



HAL
open science

Role of microorganisms in the carbon cycling of peatlands

Juanita Mora Gomez, Qian Li, Fabien Leroy, Sébastien Gogo, Fatima Laggoun-Défarge

► **To cite this version:**

Juanita Mora Gomez, Qian Li, Fabien Leroy, Sébastien Gogo, Fatima Laggoun-Défarge. Role of microorganisms in the carbon cycling of peatlands. *Le Studium Multidisciplinary Journal*, 2020, 10.34846/le-studium.193.03.fr.09-2020 . hal-03543830

HAL Id: hal-03543830

<https://hal.science/hal-03543830v1>

Submitted on 9 Feb 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

ROLE OF MICROORGANISMS IN THE CARBON CYCLING OF PEATLANDS

Juanita Mora Gomez^{1,2}, Qian Li¹, Fabien Leroy¹, Sébastien Gogo¹, Fatima Laggoun¹

¹ ISTO, CNRS UMR 7327, Université d'Orléans, BRGM, Orléans, France

² Le Studium Loire Valley Institute for Advanced Studies, Orléans, France

REPORT INFO

Fellow: **Juanita Mora Gómez**
From : Bangor University, UK
Host laboratory in region Centre-Val de Loire: Institut des Sciences de la Terre d'Orléans-ISTO
Host scientist: **Fatima Laggoun, Sébastien Gogo**
Period of residence in region Centre-Val de Loire: 04/2019-09/2020

Keywords :

extracellular enzyme activity, peatlands, peat soil, pore water, soil microbial decomposition

ABSTRACT

Peatlands are key ecosystems in the global carbon balance due in part to the slow microbial degradation of the organic matter (OM) in peat soils. Role of peatlands as powerful carbon storage systems may be threatened by climate change, leading to a potential huge release of greenhouse gases to the atmosphere. Our knowledge on the mechanisms behind the microbial OM degradation is still incomplete, and it is also essential to develop better management strategies and mitigate global change impacts. In the frame of the present fellowship, the microbial extracellular enzymatic mechanisms of the OM degradation in peat soil and pore water were studied in a French altered peatland, assessing changes in soil depth and warming effect during an annual cycle. Additionally, to the research programme, during the present fellowship a new technique for the host laboratory was implemented (protocol to measure extracellular enzyme activities in pore water and peat soil), the fellow participated in several conferences and seminars, three publications were or are in the process of being published, and a new project with the host laboratory is in developing.

1- Introduction

Peatlands are wetlands systems where soils remain temporarily or permanently waterlogged and play a strategic role in the global carbon cycle, as they keep 1/3 of the global carbon stored in the soil. In these systems, dead plant and animal material are decomposed very slowly while primary production is active leading to an accumulation of the organic matter (OM) in the form of peat (Limpens et al. 2008). OM degradation is mainly promoted by microorganisms but environmental constraints, such as low levels of pH and oxygen, slow down the organic material (OM) decomposition (Freeman et al. 2001). In the soil, OM is broken down by Extracellular Enzyme Activities (EEA) produced by microorganisms (Trivedi et al. 2016), and eventually resulting in the

emission of methane (CH₄) and carbon dioxide (CO₂) to the atmosphere (Freeman et al. 2001)

OM degradation in peatlands is sensitive to environmental variations, such as warming and drought (Fenner and Freeman 2011, Hopple et al. 2020), and changes in peatland conditions might generate an acceleration of the OM decomposition and promote greenhouse gas (GHG) production, potentially realising the huge amounts of carbon stored in their soil. Globally, this potentially high GHG emission from peatlands is of great concern hence it may act as a positive feedback sharpening global warming (Davidson and Janssens 2006). Globally, there are still many gaps in our understanding of the mechanisms behind microbial carbon cycling and the degradation of the OM in peat soil. Filling those spaces is

essential to propose mitigation strategies and solve urgent environmental issues, such as the ongoing climate change (Cavicchioli et al. 2019).

Microbial OM degradation in peatlands is shaped by different properties of the ecosystem, such as plant cover (Bragazza et al. 2013), hydrological changes (Fenner et al. 2011), oxygen availability, and variation of pH (Kang et al. 2018) or nutrients. In terms of oxygen availability, it is usually reduced in depth although vascular plants may pump oxygen inside soil through their roots producing peat microhabitats (Rupp et al. 2019). All these aspects interact with the metabolic capabilities of the microbial community dwelling in these environments to determine the OM processing, making difficult to unravel all the mechanisms involved.

In addition to the peat soil, pore water is other important component of peatland and water reaches, in some cases, more than 98% of soil weight. Traditionally, pore water is mainly considered as linked to the system hydrology where nutrients are diluted and transported, but it may also play an active role in the OM processing as some microorganisms might be favoured/harm by pore water recalcitrant conditions. This aspect has been less studied and we know very few about the microbial metabolism occurring in the porewater and potential links to the peat soil activity (Romanowicz et al. 2015). Usually, pore water microbial activity is included in the bulk peat metabolism, but it has not been clarified yet how pore water is contributing to the OM degradation and total carbon cycle in these systems.

In this context, during the *Le Studium* fellowship a research program was developed aimed to improve our understanding of microbial OM metabolism in peatlands, using as ecological model, a site where the host laboratory develops a long-term monitoring. The conducted research program involved an initial set up and standardisation of the experimental protocol for measuring EEA in peat soil and pore water in the host laboratory. It also included two research collaborations that

aimed to i) determine the effect of warming on pore water microbial metabolism (EEA) in disturbed peatlands; and ii) to study the links between microbial metabolism (EEA) in pore water and peat soil at different depths, and in relation to CO₂ production and emission at the La Guette peatland.

2- Experimental details

Study Site

La Guette peatland is a transitional acidic poor fen (pH about 4.5) located in the Centre Val de Loire. Its mean peat thickness is the 80 cm, the mean annual temperature is 6.82 °C and mean annual precipitation 737.19 mm for the period 2009-2020. Hydrology of this peatland is altered due to a road crosses, a pipeline for drinking water supplement, and a ditch for rainfall drainage; the site is now invaded by vascular plants, especially *Molinia caerulea*, *Betula spp.* and *Pinus sylvestris*, at the detriment of *Sphagnum spp.* (Gogo et al., 2011).

Standardisation of Extracellular enzyme activities

Several tests were conducted from June 2019 to August 2019 in order to standardise the experimental conditions for measuring EEA in peat soil and pore water from La Guette peatland. Hydrolases were measured by using MUF-labelled substrates (Glycosynth, Warrington, UK) and oxidases with L-DOPA (Sigma-Aldrich, Saint Louis, MO, USA). Protocol for peat soil was adapted from Dunn et al. (2013), while that for pore water was developed by the fellow based on several other protocols (German et al. 2011, Mora-Gómez et al. 2018). Standardisation consisted in: i) to define the time where linearity is preserve following the enzyme activity along the time; and ii) to define the saturation concentration of the substrate. EEA measured in this study are all part of the OM degradation of plant tissues and are associated to the carbon cycle by the degradation of cellulose (β -1,4-glucosidase), hemicellulose (β -1,4-xylosidase), and lignin-like/phenolic compounds (phenol oxidase). Some of them are related the uptake of nutrient from the soil OM, such as nitrogen (β -1,4-N-acetyl-glucosaminidase that helps to acquire

nitrogenic compounds from chitin derived oligomers), phosphorus (acid phosphatase that mineralizes organic P into phosphate), and sulphur (Arylsulfatase, involved in the acquisition of organic sulphur) (Kang and Freeman 1999, German et al. 2011)

Effect of warming on pore water EEA

EEA in pore water was studied in an experiment developed in the host laboratory as part of Qian Li thesis (Li 2021, Fig.1).

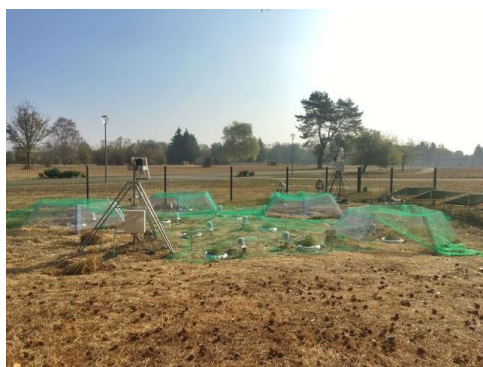


Figure 1. Warming experiment setup at ISTO laboratory campus. Photo Qian Li.

Twelve cylindrical peat monoliths were collected from La Guette peatland in June 2018. They were composed of intact vegetation (mix of dominant plant species in the field *Sphagnum* spp., *Molinia caerulea* and *Erica tetralix*) and undisturbed soil. Mesocosms were placed outside the ISTO laboratory in holes dug into the soil and they were isolated with mineral soil using bubble wrap, and they were randomly separated into two treatments: six with Open-top chambers (OTCs), which can increase air temperature and six without OTCs as control (Fig. 1). The OTCs are transparent polycarbonate hexagons, which are made in accordance with the standardized ITEX system (International Tundra Experiment). The design of OTCs allows it to obtain high solar transmittance of visible wavelength close to the natural state and minimize the transmittance of infrared wave re-emitted (Marion et al. 1997). Before placing mesocosms into the holes dug, three rhizons (Rhizosphere Research Products) for water collection were inserted into each mesocosm. Pore water for EEA measures was collected at each season from September 2019 to May 2020, and activities were measured

following the protocol standardised during the course of this fellowship.

Seasonal variation of pore water and peat metabolism with soil depth at the La Guette peatland

Two soil CO₂ profiles were installed in September 2019 in the La Guette peatland in collaboration with Fabien Leroy, postdoctoral researcher in the host institution. Both profiles were similar with a plant cover dominated by *Molinia caerulea* and *Erica tetralix*. Each profile has four CO₂ probes (GMP343, Vaisala) installed at 0, 10, 20 and 40 cm with sensors measuring the temperature and the soil water content. The data was acquired every hour and stored in acquisition station (CR1000X) powered with solar panel. Three rhizons (0.6 µm) per profile and depth were installed to collect pore water every three months, covering seasonal variation. At each sampling date peat soil was also collected in a nearby site taking care to select a place with similar plant cover than the selected for the profiles. Samples were transported to the laboratory in the ISTO and EEA in peat soil and pore water were measured following the protocol previously developed. Other variables were also measured, dissolved carbon (DOC) and total nitrogen (TN) in pore water with a Shimadzu TOC-5000 analyser, soil respiration (CH₄, CO₂) by modifying method from Li et al. (2021), and soil water content and soil organic matter were measured gravimetrically.

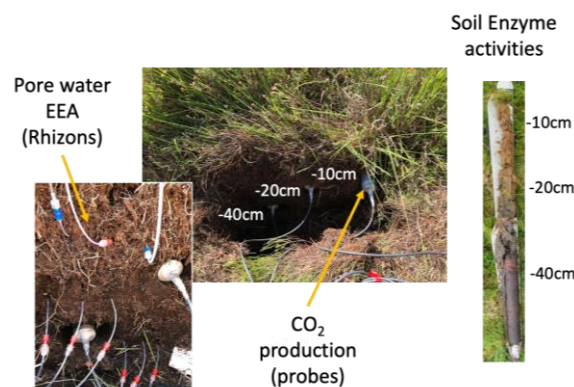


Figure 2. Depth profile installed in La Guette to monitoring EEA in pore water and CO₂ production. In parallel, soil EEA were also measured.

3- Results and discussion

Standardisation of Extracellular enzyme activities:

Defined experimental conditions after standardisation tests to measure EEA in the peat soil and pore water are summarised in table 1.

Table 1. Conditions of the enzymatic essays defined to measure the EEA in pore water and peat soil. PW= pore water.

Enzyme	Cod in text	Incubation time (min)		Substrate concentration (mM)		Function
		PW	Soil	PW	Soil	
β -1,4-glucosidase	B	30	60	0.5	0.5	Yields free glucose. Related to cellulose degradation.
Arylsulfatase	S	30	60	0.5	1	Involved in the acquisition of organic sulphur.
β -1,4-xylosidase	X	30	60	0.5	1	Degrades short xylan chains into xylose. Related to hemicellulose degradation.
β -1,4-N-acetylglucosaminidase	N	30	60	0.5	0.5	Catalyses the hydrolysis chitin derived oligomers
Acid phosphatase	P	30	60	0.5	0.5	Mineralises organic P into phosphate.
Phenol oxidase	PO X	30	10	10	5	Depolymerises lignin-like, phenolic compounds.

Developed protocol was proposed for enzymatic assays with pH and temperature at environmental conditions. Enzyme activity depends on the environmental conditions and the enzymatic potential of the microbial community (Arnosti et al. 2014). Enzymatic essay may be conducted with standard conditions (saturation concentration of the substrate and standard environmental conditions) to estimate the potential enzyme activity of an specific microbial community, but this does not allow us to know the real behaviour at field conditions (Wallenstein et al. 2010, German et al. 2011). I opted to keep substrate saturation to get optimal enzyme activity but using field environmental conditions in pH and temperature. Future studies can explore differences between enzyme activities at both potential and field condition to better allow comparisons with other study sites.

In the same way, there are also contrasting finding on the use of L-DOPA in acidic

environments, such as peatlands (Bach et al. 2013, Wiedermann et al. 2017), due to its auto-oxidation potential and sensitivity to pH. However, it has been proposed that shorth incubation times are a good alternative for using this substrate (Tahvanainen and Haraguchi 2013) and that it is suitable for peat soils (Dunn et al. 2013). Similarly, it has been proposed that L-DOPA essay may give a measure of the oxidative potential of the entire soil matrix more than the oxidative enzyme activity (Bach et al. 2013). Other substrates have been also used in soils and peatlands to measure oxidative enzyme activities, but they are less commonly used and also have technical limitations (Jassey et al. 2012, Bach et al. 2013). Future research is needed to clarify oxidative activity and L-DOPA essays in peat soils.

Effect of warming on pore water EEA:

During the study period, from summer 2019 to spring 2020, warming treatment (OTC chambers) significantly increased soil temperature in a range of 0.55 to 1.31 °C (LMM, $p < 0.03$), mainly at -5 and -15cm in depth (Fig. 3a).

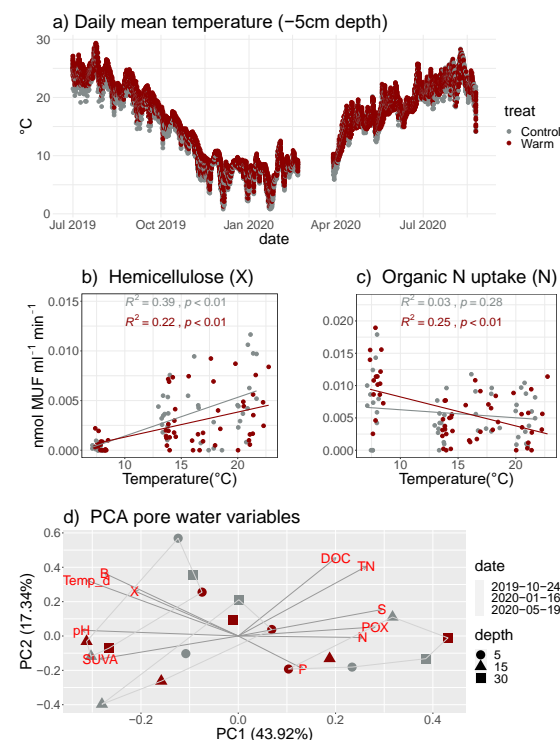


Figure 3. Effects of warming treatment on daily mean soil temperature at 5 cm (a), relationship of some enzyme activity to seasonal temperature

variation (b,c), and principal component analysis-PCA (d) of all pore water measured variables. Enzyme codes as in table 1. TN= total nitrogen, DOC=dissolve organic carbon, Temp_d= daily mean temperature of the sampling day, SUVA= absorbance measurement used to give an estimate of the aromaticity of DOC.

Correspondingly with the slight warming effect observed, we found subtle but significant effect on OM metabolism. The enzyme activities related to hemicellulose (X) and cellulose (B) degradation were reduced in warm mesocosms at the superficial soil (5cm) mainly during summer, spring and autumn (LMM, $p < 0.05$, Fig. 1b). It has been shown that extracellular enzymes are differentially sensitive to temperature depending on the environment (Wallenstein et al. 2010) but usually activity is enhanced with a rise in the temperature inside environmental ranges, what is contrary to the observed effect in X and B. Microbial activity in the pore water might have been influenced by the compounds present in the water such as nitrogen, carbon, nutrients (dissolved and particulate) and the enzymes released from the soil. Both, B and X were the only enzymes positively correlated to annual temperature variation, and also to the SUVA index (Fig. 3c), suggesting these enzymes are activated in the water when there are lower levels of labile carbon in the system. In an experimental study testing the effect of temperature and water table level on OM degradation in peatlands (Dieleman et al. 2016) SUVA index in pore water progressively declined under high water table conditions probably in association with higher plant activity under wetter conditions that potentially release labile sugar to the soil. In our study, the experimental warming with the OTC helped to keep the humidity in the soil during the warmer seasons (Li 2021) what might have stimulated plant growth in the warm mesocosms and the release of labile compounds to the pore water, reducing in turn the two enzymes, B and X that yield to simple polysaccharides.

Contrarily, we also found that the warm treatment increased the uptake of nitrogen from OM compounds associated with chitin degradation (Fig. 3c), mainly in winter. Higher

N mineralization from OM is expected under the warmer treatment as microbial metabolism might be accelerated by a temperature increase and microorganisms need basic elements for growing. Additionally, it has been observed a distinctive increase in temperature sensitivity with decreasing temperature in the N enzyme (Koch et al. 2007), what would explain the warm treatment significant effect for this enzyme principally in winter.

Seasonal variation of pore water and peat metabolism with soil depth at the La Guette peatland

We found significant seasonal variation and changes in depth profile in both pore water and soil enzymes activities (PERMANOVA, $p < 0.05$). However, not all the enzyme responded in similar manner to environmental fluctuations and while pore water activities varied in higher proportion with seasonal variation, activity in the soil was more affected by changes in depth (Fig. 4).

Seasonally, EEA might be affected but changes in water table depth, temperature, and plant metabolism (Romanowicz et al. 2015). In pore water, degradation of lignin-like (POX) and cellulose (B) compounds seasonally varied with the temperature increase through seasons, while phosphorus (P), nitrogen (N), and sulphur (S) mineralisation were not related to temperature changes (Fig. 4a). Similarly, nitrogen and phosphorus mineralisation in soil were not affected by seasonal temperature changes, as well as lignin-like compounds degradation (Fig. 4b). Some EEA also varied with depth in both soil and pore water, with general higher values at superficial soil, supporting the common funding of a more active layer in the first 10 cm of the peat soil (e.g. Bobuřká et al. 2015). Nevertheless, sulphur and phosphate mineralisation in pore water, and lignin-like compounds degradation in the soil, did not vary among depths.

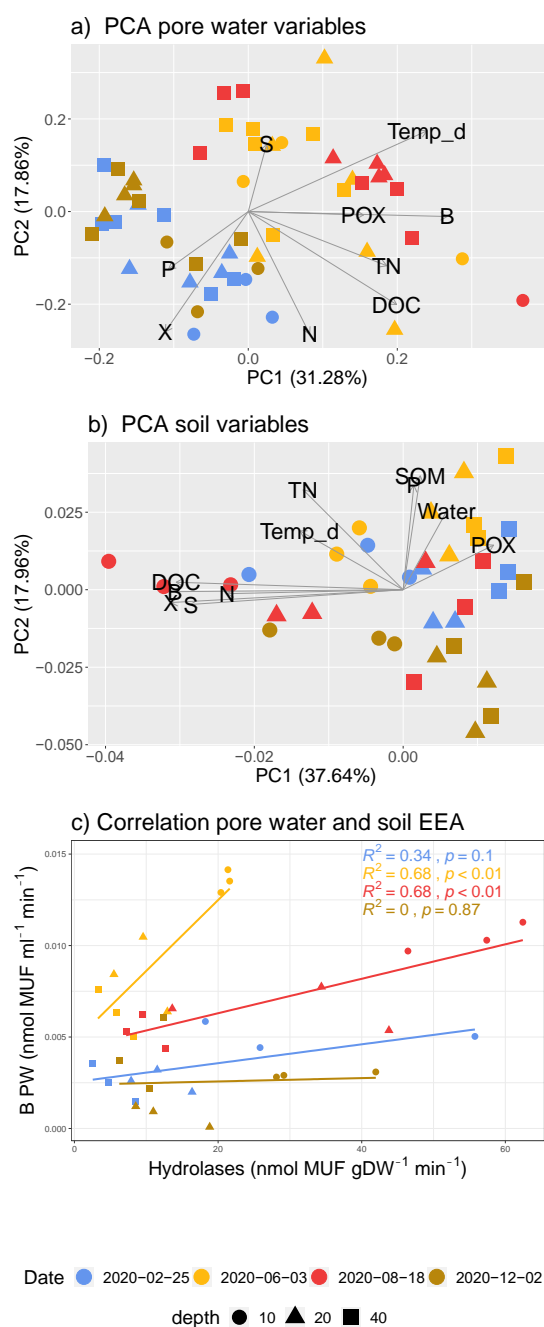


Figure 4. EEA and some environmental variables measured in pore water (a) and peat soil (b) at different soil depth and during an annual cycle (2020) in the La Guette peatland. Also, correlation between pore water and soil EEA (c) is presented. Enzyme codes as in table 1. TN= total nitrogen, DOC=dissolve organic carbon, Temp_d= daily mean temperature of the sampling day.

Processes in the soil and water were linked mainly through the DOC concentration in the pore water. Hydrolases (B,X,S,N) in the soil, except for P uptake, were positively correlated to cellulose and lignin-like compounds

degradation in the water (e.g. Fig. 4c), and all these enzymes, both in soil and pore water, were in turn also significantly correlated to the DOC concentration in the pore water (Fig. 4a,b). DOC values in pore water is usually a measure of the OM decomposition in the soil (Dieleman et al. 2016) and higher concentration reflects active OM degradation, this was confirmed in our study for soil enzyme activities. However, DOC for microbial metabolisms in the pore water might have been more related to the carbon availability for microbial consumption, that in our study, they were mainly cellulose and lignin derived degradation compounds.

Additionally, CO₂ production was measured in field and laboratory and data are currently being analysed.

4- Conclusion

OM decomposition is one of the crucial processes controlling carbon storage capacity in peatlands but mechanisms behind microbial processes involved are still not clear. The research programme carried out in the frame of the present fellowship tried to shed some light on the microbial EEA in two compartments of the peatland ecosystem, the pore water and peat soil. Our results showed a different but complementary role of the two compartments. Some EEA in pore water showed to be highly sensitive to even small temperature changes and they were linked to, but not mirrored, the microbial metabolisms in the soil. On its side, EAAs in the peat soil were more sensitive to soil depth variations, and potentially influenced EAAs in the pore water through the releasing of carbon compounds to the water as product of the soil OM degradation. Future research is needed in order to better understand regulators of EEA in the pore water and quantify its impact on the total carbon balance.

5- Perspectives of future collaborations with the host laboratory

Collaboration with the host laboratory is still active. The researcher started a new project during her fellowship on the effect of microplastics in the microbial carbon cycle of wetlands, in collaboration with other institutions. i.e. Bangor University (UK),

National University of Colombia, and Yugra University (Russia); and she is currently developing the project thanks to the Labex-Voltaire's funding support.

6- Articles published in the framework of the fellowship

It is expected to publish at least one article as part of the experimental work conducted in the host laboratory, which is currently in preparation. Additionally, the fellow collaborated in a book chapter and submitted an article on the same research topic in the framework of her Le Studium fellowship. Summary of publications is showed below:

- Qin L, Kang H, Freeman C, Mora-Gómez J, Jiang M. 2020. Chapter 10: Environmental Change and Microbial Contributions to Carbon Cycle Feedbacks. In: Jürgen Marxsen (ed). *Climate Change and Microbial Ecology: Current Research and Future Trends (Second Edition)*. Caister Academic Press. Pages: 297-326. DOI: <https://doi.org/10.21775/9781913652579.10>
- Mora-Gómez J, M. Alajmi F.E, Vargas J.O, O Kang H, Golyshin P, Freeman C. Regional and Local Constrains of Microbial Organic Matter Degradation in Moss-Dominated Peatlands. Submitted to ISME journal.
- Mora-Gómez J, Li Q, Leroy F, Gogo S, Laggoun F. Microbial organic matter degradation in pore water and soil in a French peatland: seasonal changes and responses to global warming. In prep.

Similarly, the fellow participated in one conference, one workshop, and gave two talks on her research in the regional laboratories during the fellowship. Also, she collaborated with several researchers in the host laboratory and tutored one undergraduate student. Summary of the oral communications is showed below:

- Climate, air quality, and health: long-term goals and near-term actions. June 28, 2019. Auditorium Jean Zay - Canopé Orléans, France. Mora-Gomez

J. Quantification of greenhouse gases (GHG).

- Workshop Knowledge's frontiers in water unsaturated hydrogeosystems: interface dynamics, heterogeneities & couplings. 27-28 June, 2019. ISTO, Orléans, France. Laggoun F, Gogo S, Guimbaud C, Perdereau L, Jacotot A, Ait Mansour EH, Leroy F, Mora-Gomez J, Savoie F, Chevrier S, Chalumeau G. Platform for gases Exchange at the 'Soil - Atmosphere' interface in peatlands (PESat)
- December 5, 2019. Mora-Gomez J. Microorganisms and climate change: a critical piece in the global environmental puzzle. Le Studium Thursdays. Hôtel Dupanloup, Orléans, France.

7- Acknowledgements

The fellow thanks Elodie Machado, Adrien Jacotot and Jean Sebastien Moquet for their help in the field and LE STUDIUM, Loire Valley Institute for Advanced Studies, Orléans & Tours, France. Funding was supported by the project "GHG Exchange between Soils and the Atmosphere in peatland – PESat", in the framework of the ARD 2020 PIVOTS Programme).

8- References

- Arnosti, C., C. Bell, D. L. Moorhead, R. L. Sinsabaugh, A. D. Steen, M. Stromberger, M. Wallenstein, and M. N. Weintraub. 2014. Extracellular enzymes in terrestrial, freshwater, and marine environments: Perspectives on system variability and common research needs. *Biogeochemistry* 117:5–21.
- Bach, C. E., D. D. Warnock, D. J. Van Horn, M. N. Weintraub, R. L. Sinsabaugh, S. D. Allison, and D. P. German. 2013. Measuring phenol oxidase and peroxidase activities with pyrogallol, l-DOPA, and ABTS: Effect of assay conditions and soil type. *Soil Biology and Biochemistry* 67:183–191.
- Bobušká, L., D. Fazekašová, and L. Angelovičová. 2015. Vertical Profiles of

- Soil Properties and Microbial Activities in Peatbog Soils in Slovakia. *Environmental Processes* 2:411–418.
- Bragazza, L., J. Parisod, A. Buttler, and R. D. Bardgett. 2013. Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nature Climate Change* 3:273–277.
- Davidson, E. a, and I. a Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–73.
- Dieleman, C. M., Z. Lindo, J. W. McLaughlin, A. E. Craig, and B. A. Branfireun. 2016. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry* 128:385–396.
- Dunn, C., T. G. Jones, A. Girard, and C. Freeman. 2013. Methodologies for Extracellular Enzyme Assays from Wetland Soils. *Wetlands* 34:9–17.
- Fenner, N., and C. Freeman. 2011. Drought-induced carbon loss in peatlands. *Nature Geoscience* 4:895–900.
- Fenner, N., R. Williams, H. Toberman, S. Hughes, B. Reynolds, and C. Freeman. 2011. Decomposition “hotspots” in a rewetted peatland: Implications for water quality and carbon cycling. *Hydrobiologia* 674:51–66.
- Freeman, C., N. Ostle, and H. Kang. 2001. An enzymic “latch” on a global carbon store. *Nature* 409:149.
- German, D. P., M. N. Weintraub, A. S. Grandy, C. L. Lauber, Z. L. Rinkes, and S. D. Allison. 2011. Optimization of hydrolytic and oxidative enzyme methods for ecosystem studies. *Soil Biology and Biochemistry* 43:1387–1397.
- Hopple, A. M., R. M. Wilson, M. Kolton, C. A. Zalman, J. P. Chanton, J. Kostka, P. J. Hanson, J. K. Keller, and S. D. Bridgham. 2020. Massive peatland carbon banks vulnerable to rising temperatures. *Nature Communications* 11:4–10.
- Jassey, V. E. J., G. Chiapusio, D. Gilbert, M. L. Toussaint, and P. Binet. 2012. Phenoloxidase and peroxidase activities in Sphagnum-dominated peatland in a warming climate. *Soil Biology and Biochemistry* 46:49–52.
- Kang, H., and C. Freeman. 1999. Phosphatase and arylsulphatase activities in wetland soils: Annual variation and controlling factors. *Soil Biology and Biochemistry* 31:449–454.
- Kang, H., M. J. Kwon, S. Kim, S. Lee, T. G. Jones, A. C. Johncock, A. Haraguchi, and C. Freeman. 2018. Biologically driven DOC release from peatlands during recovery from acidification. *Nature Communications* 9:1–7.
- Koch, O., D. Tscherko, and E. Kandeler. 2007. Temperature sensitivity of microbial respiration, nitrogen mineralization, and potential soil enzyme activities in organic alpine soils. *Global Biogeochemical Cycles* 21:1–11.
- Li, Q. 2021. Effet du réchauffement climatique sur le cycle du carbone dans les tourbières - approche expérimentale. Université d’Orléans.
- Li, Q., F. Leroy, R. Zocatelli, S. Gogo, A. Jacotot, C. Guimbaud, and F. Laggoun-Déforge. 2021. Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change. *Soil Biology and Biochemistry* 153.
- Limpens, J., F. Berendse, C. Blodau, J. G. Canadell, C. Freeman, J. Holden, N. Roulet, H. Rydin, and G. Schaepman-Strub. 2008. Peatlands and the carbon cycle: from local processes to global implications - a synthesis. *Biogeosciences* 5:1475–1491.
- Mora-Gómez, J., S. Duarte, F. Cássio, C. Pascoal, and A. M. Romaní. 2018. Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. *Science of The Total Environment* 621:486–496.
- Romanowicz, K. J., E. S. Kane, L. R. Potvin, A. L. Daniels, R. K. Kolka, and E. A. Lilleskov. 2015. Understanding drivers of peatland extracellular enzyme activity in the PEATcosm experiment: mixed

evidence for enzymic latch hypothesis.
Plant and Soil 397:371–386.

- Rupp, D., E. S. Kane, C. Dieleman, J. K. Keller, and M. Turetsky. 2019. Plant functional group effects on peat carbon cycling in a boreal rich fen. *Biogeochemistry* 144:305–327.
- Tahvanainen, T., and A. Haraguchi. 2013. Effect of pH on phenol oxidase activity on decaying Sphagnum mosses. *European Journal of Soil Biology* 54:41–47.
- Trivedi, P., M. Delgado-Baquerizo, C. Trivedi, H. Hu, I. C. Anderson, T. C. Jeffries, J. Zhou, and B. K. Singh. 2016. Microbial regulation of the soil carbon cycle: Evidence from gene-enzyme relationships. *ISME Journal* 10:2593–2604.
- Wallenstein, M., S. D. Allison, J. Ernakovich, J. M. Steinweg, and R. Sinsabaugh. 2010. Controls on the Temperature Sensitivity of Soil Enzymes: A Key Driver of In Situ Enzyme Activity Rates. Pages 245–258 *in* G. Shukla and A. Varma, editors. *Soil Enzymology*. Springer, Berlin, Heidelberg.
- Wiedermann, M. M., E. S. Kane, T. J. Veverica, and E. A. Lilleskov. 2017. Are colorimetric assays appropriate for measuring phenol oxidase activity in peat soils? *Soil Biology and Biochemistry* 105:108–110.

