth, being responsible for the release of N$_2$O to the atmosphere or further reduction to N$_2$. Nitrate ammonification and nitrifier denitrification as additional processes leading to the formation of N$_2$O have been discussed since in greater detail by Baggs & Phillipot (2010) and Smith (2017). The merit of the review by Smith et al. (2003) lies again in the important emphasis of the link between microbial processes and physical factors in addition to other factors, such as substrate availability and chemical factors such as soil pH (e.g. Weslien et al., 2009). This link is crucial for an understanding and prognosis of N$_2$O emissions.

Smith et al. (2003) emphasized that the anaerobic volume is affected by increases in the water-filled pore space (WFPS), where an increase in WFPS may also result in an exponential increase in N$_2$O emissions. There is still some controversy about which physical soil property is most useful for estimating N$_2$O emissions; for example the ratio of gas diffusivity within the soil to that in free air, the degree of aggregation and compaction, matric potential, WFPS and volumetric water content (for a discussion see Ball, 2013 and Smith, 2017). Smith et al. (2003) indicated that N$_2$O emissions also increase markedly with temperature. They attributed this to increases in the anaerobic volume fraction. An increase in temperature results in an increase in the size of the anaerobic zones because of increased respiration, which causes larger gradients in O$_2$. In addition, increased temperatures are also likely to lead to increased rates of denitrification per unit anaerobic volume. Both increases then favour a dramatic increase in N$_2$O emissions. In fact, the concept of anaerobic zones is a key feature of the process-based DNDC (denitrification-decomposition) model, for which there are several versions for different land uses. This model has a kinetic scheme for the anaerobic volumetric fraction (an ‘anaerobic balloon’) that is implemented to calculate the anaerobic fraction of soil in a given soil layer in
relation to O₂ diffusion and the respiratory activity of soil micro-organisms and roots (for a summary of the DNDC model see Gilhespy et al., 2014). Overall, there is no doubt that soil temperature and soil moisture are important for explaining much of the temporal variation in N₂O emissions within a site (e.g. Pilegaard et al. 2006).

Controlling factors for CH₄ emissions

For CH₄ production and transport, Smith et al. (2003) reported that ebullition and diffusion through the aerenchyma of rice and plants in natural wetlands contribute substantially to the emission of CH₄ and that the proportion of the emissions taking place by each pathway varies seasonally. The oxidation of atmospheric CH₄ to CO₂ is controlled by gas diffusivity, whereas the effect of temperature is small (Smith et al., 2003). Ball (2013) suggested that the control of gas diffusivity on the oxidation of CH₄ might not hold for all sites and that the effect of pH, moisture, temperature, and nitrogen and type of organic matter and content might be pronounced. The role of nitrogen as a regulatory factor of CH₄ oxidation has been addressed in detail by Bodelier & Laanbroek (2004), who discussed the inhibiting role of additions of nitrogenous fertilizer. The effect of WFPS on CH₄ oxidation may be seen as a hump-shaped function where the optimum oxidation occurs at 20–50% WFPS. At smaller water contents, desiccation stress and at larger water contents diffusion limitation might be inhibiting CH₄ oxidation (Dunfield, 2007). Thus, moist, well-aerated soil favours CH₄ oxidation and CO₂ exchange (Ball, 2013).

Soil structure, microbial communities and greenhouse gas emissions

Smith et al. (2003) emphasized that although the greenhouse gases are produced by microbial processes, the size of their fluxes between soil and atmosphere depends largely on soil physical factors. The transport of gases within the soil and the gas exchange between soil and atmosphere is a function of gas diffusivity, which depends on the air-filled porosity or, inversely, with the
WFPS. Most soils develop a three-dimensional architecture with pedogenesis, which is characterized by the aggregate size distribution. The distribution of aggregates largely controls almost every process in soil. This refers to the air-filled porosity or WFPS at a given matric potential (Ball, 2013) as well as to the distribution of microbial populations in soil (Nunan et al., 2003). Therefore, soil structure controls the habitat of the actors involved in the production of greenhouse gases and determines the diffusion of O$_2$ and dissolved organic matter (DOM) to fuel aerobic microbes. Consequently, inter- and intra-aggregate pore space needs to be considered. Sey et al. (2008) compared the greenhouse gas emissions from various aggregate size classes (<0.25 mm, 0.25–2 mm and 2–6 mm) and from 2-mm sieved bulk soil at different WFPS (20, 40, 80 and 80%). They found that denitrification was responsible for 95% of N$_2$O emissions in microaggregates, whereas nitrification was responsible for 97–99% of N$_2$O production in macroaggregates. This inferred that diffusion of O$_2$ was largely inhibited in microaggregates when the WFPS was 80%, whereas macroaggregates maintained aerobic conditions.

The interrelations between soil structure and greenhouse gas emissions can be readily investigated when the natural soil structure and size distribution of aggregates are disrupted due to external forces (e.g. compaction), which in turn can alter the pore size distribution and hydraulic properties (Menon et al., 2015). Beare et al. (2009) showed that the production of N$_2$O was 67 times greater in compacted than uncompacted soil at field moisture contents, and they demonstrated the effect of soil moisture on emissions of N$_2$O and CO$_2$. Deurer et al. (2012) reported enhanced carbon sequestration under the wheel tracks, probably because of reduced microbial decomposition of organic matter. Bessou et al. (2010) also found that compacted soil had smaller emissions of CO$_2$, but at the same time larger N$_2$O emissions by inducing anoxic conditions favourable for denitrification activity.

Experiments with compacted soil also help to elucidate the relation between microbial communities and greenhouse gas emissions depending on soil physical factors. So Nadian et
al. (1998) reported a significant decline in vesicular-arbuscular mycorrhizal fungi biomass at higher bulk density, and Peacock et al. (2001) found a significant reduction in microbial biomass for heavy traffic treatments. Schnurr-Pütz et al. (2006) observed that fungi, in particular, are negatively affected by soil compaction, whereas denitrifiers and methanogens appear to be more prominent. From that, the links between soil physical properties and greenhouse gas emissions can be conceptualized as in Fig. 1.

New developments in linking soil physical factors to biological processes

In their landmark paper on the interactions of soil physical factors and biological processes, Smith et al. (2003) focus on gas diffusivity, which affects soil aeration and the capacity of the soil microbial community to produce or consume CO₂, N₂O and CH₄. The concept of hotspots and hot moments (Kuzyakov & Blagodatskaya, 2015) adds the supply of the organic substrates, which is also linked partly to soil physical factors. Transport of the labile OM sources to the microbial community occurs largely through biotic activities such as the release of root exudates (Jones et al. 2004) and the detritus of soil animals (Schrader et al. 2007), but also as DOM leached from the O and A horizons (Qualls & Haines 1992). Translocation of DOM to the subsoil depends strongly on the flow paths in soil and on soil structure and precipitation events (Leinemann et al. 2016). Because DOM is mainly translocated in the inter-aggregate pore space of the soil, it is retained on aggregate surfaces, which are enriched in OM (Amelung et al. 2002), thus creating a hotspot. At the same time, the inter-aggregate pore space usually enables good aeration, leading to the release of CO₂ with microbial decomposition of the substrate. In otherwise aerobic soil, strong microenvironments may exist that are important sources of N₂O and CH₄ (Keiluweit et al. 2016). Hotspots of denitrification and methanogenesis in the intra-aggregate pore space results from slow diffusion of O₂, whereas in the rhizosphere this is caused by the inflow of very available OM from root exudation (Henry et al. 2008). This, once again, emphasizes the complex interplay of soil physical factors and biological processes
in the production of greenhouse gases in soil and their exchange between soil and atmosphere (Smith et al. 2003).

Methodological progress

The landmark paper of Smith et al. (2003) on these interactions also triggered substantially the methodological development with respect to the visualization of pores of different size, to measurement of microbial activity and the resulting O\(_2\) and CO\(_2\) partial pressures at small scales, and the development of physical and biophysical models. In the last decade much progress in the understanding of soil structure and the associated pore-space architecture has been gained by X-ray computed tomography (CT), which enables an in-situ and real-time 3-D mapping at scales of a few microns. Measured properties include porosity, pore-size distribution, tortuosity and topology (Naveed et al. 2013; Vogel et al. 2010). Peth et al. (2014) showed that synchrotron-based X-ray CT in combination with osmium staining is not only suitable for describing soil structure, but also for identifying the location of organic matter in soil, e.g. in the intra-aggregate pore space. Neutron radiography emerged as a useful method to map the water distribution within soil and its temporal changes (Oswald et al. 2008; Carminati et al. 2010), whereas the 2-D distribution of oxygen concentration can be analysed by fluorescence imaging with planar optodes (Blossfeld et al. 2011). Rudolph-Mohr et al. (2017) emphasized the great potential of combining neutron radiography with fluorescence imaging to investigate the effect of different soil moisture conditions on the oxygen patterns in soil. Such analyses may provide important input parameters for geometry-based mechanistic models.

Keith Smith also pioneered modelling of microbial respiration and denitrification at the aggregate scale by systematically incorporating factors such as oxygen supply and nitrogen concentration (Smith, 1980). Ebrahimi & Or (2015, 2016) have built on that and developed a 3-D pore-scale model that simulates the aerobic and anaerobic microbial communities within aggregates together with rates of production of N\(_2\)O and CO\(_2\) along the aggregate radius. This
model considers substrate and oxygen diffusion processes and is integrated with individual cell-based models that link soil physical processes with microbial community dynamics. Ebrahimi & Or (2016) upscaled this modelling framework to quantify depth-resolved rates of production of CO₂ and N₂O depending on small-scale environmental conditions. In a very recent model, this approach was used to quantify methane production in thawing permafrost soil, based on the microbial activity dynamics in pore networks with consideration of transport dynamics and physiological aspects of the cells (Ebrahimi & Orr, 2017).

Conclusions

Smith and co-authors expressed hope that their review would demonstrate the key roles played by soil physical factors in controlling the biological processes responsible for the exchange of greenhouse gases between soil and atmosphere. Indeed, the authors convincingly built a bridge between soil physics and soil biology. From this landmark publication and some other manuscripts, soil biophysics has developed as an emerging field within the soil sciences. Inter- and intra-aggregate pore architecture is decisive in the control of the availability of O₂ and organic substrates to microorganisms. It is thus of utmost importance not only for the production of the different greenhouse gases, but also for organic matter stabilization and biotic redox processes associated with mineral weathering and mineral transformation. The effect of biota on soil physical factors has also received increasing interest recently. This concerns, for example, the formation of aggregates by living and dead organic agents, which affects soil structure and associated pore architecture, or the rhizosphere, where water uptake by the roots strongly modifies the WFPS. Novel instrumental and modelling approaches will allow an understanding of the multiple interactions between soil physical and biotic processes in soil in relation to soil functioning and ecosystem services. This is only possible by crossing the boundaries in soils science, which is what this landmark paper emphasized.
References


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