Effect of climate warming on the carbon cycle of peatlands : experimental approach

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Résumé

1. Contexte scientifique et objectifs

Les tourbières sont les principaux écosystèmes terrestres de stockage du carbone (C) dans le monde. En effet, malgré leur faible superficie, représentant 3 à 4 % de la surface globale de la terre, elles renferment environ 30 % du stock global de C des sols. Cette forte capacité de stockage du C est principalement due aux conditions environnementales spécifiques de ces milieux, telles que la basse température, l'engorgement en eau et l'acidité, qui limitent la décomposition microbienne et favorisent l'accumulation de matière organique (MO). De plus, la végétation caractéristique (*Sphagnum* spp.) joue un rôle important dans la formation et l'extension des tourbières boréales. Elles peuvent libérer des protons (H^+) qui conduisent à un environnement oligotrophique et acide. De plus, leur litière contient des composés phénoliques résistants à la décomposition, ce qui contribue également à la faible vitesse de décomposition. En outre, les sphaignes ont la capacité de maintenir une teneur en eau élevée grâce au transport et à la rétention de l'eau par capillarité, créant ainsi des conditions anaérobies défavorables à une activité microbienne, tout au moins aérobie. En tant que tels, ces facteurs entraînent un bilan positif entre la production primaire nette, bien que faible, et la décomposition, permettant aux tourbières d'agir comme un puit de C important. A l'échelle globale, plus de 85 % des tourbières à sphaignes se trouvent dans les régions sub-boréales de l'hémisphère nord, où la température moyenne annuelle est basse et la saturation en eau du sol est importante.

Le cycle du C dans les tourbières comprend l'absorption du CO_2 par l'activité photosynthétique - production primaire brute (GPP) par la végétation de la surface terrestre ; les rejets de CO_2 des tourbières se font par la respiration de l'écosystème (ER; la somme de la respiration hétérotrophe et autotrophe) ; l'émission de CH_4 et le lessivage du carbone organique dissous (COD) souterrain. Les processus du cycle du carbone dans les tourbières sont contrôlés par de nombreux facteurs biotiques et abiotiques tels que la température, qui est un paramètre influençant directement de nombreuses réactions biochimiques dans les tourbières ainsi que le taux d'évapotranspiration de la tourbe superficielle. Le niveau de la nappe d'eau phréatique (WTD) joue également un rôle important en définissant les deux zones du sol (aérobie = acrotelme et anaérobie = catotelme), ce qui a un impact sur la disponibilité en oxygène (O_2) et donc sur les processus microbiens. De plus, la composition de la communauté végétale peut

affecter les processus de décomposition en modifiant la qualité de substrats liés à la composition de leurs litières et aussi aux de par les exsudats racinaires.

Outre ces facteurs (biotiques et abiotiques) intrinsèquement liés à l'écosystème 'tourbière', le changement climatique (notamment la hausse de température et changement des précipitations) pourrait modifier les processus du cycle du C et donc modifier significativement le stockage du C par les tourbières en les transformant en un système source émetteur de C. Si cet écosystème est perturbé par le réchauffement climatique, il peut potentiellement libérer de fortes quantités de CO_2 et de CH_4 dans l'atmosphère, qui, par l'enclenchement d'une boucle de rétroaction positive, peut aggraver à son tour le réchauffement climatique. Il est donc crucial de comprendre la rétroaction des tourbières sur l'atmosphère dans le contexte du réchauffement climatique mondial.

Depuis l'ère préindustrielle, les émissions anthropiques de gaz à effet de serre (GES) dans l'atmosphère provenant notamment des combustibles fossiles ont entraîné une augmentation significative des concentrations de CO_2, de CH_4 et d'oxyde nitreux (N_2O) qui amplifient l'effet de serre. En conséquence de la présence massive de GES dans l'atmosphère, on a estimé une augmentation de la température à la surface globale du globe au cours du 21ème siècle. Celle-ci devrait passer de 1 à 3,7 °C d'ici la fin du 21ème siècle (2081-2100) par rapport à la période entre 1986-2005. En particulier, il est à noter que l'augmentation de la température dans les régions subarctiques où se trouvent principalement les tourbières à sphaignes sera plus rapide que dans les autres régions. Ce qui est plus important encore, c'est que les rétroactions positives ou négatives de ces écosystèmes n'ont pas encore été prises en compte dans les modèles climatiques globaux.

Comme évoqué précédemment, la température contrôle de nombreux processus métaboliques liés à la photosynthèse, la respiration et l'émission de CH_4, ce qui en fait un régulateur clé des processus du cycle du carbone. Le réchauffement climatique pourrait modifier les processus microbiens dans le sol et/ou les activités physiologiques des plantes et conduire ainsi à une modification des flux de CO_2 et de CH_4 entre les tourbières et l'atmosphère et/ou de l'exportation du COD. Les résultats d'études précédentes ont montré que l'augmentation de la température induit généralement une augmentation de la fixation du CO_2 de l'atmosphère par photosynthèse. Mais parallèlement, elle pourrait aggraver les émissions de ER et de CH_4 vers l'atmosphère. De plus, le réchauffement pourrait augmenter les concentrations de COD dans l'eau interstitielle en augmentant l'activité enzymatique extracellulaire microbienne et l'apport de la végétation via les exsudats racinaires. La température influence également la

structure et l'abondance de la végétation en surface. Le réchauffement favorise la croissance des plantes vasculaires (arbustes ou graminées) mais diminue l'abondance des bryophytes et des lichens. La présence de plantes vasculaires augmente à la fois l'absorption de C par la photosynthèse et la décomposition par l'apport d'exsudats racinaires labiles et de litières facilement biodégradables. Ainsi, le bilan net de C et la réaction des tourbières au changement climatique demeurent jusque-là un sujet débattu, car la réaction de cet écosystème au réchauffement a varié en fonction de leur état initial, de la composition de la végétation et du régime climatique. En outre, la plupart des recherches se sont concentrées sur les tourbières subarctiques de l'hémisphère nord, où se trouvent la majorité des tourbières et où le réchauffement climatique devrait être plus important. Il est toujours incertain de savoir comment les tourbières tempérées réagissent au réchauffement climatique, en particulier celles situées à basse altitude qui ont subi d'importantes pressions en raison de nombreuses activités anthropiques passées.

Ainsi, afin d'estimer le fonctionnement d'une tourbière à sphaignes tempérée qui a été envahie par des plantes vasculaires sous l'effet conjugué du réchauffement climatique et d'une modification de son fonctionnement hydrologique, nous avons mené une expérience en mésocosme via un système de réchauffement expérimental et une autre expérience d'incubation. L'objectif était d'étudier l'effet de ce réchauffement climatique simulé sur les processus du cycle du C et d'évaluer les facteurs clés qui contrôlent ces processus. Plus précisément, en soumettant les mésocosmes à deux traitements thermiques: 1) température ambiante (contrôle) et 2) réchauffement modéré par un dispositif de chambres à toit ouvert (Open Top Chambers, OTCs), nous avons cherché à déterminer l'effet du réchauffement sur les flux de C gazeux à l'interface écosystème-atmosphère et la dynamique du carbone organique dissous dans les compartiments souterrains de la tourbe. La deuxième expérience qui a consisté en une incubation en laboratoire d'échantillons de tourbe présentant différents niveaux de dégradation avait pour objectif d'évaluer l'effet interactif de la température, de la disponibilité en O_2 et de la qualité du substrat sur la respiration du sol

2. Effet du réchauffement simulé par les OTCs sur les paramètres environnementaux et les communautés végétales

Les chambres à toit ouvert à réchauffement passif (ou open top chambers; OTCs), largement utilisées dans des études précédentes, ont été appliquées ici à des mésocosmes de

tourbe de 40 cm d'épaisseur et 30 cm de diamètre. Différents paramètres ont été suivis dans les placettes OTCs (6 repliquats) et les placettes témoin (6 repliquats) pendant deux années (2018 à 2020): la température de l'air, la température du sol à différentes profondeurs (5, 15 et 30 cm), la teneur en eau de la tourbe en surface, la composition de la végétation et la chimie de l'eau interstitielle souterraine (pH et conductivité).

Le monitoring montre que la température moyenne de l'air est de 0,9 °C plus élevée dans les placettes OTCs que dans les placettes témoins (14,91 ± 0,14 contre 14,01 ± 0,07 °C). A l'exception des périodes hivernales, l'amplitude thermique est plus élevée dans les placettes OTCs à comparer aux témoins en raison de l'augmentation de la température maximale. La température du sol à 5 cm a été augmentée de 1,35 °C par les OTCs. La température moyenne journalière du sol à 5 cm a été augmentée par les OTCs tout au long de l'année, et une augmentation de la température maximale et minimale journalière a été observée. La température du sol à 15 cm a été augmentée de 0,92 °C, tandis qu'à 30 cm, elle n'a pas été affectée de manière significative par les OTCs. L'effet des OTCs sur la température du sol à 15 et 30 cm a montré une forte dépendance saisonnière. Une augmentation significative de la température moyenne, maximale et minimale journalière du sol à 15 et 30 cm a été observée en automne et en hiver, tandis qu'aucun effet n'a été constaté au printemps et en été. À 5 cm, la teneur en eau de la tourbe est presque à saturation en dehors de la saison de végétation, alors qu'elle diminue pendant cette saison de végétation. Elle est plus élevée dans les placettes OTCs que dans les placettes témoins pendant la saison de végétation. Ceci peut être dû au fait que les OTCs constituent un abri au vent et réduiraient ainsi l'évapotranspiration. Durant l'expérimentation, les communautés végétales n'ont pas été impacté significative par les OTCs, tandis que les graminoïdes et les éricacées montre une tendance à une augmentation dans les mésocosmes OTCS comparé à ceux des témoins. En mai 2019, on a constaté une augmentation significative du nombre de feuilles de graminoïdes dans les placettes OTCs par rapport aux placettes témoins, ce qui indique une croissance plus rapide des graminoïdes sous traitement de réchauffement. Le pH mesuré aux 3 profondeurs n'a pas été affecté de manière significative par le traitement de réchauffement. La conductivité à 5 et 15 cm a montré des valeurs plus faibles en début de saison de végétation sous OTCs, ce qui pourrait être causé par une absorption plus élevée des nutriments par les graminoïdes davantage présents dans ces mésocosmes.

3. Flux de CO_2 et de CH_4 et bilan de C sous l'effet du réchauffement simulé

Les flux de CO_2 (GPP: Gross Primary Production et ER: Ecosystem Respiration) et de CH_4 des mésocosmes dans les placettes contrôle et les placettes OTCs ont été suivis pendant 2 ans. Les résultats montrent qu'une amélioration des GPP, des ER et des NEE a été observée, alors qu'elle ne s'est produite qu'au début ou à la fin de la saison de végétation, aucun effet de réchauffement n'a été constaté au pic de la saison de végétation. Au début de la saison de croissance, l'augmentation de ces flux semble en partie liée à la croissance plus rapide des graminoïdes sous le traitement de réchauffement. Une augmentation temporaire de l'émission de CH_4 correspondant à la baisse initiale de la WTD a été constatée. Cela est probablement dû au taux de transport plus élevé du CH_4 stocké en condition aérobie. Le fort effet des OTCs sur l'émission de CH_4 n'a été observé que lorsque la WTD a fortement diminué, ce qui suggère que l'émission de CH_4 était davantage régulée par les interactions entre la température et la WTD que par la seule température. La sensibilité à la température (Q_{10}) des flux de GPP, de ER et de l'émission de CH_4 ont tous diminué en réponse au réchauffement. Ainsi, bien qu'une augmentation des flux de C gazeux ait été observée dans notre étude, la rétroaction des tourbières à l'atmosphère sous l'augmentation de la température à long terme doit être considérée avec prudence. En raison de la sensibilité à la température des flux de C a diminué sous l'effet du réchauffement, l'augmentation des flux de C par le réchauffement peut être surestimée.

Afin d'évaluer la rétroaction des tourbières à l'atmosphère sous l'effet du réchauffement, nous avons estimé le bilan annuel de C gazeux en construisant des modèles des flux de CO_2 et de CH_4. Pour construire ces modèles, les flux de GPP, de ER et de CH_4 mesurés ont été mis en relation avec les facteurs biotiques et abiotiques par des régressions linéaires ou non linéaires. Ainsi, grâce au suivi à haute fréquence de ces facteurs, les flux de C ont pu être calculés pour obtenir un ensemble des données temporelles très détaillées. Les modèles intégrant la température ainsi que l'effet de la WTD et de la végétation ont été les plus performants pour reproduire les valeurs mesurées. Par conséquent, les modèles sélectionnés avec une bonne représentativité des valeurs mesurées ont été utilisés pour calculer les flux annuels de C et le bilan de C dans les deux traitements (OTC et témoin).

La GPP annuelle modélisée a été sensiblement augmentée par le réchauffement expérimental, avec une absorption de -602,03 ± 73,27 contre -501,39±70,44 gC m^{-2} y^{-1} dans les placettes témoins. L'augmentation de la GPP est expliquée par une biomasse aérienne plus importante (en particulier les graminoïdes et les éricacées arbustives) sous l'effet du réchauffement. En outre, elle est également liée à la GPP plus élevée des sphaignes avec une plus forte teneur en eau les placettes OTCs en été, car les OTCs constituent un abri contre le vent et réduisent donc l'évapotranspiration. Le réchauffement expérimental n'a montré aucune différence significative sur la RE (499,89 ± 102,42 et 614,84 ± 171,16 gC m^{-2} y^{-1} dans le cadre du contrôle et du traitement OTCs respectivement) et les émissions de CH_4 (15,56 ± 4,60 et 21,10 ± 8,54 gC m^{-2} y^{-1} dans le cadre du contrôle et du traitement OTCs respectivement). L'échange net de C gazeux des mésocosmes n'a pas été significativement affecté par le traitement de réchauffement, avec une émission de 14,06 ± 82,02 et 33,91 ± 136,86 gC m^{-2} y^{-1} respectivement sous contrôle et sous traitement OTCs. La contribution des émissions de CH_4 aux flux totaux de C ne représente que 0,9 à 2,2 %. La source de C était donc principalement déterminée par le rejet net de CO_2. Cependant, le potentiel de réchauffement climatique du CH_4 étant 34 fois supérieur à celui du CO_2, ce qui montre une tendance à la hausse lors du l'effet du réchauffement simulé (699,92 ± 321,14 contre 1003,40 ± 622,84 g eq CO_2 m^{-2} y^{-1} dans les placettes de contrôle et de OTCs, respectivement). Ces résultats soulignent que les différents composants impliqué dans les échanges gazeux de C de C gazeux ont réagi rapidement au réchauffement modéré, même si l'échange net de C reste, sur ce court terme, stable.

4. Dynamique du carbone organique dissous (COD) sous l'effet du réchauffement

Afin d'examiner l'effet du réchauffement sur la dynamique du COD, la quantité et la qualité de COD à 3 profondeurs (5, 15 et 30 cm) correspondant à la litière, rhizosphère des plantes vasculaires et zone/profondeur en dehors de la rhizosphère ont été mesurées. Dans l'ensemble, la concentration et la qualité du COD à ces 3 profondeurs n'ont pas été affectées par l'augmentation de la température du sol à 5 et 15 cm. Cependant, un effet significatif de la profondeur a été observé sur les variations saisonnières de la concentration en COD. La concentration du COD à 5 cm, qui se trouve dans la zone de la litière de sphaignes, a montré une tendance saisonnière claire avec une relation positive avec la température. La décomposition de la litière de sphaignes favorisée par la température et la faible WTD induisant une activité phénol-oxydase plus élevée a contribué à la concentration plus élevée de COD en

été par rapport à l'hiver. Cependant, à 15 cm, elle a progressivement diminué suite à l'abaissement de la WTD. Cela peut être attribué à la diminution de la productivité des graminoïdes et donc des exsudats racinaires en conditions sèches. La concentration de COD à 30 cm a montré une tendance similaire à 15 cm.

En outre, la qualité du COD varie en fonction de la profondeur. Le COD à 5 et 15 cm contenait plus de composés fraîchement labiles en raison de l'apport des plantes alors qu'à 30 cm, il y avait plus de composés récalcitrants. Un degré d'humification plus faible a été constaté pendant la saison de croissance. Cela pourrait être lié au fait que les GPP étaient plus élevées pendant cette période et donc que le C était plus labile en raison de l'apport de la végétation. Notre étude a souligné que l'interaction plantes-sol joue un rôle important dans la détermination de la dynamique du pool de COD. Ainsi, le changement potentiel de la composition des plantes et de la température élevée et la sécheresse qui l'accompagne à long terme peuvent conduire à un changement de la chimie du COD souterrain, avec des implications sur les processus du cycle du C dans le cadre du réchauffement climatique.

5. Effets conjugués de la température, de la disponibilité en O_2 et de la qualité du substrat sur la respiration du sol

La respiration du sol est un important flux de dioxyde de carbone (CO_2) des tourbières vers l'atmosphère. Elle est largement contrôlée par des facteurs abiotiques : la température, l'humidité du sol et la disponibilité de l'O_2. Elle est également déterminée par la qualité du substrat en termes de proportion de composés C labiles ou complexes. Ainsi, nous avons effectué une incubation de courte durée de la tourbe provenant de différentes profondeurs pour examiner la respiration du sol dans diverses conditions environnementales. Des échantillons de tourbe ont été prélevés dans des couches de 5 à 10 cm et de 35 à 40 cm et incubés à 7 températures différentes dans des conditions aérobies et anaérobies. Nos résultats montrent que la température, la disponibilité de l'O_2, la qualité du substrat et leurs interactions ont toutes un effet significatif sur la respiration du sol. Une température élevée a un effet positif sur le taux de respiration du sol en favorisant l'activité respiratoire microbienne (taux de production de CO_2/gramme de biomasse microbienne), alors qu'il existe un seuil de température entre 24 et 28 °C. Les conditions aérobies renforcent la respiration du sol et leur effet dépend de la température. La tourbe plus décomposée dans la couche de 35-40 cm a montré un taux de production de CO_2 plus faible en raison d'une quantité plus faible de carbone labile tout comme

d'une biomasse microbienne plus faible. Cependant sa sensibilité à la température (Q_{10}) était plus élevée que celle de la tourbe plus labile de la couche 5-10 cm en condition aérobie (2,20 ± 0,01 contre 1,93 ± 0,26 respectivement). Nos résultats montrent que la combinaison d'une température plus élevée et d'une augmentation de la fréquence des sécheresses stimulerait la respiration du sol, en particulier la couche souterraine avec une tourbe plus décomposée qui n'est distante que de 40 cm de la surface. Cette stimulation pourrait augmenter l'émission de CO_2 et donc accroître la possibilité d'une rétroaction positive de cet écosystème sur l'atmosphère. Ainsi, il paraît important de prendre en compte l'hétérogénéité verticale du Q_{10} afin d'améliorer l'estimation de la production de CO_2 dans les profils de tourbe.

I. ***Introduction and objectives***

I.1 Peatlands and their functions

I.1.1 Peatlands and their distribution in the world

Peatlands are wetlands, which have accumulated large quantities of carbon (C) underground. They are defined as terrestrial ecosystems with at least 30 cm depth of peat layer (Joosten and Clarke, 2002). Peat is the deposit of incompletely decomposed plant and animal constituents that has formed in place (Rydin and Jeglum, 2013). It is defined as soils consist of at least 30 % organic matters (Joosten and Clarke, 2002). Peatlands have stored around 543-612 Pg (Peta gram = 10^{15} g, or equivalent to Gigatonne) of C, representing about 30 % of global terrestrial C, in only 3-4 % of the Earth's land surface (Jackson et al., 2017; Yu et al., 2010; Yu, 2012). The accumulation of organic matter (OM) is due to the imbalance between the net primary production and the decomposition (Bragazza et al., 2009), allowing the peatlands to act as C sink. The typical environmental conditions, such as low temperature, waterlogging and acidity, limit the microbial decomposition and thus promote the OM accumulation. The vertical structure of peatlands is composed of two layers: acrotelm and catotelm. The OM is first accumulated in acrotelm, which is the upper temporarily aerobic layer above the deepest water table depth (WTD). In acrotelm, the decomposition is rapid and 90% of OM from photosynthetic origin would be degraded by microbes here (Clymo and Fogg, 1984). The catotelm corresponds to the anaerobic layer permanently saturated with water, where the decomposition is low and most of OM stored here is recalcitrant.

Depending on the dominant water supply, peatlands can be classified as two types: fens and bogs. Fens are said to be minerotrophic as they receive water from surroundings. Thus such sites are relatively rich in minerals or nutrients compared to bogs. However, bogs are ombrotrophic as these peatlands are isolated from their surroundings and the only source of water is from precipitation. As a result, they are nutrient-poor and acidic.

Peatlands can be found throughout the world from tropics to poles (Craft, 2016; Maltby and Proctor, 1996), occupying about 4 millions km^2 area in the world (Vitt, 2013). Due to the specific environmental conditions required for their development, as water-saturation, they are mostly found in areas where precipitation exceeds water losses by evapotranspiration (van Breemen, 1995), such as at north high latitudes, moist oceanic environments (Taylor, 1983), or humid mountainous regions (Cooper et al., 2012; Darlington, 1943). Majority of the earth's peatlands exist in the sub boreal regions of the northern hemisphere (more than 85 %; Fig I-1).

Tropical peatlands including mangroves and palm swamps account for around 11% of the peatland area. They are mainly located in lowland areas of Southeast Asia, especially Indonesia, and in the Amazon basin (Ellison, 2004; Lähteenoja et al., 2009; Morley, 1981; Page et al., 2011). Southern hemisphere has less temperate and boreal peatlands than in the northern hemisphere, mostly occurring in Patagonia and Tierra del Fuego with rare occurrences in Australia and islands outside the Antarctic Circle (McGlone, 2002; Yu et al., 2010).

Around 89 % of the peatlands C were estimated to be stored in northern peatlands. Tropical peatlands are estimated to contain 8% and southern hemisphere (not tropical) peatlands contain for 2% (Yu et al., 2010). However, some studies suggest that the C stock in tropical peatlands may constitute up to 19% of the global peatlands C stock (Page et al., 2011). Although boreal peatlands store more C in total, tropical peatlands have more C stored per unit of surface (Donato et al., 2011).

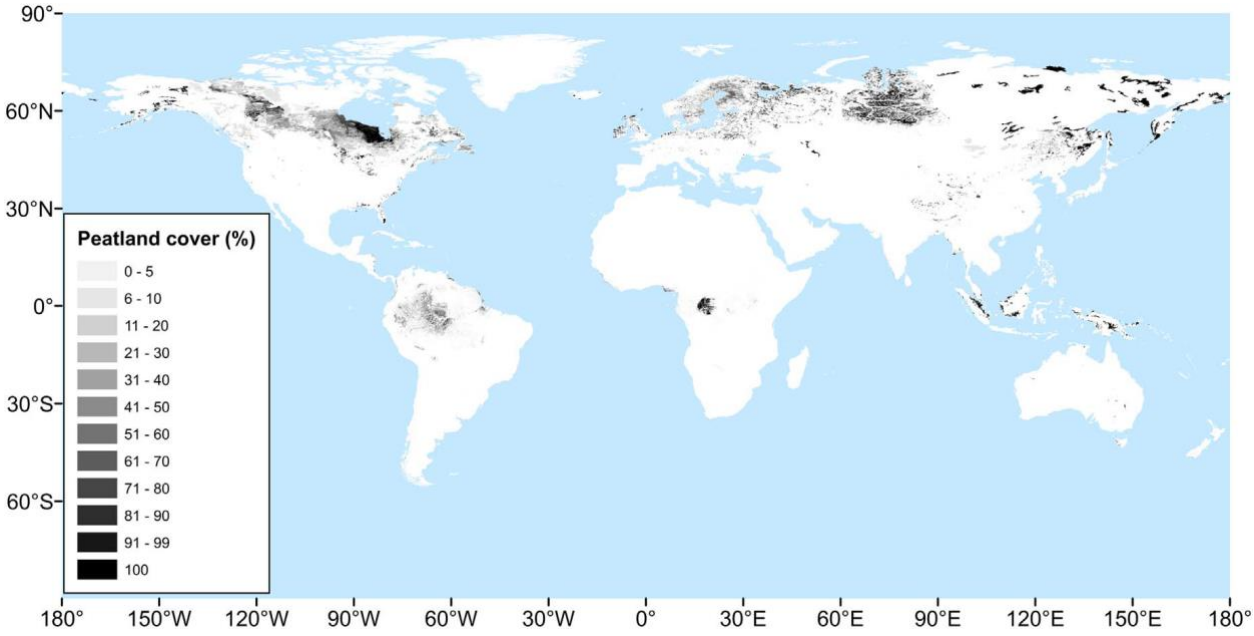

Figure I-1 Global estimation of the peatlands cover and their distribution (Xu et al., 2018).

I.1.2 The peatland engineer species: the *Sphagnum*

The development and the special features of many temperate and boreal peatlands originate from their vegetation - the peat mosses, especially the genus *Sphagnum*, which is regarded to be the builder of peatlands.

The vegetation of peatlands is mainly composed of 4 types of plants corresponding to 4 functional types (Rydin and Jeglum, 2013):

1) **Bryophytes:** including peat mosses, brown mosses, liverworts and feathermosses. They are dominant in many boreal and temperate peatlands. In particular, the genus *Sphagnum* plays an important role in the construction of peatlands.

2) **Graminoids** including grasses (Poaceae) and other plant groups with a grass-like morphology, such as sedges (*Carex spp.*), cotton grasses (*Eriophorum spp.*) and other Cyperaceae, rushes (Juncaceae), *Scheuchzeria palustris*. Some species of sedges (e.g. *Carex lasiocarpa*) and grasses (e.g. *Molinia caerulea*) covered large areas in fen. While the diversity of graminoids is generally low in *Sphagnum*-dominated peatlands, especially bogs (Rydin and Jeglum, 2013).

3) **Shrubs:** evergreen dwarf shrubs exist in many bogs (wooded bogs and hummocky parts of open bogs) and some fen, for example, *Erica tetralix* and *Calluna vulgaris*.

4) **Trees:** density is low in boreal region, while increases in temperate, subtropical, and tropical peatlands.

The important role of genus *Sphagnum* in the formation and extension of boreal peatlands results from its special characteristics. *Sphagnum* have the capacity to capture mineral cations (e.g. K^+, Ca^{2+}, and NH_4^+) and release protons (H^+) which lead to an oligotrophic and acidic environment. Meanwhile, its abilities of water transporting by capillary and water storage maintain the high water content thus create anoxic conditions (Rydin and Jeglum, 2013; Stalheim et al., 2009). All these conditions made by *Sphagnum* are harsh for other plants growth, but not to themselves, as they are adapted and tolerate such environment. The water-saturation, acidic and anoxic environment reduce the microbial decomposition and results in the OM sequestration. In addition, *Sphagnum* contains phenolic compounds, which make its litter resistant to decay, which also contributes to the low decomposition rate in this ecosystem. Consequently, the peat layer gradually builds up (Dorrepaal et al., 2005; Freeman et al., 2001).

I.1.3 C cycle in peatlands

As mentioned above, the C accumulation of peatlands is caused by the imbalance between the C uptake and the C release (Bragazza et al., 2009). Thus, to estimate the function of peatlands, it is essential to understand the processes involved in the C cycle as well as the control upon them.

The inputs of C from atmosphere to peatlands occur through the photosynthetic pathway - gross primary production (GPP) by aboveground vegetation (Fig I-2), and C is stored in living biomass and dead remains. The C releases from peatlands are through (i) ecosystem respiration (ER; the sum of heterotrophic and autotrophic respiration) under the form of CO_2 (Fig I-2), and (ii) CH_4 emission (net of CH_4 production by archaebacterial and CH_4 oxidation); (iii) belowground dissolved organic carbon (DOC) leaching.

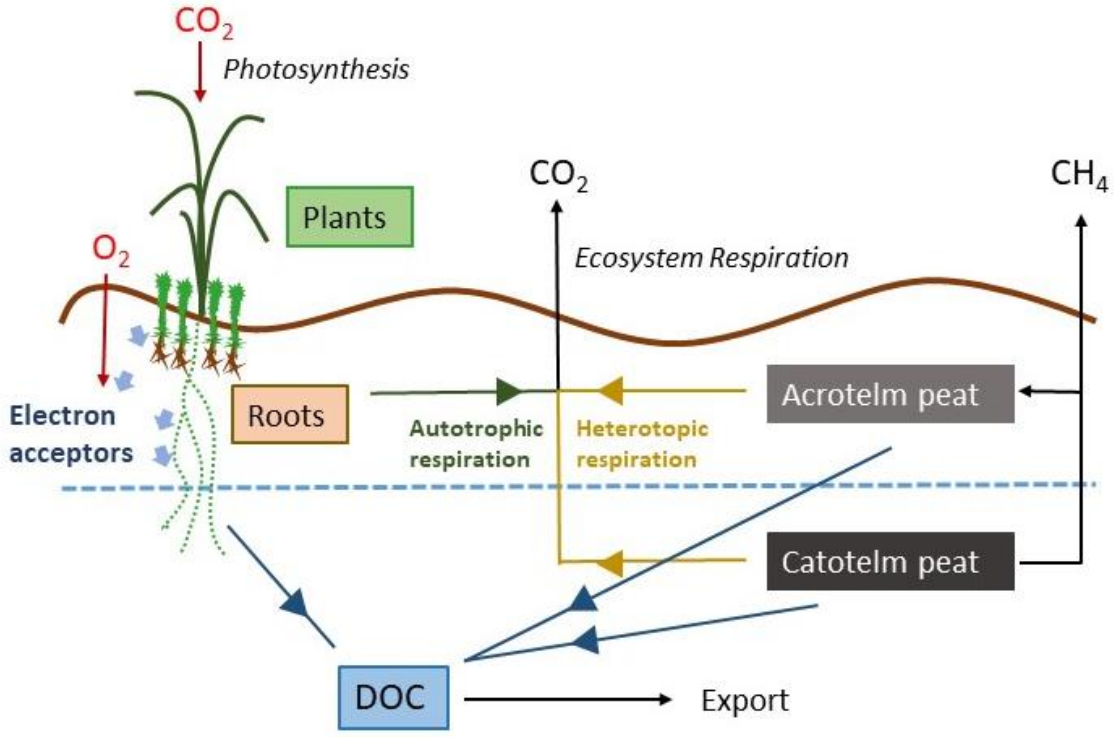

Figure I-2 Carbon cycle and biogeochemical processes in peatlands (modified from Limpens et al., 2008; Moore et al., 1998).

C cycle processes in peatlands are controlled by numerous biotic and abiotic factors (Fig. I-3). On local scale, the C cycle processes are regulated by WTD, organic matter (OM) quality, physicochemical properties of peat, hydrology condition and vegetation. The WTD which defines the boundary of aerobic/anaerobic layer influences the soil respiration and CH_4 production through controlling oxygen (O_2) availability (Blodau et al., 2004). Low WTD could increase the aerobic layer where CO_2 production is higher because of the higher efficiency of microbial degradation with O_2 supply (Moore and Dalva, 1993; Yavitt et al., 1997). However, its effect on CH_4 emission is opposite because CH_4 production occurs in strictly anaerobic condition (Fetzer et al., 1993; Heikkinen et al., 2002). OM quality in terms of degradability, which depends on the properties of precursors (Johnson and Damman, 1991) and degradation

level (Fierer et al., 2005), determined the decomposition rate. OM in peatlands consists of diverse compounds with different molecular weight: labile compounds with low molecular weight and simple structure (such as carbohydrates, amino acids and fatty acids) and more recalcitrant compounds with high molecular weight and complex structure (such as phenolic, lignin and fulvic acids; Fenner et al., 2001; Kalbitz et al., 2003). Poor-quality OM with high proportion of complex C compounds decomposes slowly, thus resulting in lower CO_2 production, while it was reported to be more sensitive to temperature change (Conant et al., 2008; Davidson and Janssens, 2006). In addition, OM quality also regulates the decomposition processes by controlling microbial community structure and diversity (Laggoun-Défarge et al., 2008). A decline of fungi biomass with peat depth was found, and the microbial community structure is strongly related to the peat organic chemistry (Sjögersten et al., 2016). Chemical properties of peat such as pH plays an important role as it can indirectly impact the decomposition processes by influencing the microbial activities and community composition (Criquet et al., 1999). Physical properties of peat, e.g. density, is another controlling factor, for example, it can affect the release of CH_4 to atmosphere by controlling the transfer of gases, as CH_4 emission depends on both production rate, transportation and oxidation (Limpens et al., 2008). Furthermore, vegetation community structure and composition strongly influence the C cycling processes. It has been reported that the presence of vascular plants in *Sphagnum*-dominated peatlands significantly enhanced GPP compared with only *Sphagnum* (1273 vs. 414 g C m^{-2} y^{-1} respectively; Leroy et al., 2019). Moreover, belowground OM pool of peatlands could be altered with plant community change. For example, the vascular plants release roots exudates thus input more labile OM, and the priming effect of these labile OM can stimulate the microbial decomposition processes (Basiliko et al., 2012; Leroy et al., 2017).

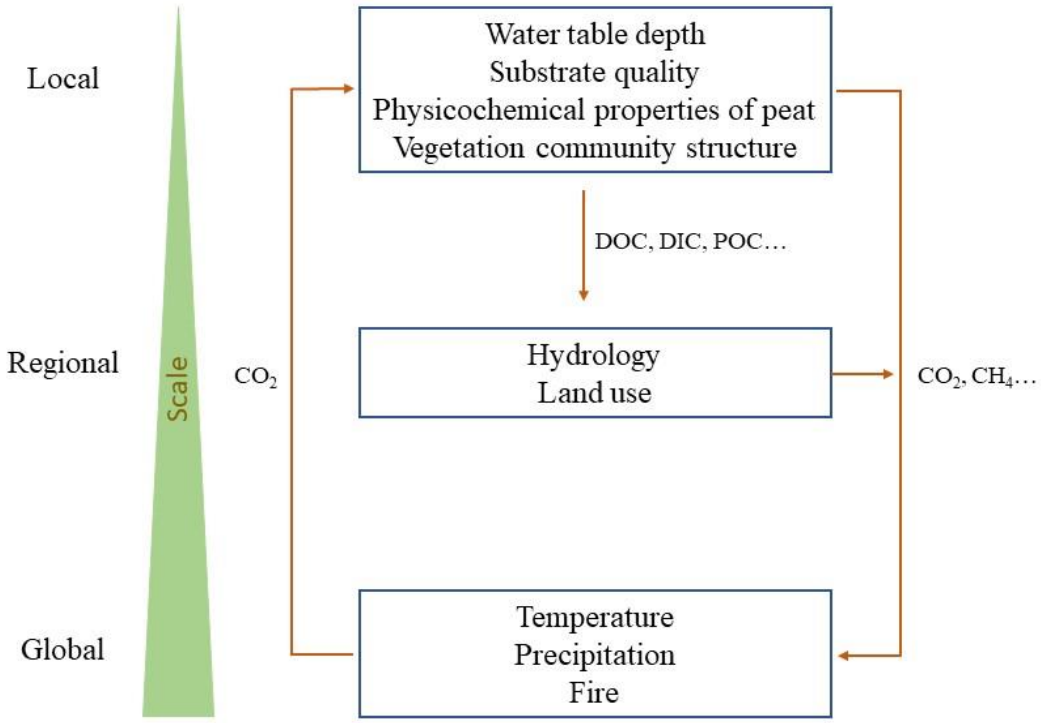

Figure I-3 The key drivers of carbon cycle processes in peatlands at different scales (modified from Limpens et al., 2008).

On the regional scale, the connection of peatlands with surrounding ecosystems influences the C export through topography and hydrology (Limpens et al., 2008). Evidence showed that the DOC leaching from peatlands promote the DOC decomposition in downstream area (Waldron et al., 2008). Anthropogenic disturbance of peatlands, especially hydrological disturbance, which happens in large areas of peatlands from Western Europe, also strongly affects the C cycle processes. It was reported that the disturbance may cause vascular plants invasion and large C emissions from peatlands, which may potentially weaken the C sink function or even turn the system into a C-source (Comont et al., 2006; Laggoun-Défarge et al., 2008; Turetsky et al., 2002).

On the global scale, precipitation, temperature and fire events are the main factors controlling the C cycle in peatlands. Precipitation amount and frequency determine the water table depth and water content of surface peat, which affect the plant communities as well as

decomposition rate. Temperature directly influences the biochemical reactions in peatlands (Limpens et al., 2008), as well as the evapotranspiration rate of surface peat (Roulet et al., 1992). Fire can be regarded as occasional accident. However, the frequency of fires events is predicted to increase in the future because of the climate change. It can cause more stored C release to atmosphere as CO_2, or it impacts the C cycle by indirectly through the release of aerosols and smoke (Limpens et al., 2008). According to Page et al. (2002), 0.19 ~ 0.23 Gt of C were emitted by fires from tropical peatlands in 1997.

Therefore, the C fluxes of peatlands are controlled by both biotic and abiotic parameters at global, regional and local scale. Furthermore, these controlling factors always interact with each other and affect the C cycle in peatlands. Particularly, temperature and precipitation are the key regulators as they provide the fundamental cold and wet environmental conditions for the formation of a such C sink ecosystem. Temperature drives the rate of many physical, chemical and biological processes and precipitation determines the water availability and balance of peatlands. However, due to the realistic and expected global climate change, these climate factors will change. Thus, whether peatlands will continue to function as C sink is still uncertain, and it depends on the potential impacts of future climatic conditions.

I.2 Global climate change and its potential impact on peatlands

I.2.1 Global climate change

Since pre-industrial era, human activities are influencing the global climate change. Anthropogenic greenhouse gas (GHG) emissions to the atmosphere mainly from fossil fuels combustion have caused significant increases in the concentrations of CO_2, CH_4 and nitrous oxide (N_2O) which amplify the greenhouse effect (Fig I-4a). Approximately 78% of total GHG emission is attributed to the CO_2 production via fossil fuel combustion during industrial period from 1970 to 2010 (IPCC, 2014; Fig I-4b), and these human activities might continue to be the dominant driver of CO_2 increase in atmosphere in next decades. According to the report of IPCC (2014), cumulative anthropogenic CO_2 emissions to the atmosphere were 2040 ± 310 Gt CO_2 during the period 1750 to 2011, with more than half of this amount were produced in the last 40 years (Fig I-4b). Nearly 40% of these GHG was stored in atmosphere (880 ± 35 Gt CO_2), the others was stored in terrestrial ecosystems (plants and soils) or in the ocean.

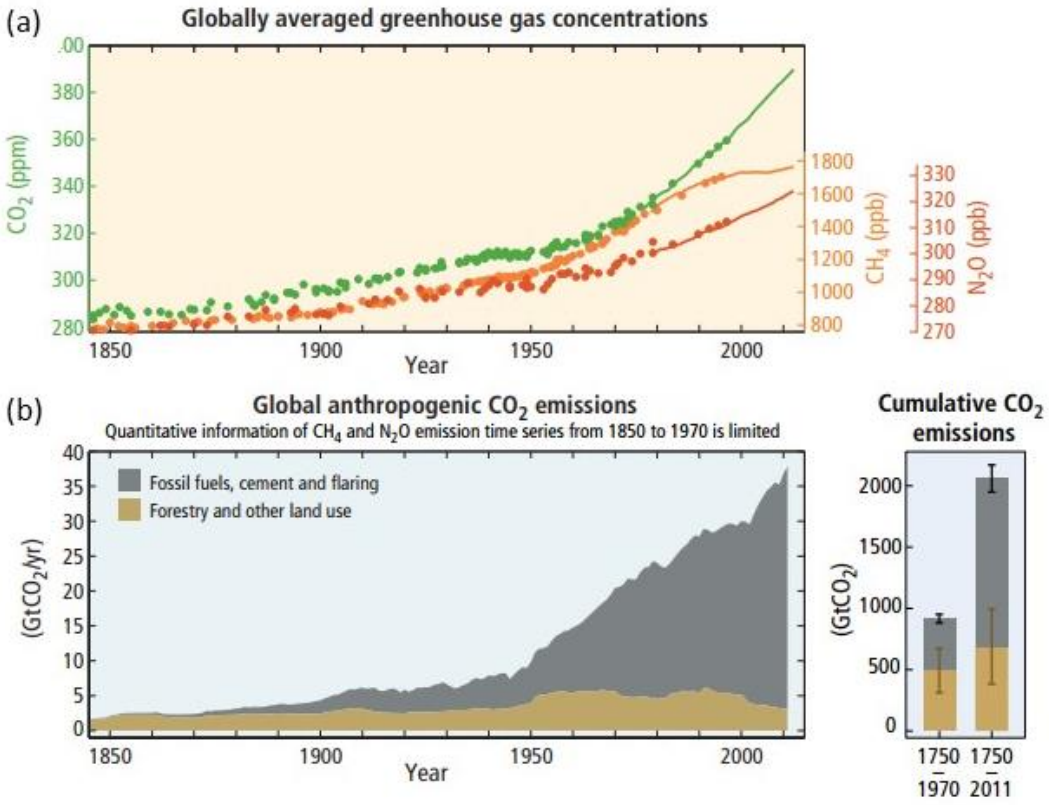

Figure I-4 Observed changes in atmospheric greenhouse gas concentrations (a) and global anthropogenic CO_2 emissions from different sources (b; IPCC, 2014).

These cumulative CO_2 emissions have an almost linear relationship with global temperature (Allen et al., 2009; Gillett et al., 2013). As a consequence of the massive GHG in atmosphere, an increase of global surface temperature over the 21st century was estimated under different assessed emission scenarios. Furthermore, strong influence of anthropogenic activities on the climate change is confirmed with growing evidence that anthropogenic GHG emissions contributed to more than half of the global surface temperature increase observed during the 1951-2010 period (IPCC, 2014). The global mean surface temperature is anticipated to rise from 1 ^{o}C to 3.7 ^{o}C by the end of the 21st century (2081–2100) relative to 1986–2005 (Fig I-5a). From the global point of view, the temperature increase in subarctic region will be faster than in other areas (Fig I-5b).

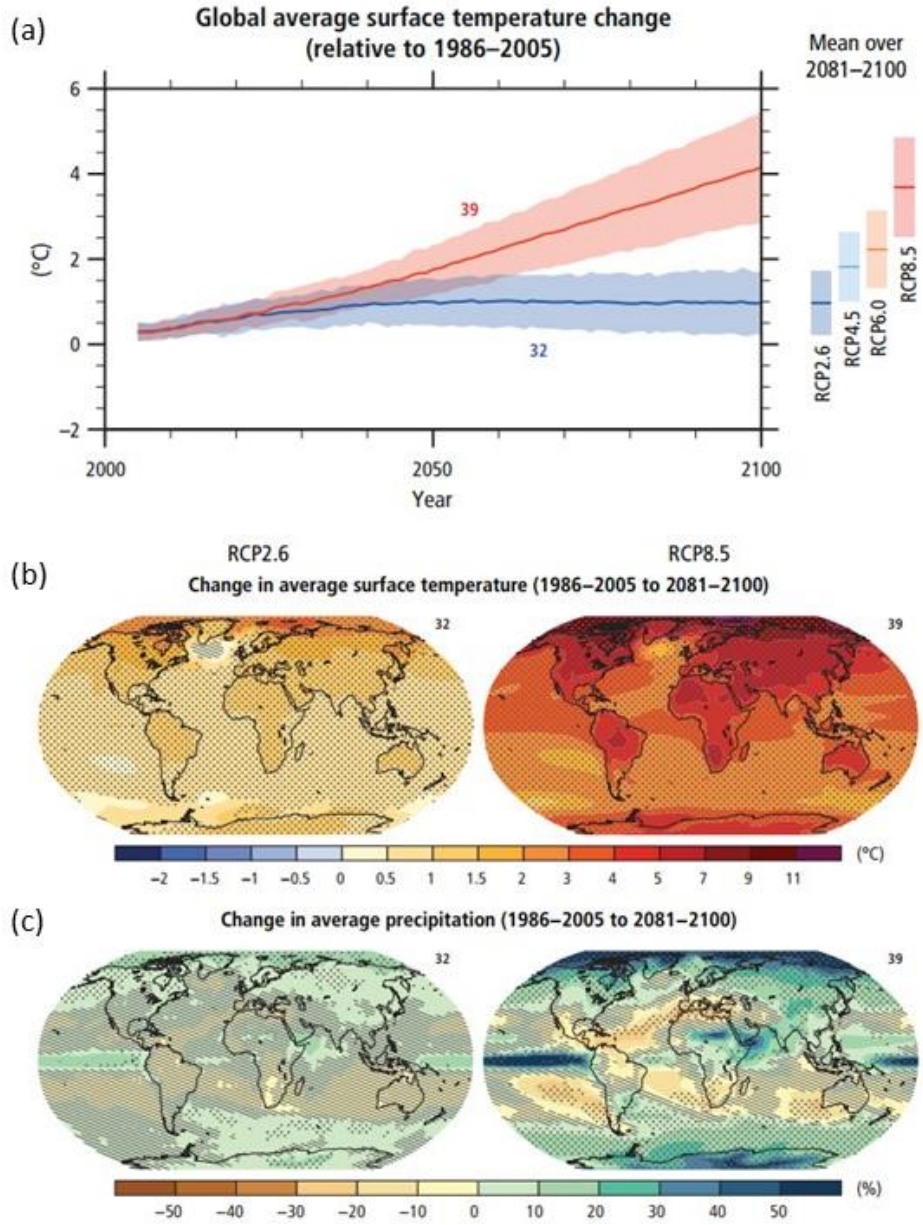

Figure I-5 Global average surface temperature change from 2006 to 2100 relative to 1986–2005 (a); Change in average surface temperature (b) and average precipitation based on multi-model mean projections for 2081–2100 relative to 1986–2005 (c; IPCC, 2014).

Evidences of "direct" effects of climate warming are already observed: e.g., glaciers/snow melting, increasing of the number of extreme heavy precipitation events and increasing meteorological disasters. Changes of precipitation is projected to be regional, with an increase of annual mean rainfall at high latitudes; while many mid-latitude and subtropical dry regions are expected to experience a decline of precipitation (Fig I-5c). In the context of climate change, the geographic area of many ecosystems, their seasonal behaviors, as well as diversity and abundance of plant species will be altered (IPCC, 2014). In return, the structure

and function shift of these ecosystems may cause positive feedback to atmosphere, which would exacerbate the global climate change. For example, the warming and drought could enhance the greenhouse gas (GHG) release from terrestrial ecosystems (Cramer et al., 2001; Heimann and Reichstein, 2008), which accelerate the climate warming. Especially those that have stored large amounts of C underground, such as peatlands, have a great potential for C release even though climate disturbance remains minor. Consequently, the assessment of the effects of climate change on the functioning of peatland ecosystems and the processes that govern the C cycle remains a major concern in the research priority.

I.2.2 Peatlands under climate change

Through the Holocene, peatlands have been a persistent sink of atmospheric CO_2 and a source of CH_4. However, this C sink function may be modified in the coming decades because of the global climate changes (Dise, 2009; Moore, 2002; Page and Baird, 2016). Therefore, the interactions between climate change stressors and peatland C cycle processes have received numerous concerns. Furthermore, considering the large C stock of peatlands, these ecosystems have large potential to release substantial amount of C to the atmosphere. Thus, the anticipation of peatlands stability in terms of their structure and functions under the context of global change is of great importance, especially in long-term.

Previous studies have found the variability of different plant communities in response to warming. The warming condition benefit the growth of vascular plants (shrubs or graminoids) but decreased the abundance of bryophytes and lichens (Buttler et al., 2015; Jónsdóttir et al., 2005; Walker et al., 2006). The high abundance of vascular plants induced by warming could increase the C uptake of peatlands because of their high primary productivity (Gavazov et al., 2018; Leroy et al., 2019). However, their root exudates also supply labile C input into belowground which provide additional energy to microbes and could accelerate the decomposition of "old" OM via the priming effect (Gavazov et al., 2018; Girkin et al., 2018). Thus, this shift of plant community composition has implications on the C cycle in peatlands. Whereas, the response of aboveground vegetation to climate warming in long-term cannot be simply predicted and depends on the response of individual plants. As Hollister et al., (2005a) and Weltzin et al., (2003) have shown, the response of plants to warming showed species-specific and their response depends on the initial vegetation composition of the study site. Furthermore, the rapid response of plant communities to warming was mainly caused by the change of growth and biomass allocation. However, their long-term response could be a result

of both initial responses and plant-plant interactions (e.g. competition between species) (Hollister et al., 2005b), which brings challenge when predict the changes in plant community composition under changing climate.

Temperature controls the metabolic processes related to microbial and plant activities (Lloyd and Taylor, 1994; Medlyn et al., 2002; Weltzin et al., 2000), which makes it a key regulator of C cycle processes. Generally, an increase of temperature could induce a rise of photosynthesis (e.g. Chivers et al., 2009; Flanagan and Syed, 2011). Also, the enhancement of ER by temperature increase was also observed in previous studies (e.g. Chivers et al., 2009; Flanagan and Syed, 2011; Updegraff et al., 2001; Voigt et al., 2017). Dorrepaal et al., (2009) observed an over 50 % increase of ecosystem respiration from peat induced by approximately 1 ^{o}C temperature rise and large proportion of this increase comes from subsurface. Moreover, CH_4 emissions and oxidation are also strongly correlated with temperature (Segers, 1998). Additionally, warming could enhance the DOC concentrations in pore water through increasing both microbial extracellular enzyme activity which regulate the decomposition rate and root exudates production, which may increase the C losses by leaching (Bonnett et al., 2006; Dieleman et al., 2016; Fenner et al., 2007; C. Freeman et al., 2001; Kane et al., 2014).

WTD is also an important control on C cycle in peatlands (Blodau et al., 2004; Moore and Dalva, 1993). Under the condition of WTD drawdown induced by drought, CO_2 emission is expected to be largely increased as a result of the higher decomposition rate of OM and microbial inhibitors (such as phenolic compounds) when exposure to aerobic conditions (Blodau et al., 2004; Fenner and Freeman, 2011; Hribljan et al., 2014; Moore and Dalva, 1993; Yavitt et al., 1997). However, the decrease of WTD would cause a decline of CH_4 release, because the occurrence of oxygen is unfavorable for the methanogenesis activity, and at the same time increase the oxidation of CH_4 (Bridgham et al., 2013; Heikkinen et al., 2002; Segers, 1998).

Overall, numerous studies tried to elucidate the impact of climate change on peatlands (Dieleman et al., 2015; Laine et al., 2019; Pearson et al., 2015; Updegraff et al., 2001). However, the C cycle processes in these ecosystems are influenced by multiple climate variables, as well as their co-effects. Thus, the estimation of the stability of peatlands C stock is still challenging. More importantly, the response of C cycle to climate change varies with region, environmental condition, vegetation composition and initial state of peatlands. Therefore, examination of various C cycle processes under changing environment in specific sites is essential to address the precise feedback of peatlands to climate change.

A study predicted that the C sink of intact natural peatlands will maintain and increase slightly until around 2100. However, their feedbacks to global warming are expected to switch from negative to positive, suggesting a decrease of C sink in response to warming at the end of 21st century (Gallego-Sala et al., 2018). Nevertheless, large amount of boreal and temperate peatlands, which have suffered widespread anthropogenic disturbance (drainage, peat cutting, land use change), has been transformed to a net C source. Furthermore, the C release from these disturbed sites was estimated to increase in the next century (Leifeld et al., 2019). Restoring the C sink, or at least decreasing the source function of the disturbed peatlands can be a tool to achieve a decline of the global warming by 1.5-2.0 °C relative to pre-industrial times as was set in the Paris Agreement. Following this task, a net zero GHGs emissions by 2050 is required (Rogelj, et al.). Therefore, the estimation of the role of disturbed peatlands as either a sink or source of C under the projected climate change is necessary.

I.3 Scientific questions and objectives

Northern peatlands are important terrestrial ecosystems providing large C reservoir. Climate scenarios projections suggest that they will experience higher temperature in the future than now. More importantly, the contribution of the feedback of peatland ecosystems to atmosphere has not been taken into account in the global climate models (Sanderman et al., 2017; Walsh et al., 2017). Thus, the estimation of the function of peatlands in the context of climate warming is of great importance, especially the disturbed temperate peatlands, which may act as a C source in the future. In order to predict the fate of C stored in peatlands, it is critical to understand the change of key processes involved in the C cycle under temperature elevation. Accordingly, this thesis mainly focus on the effect of warming on the i) gaseous C fluxes (CO_2 and CH_4) at the ecosystem-atmosphere interface, ii) dynamics of belowground DOC pool, and iii) CO_2 production of peat in interaction with oxygen (O_2) availability and peat quality (Fig I-6).

To study the warming effect on the CO_2 and CH_4 fluxes and DOC pool, a mesocosm experiment was conducted. The mesocosms from a temperate *Sphagnum* peatland (La Guette) which has been invaded by vascular plants (especially *Molinia caerulea*) were submitted to two temperature treatments: 1) ambient (Control) and 2) moderate warming by open-top chambers (OTCs). We examined how this experimental warming will affect:

- the physical and chemical parameters of peat profile and the plant community structure: in Chapter III,

- the CO_2, CH_4 fluxes and C balance of peatlands: in Chapter IV,

- the quantity and quality of DOC in vertical peat profile: in Chapter V,

To study the role of abiotic and biotic factors (temperature, O_2 availability and peat quality) on the controlling of soil respiration, a laboratory incubation experiment was conducted with peat in different degradation states in order to determined:

- the abiotic and biotic drivers of CO_2 production and its sensitivity to temperature change: in Chapter VI.

Chapter III: Environmental parameters and aboveground vegetation community change under the effect of open-top chambers (OTCs)

The passive warming open top chambers (OTCs) are widely used to manipulate the experimental warming by trapping the solar energy and avoid any undesirable effect of unnatural precipitation and concentrated greenhouse gas (Marion et al., 1997). Thus, an increase of air temperature and the induced elevation of soil temperature are expected (Hollister et al., 2006; Marion et al., 1997; Walker et al., 2006). Also, the increase of soil temperature will enhance the evapotranspiration and thus decline the soil moisture, especially the surface layer. The higher temperature has multiple effect on different vegetation communities, with facilitation on vascular plants at the detriment of bryophytes (Bragazza et al., 2013; Buttler et al., 2015; Dieleman et al., 2015). The pore water pH was strongly associated to the physiology of plants, as *Sphagnum* can release protons (H^+) thus acidify the environment (Rydin and Jeglum, 2013). Thus, the higher plant activities induced by the increasing soil temperature could decrease the pH of pore water at surface layer peat. Moreover, the higher nutrient uptake by vegetation due to the increased soil temperature would decrease the conductivity of pore water. Therefore, the warming effect on different physico-chemical variables induced by OTCs was examined in this chapter. The physical properties (temperature, water content) of peat and chemical properties (pH and conductivity) of pore water at different depth (5. 15 and 30 cm) of mesocosms were measured. In addition, the aboveground vegetation community structure was monitored.

We hypothesized that:

- 1) mean air temperature and soil temperature at 5 and 15 cm depth will be increased by OTCs, while the OTCs effect on soil temperature at 30 cm will not be significant;

- 2) OTCs will decrease the water content of surface peat at 5 cm by enhancing the evapotranspiration;
- 3) pH and conductivity of pore water will decrease under OTCs at 5 cm layer;
- 4) the warming effect induced by OTCs will facilitate the growth of vascular plants (including graminoids and ericaceous shrub) and will increase their abundance.

Chapter IV: Effect of climate warming on the CO_2 and CH_4 fluxes and C balance of peatlands

As mentioned above (I.2.2), the warming is expected to enhance both GPP, ER and CH_4 emission. As a result, it is difficult to estimate the net gaseous C balance of peatlands. Previous research on the subarctic peatlands indicated that the warming tended to diminish the C accumulation in peatlands (e.g. Jones et al., 1998; Malmer et al., 2005; Voigt et al., 2017). Thus, in this chapter we determined the feedback of peatlands to atmosphere under the experimental warming. First, we measured the CO_2 fluxes (GPP, ER, net CO_2 exchange) and CH_4 emission under control and warming treatment (Fig I-6). Furthermore, we determined the temperature sensitivity of CO_2 and CH_4 fluxes under both treatments to understand the precise response of C fluxes to temperature change. Second, in order to estimate the annual C balance, models of CO_2 and CH_4 fluxes were proposed by studying the relationship between measured C fluxes components (CO_2 and CH_4) and biotic and abiotic factors. Different models were tested and the ones with the best performances were selected. Third, the modelled annual CO_2, CH_4 fluxes and the C budget as well as the global warming potential of two treatments were calculated.

The hypotheses are:

- 1) the elevated temperature induced by OTCs will increase both CO_2 uptake by photosynthesis and CO_2 release through respiration;
- 2) CH_4 emission will enhanced by warming;
- 3) the increasing temperature will diminish the C sink functioning of this ecosystem.

Chapter V: Dynamics of dissolved organic carbon (DOC) pool under experimental warming

Temperature is a key regulator of microbial decomposition processes. Thus, changes in DOC concentration (as both product of and substrate for microbes) under warming treatment are expected (Moore and Dalva, 2001). The DOC concentration depends on the balance

between DOC production and consumption, while both DOC production and C mineralization could be stimulated by the increasing temperature. Previous studies emphasized that the increasing DOC concentration mainly results from the enhanced labile C input from root exudates, which also increased the lability of DOC (Dieleman et al., 2016; Kane et al., 2014). Furthermore, the extensive root systems of vascular plants present in subsurface peat while the *Sphagnum* and their litters exit in surface layer, thus due to the effect of plant-microorganism interactions (Girkin et al., 2018; Kuzyakov et al., 2000; Straková et al., 2010), the dynamics of belowground DOC pool could exhibite vertical heterogeneity. In this chapter, the quantity and quality of pore water DOC at three depth (-5. -15 and -30 cm) of the mesocosms were investigated. These three depths corresponded to (i) the zone under the effect of *Sphagnum* litter, (ii) near the roots of vascular plants and (iii) out of rhizosphere. DOC concentration, aromaticity and fluorescence indices were measured (Fig I-6).

We hypothesized that:

- 1) the DOC concentration will increase due to higher vegetation input under warming treatment, especially at surface and subsurface layer where an increase of soil temperature was prevailing;
- 2) the lability of DOC pool will increase due to the enhancement of plant derived labile root exudates, especially at the depth of vascular plants roots.

Chapter VI: Abiotic and biotic drivers of soil respiration in peat and its sensitivity to temperature change

Soil respiration is an important efflux of CO_2 from peatlands to the atmosphere. Dorrepaal et al., (2009) reported that about 70 % ER in peat soil is accounted by heterotrophic respiration. Thus we are also interested in how it will respond to different environmental variables change. Soil respiration is largely controlled by abiotic factors: temperature, soil moisture and O_2 availability (Szafranek-Nakonieczna and Stepniewska, 2014; Wang et al., 2010). In addition, OM quality also determines the soil respiration rate as well as its temperature sensitivity (Conant et al., 2008; Davidson and Janssens, 2006). In order to elucidate the role of abiotic and biotic factors (temperature, peat quality, O_2 availability as well as microbial biomass) and their interactions in regulating the soil respiration of peat, an incubation experiment with peat of different degradation states was conducted. Meanwhile, the temperature sensitivity of CO_2 production in vertical profile of peat was determined.

The hypotheses are:

- 1) High temperature and aerobic conditions enhance CO_2 production;
- 2) Deep layer peat with more decomposed OM has a lower CO_2 production, while it is more sensitive to temperature change;
- 3) Peat quality affects the microbial biomass and their interactions control the CO_2 production from peat.

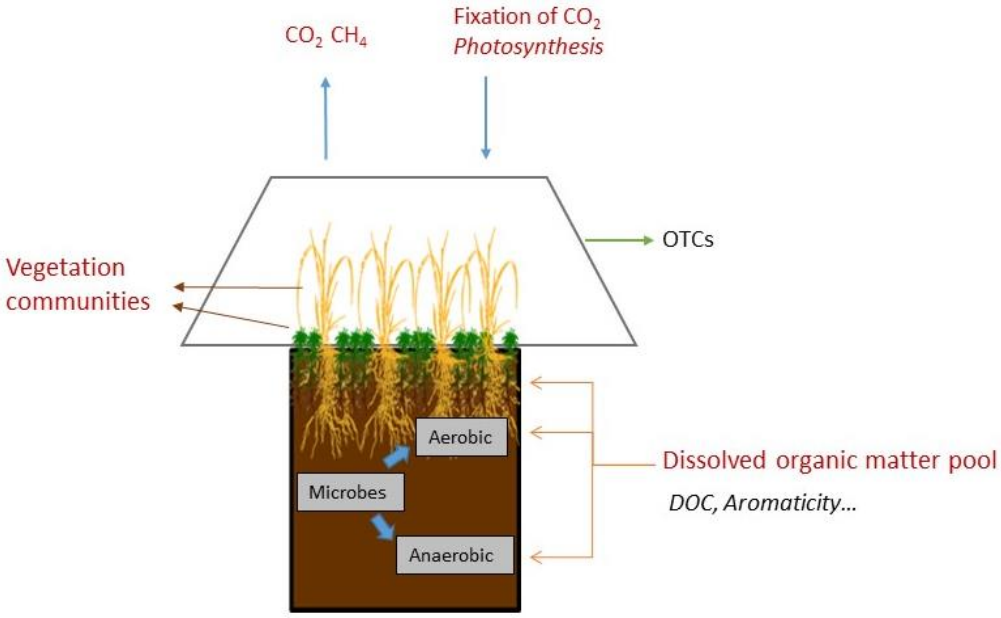

Figure I-6 Variables analyzed of mesocosms under the effect of OTCs.

References

Allen, M. R., Frame, D. J., Huntingford, C., Jones, C. D., Lowe, J. A., Meinshausen, M., et al. (2009). Warming caused by cumulative carbon emissions towards the trillionth tonne. *Nature* 458, 1163–1166. doi:10.1038/nature08019.

Basiliko, N., Stewart, H., Roulet, N. T., and Moore, T. R. (2012). Do Root Exudates Enhance Peat Decomposition? *Geomicrobiol. J.* 29, 374–378. doi:10.1080/01490451.2011.568272.

Blodau, C., Basiliko, N., and Moore, T. R. (2004). Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry* 67, 331–351. doi:10.1023/B:BIOG.0000015788.30164.e2.

Bonnett, S. A. F., Ostle, N., and Freeman, C. (2006). Seasonal variations in decomposition processes in a valley-bottom riparian peatland. *Sci. Total Environ.* 370, 561–573. doi:10.1016/j.scitotenv.2006.08.032.

Bragazza, L., Buttler, A., Siegenthaler, A., and Mitchell, E. A. D. (2009). Plant litter decomposition and nutrient release in peatlands. *GMS* 184, 99–110. doi:10.1029/2008GM000815.

Bragazza, L., Parisod, J., Buttler, A., and Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nat. Clim. Change* 3, 273–277. doi:10.1038/nclimate1781.

Bridgham, S. D., Cadillo-Quiroz, H., Keller, J. K., and Zhuang, Q. (2013). Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. *Glob. Change Biol.* 19, 1325–1346. doi:10.1111/gcb.12131.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., et al. (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *J. Veg. Sci.* 26, 964–974. doi:10.1111/jvs.12296.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2009). Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO2 Fluxes in an Alaskan Rich Fen. *Ecosystems* 12, 1329–1342. doi:10.1007/s10021-009-9292-y.

Clymo, R. S., and Fogg, G. E. (1984). The limits to peat bog growth. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 303, 605–654. doi:10.1098/rstb.1984.0002.

Comont, L., Laggoun-Défarge, F., and Disnar, J.-R. (2006). Evolution of organic matter indicators in response to major environmental changes: The case of a formerly cut-over peat bog (Le Russey, Jura Mountains, France). *Org. Geochem.* 37, 1736–1751. doi:10.1016/j.orggeochem.2006.08.005.

Conant, R. T., Steinweg, J. M., Haddix, M. L., Paul, E. A., Plante, A. F., and Six, J. (2008). Experimental Warming Shows That Decomposition Temperature Sensitivity Increases with Soil Organic Matter Recalcitrance. *Ecology* 89, 2384–2391. doi:10.1890/08-0137.1.

Cooper, D. J., Chimner, R. A., and Merritt, D. M. Western Mountain Wetlands. 17.

Craft, C. (2016). "7 - Peatlands," in *Creating and Restoring Wetlands*, ed. C. Craft (Boston: Elsevier), 161–192. doi:10.1016/B978-0-12-407232-9.00007-5.

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., et al. (2001). Global response of terrestrial ecosystem structure and function to CO2 and climate change:

results from six dynamic global vegetation models. *Glob. Change Biol.* 7, 357–373. doi:https://doi.org/10.1046/j.1365-2486.2001.00383.x.

Criquet, S., Tagger, S., Vogt, G., Iacazio, G., and Le Petit, J. (1999). Laccase activity of forest litter. *Soil Biol. Biochem.* 31, 1239–1244. doi:10.1016/S0038-0717(99)00038-3.

Darlington, H. C. (1943). Vegetation and Substrate of Cranberry Glades, West Virginia. *Bot. Gaz.* 104, 371–393. doi:10.1086/335148.

Davidson, E. A., and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173. doi:10.1038/nature04514.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Glob. Change Biol.* 21, 388–395. doi:10.1111/gcb.12643.

Dieleman, C. M., Lindo, Z., McLaughlin, J. W., Craig, A. E., and Branfireun, B. A. (2016). Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry* 128, 385–396. doi:10.1007/s10533-016-0214-8.

Dise, N. B. (2009). Peatland Response to Global Change. *Science* 326, 810–811. doi:10.1126/science.1174268.

Donato, D. C., Kauffman, J. B., Murdiyarso, D., Kurnianto, S., Stidham, M., and Kanninen, M. (2011). Mangroves among the most carbon-rich forests in the tropics. *Nat. Geosci.* 4, 293–297. doi:10.1038/ngeo1123.

Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., and Logtestijn, R. S. P. V. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *J. Ecol.* 93, 817–828. doi:10.1111/j.1365-2745.2005.01024.x.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., et al. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* 460, 616–619. doi:10.1038/nature08216.

Ellison, A. M. (2004). Wetlands of Central America. *Wetl. Ecol. Manag.* 12, 3–55. doi:10.1023/B:WETL.0000016809.95746.b1.

Fenner, N., and Freeman, C. (2011). Drought-induced carbon loss in peatlands. *Nat. Geosci.* 4, 895–900. doi:10.1038/ngeo1323.

Fenner, N., Freeman, C., Hughes, S., and Reynolds, B. (2001). Molecular weight spectra of dissolved organic carbon in a rewetted Welsh peatland and possible implications for water quality. *Soil Use Manag.* 17, 106–112. doi:10.1111/j.1475-2743.2001.tb00015.x.

Fenner, N., Ostle, N. J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B., et al. (2007). Elevated CO2 Effects on Peatland Plant Community Carbon Dynamics and DOC Production. *Ecosystems* 10, 635–647. doi:10.1007/s10021-007-9051-x.

Fetzer, S., Bak, F., and Conrad, R. (1993). Sensitivity of methanogenic bacteria from paddy soil to oxygen and desiccation. *FEMS Microbiol. Ecol.* 12, 107–115. doi:10.1111/j.1574-6941.1993.tb00022.x.

Fierer, N., Craine, J. M., McLauchlan, K., and Schimel, J. P. (2005). Litter Quality and the Temperature Sensitivity of Decomposition. *Ecology* 86, 320–326. doi:10.1890/04-1254.

Flanagan, L. B., and Syed, K. H. (2011). Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Glob. Change Biol.* 17, 2271–2287. doi:10.1111/j.1365-2486.2010.02378.x.

Freeman, C., Evans, C. D., Monteith, D. T., Reynolds, B., and Fenner, N. (2001a). Export of organic carbon from peat soils. *Nature* 412, 785–785. doi:10.1038/35090628.

Freeman, C., Ostle, N., and Kang, H. (2001b). An enzymic "latch" on a global carbon store. *Nature* 409, 149–149. doi:10.1038/35051650.

Gallego-Sala, A. V., Charman, D. J., Brewer, S., Page, S. E., Prentice, I. C., Friedlingstein, P., et al. (2018). Latitudinal limits to the predicted increase of the peatland carbon sink with warming. *Nat. Clim. Change* 8, 907–913. doi:10.1038/s41558-018-0271-1.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., et al. (2018). Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. *Glob. Change Biol.* 24, 3911–3921. doi:10.1111/gcb.14140.

Gillett, N. P., Arora, V. K., Matthews, D., and Allen, M. R. (2013). Constraining the Ratio of Global Warming to Cumulative CO2 Emissions Using CMIP5 Simulations. *J. Clim.* 26, 6844–6858. doi:10.1175/JCLI-D-12-00476.1.

Girkin, N. T., Turner, B. L., Ostle, N., Craigon, J., and Sjögersten, S. (2018). Root exudate analogues accelerate CO2 and CH4 production in tropical peat. *Soil Biol. Biochem.* 117, 48–55. doi:10.1016/j.soilbio.2017.11.008.

Heikkinen, J. E. P., Elsakov, V., and Martikainen, P. J. (2002). Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia. *Glob. Biogeochem. Cycles* 16, 62-1-62–15. doi:10.1029/2002GB001930.

Heimann, M., and Reichstein, M. (2008). Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* 451, 289–292. doi:10.1038/nature06591.

Hollister, R. D., Webber, P. J., and Bay, C. (2005a). Plant Response to Temperature in Northern Alaska: Implications for Predicting Vegetation Change. *Ecology* 86, 1562–1570.

Hollister, R. D., Webber, P. J., Nelson, F. E., and Tweedie, C. E. (2006). Soil Thaw and Temperature Response to Air Warming Varies by Plant Community: Results from an Open-top Chamber Experiment in Northern Alaska. *Arct. Antarct. Alp. Res.* 38, 206–215. doi:10.1657/1523-0430(2006)38[206:STATRT]2.0.CO;2.

Hollister, R. D., Webber, P. J., and Tweedie, C. E. (2005b). The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Glob. Change Biol.* 11, 525–536. doi:10.1111/j.1365-2486.2005.00926.x.

Hribljan, J. A., Kane, E. S., Pypker, T. G., and Chimner, R. A. (2014). The effect of long-term water table manipulations on dissolved organic carbon dynamics in a poor fen peatland. *J. Geophys. Res. Biogeosciences* 119, 577–595. doi:10.1002/2013JG002527.

IPCC (2014). Climate Change 2014: Synthesis Report. Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N.K., Edenhofer, O., Elgizouli, I., Field, C.B., Forster, P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., Hegerl, G., Howden, M., Jiang, K., Jimenez Cisneroz, B., Kattsov, V., Lee, H., Mach, K.J., Marotzke, J., Mastrandrea, M.D., Meyer, L., Minx, J., Mulugetta, Y., O'Brien, K., Oppenheimer, M., Pereira, J.J., Pichs-Madruga, R., Plattner, G.-K., Pörtner, H.-O., Power, S.B., Preston, B., Ravindranath, N.H., Reisinger, A., Riahi, K.,

Rusticucci, M., Scholes, R., Seyboth, K., Sokona, Y., Stavins, R., Stocker, T.F., Tschakert, P., van Vuuren, D., van Ypserle, J.-P., 2014. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, EPIC3Geneva, Switzerland, IPCC, 151 p., pp. 151, ISBN: 978-92-9169-143-2. IPCC, Geneva, Switzerland.

Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., and Piñeiro, G. (2017). The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls. *Annu. Rev. Ecol. Evol. Syst.* 48, 419–445. doi:10.1146/annurev-ecolsys-112414-054234.

Johnson, L. C., and Damman, A. W. H. (1991). Species-Controlled Sphagnum Decay on a South Swedish Raised Bog. *Oikos* 61, 234–242. doi:10.2307/3545341.

Jones, M. H., Fahnestock, J. T., Walker, D. A., Walker, M. D., and Welker, J. M. (1998). Carbon Dioxide Fluxes in Moist and Dry Arctic Tundra during the Snow-free Season: Responses to Increases in Summer Temperature and Winter Snow Accumulation. *Arct. Alp. Res.* 30, 373–380. doi:10.1080/00040851.1998.12002912.

Jónsdóttir, I. S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., and Hjartarson, H. (2005). Variable sensitivity of plant communities in Iceland to experimental warming. *Glob. Change Biol.* 11, 553–563. doi:10.1111/j.1365-2486.2005.00928.x.

Joosten, H., and Clarke, D. (2002). Wise use of mires and peatlands. *Int. Mire Conserv. Group Int. Peat Soc.* 304.

Kalbitz, K., Schmerwitz, J., Schwesig, D., and Matzner, E. (2003). Biodegradation of soil-derived dissolved organic matter as related to its properties. *Geoderma* 113, 273–291. doi:10.1016/S0016-7061(02)00365-8.

Kane, E. S., Mazzoleni, L. R., Kratz, C. J., Hribljan, J. A., Johnson, C. P., Pypker, T. G., et al. (2014). Peat porewater dissolved organic carbon concentration and lability increase with warming: a field temperature manipulation experiment in a poor-fen. *Biogeochemistry* 119, 161–178. doi:10.1007/s10533-014-9955-4.

Kuzyakov, Y., Friedel, J. K., and Stahr, K. (2000). Review of mechanisms and quantification of priming effects. *Soil Biol. Biochem.* 32, 1485–1498. doi:10.1016/S0038-0717(00)00084-5.

Laggoun-Défarge, F., Mitchell, E., Gilbert, D., Disnar, J.-R., Comont, L., Warner, B. G., et al. (2008). Cut-over peatland regeneration assessment using organic matter and microbial indicators (bacteria and testate amoebae). *J. Appl. Ecol.* 45, 716–727. doi:10.1111/j.1365-2664.2007.01436.x.

Laggoun-Défarge, F., Mitchell, E., Gilbert, D., Disnar, J.-R., Comont, L., Warner, B. G., et al. (2008). Cut-over peatland regeneration assessment using organic matter and microbial indicators (bacteria and testate amoebae). *J. Appl. Ecol.* 45, 716–727. doi:10.1111/j.1365-2664.2007.01436.x.

Lähteenoja, O., Ruokolainen, K., Schulman, L., and Oinonen, M. (2009). Amazonian peatlands: an ignored C sink and potential source. *Glob. Change Biol.* 15, 2311–2320. doi:10.1111/j.1365-2486.2009.01920.x.

Laine, A. M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., et al. (2019). Warming impacts on boreal fen CO_2 exchange under wet and dry conditions. *Glob. Change Biol.* 25, 1995–2008. doi:10.1111/gcb.14617.

Leifeld, J., Wüst-Galley, C., and Page, S. (2019). Intact and managed peatland soils as a source and sink of GHGs from 1850 to 2100. *Nat. Clim. Change* 9, 945–947. doi:10.1038/s41558-019-0615-5.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., and Laggoun-Défarge, F. (2017). Vegetation composition controls temperature sensitivity of CO2 and CH4 emissions and DOC concentration in peatlands. *Soil Biol. Biochem.* 107, 164–167. doi:10.1016/j.soilbio.2017.01.005.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., et al. (2019). CO_2 and CH_4 budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*. *Biogeosciences* 16, 4085–4095. doi:https://doi.org/10.5194/bg-16-4085-2019.

Limpens, J., Berendse, F., Blodau, C., Canadell, J. G., Freeman, C., Holden, J., et al. (2008). Peatlands and the carbon cycle: from local processes to global implications ? a synthesis. *Biogeosciences Discuss.* 5, 1379–1419.

Lloyd, J., and Taylor, J. A. (1994). On the Temperature Dependence of Soil Respiration. *Funct. Ecol.* 8, 315–323. doi:10.2307/2389824.

Malmer, N., Johansson, T., Olsrud, M., and Christensen, T. R. (2005). Vegetation, climatic changes and net carbon sequestration in a North-Scandinavian subarctic mire over 30 years. *Glob. Change Biol.* 11, 1895–1909. doi:https://doi.org/10.1111/j.1365-2486.2005.01042.x.

Maltby, E., and Proctor, M. C. F. (1996). Peatlands: their nature and role in the biosphere. Available at: http://inis.iaea.org/Search/search.aspx?orig_q=RN:28074144 [Accessed May 15, 2020].

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., et al. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.* 3, 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x.

McGlone, M. S. (2002). The Late Quaternary peat, vegetation and climate history of the Southern Oceanic Islands of New Zealand. *Quat. Sci. Rev.* 21, 683–707. doi:10.1016/S0277-3791(01)00044-0.

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., et al. (2002). Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant Cell Environ.* 25, 1167–1179. doi:10.1046/j.1365-3040.2002.00891.x.

Moore, P. D. (2002). The future of cool temperate bogs. *Environ. Conserv.* 29, 3–20. doi:10.1017/S0376892902000024.

Moore, T. R., and Dalva, M. (1993). The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *J. Soil Sci.* 44, 651–664. doi:10.1111/j.1365-2389.1993.tb02330.x.

Moore, T. R., and Dalva, M. (2001). SOME CONTROLS ON THE RELEASE OF DISSOLVED ORGANIC CARBON BY PLANT TISSUES AND SOILS. *Soil Sci.* 166, 38–47.

Moore, T. R., Roulet, N. T., and Waddington, J. M. (1998). Uncertainty in Predicting the Effect of Climatic Change on the Carbon Cycling of Canadian Peatlands. *Clim. Change* 40, 229–245. doi:10.1023/A:1005408719297.

Morley, R. J. (1981). Development and Vegetation Dynamics of a Lowland Ombrogenous Peat Swamp in Kalimantan Tengah, Indonesia. *J. Biogeogr.* 8, 383–404. doi:10.2307/2844758.

Page, S. E., and Baird, A. J. (2016). Peatlands and Global Change: Response and Resilience. *Annu. Rev. Environ. Resour.* 41, 35–57. doi:10.1146/annurev-environ-110615-085520.

Page, S. E., Rieley, J. O., and Banks, C. J. (2011). Global and regional importance of the tropical peatland carbon pool. *Glob. Change Biol.* 17, 798–818. doi:10.1111/j.1365-2486.2010.02279.x.

Page, S. E., Siegert, F., Rieley, J. O., Boehm, H.-D. V., Jaya, A., and Limin, S. (2002). The amount of carbon released from peat and forest fires in Indonesia during 1997. *Nature* 420, 61–65. doi:10.1038/nature01131.

Pearson, M., Penttilä, T., Harjunpää, L., Laiho, R., Laine, J., Sarjala, T., et al. Effects of temperature rise and water-table-level drawdown on greenhouse gas fluxes of boreal sedge fens. 20, 17.

Rogelj, J. et al. in Global Warming of 1.5° C: An IPCC Special Report (eds Masson-Delmotte, V. et al.) Ch. 2 (IPCC, 2018).

Roulet, N., Moore, T., Bubier, J., and Lafleur, P. (1992). Northern fens: methane flux and climatic change. *Tellus B* 44, 100–105. doi:10.1034/j.1600-0889.1992.t01-1-00002.x.

Rydin, H., and Jeglum, J. K. (2013). *The Biology of Peatlands, 2e*. OUP Oxford.

Sanderman, J., Hengl, T., and Fiske, G. J. (2017). Soil carbon debt of 12,000 years of human land use. *Proc. Natl. Acad. Sci.* 114, 9575–9580. doi:10.1073/pnas.1706103114.

Segers, R. (1998). Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry* 41, 23–51. doi:10.1023/A:1005929032764.

Sjögersten, S., Caul, S., Daniell, T. J., Jurd, A. P. S., O'Sullivan, O. S., Stapleton, C. S., et al. (2016). Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. *Soil Biol. Biochem.* 98, 42–53. doi:10.1016/j.soilbio.2016.03.016.

Stalheim, T., Ballance, S., Christensen, B. E., and Granum, P. E. (2009). Sphagnan – a pectin-like polymer isolated from Sphagnum moss can inhibit the growth of some typical food spoilage and food poisoning bacteria by lowering the pH. *J. Appl. Microbiol.* 106, 967–976. doi:10.1111/j.1365-2672.2008.04057.x.

Straková, P., Anttila, J., Spetz, P., Kitunen, V., Tapanila, T., and Laiho, R. (2010). Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. *Plant Soil* 335, 501–520. doi:10.1007/s11104-010-0447-6.

Szafranek-Nakonieczna, A., and Stepniewska, Z. (2014). Aerobic and anaerobic respiration in profiles of Polesie Lubelskie peatlands. *Int. Agrophysics* 28. Available at: http://yadda.icm.edu.pl/yadda/element/bwmeta1.element.agro-9a68ce86-a247-40f5-ae04-41017c4101d4 [Accessed May 31, 2020].

Taylor, J. A. (1983). peatlands of Great Britain and Ireland. *Ecosyst. World*. Available at: https://agris.fao.org/agris-search/search.do?recordID=US201302603377 [Accessed May 15, 2020].

Turetsky, M., Wieder, K., Halsey, L., and Vitt, D. (2002). Current disturbance and the diminishing peatland carbon sink. *Geophys. Res. Lett.* 29, 21-1-21–4. doi:10.1029/2001GL014000.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., and Harth, C. (2001). Response of Co2 and Ch4 Emissions from Peatlands to Warming and Water Table Manipulation. *Ecol. Appl.* 11, 311–326. doi:10.1890/1051-0761(2001)011[0311:ROCACE]2.0.CO;2.

van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends Ecol. Evol.* 10, 270–275. doi:10.1016/0169-5347(95)90007-1.

Vitt, D. H. (2013). "Peatlands☆," in *Encyclopedia of Ecology (Second Edition)*, ed. B. Fath (Oxford: Elsevier), 557–566. doi:10.1016/B978-0-12-409548-9.00741-7.

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Glob. Change Biol.* 23, 3121–3138. doi:10.1111/gcb.13563.

Waldron, S., Flowers, H., Arlaud, C., Bryant, C., and Mcfarlane, S. (2008). The significance of organic carbon and nutrient export from peatland-dominated landscapes subject to disturbance. *Biogeosciences Discuss.* 5, 1139–1174.

Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., et al. (2006). Plant community responses to experimental warming across the tundra biome. *Proc. Natl. Acad. Sci. U. S. A.* 103, 1342–1346. doi:10.1073/pnas.0503198103.

Walsh, B., Ciais, P., Janssens, I. A., Peñuelas, J., Riahi, K., Rydzak, F., et al. (2017). Pathways for balancing CO 2 emissions and sinks. *Nat. Commun.* 8, 14856. doi:10.1038/ncomms14856.

Wang, X., Li, X., Hu, Y., Lv, J., Sun, J., Li, Z., et al. (2010). Effect of temperature and moisture on soil organic carbon mineralization of predominantly permafrost peatland in the Great Hing'an Mountains, Northeastern China. *J. Environ. Sci.* 22, 1057–1066. doi:10.1016/S1001-0742(09)60217-5.

Weltzin, J. F., Bridgham, S. D., Pastor, J., Chen, J., and Harth, C. (2003). Potential effects of warming and drying on peatland plant community composition. *Glob. Change Biol.* 9, 141–151. doi:10.1046/j.1365-2486.2003.00571.x.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., and Chapin, C. T. (2000). Response of Bog and Fen Plant Communities to Warming and Water-Table Manipulations. *Ecology* 81, 3464–3478. doi:10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2.

Xu, J., Morris, P. J., Liu, J., and Holden, J. (2018). PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. *CATENA* 160, 134–140. doi:10.1016/j.catena.2017.09.010.

Yavitt, J. B., Williams, C. J., and Wieder, R. K. (1997). Production of methane and carbon dioxide in peatland ecosystems across North America: Effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiol. J.* 14, 299–316. doi:10.1080/01490459709378054.

Yu, Z. C. (2012). Northern peatland carbon stocks and dynamics: a review. *Biogeosciences* 9, 4071–4085. doi:https://doi.org/10.5194/bg-9-4071-2012.

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., and Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* 37. doi:10.1029/2010GL043584.

II. ***Materials and methods***

II.1 Introduction

Like mentioned in Chapter I, the climate change is becoming more and more alarming. Thus, the questions concerning the dynamics of the C stock in peatlands are of great importance. Previous studies have reported that the response of peatland ecosystems to climate warming showed large spatial heterogeneity (e.g. Waddington et al., 1998; Bubier et al., 2002; Chivers et al., 2009; Gillett et al., 2013; Ward et al., 2013), as such, their precise feedbacks to atmosphere and the magnitude remains large uncertainties. Up to now, most of research focus on the boreal peatlands in the northern hemisphere where majority of peatlands are located (e.g. Aurela et al., 2004; Chivers et al., 2009; Dieleman et al., 2015; Laine et al., 2019; Munir et al., 2015; Voigt et al., 2017). However, there is still a large gap in how temperate peatlands will respond to the warming climate. Temperate low-latitude peatlands are already below the temperature which is the projected level of subarctic regions in the future. Furthermore, they have suffered high anthropogenic pressures (e.g. hydrological disturbance; peat cutting or nutrient amendment) and a vegetation shift has occurred. Here, in this research, we focused on a temperate peatland which has suffered hydrological disturbance (drainage) for decades. This disturbance accelerated the invasion of vascular plants, which affects the C storage of this ecosystem. A restoration work was conducted in 2014 to raise the water table level and restore the favorable hydrological condition of this peatland. The effect of such actions was monitored for three years (2014-2016) and preliminary results have detected a restoration of hydrology and vegetation (Laggoun-Défarge et al., 2016). However, its sustainable maintenance in long-term needs to be investigated. In particular, under the context of climate warming, the structure and functioning of this ecosystem are of great concerns. Thus, it is necessary to identify the key processes controlling the C accumulation in peat.

To understand the C cycle of the peatland in response to the long-term climate warming, mesocosms and lab incubation experiment was conducted (see section I.3). The mesocosm experiment set up is a trade off between “experimental control” and “ecological reality”. The mesocosms are intact peat monoliths with vegetation, and the experiment was carried out in an outdoor environment condition which is similar as in field. Moreover, the mesocosm allow us to control isolated variables easily. There have been numerous research to manipulate experimental warming in order to simulate the forecasted global temperature rise, thus various heating method were developed and tested for their efficacy (Chapin and Bloom, 1976; Hillier et al., 1994; Marion et al., 1997; Tissue and Oechel, 1987). Among those, passive warming

open-top chambers (OTCs) which was developed for the international tundra experiment (ITEX; Henry and Molau, 1997), are widely used due to their numerous advantages. For example, the temperature increase of OTCs is achieved by trapping solar energy than directly change of energy, which largely avoid undesirable ecological effect (Marion et al., 1997). In addition, the design of open top minimizes the unnatural solar irradiation and precipitation, and the unsealed bottom allow the air circulation to avoid greenhouse effect (Dabros et al., 2010; Hollister and Webber, 2000). The experimental approach and measurements of mesocosm experiment are described in section II.2.

Soil respiration is a large efflux of CO_2 from peatlands to the atmosphere (Dorrepaal et al., 2009). A lab incubation experiment was conducted to study the soil respiration. With this set up, it is possible to precisely control individual environmental variables (e.g. temperature, O_2 availability), which make it possible to characterize the different abiotic and biotic drivers as well as their interactions on soil respiration. The experimental approach and measurements of incubation experiment are described in section II.3.

II.2 Study site

The study site was La Guette peatland, a transitional acidic poor fen (pH about 4.5) located in central France region Centre Val de Loire (Neuvy-sur-Barangeon, Cher, 47°19' North, 2°14' East; Fig. II-1). The open parts of the peatland extends over twenty hectares with a mean peat thickness of 80 cm and maximum thickness reaching to 180 cm. The mean annual temperature was 6.82 °C and mean annual precipitation was 737.19 mm in the period 2009–2020. Typical plant species of La Guette were *Sphagnum cuspidatum, Sphagnum palustre* and *Sphagnum rubellum*, *Eriophorum augustifolium*, *Erica tetralix* and *Calluna vulgaris*. A road crosses the peatland at the output in the south-west part of the site (Fig. II-1). The presence of this road as well as other facilities (such as pipeline for drinking water supplement and ditch for rainfall drainage) increase the drainage of this peatland (Fig. II-1). As a consequence of the hydrological disturbance and the wild-fire in 1974, 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).

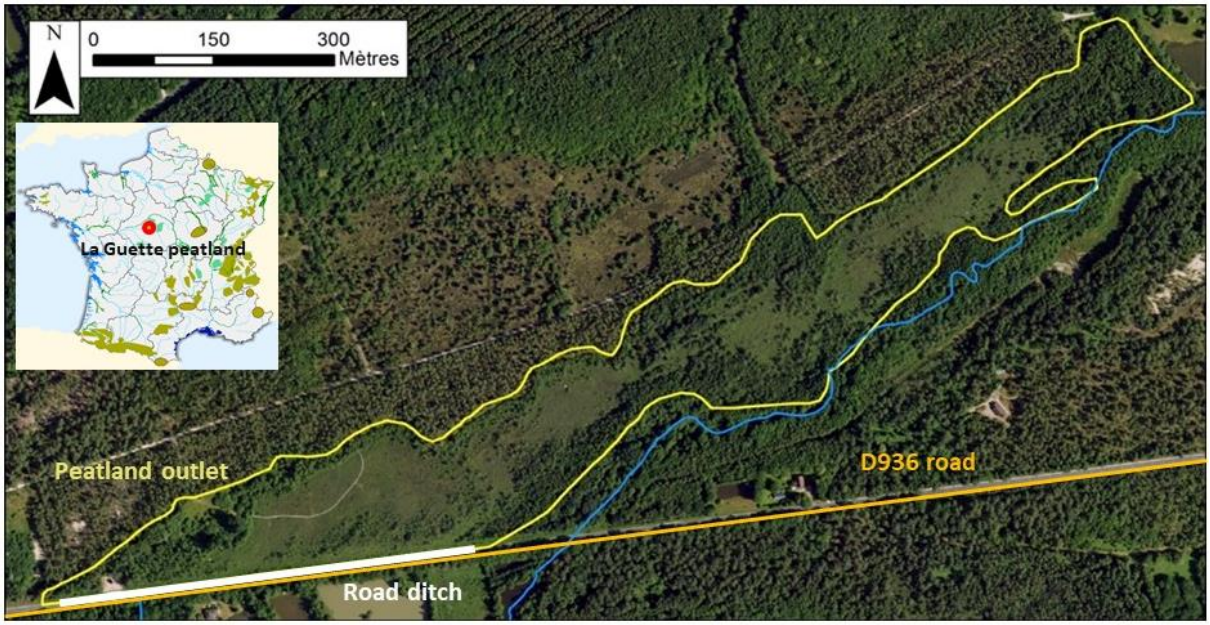

Figure II-1 Location and the map of La Guette peatland.

II.3 Mesocosm experiment

II.3.1 Sampling strategy and experimental approach

Twelve intact cylindrical peat monoliths 40 cm high and 30 cm in diameter (Fig. II-2a), designed following Dieleman et al., (2015) and Fenner et al., (2007), were collected from La Guette peatland in June 2018. The sampling locations were selected to ensure that all the mesocosms contained a representative species assemblage, including mosses, graminoids and ericaceous shrubs, so that the behavior of mesocosms can represent the whole study site. After collection, these mesocosms were sealed at the bottom by fixing PVC boards underneath (Fig. II-2a).

These mesocosms were placed outside the ISTO laboratory in holes dug into the soil and they were isolated from mineral soil with bubble wrap in July 2018 (Fig. II-2b, d). They were randomly separated into two treatments: six with open-top chambers (OTCs), which can increase air temperature and another six without OTCs as control. The OTCs are transparent polycarbonate hexagons, which are made in accordance with the standardized ITEX system (International Toundra 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). They are 60 cm high, the distance between

parallel sides is 150 cm at the top and 210 cm at the bottom. The OTCs are raised 10 cm from the soil surface to let the air circulation and avoid GHG accumulation in chambers (Fig. II-2c). The mesocosms were protected by covering nets above them to avoid the disturbance from birds (Fig. II-2d).

The air temperature was monitored with temperature probes (Campbell Scientific T107, USA) installed near each mesocosms at 10 cm above the surface of soil (Fig. II-7) to examine the warming effect induced by OTCs. The soil temperature at 5, 15 and 30 cm depth were monitored with temperature probes (Campbell Scientific T107, USA) inserted into each mesocosm through the holes on PVC tubes (Fig. II-7), in order to examine the effect of warming on soil in vertical profile. The air temperature increase is expected to influence the evapotranspiration of vegetation and surface peat layer, which would further change the soil moisture. Thereby, the water content of surface *Sphagnum* peat at 5 cm depth was monitored by vertically inserting water moisture probes (Decagon EC-5, METER group USA) into *Sphagnum* part of mesocosms (Fig. II-7). The temperature and relative humidity of the ambient air was monitored by temperature and relative humidity probes (Campbell Scientific CS215, USA), the solar radiation of the ambient environment was monitored by a PAR sensor (SP-LITE pyranometer, Campbell Scientific, USA), the precipitation was monitored by a tipping bucket rain gauge (Campbell Scientific AGR100), the wind speed and direction of the ambient environment were monitored by a wind monitor (Campbell Scientific 05103, USA), and the atmospheric pressure of the ambient environment was monitored by a barometric pressure sensor (Campbell Scientific CS100, USA). These probes were connected to dataloggers (Campbell Scientific CR800, USA) in the weather stations installed near the study site (Fig. II-2d) and the data were recorded every 5 min.

The water supply in mesocosms was mainly from the natural precipitation, but to maintain a similar WTD in all mesocosms during drought summer, water was supplemented by water collected from the drainage ditch near La Guette peatland when necessary, as this water has similar properties as pore water in La Guette peatland (e.g. pH, conductivity). WTD was measured manually by a piezometer installed in each mesocosm every week (Fig. II-7). The percentage cover of each vegetation species: bryophytes (*Sphagnum* spp.), graminoids (*Molinia caerulea* and *Eriophorum augustifolium*) and ericaceous shrubs (*Erica tetralix* and *Calluna vulgaris*) were measured in each mesocosm during the monitoring, and the number of graminoids leaves were recorded.

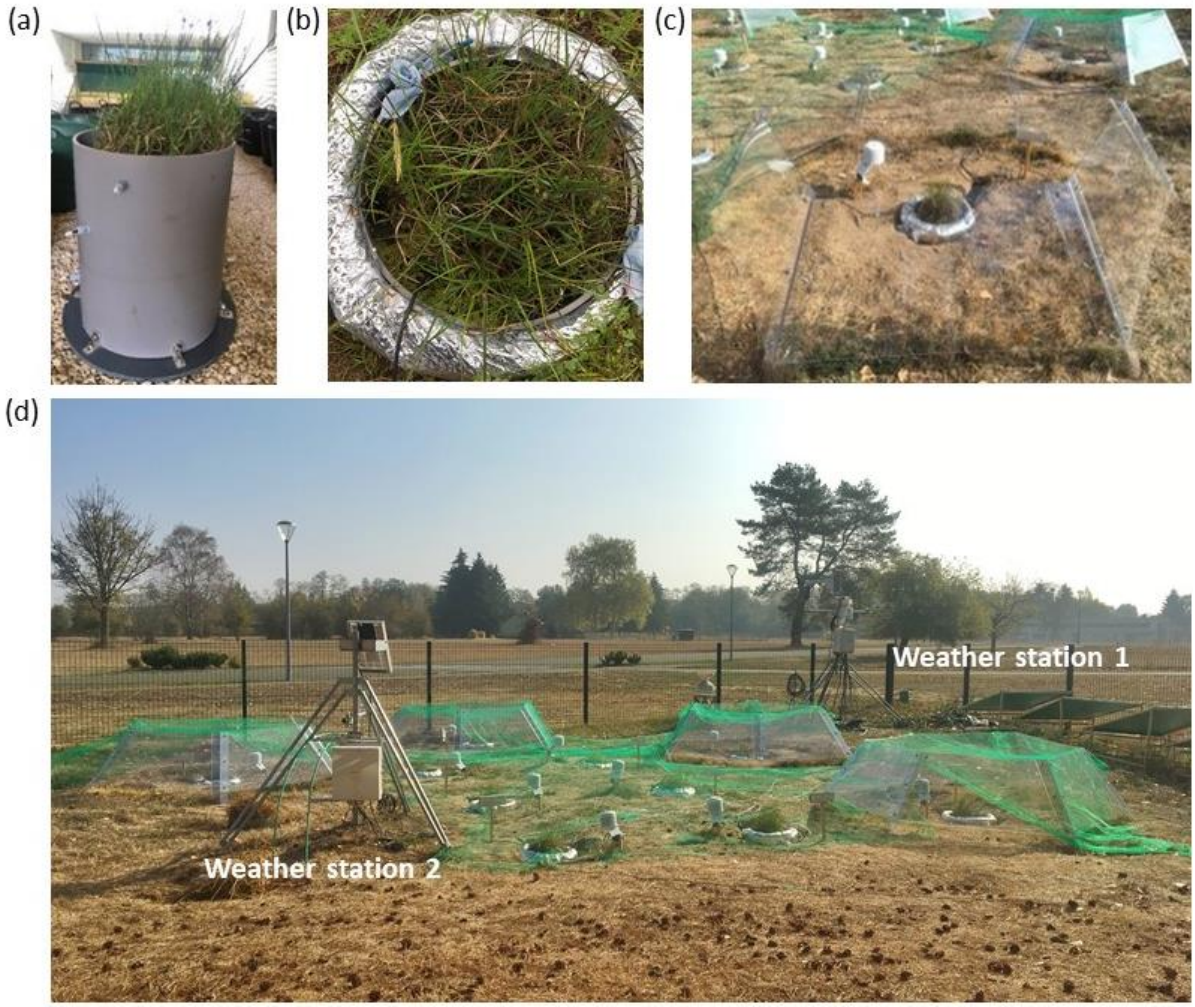

Figure II-2 Mesocosm of 40 cm in thickness and 30 cm in diameter collected from La Guette peatland (a); Mesocosms were buried in mineral soil and isolated by bubble warp from surrounding environment; (b) Mesocosms subjected to warming treatment with Open-top chambers (OTCs); (c) The study site outside of laboratory ISTO for the mesocosms under two treatments (control and OTCs treatment) with two weather stations monitoring the environmental variables (d).

II.3.2 CO_2 and CH_4 fluxes measurements

CO_2 and CH_4 flux measurements were carried out for 2 years from August 2018 to July 2020 at a frequency of twice per month during the growing season (August–October 2018, April–October 2019 and April–July 2020), and once per month in winter (November 2018–March 2019, November 2019–March 2020). However, because of the lockdown of Covid-19, the monitoring between March-May 2020 was stopped. The CO_2 and CH_4 flux measurements were carried out with a static chamber method (e.g. Leroy et al., 2019). The chamber was equipped with a low-speed battery-operated fan to circulate the air inside the chamber during

measurements. Between measurements, the chamber was air-flushed to equilibrate the headspace concentration with that of the ambient air.

The CO_2 measurements were performed using a CO_2 sensor (Vaisala Carbocap GMP343, Finland) inserted into the chamber. The transparent chamber was used to measure the net ecosystem exchange (NEE; Fig II-3a), which is the difference between the ecosystem respiration (ER) and the gross primary production (GPP). The ER was measured by covering the chamber with an opaque cover to prevent the photosynthesis (Fig II-3c). The NEE was measured under different light conditions which were artificially modulated by adding different numbers of plastic nets above the mesocosms (Fig II-4a). In this case, the light response of GPP was assessed and it was used to calculate the GPP modelling parameters (Fig II-4b). During the measurement, the CO_2 concentration (ppm) was recorded every 5 s. The measurements were performed until a clear linear slope of CO_2 concentration versus time was obtained, but for a maximum of 5 min (Fig II-3b, d). During the CO_2 measurements, the air temperature and humidity inside the chamber were also measured with a temperature and humidity meter (Vaisala Humicap HM70, Finland) inserted into the chamber. The photosynthetically active radiation (PAR; mol m^{-2} s^{-1}), which is measured as the photosynthetic photon flux density (PPFD) was measured with a PAR sensor (SDEC JYP 1000, France) placed on the top of chamber. The PAR was measured at the beginning and at the end of each CO_2 measurement, and their mean was used to represent the PAR during this measurement.

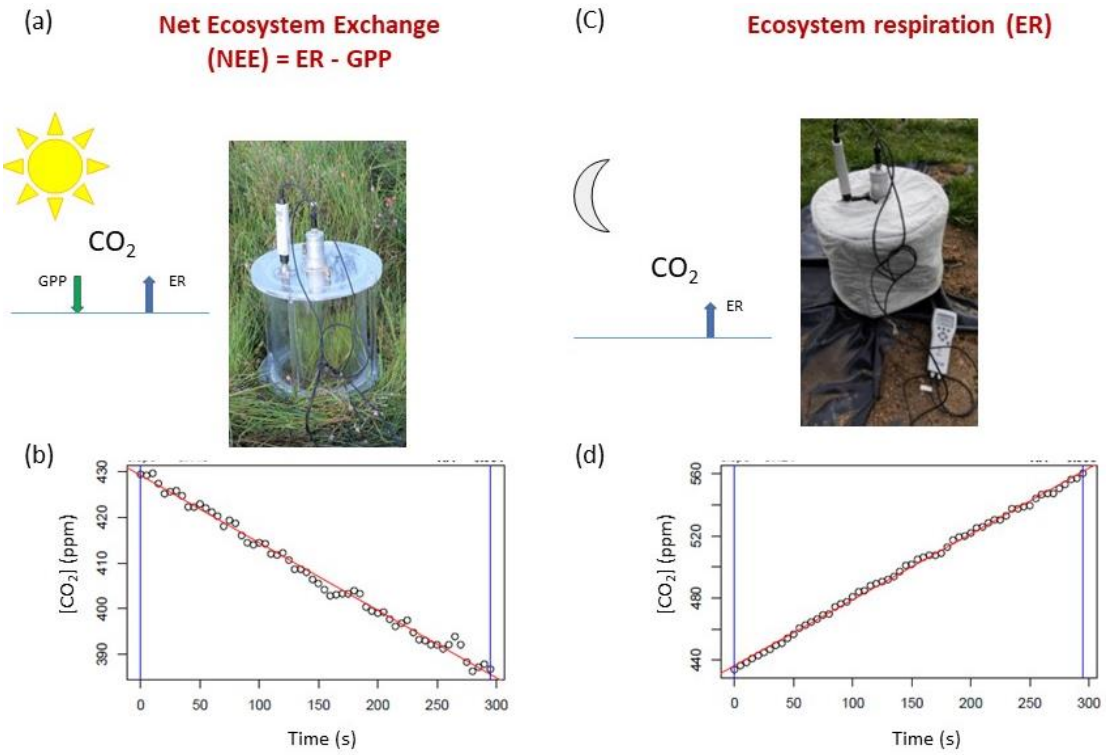

Figure II-3 Measurement of net ecosystem exchange (NEE) with transparent chamber (a) and the corresponding slope of decreasing CO_2 concentration against time which represents the absorption of CO_2 (ppm/s; b); Measurement of ecosystem respiration (ER) and the corresponding slope of increasing CO_2 concentration against time which represents the release of CO_2 (ppm/s; b).

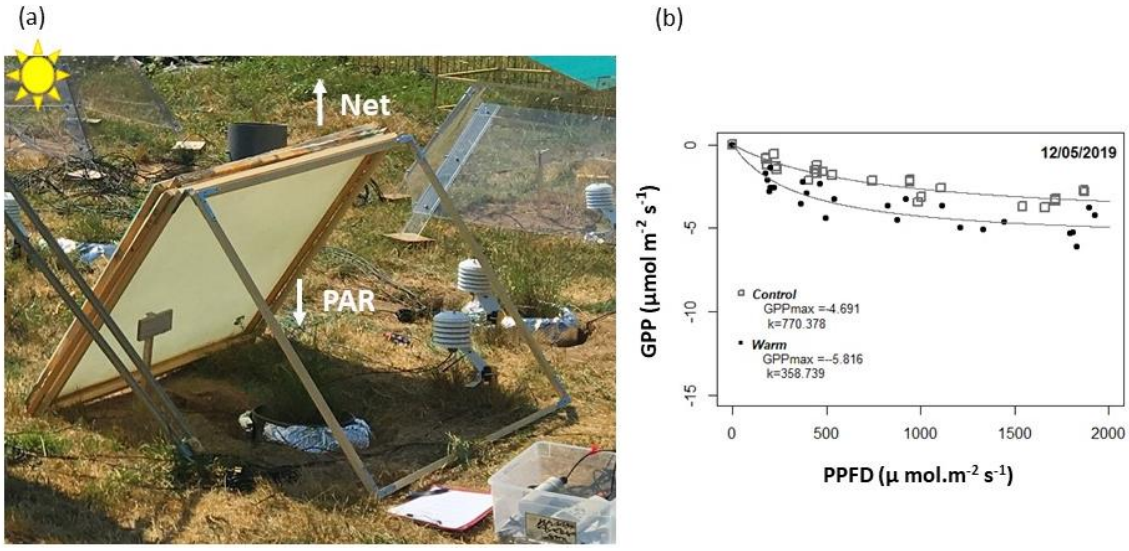

Figure II-4 Measurement of net ecosystem exchange (NEE) with different numbers of nets to decrease the photosynthetically active radiation (PAR) towards mesocosms (a) and the response curve of GPP to varying PPFD (b) was achieved from this measurement.

The CH_4 emissions were measured using a LGR Ultra-portable Greenhouse Gas Analyzer (Los Gatos Research, USA; Fig II-5) connected to the transparent chamber. The measurement of CH_4 concentration (ppm) also lasted until a clear linear slope of CH_4 concentration versus time was obtained, but for a maximum of 5 min. lasted for a maximum of 5 min (Fig II-5b).

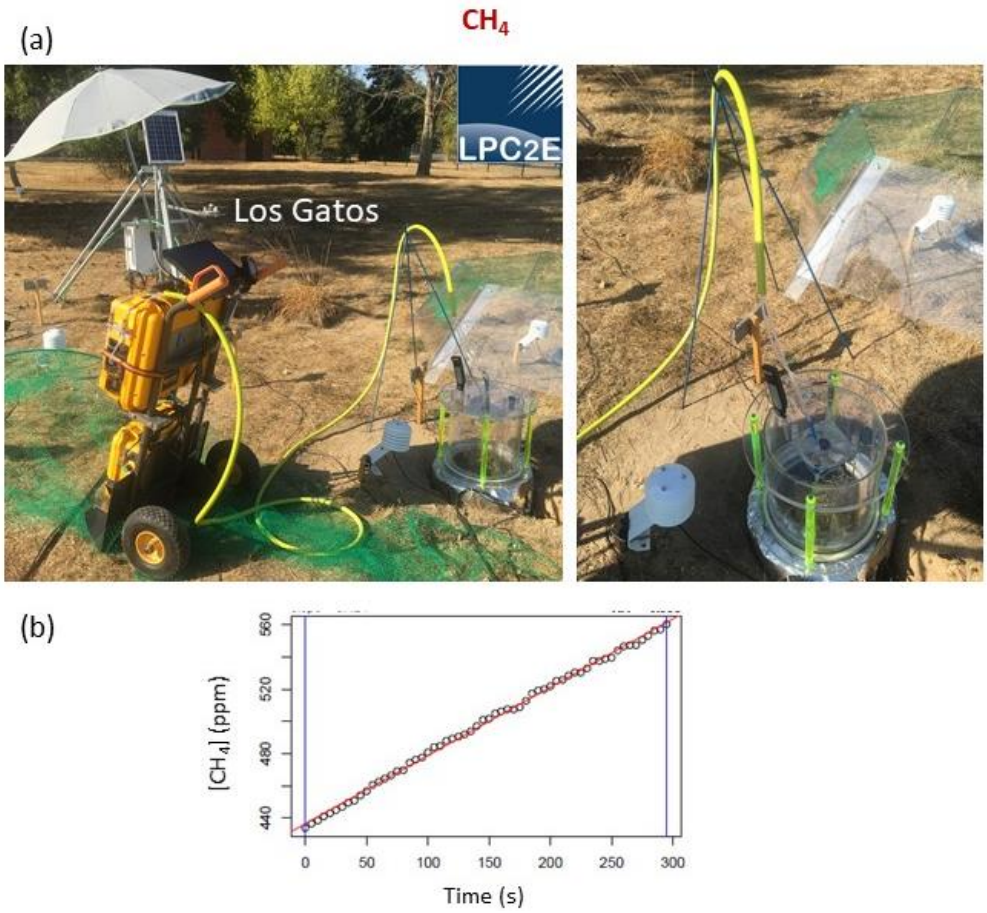

Figure II-5 Measurement of CH_4 was carried out by Los Gatos with a transparent sealed chamber and the slope of increasing CH_4 concentration against time was corresponding to the release of CH_4 (ppm/s).

The CO_2 and CH_4 concentrations measured during the first 30 s of measurement were always excluded to remove the fluctuation caused by the placement of the chamber (e.g. ebullition). If saturation occurred at the end of the measurement, the data were also excluded to keep only the linear slope. If ebullition occurred during the CH_4 measurement, the measurement was repeated to include only the diffusive emissions of CH_4. Atmosphere was regarded as the reference for C fluxes, thus positive values of CO_2/CH_4 fluxes indicated an emission to atmosphere and negative values indicated an uptake by the ecosystem.

The flux of CO_2/CH_4 (μmol m^{-2} s^{-1}) was calculated by Eq.II-1:

$$F_{CO_2/CH_4} = \frac{\left(\frac{V}{A}\right)\times\left(\frac{d_c}{d_t}\right)\times Pat_m}{R\times(T+273.15)} \quad \text{Eq. II-1}$$

where R is the gas constant at 273.15 K (8.314 m^3 Pa K^{-1} mol^{-1}); T is the temperature inside the chamber (°C); V is the volume of the chamber (m^3); A is the surface area of the chamber (m^2); Pat_m is the atmospheric pressure (Pa); dc/dt is the CO_2/CH_4 concentration change against time (ppm s^{-1}) calculated using linear regression.

II.3.3 Pore water sampling and physicochemical analysis

Pore water samples were taken from 3 depths (5, 15 and 30 cm) of mesocosms and analyzed for the 2 years of the monitoring (from August 2018 to July 2020). Before placing mesocosms into the holes dug in the mineral soil, three rhizons (Rhizosphere Research Products) for water collection were inserted into each mesocosm through the holes on PVC tubes at 5, 15 and 30 cm depth (Fig II-7). Then water samples were collected from each mesocosm and considered as T_0. After that, mesocosms were placed in to holes in mineral soil and pore water was sampled after each CO_2 and CH_4 measurement. When sampling pore water, syringes were connected with rhizons, and vacuum has been created in syringes to let water coming out (Fig II-6). After sampling, the pH and conductivity of the samples were measured by pH and conductivity meters. Then samples were filtered at 0.45 μm mesh and stored in vials at 4°C for the measurement of dissolved organic carbon (DOC), aromaticity ($SUVA_{254}$) and natural fluorescence.

DOC, $SUVA_{254}$ and natural fluorescence of pore water samples at T_0 were measured. During the 2 years of monitoring, the DOC and $SUVA_{254}$ were measured after each CO_2 and CH_4 measurement. The natural fluorescence was measured with low frequency (July, September, December in 2018 and April, May, July, September, December in 2019).

Figure II-6 Collection of pore water with syringes from 5, 15 and 30 cm depth of mesocosms.

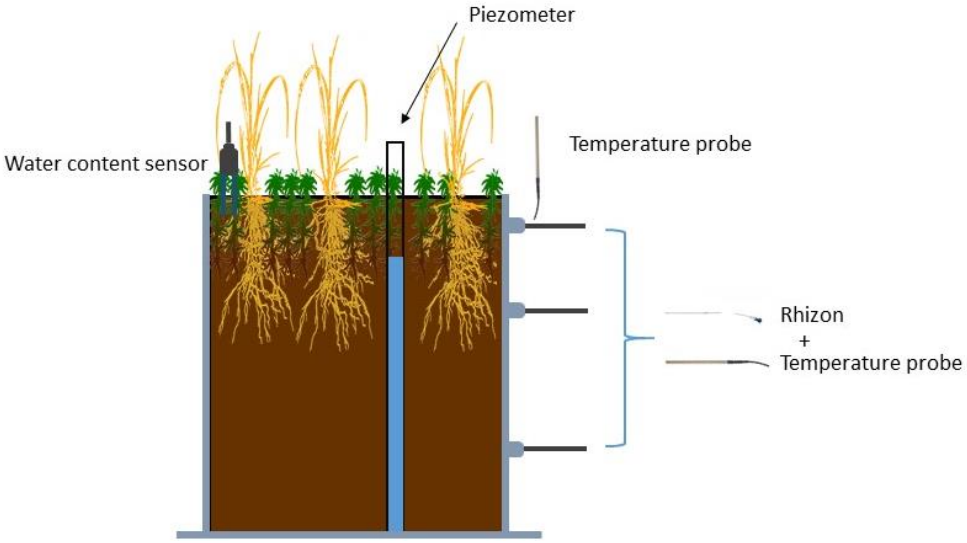

Figure II-7 Mesocosm and the temperature probes installed for monitoring the air temperature at 10 cm above soil surface and soil temperature at 5, 15 and 30 cm depth; water moisture sensor for monitoring the water content at 5 cm of peat; piezometer for the measurement of water table depth (WTD); rhizons installed for the pore water sampling from 5, 15 and 30 cm depth.

II.4 Incubation experiment

Peat samples were taken from a near soil surface layer (5-10 cm) and a subsurface layer (35-40 cm) at four different *Sphagnum* locations on April 2019 in La Guette peatland. The samples from these four locations were used as replicates. The two layers corresponded to less and more decomposed peat, respectively. Eight collected samples were homogenized separately and stored at 4 ^{o}C. Subsamples of 10g from 5-10 cm depth and 30 g from 35-40 cm depth were transferred into 250 mL jars, sealed and vacuumed, then flushed with pure nitrogen (N_2) or air for anaerobic and aerobic incubation (16 for each condition including 2 replicates for each of the 8 collected samples), respectively. The jars were incubated at constant temperature in FitoClima 1200 incubator (Aralab) for 7 days. Each day, 5 mL gas was collected and CO_2 concentration was analyzed by LGR Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, Inc. CA) and replaced by same volume of N_2/air to maintain pressure. These processes were reproduced every week under 7 temperatures between 4 and 28 °C, in 4 °C step. Soil respiration rate was calculated by the linear regression of CO_2 concentration versus time. The temperature sensitivity (Q_{10}) was determined following Lloyd and Taylor, (1994):

Peat total carbon and nitrogen (TC, TN) and water extractable organic carbon (WEOC) of the eight collected samples were measured. Microbial biomass carbon of the eight collected samples and samples after incubation were analysed.

References

Aurela, M., Laurila, T., and Tuovinen, J.-P. (2004). The timing of snow melt controls the annual CO2 balance in a subarctic fen. *Geophys. Res. Lett.* 31. doi:10.1029/2004GL020315.

Bubier, J., Crill, P., and Mosedale, A. (2002). Net ecosystem CO2 exchange measured by autochambers during the snow-covered season at a temperate peatland. *Hydrol. Process.* 16, 3667–3682. doi:10.1002/hyp.1233.

Chapin, F. S., and Bloom, A. (1976). Phosphate Absorption: Adaptation of Tundra Graminoids to a Low Temperature, Low Phosphorus Environment. *Oikos* 27, 111–121. doi:10.2307/3543439.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2009). Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO2 Fluxes in an Alaskan Rich Fen. *Ecosystems* 12, 1329–1342. doi:10.1007/s10021-009-9292-y.

Dabros, A., Fyles, J. W., and Strachan, I. B. (2010). Effects of open-top chambers on physical properties of air and soil at post-disturbance sites in northwestern Quebec. *Plant Soil* 333, 203–218. doi:10.1007/s11104-010-0336-z.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Glob. Change Biol.* 21, 388–395. doi:10.1111/gcb.12643.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., et al. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* 460, 616–619. doi:10.1038/nature08216.

Fenner, N., Ostle, N. J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B., et al. (2007). Elevated CO2 Effects on Peatland Plant Community Carbon Dynamics and DOC Production. *Ecosystems* 10, 635–647. doi:10.1007/s10021-007-9051-x.

Gillett, N. P., Arora, V. K., Matthews, D., and Allen, M. R. (2013). Constraining the Ratio of Global Warming to Cumulative CO2 Emissions Using CMIP5 Simulations. *J. Clim.* 26, 6844–6858. doi:10.1175/JCLI-D-12-00476.1.

Gogo, S., Laggoun-Défarge, F., Delarue, F., and Lottier, N. (2011). Invasion of a Sphagnum-peatland by Betula spp and Molinia caerulea impacts organic matter biochemistry. Implications for carbon and nutrient cycling. *Biogeochemistry* 106, 53–69. doi:10.1007/s10533-010-9433-6.

Henry, G. H. R., and Molau, U. (1997). Tundra plants and climate change: the International Tundra Experiment (ITEX). *Glob. Change Biol.* 3, 1–9. doi:https://doi.org/10.1111/j.1365-2486.1997.gcb132.x.

Hillier, S. H., Sutton, F., and Grime, J. P. (1994). A New Technique for the Experimental Manipulation of Temperature in Plant Communities. *Funct. Ecol.* 8, 755–762. doi:10.2307/2390235.

Hollister, R. D., and Webber, P. J. (2000). Biotic validation of small open-top chambers in a tundra ecosystem. *Glob. Change Biol.* 6, 835–842. doi:10.1046/j.1365-2486.2000.00363.x.

Laggoun-Défarge, F., Gogo, S., Bernard-Jannin, L., Guimbaud, C., Zocatelli, R., Rousseau, J., et al. (2016). Does hydrological restoration affect greenhouse gases emission and plant dynamics in sphagnum peatlands? in.

Laine, A. M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., et al. (2019). Warming impacts on boreal fen CO_2 exchange under wet and dry conditions. *Glob. Change Biol.* 25, 1995–2008. doi:10.1111/gcb.14617.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., et al. (2019). CO_2 and CH_4 budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*. *Biogeosciences* 16, 4085–4095. doi:https://doi.org/10.5194/bg-16-4085-2019.

Lloyd, J., and Taylor, J. A. (1994). On the Temperature Dependence of Soil Respiration. *Funct. Ecol.* 8, 315–323. doi:10.2307/2389824.

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., et al. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.* 3, 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x.

Munir, T. M., Perkins, M., Kaing, E., and Strack, M. (2015). Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water-table-lowering simulations of climate change. *Biogeosciences* 12, 1091–1111. doi:https://doi.org/10.5194/bg-12-1091-2015.

Tissue, D. T., and Oechel, W. C. (1987). Response of Eriophorum Vaginatum to Elevated CO_2 and Temperature in the Alaskan Tussock Tundra. *Ecology* 68, 401–410. doi:10.2307/1939271.

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Glob. Change Biol.* 23, 3121–3138. doi:10.1111/gcb.13563.

Waddington, J. M., Griffis, T. J., and Rouse, W. R. (1998). Northern Canadian Wetlands: Net Ecosystem CO2 Exchange and Climatic Change. *Clim. Change* 40, 267–275. doi:10.1023/A:1005468920206.

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., and Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecol. Lett.* 16, 1285–1293. doi:10.1111/ele.12167.

III. ***Environmental parameters and aboveground vegetation community change under the effect of open-top chambers (OTCs)***

III.1 Introduction

The increasing earth surface temperature and the anticipated greater global warming in the next century have raised the research on terrestrial ecosystem response to the climate change (IPCC 2014), especially those who stored large quantities of carbon, such as peatlands. Their feedbacks to atmosphere under the context of climate warming are of great importance (Gorham, 1991; Page and Baird, 2016), as small changes in the dynamics of carbon (C) cycle may lead to markedly C release and exacerbate the global warming.

The ITEX OTCs was a standard and widely used method for field manipulations of simulated climate warming. Previous studies have reported a rise of mean air temperature ranging from 0.6-3 ^{o}C with OTCs treatment (Hollister et al., 2006; Marion et al., 1997; Walker et al., 2006). This temperature increase was in the range of predicted Earth surface temperature increase by the end of 21st century (IPCC 2014). In addition, OTCs could induce stronger temperature extremes (especially daytime maxima) compared with ambient environment, which could be attributed to less air exchange inside chambers caused by the wind sheltering of OTCs (Bokhorst et al., 2011; Dabros et al., 2010). The response of soil temperature to OTCs varied among experimental sites (Hollister et al., 2006). Marion et al., (1997) detected a warming effect of OTCs on the soil. However, Dabros et al., (2010) found a cooler soil at -12 and -20 cm under OTCs treatment which was caused by the earlier snow thawing and exposure of soil to cold temperature. These studies mainly focus on the soil temperature in subsurface layer, while changes of deeper soil temperature (eg. less than -30 cm) in response to OTCs are less reported. OTCs also affected other microclimate variables such as soil moisture. Dabros et al., (2010) reported a decrease of soil moisture as a consequence of higher evapotranspiration under the increased air temperature induced by OTCs. While no significant effect of OTCs treatment on the soil moisture were observed in the study of Marion et al., (1997). The water loss by evapotranspiration was driven by the microenvironment, such as air temperature, vegetation communities and wind. Thus, both biotic and abiotic factors should be integrated to determine the soil moisture in response to OTCs. Furthermore, the response of vegetation to experimental warming varies among different communities. Vascular plants benefit from the increasing temperature, while the abundance of bryophytes and lichens decreased because of warming (Hollister et al., 2005b, 2005a; Jónsdóttir et al., 2005; Walker et al., 2006). The induced temperature, soil moisture change as well as the shift of vegetation composition would potentially influence the microbial processes and nutrients availability and thus the

belowground pore water chemistry. The pore water pH was strongly associated to the physiology of plants, as *Sphagnum* can release protons (H^+) thus acidifying the environment (Rydin and Jeglum, 2013). Also, the uptake of nutrients by plants was expected to be enhanced by higher temperature (Dabros and Fyles, 2010) and this could impact the conductivity of pore water.

As a consequence of the inconsistent effect of OTCs across regions, climate regimes and vegetation community compositions (Bokhorst et al., 2013; Hollister et al., 2006; Marion et al., 1997; Piikki et al., 2008), the environmental parameters change induced by OTCs should be characterized. In this case, the response of biogeochemical processes (e.g. OM decomposition, plant-plant interactions and plant-soil interactions) under experimental warming can be related and predicted. The objectives of this chapter are to: 1) characterize the air, vertical soil temperature and the surface peat moisture change under the effect of OTCs in mesocosms; 2) determine the response of vegetation communities to experimental warming; 3) examine the effect of OTCs on the pH and conductivity of pore water. The hypothesis are: 1) air temperature and soil temperature at 5 and 15 cm depth will be increased by OTCs, while the soil temperature at 30 cm will not be changed; 2) OTCs will decrease the water content of surface peat at 5 cm by enhancing the evapotranspiration; 3) pH and conductivity of pore water will decrease under OTCs at 5 cm depth; 4) the warming effect induced by OTCs will facilitate the growth of vascular plants (including graminoids and ericaceous shrub) and increase their abundance.

III.2 Materials and methods

III.2.1 Mesocosm experiment, monitoring of environmental variables and vegetation

Mesocosm experiment, sampling strategy, monitoring of environmental variables and vegetation cover were described in II.3.1 chapter.

The soil moisture sensors (Decagon EC-5) were calibrated with peat of different water content. 15 cylindrical peat monoliths (10 cm in diameter and 12 cm in thickness) of water-saturated peat were collected from La Guette peatland. The soil moisture sensors were vertically inserted into each sample and connected with a dataloggers (Campbell Scientific CR800) to monitoring the output value of sensors. These samples were dried at room temperature with a fen to accelerate the dryness. Three of them were randomly selected every week to

gravimetrically determine the volumetric water content (VWC; %). To do so, the wet weight of samples was measured. Then the dry weight was measured after completely drying at 30 °C for more than 72 h. As such, the volumetric water content was calculated. The output millivolt (mV) value of sensors and the gravimetrically determined VWC were corrected with linear regression:$VWC\ (\%) = 575.98 \times mV - 82.581$ (R^2=0.97).

In September 2019, the *Sphagnum* in some mesocosms (two plots under control and one plot under OTCs) were disturbed by birds. To maintain the vegetation communities in mesocosms, new *Sphagnum* were collected from La Guette peatland and put back to the disturbed places. A vegetation Index (VI) was calculated (Eq. III-1) by summing the percentage of vegetation cover in each mesocosm following three distinct plant strata: the bryophytes (*Sphagnum* spp.), graminoids (*Molinia caerulea* and *Eriophorum augustifolium*), and ericaceous shrub (*Erica tetralix* and *Calluna vulgaris*) strata divided by the total potential cover TC (TC = n x 100, n being the number of vegetation strata recorded):

$$VI = \frac{BS+GS+SS}{TC} \quad \text{Eq.III-1}$$

where BS, GS and SS represent the percentages of cover of bryophytes, graminoids and ericaceous shrub strata and TC represents the total maximum potential cover of the three strata.

III.2.2 Sampling and analysis of pH and conductivity

The sampling and analysis of pH and conductivity of pore water were described in II.3.3 chapter.

III.2.3 Data treatment and statistics

The air and soil temperature at 5, 15 and 30 cm depth were recorded every 5 min by datalogger. Extreme values caused by technical problems were removed before data treatment. For air temperature or soil temperature at 3 depths in each mesocosm, the daily mean, maximum and minimum temperature were calculated based on the 5 min dataset. The mean air/soil temperature during August 2018 and July 2020 were calculated based on the daily dataset. The daily mean, maximum and minimum temperature were averaged for each season, then the mean value for each treatment was calculated by averaging each replicate. As such, the difference between control and OTCs treatment was calculated for each season. The daily thermal amplitude was calculated as the difference between daily maximum and minimum temperature.

Then the daily thermal amplitude was averaged for each month. The data treatment was conducted by R 3.6.3 processing software.

Soil water content at 5 cm was also recorded every 5 min by datalogger. First, the extreme values caused by technical problems were removed before data treatment. Then the daily mean water content in each mesocosm was calculated. After, the mean value for each month was calculated based on the daily dataset.

One-way ANOVA was used to determine the effect of OTCs on the daily mean, maximum and minimum air and soil temperature for different seasons by comparing control plots with OTCs plots (R 3.6.3).

III.3 Results

III.3.1 Air and soil temperatures

III.3.1.1 Mean air and soil temperatures and their inter-annual variations

The daily mean air temperature at 10 cm above the soil surface ranged from -1.99 to 34.01 ºC during the 2 years monitoring (Fig. III-1a). On average, it was 0.9 °C higher in OTCs plots than in control plots (14.91±0.14 vs 14.01±0.07 °C; Table III-1). The daily mean soil temperature ranged from 0.28 to 28.30 ºC at 5 cm, from 1.71 to 28.21 ºC at 15 cm and from 2.93 to 27.14 at 30 cm (Fig. III-1b, c and d). On average, the soil temperature was increased 1.35 °C by OTCs at 5 cm depth and 0.92 °C at 15 cm depth. However, at 30 cm it was not significantly affected by OTCs treatment (Table III-1). In addition, the fluctuation of air temperature among different dates was stronger than soil temperature, and fluctuation of soil temperature decreased with depth (Fig. III-1a, b, c and d).

III.3.1.2 Seasonal variations of OTCs effect on air and soil temperatures

OTCs raised the daily mean air temperature in most of the months at the exception of winter months (November and December 2018, January and December 2019 and January 2020; Fig. III-1a and Table III-2). The increase of daily mean air temperature in different seasons ranged from 0.15 to 1.59 ºC with an obvious seasonal change, which was higher in summer and lower in winter. In addition, the daily maximum air temperature was significantly increased in OTCs, which was up to 4.97 ºC during summer 2019. However, there was no significant effect

of OTCs on daily minimum air temperature (Table III-2). Therefore, the increase of daily mean air temperature could be attributed to the enhancement of daily maximum temperature by OTCs.

In comparison of control plots, daily mean soil temperature at 5 cm was increased in OTCs plots during the whole year except spring 2020, and the increase ranged from 0.55 to 1.31 ºC in different seasons (Fig. III-1b and Table III-2). Furthermore, the warming effect of OTCs on daily maximum and minimum soil temperature at 5 cm was also found (increase between 0.62 to 1.81 ºC for maximum and 0.56 to 1.19 ºC for minimum temperature). Nevertheless, the increase of daily maximum soil temperature mainly happened in 2019 and the daily minimum soil temperature was mainly increased out of growing season (Table III-2). Therefore, the increase of daily mean soil temperature at 5 cm can be considered to be a result of the increase of either daily maximum or minimum temperature or both, depending on seasons. A different behavior was found during spring 2020, with no significant difference of OTCs on daily mean, maximum and minimum soil temperature.

The OTCs effect on soil temperature at -15 and -30 cm showed strong seasonal dependence. Significant increase of daily mean, maximum and minimum soil temperature at 15 and 30 cm in OTCs plots occurred simultaneously during autumn and winter (Fig. III-1c, d and Table III-2). While during spring and summer, only daily mean soil temperature at 15 cm was increased during summer 2018 and daily minimum soil temperature at 15 cm was increased during spring and summer 2019. In a vertical profile, the soil warming effect of OTCs decreased with depth. At 15 cm, the increase of daily means soil temperature ranged from 0.50 and 0.68 ºC, and it was between 0.34 to 0.48 ºC at 30 cm (Table III-2).

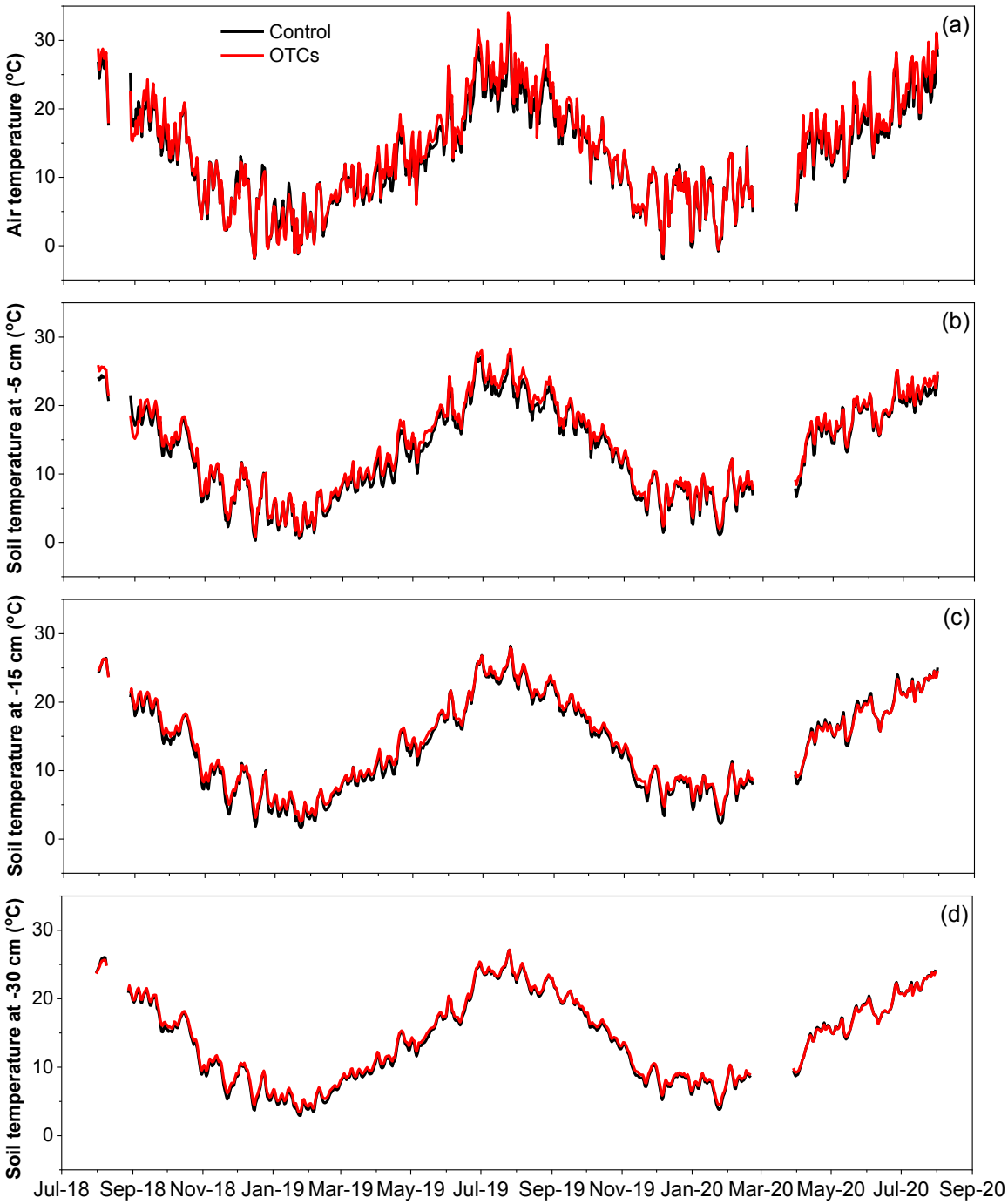

Figure III-1 Daily mean air temperature (°C) at 10 cm above soil surface (a), soil temperature (°C) at 5 cm (b), 15 cm (c) and 30 cm (d) depth of mesocosms under control and OTCs treatments from August 2018 to July 2020.

Table III-1 Mean value of air temperature (Ta), soil temperature (Ts) at 5, 15 and 30 cm, water table depth (WTD) and water content of surface peat at 5 cm depth from August 2018 to July 2020. Significant differences of ANOVAs are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Data are presented as mean ±SD, n=6.

	Mean		Significance
	Control	OTCs	
Ta (ºC)	14.01±0.07	14.91±0.14	***
Ts at 5 cm (ºC)	13.85±0.42	15.20±0.32	**
Ts at 15 cm (ºC)	14.38±0.17	15.30±0.33	**
Ts at 30 cm (ºC)	14.77±0.10	14.94±0.32	
WTD (cm)	-6.80±0.47	-6.68±1.08	
Water content (%)	65.87±3.53	70.71±7.51	

Table III-2 The seasonal averaged differences of daily mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) temperature (°C) between control and OTCs treatments for air temperature at 10 cm above soil surface (ΔTA), soil temperature at 5 cm (ΔTS5), 15 cm (ΔTS15) and 30 cm (ΔTS30) depth of mesocosms in different season from August 2018 to July 2020. Significant differences of one-way ANOVA are expressed as *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ (n=6).

		2018			2019				2020
		Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
ΔTA	**T_{mean}**	1.33***	0.13	0.19	1.49***	1.59***	0.20***	0.15**	1.22**
	T_{max}	4.44***	1.50***	2.04***	4.73***	4.97***	1.20***	1.40***	4.64***
	T_{min}	-0.24	-0.12	-0.26	0.05	0.12	0.08	-0.04	0.21
ΔTS5	**T_{mean}**	1.31**	0.55***	0.59***	1.13**	1.16**	0.60**	0.59***	0.50
	T_{max}	1.73	0.62**	0.57	1.39*	1.81**	0.65****	0.68***	0.89
	T_{min}	0.98	0.61*	0.56*	1.19**	1.12	0.62*	0.57**	0.49
ΔTS15	**T_{mean}**	0.65*	0.68**	0.54***	0.54	0.47	0.65**	0.50***	-0.12
	T_{max}	0.56	0.57***	0.40**	0.38	0.35	0.58**	0.37**	-0.33
	T_{min}	0.75	0.77**	0.65***	0.71**	0.67*	0.70**	0.57**	0.05
ΔTS30	**T_{mean}**	0.28	0.48**	0.41***	0.42	0.22	0.40**	0.34**	-0.05
	T_{max}	0.25	0.47***	0.44***	0.51	0.3	0.41***	0.36**	0.01
	T_{min}	0.29	0.48*	0.38*	0.32	0.05	0.39*	0.34	-0.13

III.3.1.3 Daily thermal amplitude of air and soil temperature

The daily thermal amplitude (difference between daily maximum and minimum value) of air temperature fluctuated strongly during the year, while it was obviously lower for soil temperature and decreased with depth (Fig. III-2). The daily thermal amplitude of air temperature was significantly higher under OTCs treatment in all months during the 2 years of monitoring (Fig. III-2), which was result from the increase of daily maximum air temperature. OTCs treatment had no significant effect on the daily thermal amplitude in soil at 3 depths.

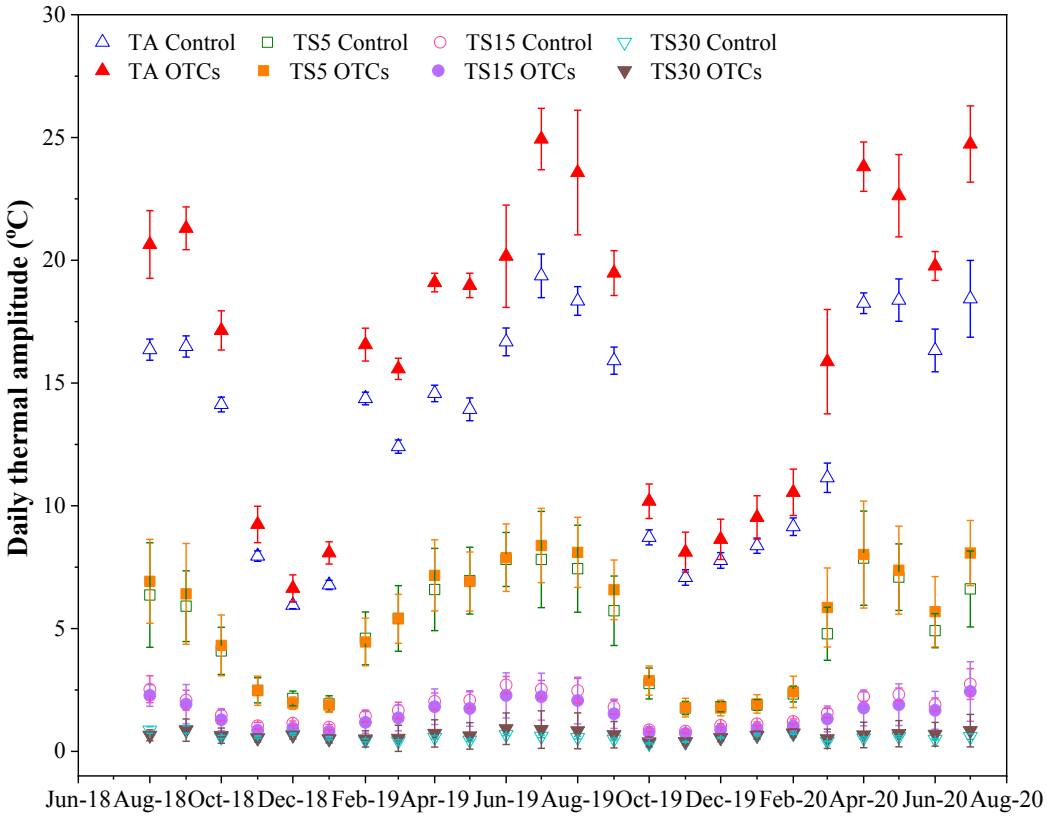

Figure III-2 Monthly averaged daily thermal amplitude (°C) of air temperature (TA) and soil temperature at 5 cm (TS5), 15 cm (TS15) and 30 cm (TS30) depth of mesocosms under control and OTCs treatments in each month from August 2018 to July 2020.

III.3.2 Soil water content

The water content of peat at 5 cm depth varies between 82 to 93 % for both treatments when out of growing season, suggesting the high moisture condition of surface peat most of the time. However, during growing season, water content decreased and reached the lowest values in July 2020 (15.62 ± 5.48 % for control and 22.91 ± 7.75 % for OTCs plots; Fig III-3). The

drier condition in 2020 began from April, while in 2019 it happened from July, suggesting the hotter or drier climate comes earlier and lasts longer in 2020 compared with 2019. OTCs plots showed higher water content than control during the growing season, while no significant differences were found when out of growing season.

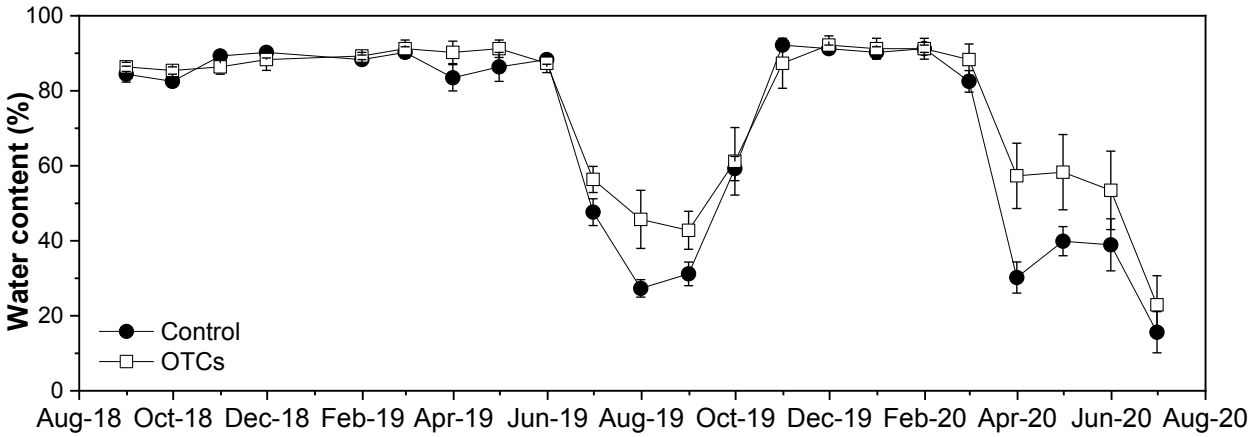

Figure III-3 Monthly averaged daily mean volumetric water content (%) of surface peat at 5 cm depth in mesocosms under control and OTCs treatment from July 2018 to July 2020. Error bar represents the standard error of the mean (SEM).

III.3.3 Water table depth

Water table depth (WTD) of mesocosms ranged from -0.4 to -19 cm during the 2 years of monitoring, with higher level in winter and lower level in summer. The mean WTD was similar between the two treatments (Table III-1). When out of growing season, the water in mesocosms mainly comes from the precipitation, which maintained the WTD above -5 cm most of time. While during growing season, because of high temperature and low frequency of rainfall, water was supplemented by water collected from the drainage ditch near La Guette peatland to maintain a similar water table depth (WTD) in all mesocosms. In summer 2018, water was added manually to mesocosms once in the middle of August. In summer 2019, water was manually added each week or every two weeks during middle of July to middle of August, depends on the detected WTD. After setting up the mesocosms, WTD decreased and reached around -10 ~ -12 cm during July and August for both treatments. While it tended to increase after that and maintained above -7 cm from September 2018 to May 2019. From June 2019, WTD showed a dramatic decline and reached -19 ~ -16 cm during July and August 2019. During this period, there are some extreme drought dates so that the WTD was too low to be

detected, which lead to a data missing in some mesocosms and large difference between the two treatments. In September, WTD increased while it was still low (about - 15 cm). After October 2019, WTD stayed above -5 cm until May 2020 (Fig III-4).

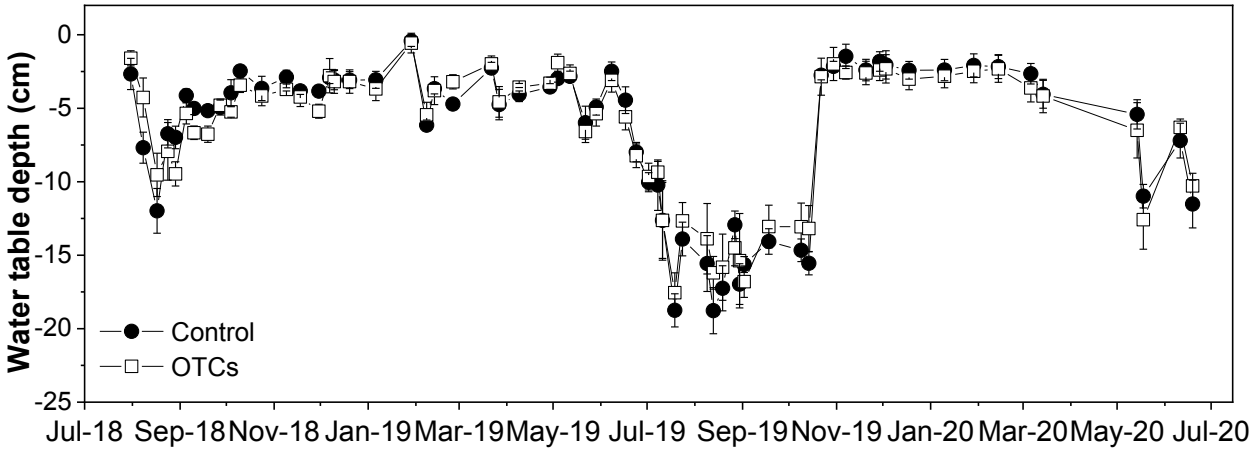

Figure III-4 Water table depth (WTD; cm) in mesocosms under control and OTCs treatment. Error bar represents the standard error of the mean (SEM).

III.3.4 Vegetation

During the whole monitoring period, the percentage cover of *Sphagnum* showed an increasing trend with time. In September 2019, it increased 119.5 % and 104.7 % compared with T_0 for control and OTCs, respectively. However, there was a slight decrease in September 2018 for both treatments. This was caused by the disturbance of *Sphagnum* by birds. In comparison of the two treatments, the *Sphagnum* cover showed no significant difference during the monitoring. The percentage of graminoids (*Molinia caerulea* and *Eriophorum augustifolium*) cover exhibited a trend of increase from installation to September 2018 for both treatments. Then it continually increased under OTCs treatment while showed a slight decrease in control at the end of growing season 2018 (Fig. III-5b), indicating that the warmer temperature in OTCs may extend the green living time of graminoids. In the growing season 2019, the graminoids cover showed a trend of slight increase until September 2019 (Fig. III-5b). There was no significant difference between the two treatments during monitoring. The leaf number of graminoids showed a seasonal variation, with a continually increase during the growing season in both 2018 and 2019 while decrease from the end of September (out of growing season). It was higher in 2019 compared with 2018, with more than double leaves in September 2019 compared with the initial value (2.94 and 2.54 times of T_0 in control and OTCs

plots, respectively; Fig. III-5e). The increase of graminoids leaf number but not their percentage of vegetation cover indicated that their density in specific area increased. A significant higher leaf number in OTCs plots compared with control was found in May 2019 (140 ± 13 in control and 196 ± 21 in OTCs plots; p=0.04), which indicates a faster growth of graminoids under warming treatment. The percentage of ericaceous shrub (*Erica tetralix* and *Calluna vulgaris*) cover maintained constant during monitoring and showed no significant difference between the two treatments (Fig. III-5c).

An gradually increase of vegetation index (VI) with time was found under both control and OTCs treatment (Fig. III-5e). This can be attributed to the increase of the *Sphagnum* cover during monitoring (Fig. III-5a). When comparing the two treatments, the increasing of VI along time under OTCs was stronger than control (increase of 33.1 and 45.5 % in control and OTCs plots, respectively when comparing September 2019 and T_0; Fig. III-5e), suggesting that the warming treatment facilitates the growth of vegetation than ambient temperature. This promotion of vegetation growth by warming treatment mainly results from the facilitation on graminoids and ericaceous cover. In September 2019, the graminoids cover increased 12.1 % and 26.6 % and shrub cover decreased 25.0 % but increased 45.5 % under control and OTCs treatment, respectively (Fig. III-5b and c).

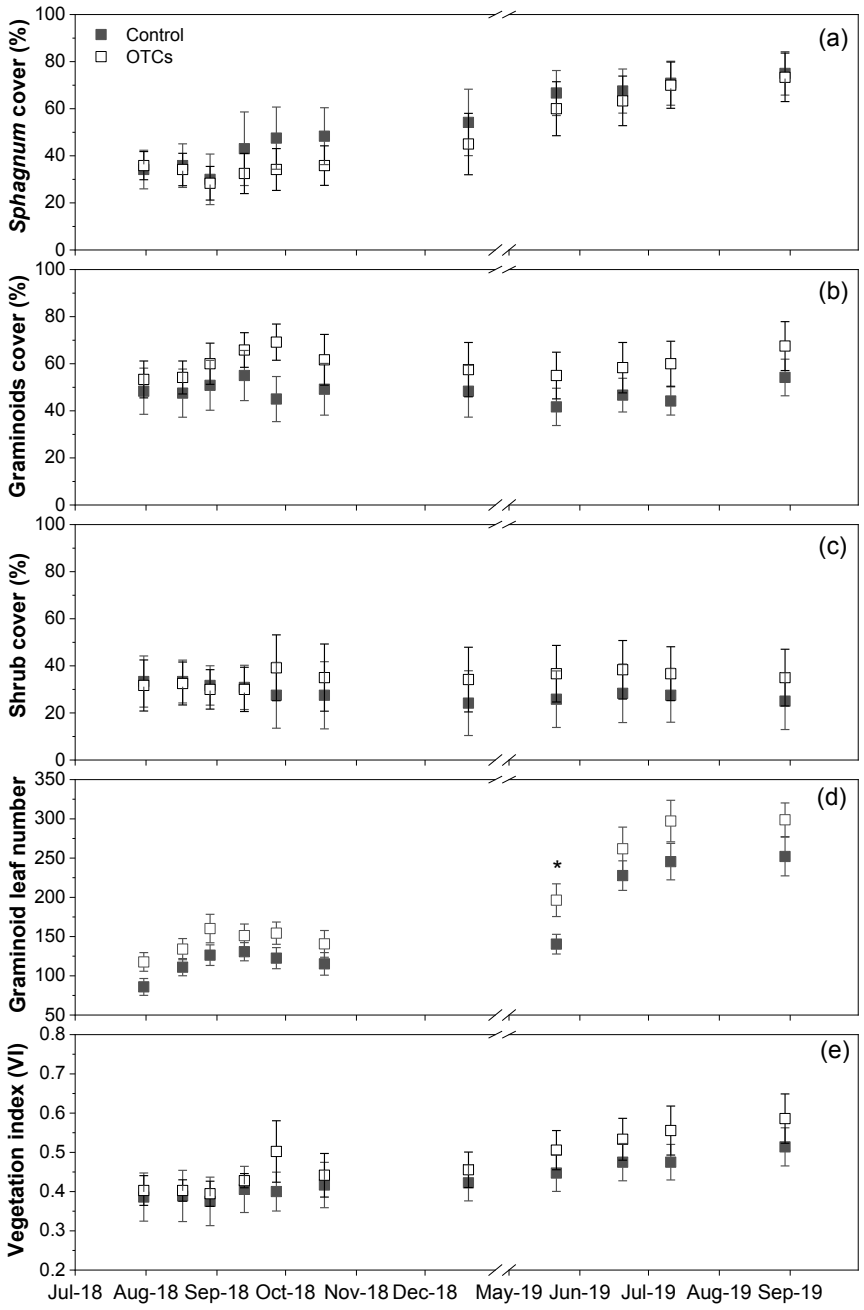

Figure III-5 Percentage cover (%) of bryophytes (*Sphagnum*; a), graminoids (*Molinia caerulea* and *Eriophorum augustifolium*; b) and ericaceous shrubs (c), leaf number of graminoids (*Erica tetralix* and *Calluna vulgaris*; d) and vegetation index (VI; e) from July 2018 to September 2019. Error bar represents the standard error of the mean (SEM). Significant differences of one-way ANOVA are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

III.3.5 pH and conductivity of pore water

pH value of pore water in mesocosms ranged between 3.78 and 4.81 (Fig III-6 a, b, c). The seasonal variation of pH at 3 depths showed different behaviors. pH at 5 cm varied strongly

with season, with high values during winter and low values during summer. The highest pH occurred in December 2018 (4.81 ± 0.11 of control and 4.68 ± 0.05 of OTCs plots) and the lowest occurred in July 2019 (3.85 ± 0.02 of control and 3.95 ± 0.15 of OTCs plots; Fig III-6 a). At -15 cm, pH exhibited similar seasonal variation, ranging from 3.91 to 4.56 (Fig III-6 b). However, the seasonal amplitude of pH at 30 cm was lower than that at 5 and 15 cm, with values ranging from 4.10 to 4.69 (Fig III-6 c). When comparing the two treatments, significant difference was only observed at 5 cm in December 2019 with higher pH in OTCs plots than control (4.17 ± 0.03 and 4.34 ± 0.10 for control and OTCs treatment, respectively; $p<0.05$).

Conductivity of pore water from mesocosms ranged between 52.72 and 169.07 µS/cm (Fig III-7 a, b, c). At 5 cm, conductivity was above 100 µS/cm during September 2018, August and September 2019, which was higher than the other periods of the year. When comparing both treatments, significantly higher conductivity in control plots than OTCs were observed in May (91.34 ± 2.45 and 68.90 ± 2.69 µS/cm for control and OTCs, respectively; $p<0.001$) and June 2019 (71.22 ± 2.14 and 52.72 ± 3.26 µS/cm for control and OTCs, respectively; $p<0.01$; Fig III-7 a). Conductivity at 15 cm ranged from 59.52 and 128.82 µS/cm, with less seasonal variation than at 5 cm. Higher values (>100 µS/cm) were observed in September and December 2018 as well as August and September 2019, while values were below 100 µS/cm during other periods. Significant higher values in control plots than OTCs were found in May (91.20 ± 3.42 and 73.80 ± 2.79 µS/cm for control and OTCs, respectively; $p<0.01$), June (90.55 ± 3.55 and 74.66 ± 2.60 µS/cm at 19th June; $p<0.01$; 89.63 ± 4.05 and 75.82 ± 2.58 µS/cm at 26th June for control and OTCs, respectively; $p<0.05$; Fig III-7 b) and December 2019 (109.85 ± 1.61 and 87.16 ± 8.59 µS/cm for control and OTCs, respectively; $p<0.05$). At 30 cm, the conductivity remains stable and similar for both treatments during the monitoring.

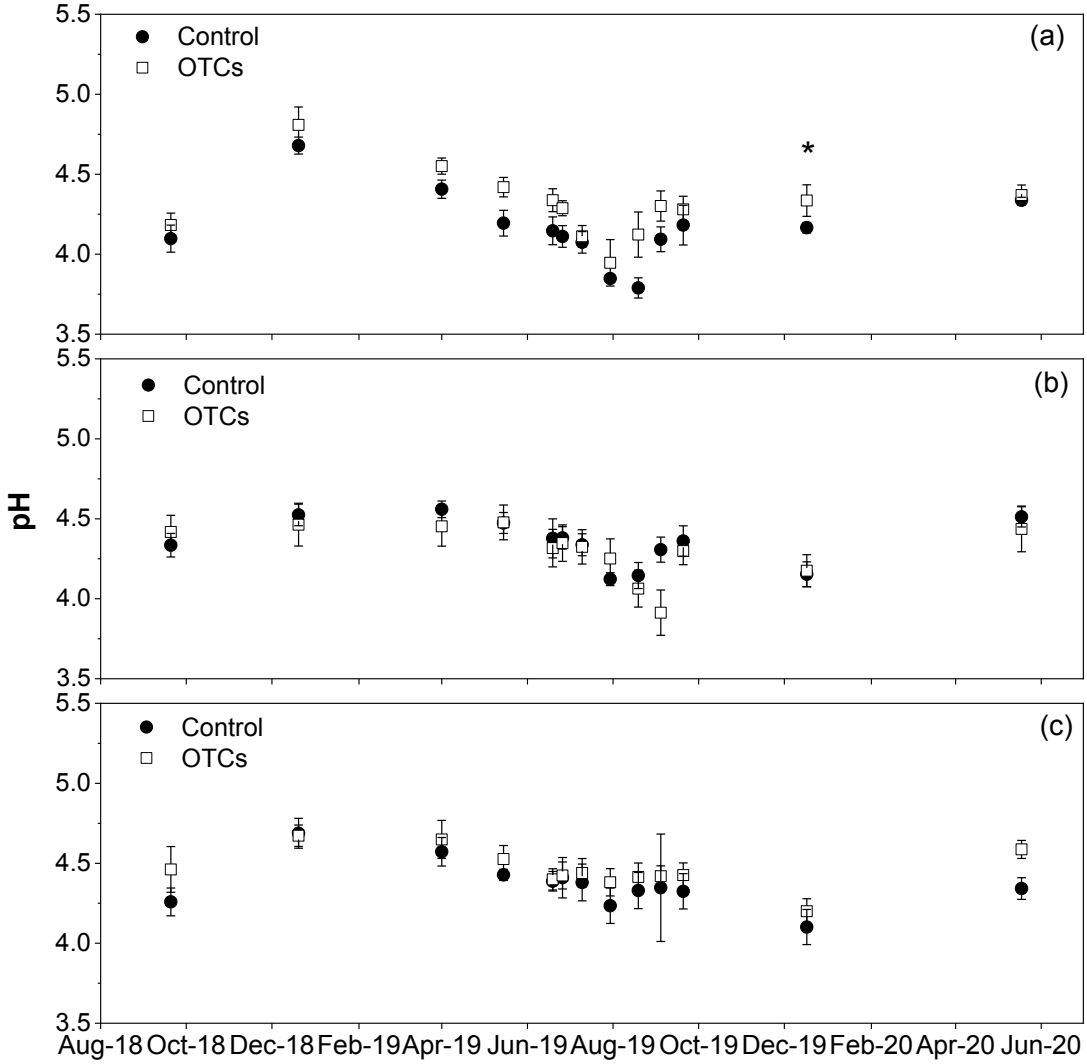

Figure III-6 pH of pore water from 5 (a), 15 (b) and 30 cm (c) of mesocosms under control and OTCs treatment. Error bar represents the standard error of the mean (SEM). Significant differences of one-way ANOVA are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$

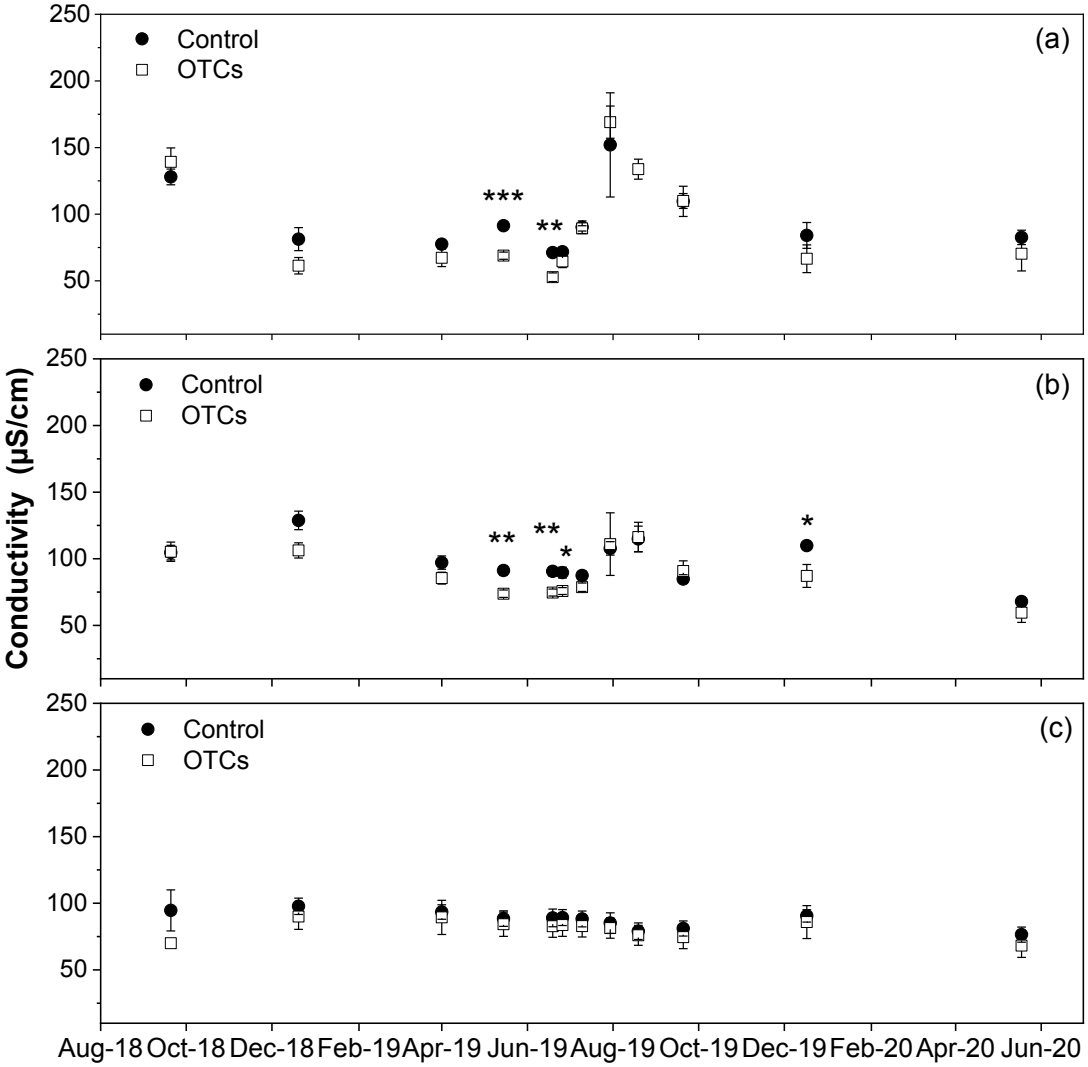

Figure III-7 Conductivity (µS/cm) of pore water from 5 (a), 15 (b) and 30 cm (c) of mesocosms under control and OTCs treatment. Error bar represents the standard error of the mean (SEM). Significant differences of one-way ANOVA are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

III.4 Discussion

III.4.1 Effect of OTCs on air and soil temperatures

The increase of air temperature under OTCs observed in our mesocosms experiment was similar with the *in situ* observation reported by Delarue et al., (2011). Moreover, we found that the increase of daily mean air temperature by OTCs treatment was result from the rise of daily maximum air temperature, but not the daily minimum air temperature. This result was in

agreement with the *in situ* monitoring in the experimental station of Frasne peatland (Delarue et al., 2011). However, the air warming effect of OTCs was stronger in our study compared with the *in situ* monitoring (increase up to 1.84 and 5.33 °C in our study and up to 1.0 and 4.5 °C of *in situ* monitoring for daily mean and maximum air temperature, respectively). In addition, a rise in mean (+ 0.8 °C), maximum (+ 2.3 °C) and minimum (+ 0.4 °C) air temperature by OTCs was observed *in situ* after 2.5 years of monitoring, which indicated that OTCs may need longer time to have significant passive effect. This delay of OTCs effect may be caused by the colder environment *in situ* due to its location in the Jura mountains, which confirmed the dependence of experimental warming effect of OTCs on local climate (Bokhorst et al., 2013).

In our study, an increase of soil temperature at 5 cm depth of mesocosms was observed during the whole monitoring except spring 2020. This result was not supported by the *in situ* monitoring, where an increase of daily mean soil temperature at 7 cm depth was only observed in March and it was caused by the rise of minimum temperature (Delarue et al., 2011). However, Lou et al., (2014) reported an increase of annual peat temperature at 10 cm depth of mesocosms, which is in accordance with our results. The difference between mesocosms experiment and *in situ* monitoring may be caused by the faster heat diffusion of soil in the latter situation. Mesocosms are closed systems, which are isolated from mineral soil by PVC tubes and plastic bubble wrap in our case. Whereas the peat *in sit*u is connected with their surroundings so that the thermal exchange of soil was stronger, which lead to the absence of significant difference between control and OTCs treatment. Additionally, the soil temperature change also related to the water content of soil. Heat diffuses faster in water than in air, thus, lower soil moisture lead to higher resistance to thermal diffusion (Dabros and Fyles, 2010). The soil moisture at 5 cm depth of mesocosms was lower in control than in OTCs plots during growing seasons (Fig III-3), and as such, the drier soil in control plots may result in a decrease of thermal conductivity, which induced the lower soil temperature compared with OTCs plots. The daily thermal amplitude of soil showed no significant differences between the two treatments in our study (Fig. III-2). However Delarue et al., (2011) found that it was significantly lower under OTCs treatment than control at 7 cm peat. These inconsistent results may be attributed to the increase of both daily maximum and minimum soil temperature by OTCs in our study, which offset each other and thus did not change the thermal amplitude. No monitoring of the soil temperature deeper than 7 cm was conducted *in situ*. Thus, it is not possible to compare the deep soil temperature (15 and 30 cm) change of mesocosms with *in situ* monitoring.

When comparing the response of soil temperature to OTCs in different depth, soil temperature at 5 cm responded to OTCs during all year round, while the soil temperature at 15 and 30 cm were only increased when out of growing season. This vertical difference suggested that surface layer of soil are more sensitive to air temperature change than deeper soil layer. Therefore, the change of biochemical processes in surface layer peat should be the priority when investigate the response of ecosystem processes to climate warming.

III.4.2 Soil moisture under OTCs

The seasonal variation of surface peat water content was in accordance with the measured WTD (Fig III-3 and III-4), which was lower during the growing season. This was result from the hot weather and low frequency of precipitation during this season and cold weather combined with higher rainfall during winter, i.e. out of growing season. We hypothesized that the OTCs would decreased the surface peat moisture as the water losses through evapotranspiration would be enhanced by the higher air temperature induced by OTCs (Aerts, 2006; Dabros and Fyles, 2010). However, the observed higher water content with OTCs compared to control during growing season (Fig III-3) was opposite to our hypothesis. The evaporative losses of water from surface peat were controlled by several microenvironmental factors, such as temperature, wind and plants, as well as their interplay (Dabros et al., 2010). Furthermore, the reduction of evaporation as a consequence of the blocking of wind by OTCs was reported in previous study (Boeck et al., 2012). Thereby, the reduction of wind flow through the soil surface caused by OTCs may be a reason for such results. Also, the inconsistent results from different research studies may be caused by their contrasting environment conditions which drive a dominance of different controlling factors. Similar results were found by Delarue et al., (2015) with increased peat moisture under OTCs from *in situ* monitoring. They interpreted the raised surface peat moisture under OTCs by the interactions between air temperature and ground water level. The water table level was a stronger controlling factor on peat moisture in comparison to air temperature, thus the increasing surface peat moisture may be caused by the compensation of capillary flow. These results emphasized that it is necessary to measure the effect of OTCs on the wind speed and direction in the further OTCs experiments. Moreover, the interactions between microenvironmental parameters and vegetation communities should be determined to better understand the effect of OTCs on surface soil moisture.

III.4.3 Vegetation communities change under OTCs

OTCs did not induce a significant change of vegetation communities within the 2 years monitoring. This is inconsistent with previous studies which reported a significant effect of OTCs on plant species including bryophytes, graminoids and shrubs (Buttler et al., 2015; Hollister et al., 2005b; Jónsdóttir et al., 2005; Walker et al., 2006). However, these studies found the response of plant communities to OTCs treatment after 3-8 years monitoring, indicating that the length of our experiment (2 years) may be not long enough to have noticeable effect on vegetation. This result indicated that the duration of treatment play an important role in determining the response of vegetation species to moderate warming. Although no significant effect on the vegetation was observed, the increase of vegetation index (VI) with time was stronger under OTCs treatment compared with control. This was result from the stronger increase of graminoids and shrub cover with OTCs, while the increase of *Sphagnum* species was lower in OTCs plots than control. This trend was consistent with previous results that vascular plants take more advantage of warming than bryophytes, thus elevated temperature enhanced the abundance of vascular plant but decreased the bryophytes (Hollister et al., 2005b; Jónsdóttir et al., 2005; Walker et al., 2006). The variability of experimental warming effect on the growth patterns among different community species indicated that each species responded individually to the changing environment (Hollister et al., 2005a). Inherent differences with respect to species adaptations to environmental conditions may be responsible for the various response of species to experimental warming, with some conditions that were beneficial to specific species but detrimental to others. Hollister et al., (2005b) examined the short-term (after two growing seasons) and long-term (after three to five growing seasons) plant response to experimental warming. They found that the short-term vegetation response to warming mainly lead to a modification in growth depends on the initial state of vegetation cover, while in long-term the competitive interactions between different species also affect the plant composition change. Therefore, to understand how the plant community will respond to experimental warming in specific site, longer time monitoring is necessary.

III.4.4 Effect of OTCs on pH and conductivity of pore water

Significant seasonal variations of pH at 5 and 15 cm depths of mesocosms were observed, but the inter-annual amplitude of pH at 30 cm (out of rhizosphere) was low. This result suggested that the pH of pore water is strongly influenced by the vegetation and their litters/roots. *Sphagnum* has the capacity to capture mineral cations (e.g. K^+, Ca^{2+}, and NH_4^+) by

releasing protons (H^+) thus acidify the environment (Rydin and Jeglum, 2013). This mechanism could explain the lower values of pH during growing season when the physiological activities of *Sphagnum* was high compared with the higher values in winter at 5 cm depth. The pH at 15 cm depth showed similar but slighter seasonal variations as this layer is farther to the surface than at 5 cm, thus was less impacted by *Sphagnum*. However, due to the transfer of ions from surface peat, pH in this layer also showed a seasonal change. In addition, the low WTD and water content at 5 cm depth in summer may also be responsible, at least partly, for the decreasing pH in the same period. The reduction of pH in peatlands as a consequence of drought was reported before (Juckers and Watmough, 2014; Tipping et al., 2003). Moreover, the lower soil moisture of at 5 cm depth would lead to the higher concentration of H^+ and thus lower pH.

The inter-annual variation of conductivity decreased with depth, suggesting it is also linked with vegetation and their litters/roots. The large increase of conductivity at 5 cm depth in summer 2019 for both treatments was surprising, as it was expected to decrease because plants take up larger amount of nutrients during growing season compared with winter. However, some previous research reported an increase of metal ions concentration in pore water with the decreasing pH, as the higher H^+ concentration at low pH level compete with metal ions for binding sites on peat, which lead to more free metal ions in pore water (Adkinson et al., 2011; Brown et al., 2000; Sader et al., 2011; Tipping et al., 2003). In addition, the lower water content at 5 cm depth lead to the condensation of ions, which may also contributed to the increased conductivity in summer. Lower conductivity under OTCs treatment was observed at 5 and 15 cm depths during May and June in comparison with control. As graminoids leaf number was significantly higher in OTCs plots than control in May 2019, thus the lower conductivity may result from the stronger plants uptake of nutrients during early growing season under OTCs treatment.

III.5 Conclusion

During the monitoring of 2 years, an increase of air and soil temperature by OTCs was observed. OTCs increased the mean air temperature and its daily amplitude, which was caused by the increase of daily maximum temperature. The response of soil temperature to OTCs treatment varied with depth. Soil temperature at 5 cm was raised in the whole year, while at 15 and 30 cm it was only increased out of growing season. Peat moisture at 5 cm depth was higher in OTCs plots compared with control during growing season. The vegetation community was not changed by OTCs, while the increase of graminoids and shrub cover over time was stronger

under OTCs treatment than control, but *Sphagnum* showed opposite trend. The pore water pH and conductivity was strongly impacted by vegetation, thus at 5 and 15 cm depths they showed strong seasonal variation, but maintained constant at 30 cm. pH under the two treatments was not significantly different. Conductivity at 5 and 15 cm was lower with OTCs than control in May and June 2019. This result corresponded to the higher graminoids leaf number in the same period which lead to a higher nutrient uptake and thus lower conductivity of pore water.

Our results confirmed that the OTCs efficiently induced a moderate air temperature increase of about 1 ^{o}C, which was in the range of predicted Earth surface temperature increase by the end of 21st century (IPCC, 2014). Therefore, using of this device allow us to simulate the climate warming. However, to assess the plant community change in response to warming, long-term monitoring is necessary. The examination of air, soil temperature, above ground vegetation, as well as the belowground pore water chemistry could bring us information which would help to address the change of CO_2 and CH_4 fluxes (Chapter IV) and DOC pool (Chapter V) of this ecosystem.

References

Adkinson, A.C., Syed, K.H., Flanagan, L.B., 2011. Contrasting responses of growing season ecosystem CO2 exchange to variation in temperature and water table depth in two peatlands in northern Alberta, Canada. Journal of Geophysical Research: Biogeosciences 116. doi:10.1029/2010JG001512

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology 94, 713–724. doi:10.1111/j.1365-2745.2006.01142.x

Boeck, H.J.D., Groote, T.D., Nijs, I., 2012. Leaf temperatures in glasshouses and open-top chambers. New Phytologist 194, 1155–1164. doi:10.1111/j.1469-8137.2012.04117.x

Bokhorst, S., Huiskes, A., Aerts, R., Convey, P., Cooper, E.J., Dalen, L., Erschbamer, B., Gudmundsson, J., Hofgaard, A., Hollister, R.D., Johnstone, J., Jónsdóttir, I.S., Lebouvier, M., Vijver, B.V. de, Wahren, C.-H., Dorrepaal, E., 2013. Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. Global Change Biology 19, 64–74. doi:10.1111/gcb.12028

Bokhorst, S., Huiskes, A., Convey, P., Sinclair, B.J., Lebouvier, M., Van de Vijver, B., Wall, D.H., 2011. Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. Polar Biology 34, 1421–1435. doi:10.1007/s00300-011-0997-y

Brown, P.A., Gill, S.A., Allen, S.J., 2000. Metal removal from wastewater using peat. Water Research 34, 3907–3916. doi:10.1016/S0043-1354(00)00152-4

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., Bragazza, L., 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. Journal of Vegetation Science 26, 964–974. doi:10.1111/jvs.12296

Dabros, A., Fyles, J.W., 2010. Effects of open-top chambers and substrate type on biogeochemical processes at disturbed boreal forest sites in northwestern Quebec. Plant and Soil 327, 465–479. doi:10.1007/s11104-009-0077-z

Dabros, A., Fyles, J.W., Strachan, I.B., 2010. Effects of open-top chambers on physical properties of air and soil at post-disturbance sites in northwestern Quebec. Plant and Soil 333, 203–218. doi:10.1007/s11104-010-0336-z

Delarue, F., Buttler, A., Bragazza, L., Grasset, L., Jassey, V.E.J., Gogo, S., Laggoun-Défarge, F., 2015. Experimental warming differentially affects microbial structure and activity in two contrasted moisture sites in a Sphagnum-dominated peatland. Science of The Total Environment 511, 576–583. doi:10.1016/j.scitotenv.2014.12.095

Delarue, F., Laggoun-Défarge, F., Buttler, A., Gogo, S., Jassey, V.E.J., Disnar, J.-R., 2011. Effects of short-term ecosystem experimental warming on water-extractable organic matter in an ombrotrophic Sphagnum peatland (Le Forbonnet, France). Organic Geochemistry 42, 1016–1024. doi:10.1016/j.orggeochem.2011.07.005

Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecological Applications 1, 182–195. doi:10.2307/1941811

Hollister, R.D., Webber, P.J., Bay, C., 2005a. Plant Response to Temperature in Northern Alaska: Implications for Predicting Vegetation Change. Ecology 86, 1562–1570. doi:10.1890/04-0520

Hollister, R.D., Webber, P.J., Nelson, F.E., Tweedie, C.E., 2006. Soil Thaw and Temperature Response to Air Warming Varies by Plant Community: Results from an Open-top Chamber Experiment in Northern Alaska. Arctic, Antarctic, and Alpine Research 38, 206–215. doi:10.1657/1523-0430(2006)38[206:STATRT]2.0.CO;2

Hollister, R.D., Webber, P.J., Tweedie, C.E., 2005b. The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. Global Change Biology 11, 525–536. doi:10.1111/j.1365-2486.2005.00926.x

IPCC (2014). Climate Change 2014: Synthesis Report. Pachauri, R.K., Allen, M.R., Barros, V.R., Broome, J., Cramer, W., Christ, R., Church, J.A., Clarke, L., Dahe, Q., Dasgupta, P., Dubash, N.K., Edenhofer, O., Elgizouli, I., Field, C.B., Forster, P., Friedlingstein, P., Fuglestvedt, J., Gomez-Echeverri, L., Hallegatte, S., Hegerl, G., Howden, M., Jiang, K., Jimenez Cisneroz, B., Kattsov, V., Lee, H., Mach, K.J., Marotzke, J., Mastrandrea, M.D., Meyer, L., Minx, J., Mulugetta, Y., O'Brien, K., Oppenheimer, M., Pereira, J.J., Pichs-Madruga, R., Plattner, G.-K., Pörtner, H.-O., Power, S.B., Preston, B., Ravindranath, N.H., Reisinger, A., Riahi, K., Rusticucci, M., Scholes, R., Seyboth, K., Sokona, Y., Stavins, R., Stocker, T.F., Tschakert, P., van Vuuren, D., van Ypserle, J.-P., 2014. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change, EPIC3Geneva, Switzerland, IPCC, 151 p., pp. 151, ISBN: 978-92-9169-143-2. IPCC, Geneva, Switzerland.

Jónsdóttir, I.S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., Hjartarson, H., 2005. Variable sensitivity of plant communities in Iceland to experimental warming. Global Change Biology 11, 553–563. doi:10.1111/j.1365-2486.2005.00928.x

Juckers, M., Watmough, S.A., 2014. Impacts of simulated drought on pore water chemistry of peatlands. Environmental Pollution 184, 73–80. doi:10.1016/j.envpol.2013.08.011

Lou, X.-D., Zhai, S.-Q., Kang, B., Hu, Y.-L., Hu, L.-L., 2014. Rapid Response of Hydrological Loss of DOC to Water Table Drawdown and Warming in Zoige Peatland: Results from a Mesocosm Experiment. PLOS ONE 9, e109861. doi:10.1371/journal.pone.0109861

Marion, G.M., Henry, G.H.R., Freckman, D.W., Johnstone, J., Jones, G., Jones, M.H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A.N., Svoboda, J., Virginia, R.A., 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems. Global Change Biology 3, 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x

Page, S.E., Baird, A.J., 2016. Peatlands and Global Change: Response and Resilience. Annual Review of Environment and Resources 41, 35–57. doi:10.1146/annurev-environ-110615-085520

Piikki, K., De Temmerman, L., Högy, P., Pleijel, H., 2008. The open-top chamber impact on vapour pressure deficit and its consequences for stomatal ozone uptake. Atmospheric Environment 42, 6513–6522. doi:10.1016/j.atmosenv.2008.04.014

Rydin, H., Jeglum, J.K., 2013. The Biology of Peatlands, 2e. OUP Oxford.

Sader, J.A., Hattori, K., Hamilton, S., Brauneder, K., 2011. Metal binding to dissolved organic matter and adsorption to ferrihydrite in shallow peat groundwaters: Application to diamond exploration in the James Bay Lowlands, Canada. Applied Geochemistry 26, 1649–1664. doi:10.1016/j.apgeochem.2011.04.022

Tipping, E., Smith, E.J., Lawlor, A.J., Hughes, S., Stevens, P.A., 2003. Predicting the release of metals from ombrotrophic peat due to drought-induced acidification. Environmental Pollution 123, 239–253. doi:10.1016/S0269-7491(02)00375-5

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103, 1342–1346. doi:10.1073/pnas.0503198103

IV. ***Effect of warming on the CO_2 and CH_4 fluxes and C balance of peatlands***

IV.1 CO_2 and CH_4 fluxes and their temperature sensitivity under experimental warming

IV.1.1 Introduction

Temperature is a central control on the metabolic processes related to both photosynthetic and ER processes (Lloyd and Taylor , 1994; Medlyn et al., 2002; Weltzin et al., 2000). Thus, all these processes could be accelerated by the increasing temperature and resulting in the alteration of C balance in peatlands. The response of CO_2 exchange and CH_4 emission to the projected climate warming are widely studied in different types of peatlands with various approaches (e.g. Chivers et al., 2009; Dieleman et al., 2015; Dorrepaal et al., 2009; Flanagan and Syed, 2011; Laine et al., 2019; Voigt et al., 2017). However, their results varied largely due to the differences in vegetation type and climate regime. In addition, few of them investigated the temperature sensitivity of C fluxes in response to warming. Temperature sensitivity of C fluxes, which indicates the precise response of C fluxes to temperature change, is an important parameter in the ecosystem models (Knorr et al., 2005). One of the major indicator for temperature sensitivity is the $Q_{10,}$ representing how much the rate of processes change with a temperature increase of 10 ^{o}C. Thus, understanding how the Q_{10} of C fluxes respond to elevated temperature could help to predict precisely the feedback of C cycle in a warmer climate.

In this study, to examine the response of CO_2 exchange, CH_4 emission as well as their temperature sensitivity to experimental warming, a mesocosms experiment was conducted. As indicated before, peat mesocosms from a temperate *Sphagnum* peatland which was invaded by vascular plants (especially *Molinia caerulea*) were submitted to two temperature treatments: ambient (Control) and moderate experimental warming by open-top chambers (OTCs). GPP, ER and CH_4 emission were measured for 2 years, air and soil temperature at 3 depths (5, 15 and 30 cm) were monitored. The temperature sensitivity of C fluxes was calculated under both treatments. Our objectives were to 1) determine the response of CO_2 and CH_4 fluxes to experimental warming; 2) the temperature sensitivity of GPP, ER and CH_4 emission under warming treatment.

IV.1.2 Materials and methods

IV.1.2.1 Experimental design and sampling strategy

The sampling and mesocosms experiment were described in section II.3.1.

IV.1.2.2 CO_2 and CH_4 fluxes measurements

The method of CO_2 and CH_4 flux measurements was described in section II.3.2. The measurement of NEE (Net Ecosystem Exchange) and ER (Ecosystem Respiration) was conducted under full light (PAR > 1000 μmol m^{-2} s^{-1}) and the GPP (Gross Primary Production) was calculated as the sum of NEE and ER.

IV.1.2.3 Temperature sensitivity of CO_2 and CH_4 fluxes

The measured GPP, ER and CH_4 emission were related to the air and soil temperature at 5 cm, 15 cm and 30 cm depth with exponential regression. The exponential regression was fitted for each mesocosm under both treatment individually. Temperature sensitivity was expressed through the temperature coefficient (Q_{10}) and it was calculated for each mesocosm separately (Lloyd and Taylor, 1994):

$$Q_{10} = e^{10b} \quad \text{Eq.IV-1}$$

where b is derived from the van't Hoff equation which described the exponential relationship between C fluxes and temperature as follow:

$$k = ae^{bT} \quad \text{Eq.IV-2}$$

where k is the GPP, ER or CH_4 emission fluxes; T is temperature (^oC); and a and b are fitting parameters.

IV.1.2.4 Statistics

The differences of GPP, ER, NEE and CH_4 emission between control and OTCs plots in different periods of growing season [early growing season (EG; April-May), middle growing season (MG: June-August), late growing season (LG: September) and the whole growing season in 2019 (WG: April-September)] were analyzed with two way repeated measure

ANOVA, with time as within subject and control/warming treatment as between-group factor. The difference of annual air and soil temperature and Q_{10} under control and OTCs treatment were tested by one-way ANOVA. The nonlinear regression of GPP, ER, CH_4 emission with temperature were analyzed in R (R 3.6.3, R Core Team 2020).

IV.1.3 Results

IV.1.3.1 Measured CO_2 and CH_4 fluxes

GPP and ER showed significant seasonal variations with high absolute values during summer and low absolute values during winter (Fig. IV-1a and b). NEE, the balance between GPP and ER, showed negative values (Fig. IV-1c), which indicate a net uptake of CO_2. NEE also varied with seasons with lower values during summer and higher values in winter, suggesting that the mesocosms acted as a stronger CO_2 sink in summer than in winter. The experimental warming effect on the CO_2 fluxes depends on the periods (Fig. IV-1a, b and c). The GPP was significantly enhanced by OTCs during early growing season (EG; $p < 0.001$) and late growing season (LG; $p < 0.05$) in 2019, while no significant difference was observed in 2018 ($p = 0.41$), during middle growing season in 2019 (MG; $p = 0.60$) and the whole growing season in 2019 (WG; $p = 0.21$; Fig. IV-1a). The ER was significantly increased by OTCs during LG 2018 ($p < 0.01$), EG ($p < 0.05$) and LG 2019 ($p < 0.01$; Fig. IV-1b). The significant effect of OTCs on NEE was only found in EG 2019 ($p < 0.01$; Fig. IV-1c).

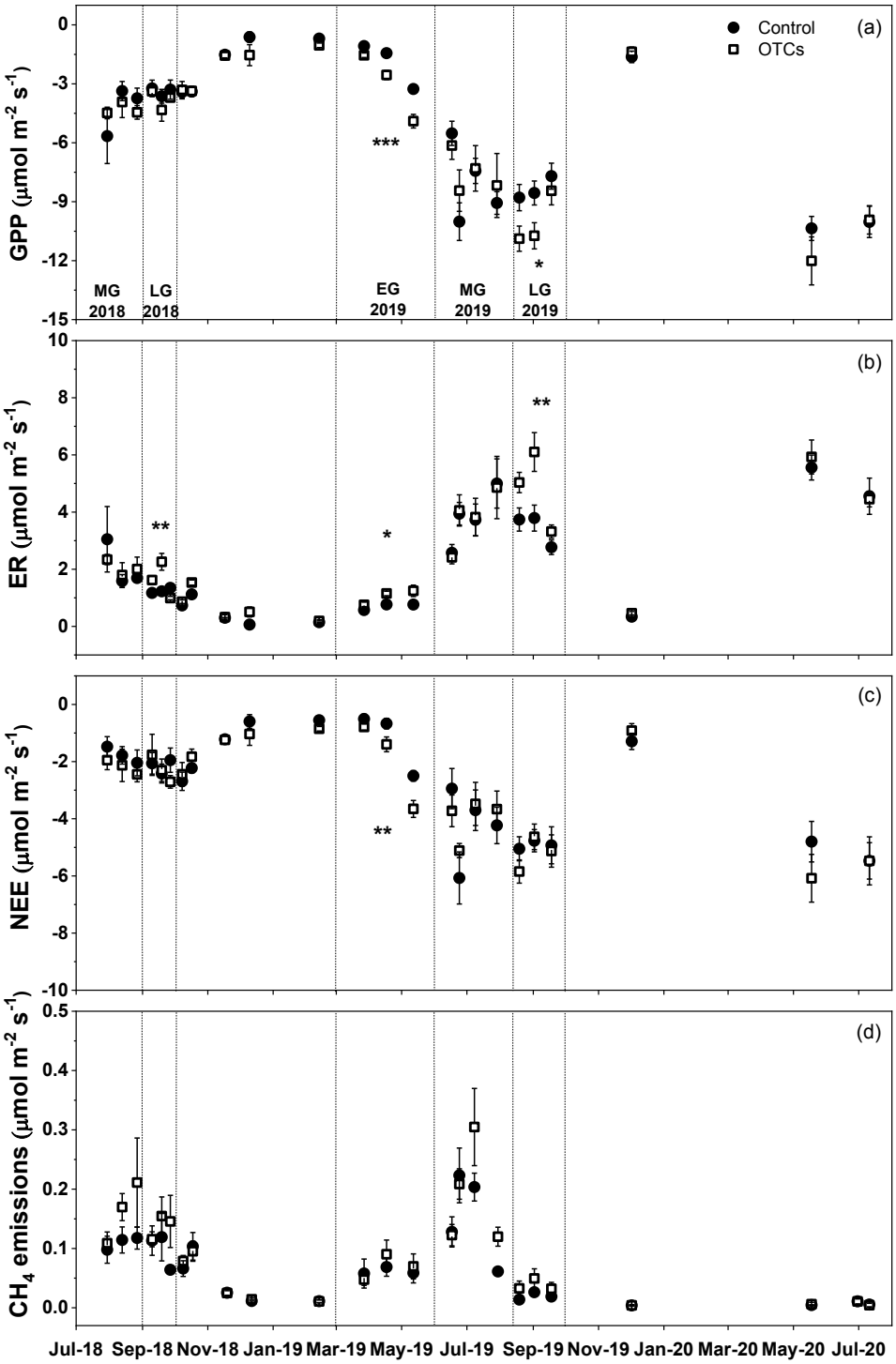

Figure IV-1 Measurements of gross primary production (GPP; a), ecosystem respiration (ER; b), net ecosystem exchange (NEE; c) and CH_4 emissions (d) in control and OTCs plots (±SEM; n=6) from August 2018 to July 2020. Significant differences of repeated measure ANOVA in early (LG), middle (MG) and late growing season (LG) are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

CH_4 emissions showed highest values in July 2019 and lowest values in winter (Fig. IV-1d). Nevertheless, low values were also found during August to September 2019 and May to July 2020 (Fig. IV-1d), corresponding to the low WTD (lower than -10 cm) in these periods (Fig III-4). However, a dramatic increase of CH_4 emissions was observed when WTD began to drop down in June and July 2019 (Fig IV-1d and Fig III-4). CH_4 emission was not significantly affected by warming treatment during any period of growing season (Fig. IV-1d).

IV.1.3.2 Temperature sensitivity of C fluxes

An exponential function, with air and soil temperature at -5, -15 and -30 cm depth as explaining variables, was adjusted to the measured GPP, ER and CH_4 emissions. Results showed that GPP and ER were best fitted with soil temperature at -30 cm, CH_4 emission was best fitted with soil temperature at -5 cm (Table IV-1). The Q_{10} of GPP with soil temperature at -30 cm decreased with OTCs compared with control (1.97±0.38 vs. 2.49±0.43; Fig. IV-2; Table IV-2). ER showed lower sensitivity to soil temperature at -30 cm under OTCs treatment with Q_{10} of 2.71±0.32 compared with 3.48±0.70 for control (Fig. IV-3; Table IV-2). The CH_4 was less sensitive to soil temperature at -5 cm under the effect of OTCs with Q_{10} of 2.71±0.32 compared with 3.48±0.70 for control (Fig. IV-4; Table IV-2). These results suggested that all C fluxes were less sensitive to temperature under warming.

Table IV-1 Nonlinear regression determination coefficient (r^2) of ecosystem respiration (ER), gross primary production (GPP) and methane emissions (CH_4) with air (Ta) and soil temperature (Ts) at 5, 15 and 30 cm depth. The number in bold represents the highest r^2.

	Determination coefficient (r^2)					
	Control			OTCs		
	ER	GPP	CH_4	ER	GPP	CH_4
Ta	0.40^{+++}	0.42^{---}	0.22^{+++}	0.26^{+++}	0.25^{---}	0.21^{+++}
Ts at 5 cm	0.42^{+++}	0.44^{---}	$\mathbf{0.35}^{+++}$	0.27^{+++}	0.29^{---}	$\mathbf{0.28}^{+++}$
Ts at 15 cm	0.46^{+++}	0.46^{---}	0.26^{+++}	0.38^{+++}	0.29^{---}	0.28^{+++}
Ts at 30 cm	$\mathbf{0.46}^{+++}$	$\mathbf{0.47}^{---}$	0.17^{+++}	$\mathbf{0.385}^{+++}$	$\mathbf{0.30}^{--}$	0.26^{+++}

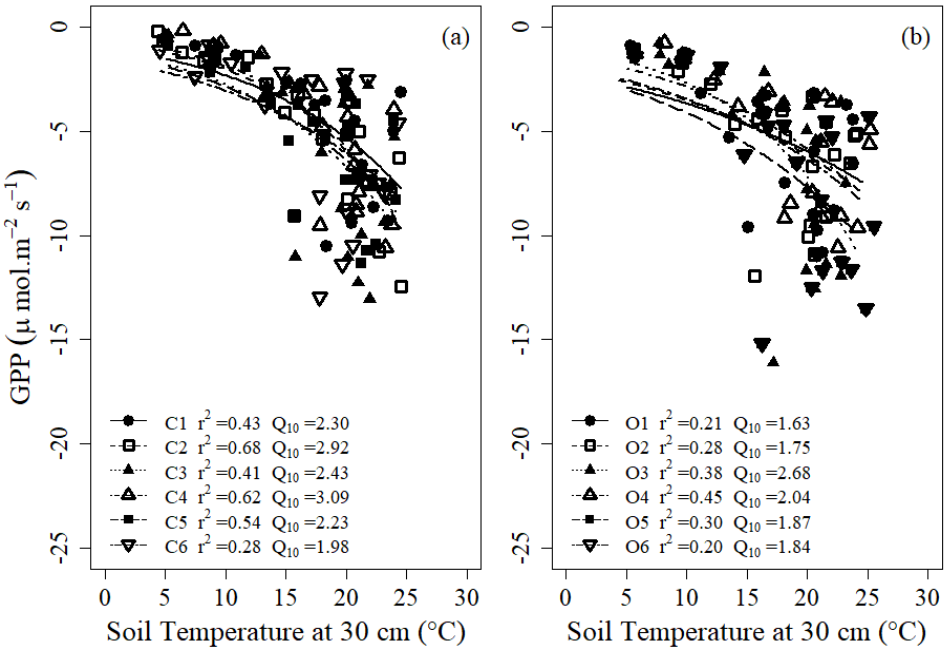

Figure IV-2 Exponential fitting of GPP and soil temperature at 30 cm depth for each replicate under control (C1-C6; a) and OTCs treatments (O1-O6; b) and the calculated Q_{10}.

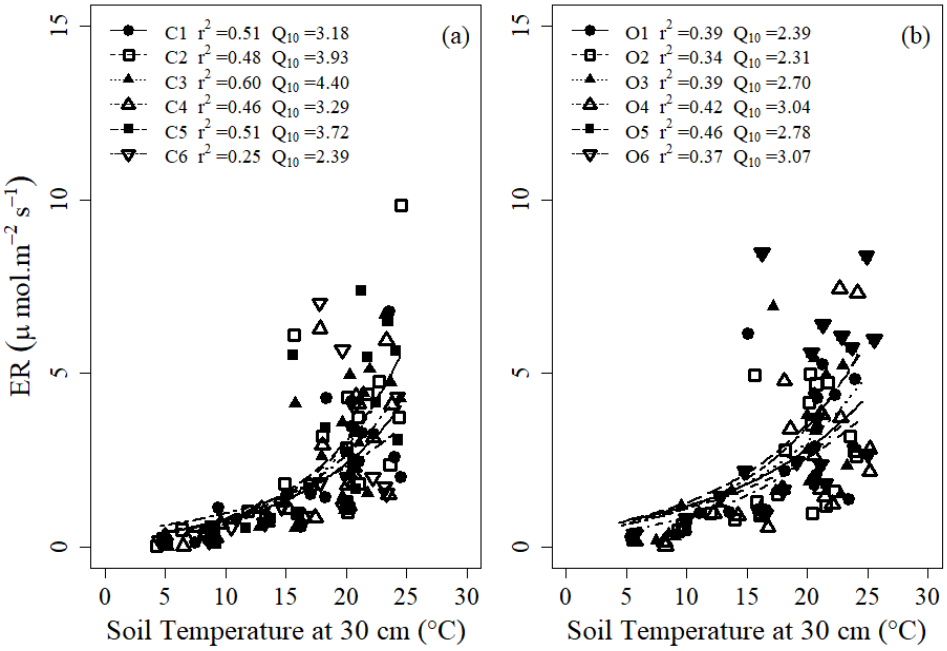

Figure IV-3 Exponential fitting of ER and soil temperature at 30 cm depth for each replicate under control (C1-C6; a) and OTCs treatments (O1-O6; b) and the calculated Q_{10}.

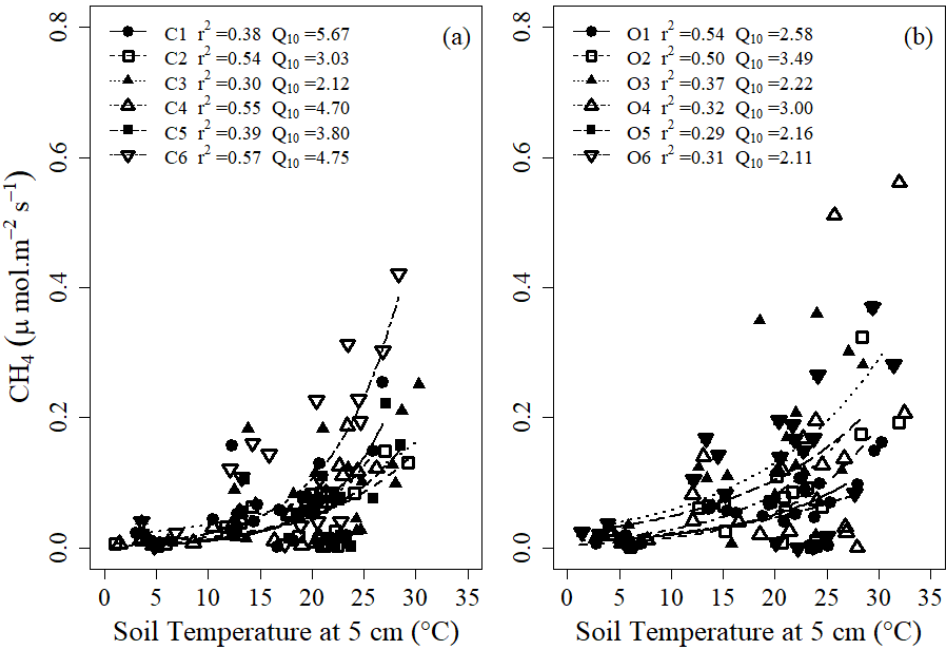

Figure IV-4 Exponential fitting of CH_4 emission and soil temperature at 5 cm depth for each replicate under control (C1-C6; a) and OTCs treatments (O1-O6; b) and the calculated Q_{10}.

Table IV-2 Q_{10} value of GPP and ER to soil temperature at 30 cm, and CH_4 emission to soil temperature at 5 cm under control and OTCs treatment. Significant differences of one way ANOVA are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Data are presented as mean ±SD, n=6

	Control	OTCs	*p*
GPP	2.49±0.43	1.97±0.38	*
ER	3.48±0.70	2.71±0.32	*
CH_4	4.01±0.45	2.59±0.39	*

IV.1.4 Discussion

IV.1.4.1 Warming effect on the measured CO_2 and CH_4 fluxes

The effect of warming on the CO_2 fluxes showed a clear seasonality. The significant effect of OTCs on GPP only occurred in 2019, during both early and late stage of growing season. The temperature effect on ER was observed from the late growing season in 2018, and it was also found during early and late stage of growing season in 2019. As the balance of GPP

and ER, the significant difference of NEE between the two treatments was only found during early growing season in 2019. This result suggested that in other periods, the change in GPP may offset that of ER and resulting in no difference in NEE. The observed earlier OTCs effect on ER than GPP may be caused by the other controlling factors on GPP, such as photosynthetic radiation, which is a dominant control on the photosynthesis (Blodau, 2002). The seasonal variability of warming effect on the CO_2 fluxes was also found by previous research in forest soils (Song et al., 2018). Similar with our results, they observed warming effect on CO_2 fluxes in early and late period of growing season, but no effect was found during the peak of summer. The strong effect of experimental warming during late growing season may be caused by the energy accumulation during the whole growing season (Song et al., 2018). Nevertheless, the strong OTCs effect in early growing season could be attributed to the vegetation growth. The number of graminoids leaf increased 47.1 % in May 2019 compared with winter 2018 under OTCs treatment, which was higher than that of 26.2 % in control plots (Fig. III-5). Furthermore, it has been reported that the presence of graminoids, especially *Molinia caerulea*, responsible for the higher GPP and ER compared with *Sphagnum* alone (Leroy et al., 2019). Thus, the warmer environment in OTCs facilitates the growth of vegetation, implying a faster growth of graminoids compared to control. And this leads to a higher GPP and ER during this period. Although CO_2 fluxes were impacted by warming treatment in different period, whereas no significant effect of warming was found throughout the whole growing season (Table IV-3).

CH_4 emission was controlled by both temperature and WTD (Fig. IV-1d). The CH_4 emission depends on both production, oxidation and transportation rates (Limpens et al., 2008). Therefore, the temporary increase of CH_4 emission corresponding to the WTD drop down could be attributed to the higher transportation rate of stored CH_4 in aerobic than anaerobic peat. The increase of aerobic layer following the decreasing WTD could accelerate the diffusion of CH_4 from deep peat to atmosphere because of more gas spaces in soil (Blodau, 2002; Kettunen et al., 1996; Moore and Dalva, 1993; Shannon and White, 1994). In comparison of the two treatments, a higher CH_4 emission under warming treatment was only found at the beginning and in the middle of July, corresponding to the dramatic decrease of WTD. This result suggested that larger amount of CH_4 may be produced and stored under warming treatment, and then transported to atmosphere when WTD decreased. In addition, WTD was reported to be a stronger regulator on CH_4 emissions than temperature (Roulet et al., 1992; Turetsky et al., 2008), and thus the fluctuation of WTD may amplified the effect of warming. Our results highlighted that the interactions of temperature and WTD had stronger effect on CH_4 emission to

atmosphere than solely temperature. Therefore, the further climate of higher temperature combined with increased frequency of drought would lead to higher CH_4 emission from peatlands, which could exacerbate the global warming and diminish the C storage of peatlands.

IV.1.4.2 Decreasing Q_{10} of C fluxes under warming

The temperature sensitivity of GPP, ER and CH_4 emissions all decreased under warming treatment in our study (Table IV-4). Several studies have reported a decreasing Q_{10} of CO_2 fluxes with increasing temperature in forest soils (Fang et al., 2010; Song et al., 2018). Xu and Qi, (2001) implied that the response of Q_{10} to temperature was related to the soil moisture, with a greater Q_{10} under higher soil moisture. However, we found an opposite trend in our study, in which a lower Q_{10} was observed in OTCs plots with a higher moisture in surface peat (Fig III-3). Wang et al., (2006) reported an unimodal relationship between Q_{10} and soil water content. Q_{10} of soil respiration increased with soil water content until a threshold then declined, which may be caused by the limitation of oxygen in high soil moisture. In addition, in our study, the surface peat moisture only showed higher values under OTCs treatment than control during July to September 2019 and April to July 2020, but it maintained similar for both treatments in other periods. Thus, this difference in short period may cannot induce an effect on Q_{10} of C fluxes in the whole year.

Tjoelker et al., (2001) reported a significant decline of Q_{10} of plant respiration with increasing temperature. According to Atkin and Tjoelker, (2003), this result was related to the limitation of respiratory capacity at low temperature and the limitation of substrate availability at high temperature. Also, the soil respiration was confirmed to acclimate to warming (Luo et al., 2001), probably due to the readily depletion of labile substrate (Kirschbaum, 2004). In addition, the acclimation of photosynthesis to higher temperature was likely result from the inactivation of Rubisco induced by moderate heat stress (Sharkey, 2005), or the increase of optimum temperature for photosynthesis (Kattge and Knorr, 2007; Way and Yamori, 2014). Considering CH_4, only MA et al., (2017) reported a decreasing Q_{10} of CH_4 production and a decreasing potential of CO_2 conversion to CH_4 in response to warming. As such, more laboratory experiments are required to fully investigate the temperature-dependence of Q_{10} for CH_4 emission. Although warming induced more C release to atmosphere, the decreasing temperature sensitivity implied that the processes linked to the C fluxes could acclimate to the increasing temperature. Therefore, the decreasing Q_{10} with warming should be taken into

account in the estimation of C fluxes in response to increasing temperature to improve the accuracy.

IV.1.5 Conclusion

In conclusion, the experimental warming significantly affected the C fluxes but its effect varied with periods. Both GPP, ER were significantly increased by OTCs during early growing season, due to the faster growth of graminoids under warming treatment. Moreover, significant effect was also found during late of growing season, but no effect in the peak of growing season. The strong effect of OTCs on CH_4 emission was only observed when higher temperature interacted with the drop down of WTD. However, the temperature sensitivity (Q_{10}) of GPP, ER and CH_4 emission all declined in response to warming. Our results highlighted that the warming induced stronger gaseous C fluxes between peatlands and atmosphere. However, as the temperature sensitivity of C fluxes declined under warming, this enhancement effect in long-term maybe overestimated.

References

Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends in Plant Science 8, 343–351. doi:10.1016/S1360-1385(03)00136-5

Blodau, C., 2002. Carbon cycling in peatlands — A review of processes and controls. Environmental Reviews 10, 111–134. doi:10.1139/a02-004

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W., McGuire, A.D., 2009. Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO2 Fluxes in an Alaskan Rich Fen. Ecosystems 12, 1329–1342. doi:10.1007/s10021-009-9292-y

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., Lindo, Z., 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Global Change Biology 21, 388–395. doi:10.1111/gcb.12643

Dorrepaal, E., Toet, S., van Logtestijn, R.S.P., Swart, E., van de Weg, M.J., Callaghan, T.V., Aerts, R., 2009. Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. Nature 460, 616–619. doi:10.1038/nature08216

Fang, H.J., Yu, G.R., Cheng, S.L., Zhu, T.H., Wang, Y.S., Yan, J.H., Wang, M., Cao, M., Zhou, M., 2010. Effects of multiple environmental factors on CO2 emission and CH4 uptake from old-growth forest soils. Biogeosciences 7, 395–407. doi:https://doi.org/10.5194/bg-7-395-2010

Flanagan, L.B., Syed, K.H., 2011. Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. Global Change Biology 17, 2271–2287. doi:10.1111/j.1365-2486.2010.02378.x

Kattge, J., Knorr, W., 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. Plant, Cell & Environment 30, 1176–1190. doi:https://doi.org/10.1111/j.1365-3040.2007.01690.x

Kettunen, A., Kaitala, V., Alm, J., Silvola, J., Nykänen, H., Martikainen, P.J., 1996. Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland. Global Biogeochemical Cycles 10, 457–471. doi:10.1029/96GB01609

Kirschbaum, M.U.F., 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Global Change Biology 10, 1870–1877. doi:10.1111/j.1365-2486.2004.00852.x

Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil carbon turnover to warming. Nature 433, 298–301. doi:10.1038/nature03226

Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H., Tuittila, E., 2019. Warming impacts on boreal fen CO 2 exchange under wet and dry conditions. Global Change Biology 25, 1995–2008. doi:10.1111/gcb.14617

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., Shuguang, W., Laggoun-Défarge, F., 2019. CO2 and CH4 budgets and global warming potential modifications in Sphagnum-dominated peat mesocosms invaded by Molinia caerulea. Biogeosciences 16, 4085–4095. doi:https://doi.org/10.5194/bg-16-4085-2019

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G., 2008. Peatlands and the carbon cycle: from local processes to global implications ? a synthesis. Biogeosciences Discussions 5, 1379–1419.

Lloyd, J., Taylor, J.A., 1994. On the Temperature Dependence of Soil Respiration. Functional Ecology 8, 315–323. doi:10.2307/2389824

Luo, Y., Wan, S., Hui, D., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625. doi:10.1038/35098065

MA, S., Huang, Y., Jiang, J., Ricciuto, D.M., Hanson, P.J., Luo, Y., 2017. Acclimation of methane production weakens ecosystem response to climate warming in a northern peatland. AGU Fall Meeting Abstracts 42.

Medlyn, B.E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P.C., Kirschbaum, M.U.F., Roux, X.L., Montpied, P., Strassemeyer, J., Walcroft, A., Wang, K., Loustau, D., 2002. Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. Plant, Cell & Environment 25, 1167–1179. doi:10.1046/j.1365-3040.2002.00891.x

Moore, T.R., Dalva, M., 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. Journal of Soil Science 44, 651–664. doi:10.1111/j.1365-2389.1993.tb02330.x

Roulet, N., Moore, T., Bubier, J., Lafleur, P., 1992. Northern fens: methane flux and climatic change. Tellus B 44, 100–105. doi:10.1034/j.1600-0889.1992.t01-1-00002.x

Shannon, R.D., White, J.R., 1994. A three-year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry 27, 35–60. doi:10.1007/BF00002570

Sharkey, T.D., 2005. Effects of moderate heat stress on photosynthesis: importance of thylakoid reactions, rubisco deactivation, reactive oxygen species, and thermotolerance provided by isoprene. Plant, Cell & Environment 28, 269–277. doi:https://doi.org/10.1111/j.1365-3040.2005.01324.x

Song, X., Wang, G., Hu, Z., Ran, F., Chen, X., 2018. Boreal forest soil CO2 and CH4 fluxes following fire and their responses to experimental warming and drying. Science of The Total Environment 644, 862–872. doi:10.1016/j.scitotenv.2018.07.014

Tjoelker, M.G., Oleksyn, J., Reich, P.B., 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. Global Change Biology 7, 223–230. doi:https://doi.org/10.1046/j.1365-2486.2001.00397.x

Turetsky, M.R., Treat, C.C., Waldrop, M.P., Waddington, J.M., Harden, J.W., McGuire, A.D., 2008. Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. Journal of Geophysical Research: Biogeosciences 113. doi:10.1029/2007JG000496

Voigt, C., Lamprecht, R.E., Marushchak, M.E., Lind, S.E., Novakovskiy, A., Aurela, M., Martikainen, P.J., Biasi, C., 2017. Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. Global Change Biology 23, 3121–3138. doi:10.1111/gcb.13563

Wang, C., Yang, J., Zhang, Q., 2006. Soil respiration in six temperate forests in China. Global Change Biology 12, 2103–2114. doi:10.1111/j.1365-2486.2006.01234.x

Way, D.A., Yamori, W., 2014. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynthesis Research 119, 89–100. doi:10.1007/s11120-013-9873-7

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K., Chapin, C.T., 2000. Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81, 3464–3478. doi:10.1890/0012-9658(2000)081[3464:ROBAFP]2.0.CO;2

Xu, M., Qi, Y., 2001. Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevadan Forest. Global Biogeochemical Cycles 15, 687–696. doi:10.1029/2000GB001365

IV.2 Model construction for the time-integrated CO_2 and CH_4 fluxes

IV.2.1 Introduction

As an important carbon (C) storage terrestrial ecosystem, peatlands and the stability of their carbon stock have received considerable attention, especially under the context of global climate change (Gorham, 1991; Page and Baird, 2016; Yu et al., 2011). In order to understand the response of such ecosystem to climate warming and predict its function (remain C sink or switch to C source), the estimation of annual C balance of peatlands is essential (Olson et al., 2013). To do so, CO_2 and CH_4 fluxes are usually measured through chamber approach with a frequency of several days to fortnight intervals (Alm et al., 2007; Leroy et al., 2019; Waddington and Roulet, 1996). These measured values under short time monitoring cannot represent the fluxes between two measurements at different dates, as C fluxes vary largely with environmental factors (e.g. temperature, solar irradiation or soil moisture). Therefore, it is necessary to relate the measured C fluxes components (CO_2 and CH_4) to biotic and abiotic factors. Then, with the high frequency monitoring of these factors, the C fluxes can be calculated to obtain a dataset with high time frequency.

Numerous research had attempted to construct simple model for CO_2 exchange. Generally, they modelled net CO_2 exchange by partitioning it into two components: light dependent gross primary production (GPP) and light independent ecosystem respiration (ER), then they were modelled separately. The modelling of GPP by both rectangular hyperbolic or nonrectangular hyperbolic light response model were widely reported (e.g. Veenendaal et al., 2007; Waddington et al., 2010; Whiting et al., 1992). The incorporation of the seasonal change temperature and vegetation index in the GPP models was demonstrated to improve their performance (e.g. Bubier et al., 1999; Burrows et al., 2005; Görres et al., 2014; Wilson et al., 2007a). Similarly, in spite of modelling ER by a nonlinear regression of temperature (e.g. Beyer et al., 2015; Elsgaard et al., 2012; Hoffmann et al., 2015), the introducing of WTD and vegetation index showed better fit to the data (e.g. Kandel et al., 2013; Renou-Wilson et al., 2014; Shaver et al., 2013). In contrast, there are less studies that modelled CH_4 emissions by simple models compared with CO_2. This is caused by the complicated mechanisms which controls the emission of CH_4 (Limpens et al., 2008). The CH_4 models from different studies showed various abilities (e.g. Bortoluzzi et al., 2006; Laine et al., 2007; Schrier-Uijl et al.,

2010a). Therefore, measurements of CH_4 fluxes with higher frequency and monitoring of more detailed environmental factors may be needed in order to better describe the dynamics of CH_4 fluxes.

In this study, the measured CO_2 and CH_4 fluxes were linked to biotic and abiotic factors, including temperature, water table depth (WTD) and vegetation. Models from literature research were used and modify with our data, then they were calibrated and evaluated. The models with which the modelled data showed best agreement with measured data were selected in order to calculate the annual C fluxes components and C budget of mesocosms. These results are presented in the next chapter.

IV.2.2 Materials and methods

IV.2.2.1 Models of net ecosystem exchange (NEE)

Net ecosystem exchange (NEE) is the net CO_2 exchange between peatland ecosystem and atmosphere, which is calculated from the balance between GPP (absorption of CO_2 by gross primary production) and ER (release of CO_2 by ecosystem respiration). In this study, GPP is negative, which indicates an uptake of CO_2 by mesocosms and ER is positive, suggesting an output of CO_2 from mesocosms. Thus, the negative NEE represents a net CO_2 input into the ecosystem and in contrast, the positive NEE represents a net CO_2 release to atmosphere. ER includes both heterotrophic respiration by soil decomposition and autotrophic respiration by plants. Therefore, the estimation of NEE was through the modelling of GPP and ER separately.

IV.2.2.2 Models of gross primary production (GPP)

In order to identify the parameter which described the variation of GPP, first the measured GPP data were correlated to abiotic and biotic parameters, including air and soil temperature at the 3 depths, WTD, PAR, number of graminoids leaf and vegetation index (VI) with linear regression.

The relationship between GPP and PPFD was often described by a rectangular hyperbolic saturation curve (Eq.IV-3; Thornley and Johnson 1990), which was in the same form of Michaelis-Menten equation (Johnson and Goody, 2011):

$$GPP = \frac{GPP_{max} \times PAR}{k + PAR} \qquad \text{Eq.IV-3}$$

where GPP_{max} (μmol m^{-2} s^{-1}) is the asymptotic maximum GPP at light saturation, PAR (μmol m^{-2} s^{-1}) is the photosynthetically active radiation and k (μmol photon m^{-2} s^{-1}) is the half-saturation constant.

In some previous studies, Eq.IV-3 was modified by adding other variables (e.g. WTD, temperature or vegetation index) which are related to GPP (e.g. Laine et al., 2019; Samaritani et al., 2011; Tuittila et al., 1999; Wilson et al., 2007). Following Kandel et al., (2013), the temperature sensitivity of photosynthesis (Eq.IV-4; Raich et al., 1991; Mahadevan et al., 2008) was added to Eq.IV-3:

$$T_{scale} = \frac{(T-T_{min})(T-T_{max})}{(T-T_{min})(T-T_{max})-(T-T_{opt})^2} \quad \text{Eq.IV-4}$$

where T is the measured air temperature (°C). T_{min}, T_{max} and T_{opt} are minimum, maximum and optimum air temperature (°C) for photosynthesis, respectively. Following Leroy et al. (2019), they were set as 0, 20 and 40 °C, respectively.

Then the effect of vegetation and WTD which showed correlation with GPP were included into equation. The performance of model was examined by linearly adding WTD, number of graminoids leaves or vegetation index (VI; calculated by Eq.III-1) to Eq.IV-3. The best fit was found when WTD, number of graminoids leaves and VI were all included into Eq.IV-3 (the second part of the right-hand of Eq.IV-5), thus the GPP_1 model was constructed as follow:

$$GPP\_1 = \frac{GPP_{max} \times PAR}{k+PAR} \times (a \times Graminoid_{leaves} + b \times VI + c \times \frac{WTD}{WTD_{ref}}) \times T_{scale} \quad \text{Eq.IV-5}$$

where the $Graminoid_{leaves}$ is the number of graminoids (*Molinia caerulea* and *Eriophorum augustifolium*) leaves. VI is the vegetation index (Eq.1). WTD is the water table depth (cm), and its reference value, WTD_{ref}, was set at -25 cm, which was the lowest value we observed in the mesocosms. Coefficients a, b and c are fitted parameters.

Secondly, the GPP was modelled by a modified version of Eq.IV-3 (Johnson and Thornley, 1984; Whiting, 1994):

$$GPP\_2 = \frac{i \times PAR \times GPP_{max}}{i \times PAR + GPP_{max}} \quad \text{Eq.IV-6}$$

where i (μmol CO_2 μmol per photon) is the initial slope of the photosynthetic light response, GPP_{max} (μmol m^{-2} s^{-1}) and PAR (μmol m^{-2} s^{-1}) are the same as in Eq.IV-3.

Bortoluzzi et al., (2006) reported that the GPP_{max} can be well described based on the equation suggested by June et al., (2004). In addition, they introduced the effect of vegetation in the equation. Following them, we linearly added the number of graminoids leaves which strongly correlated with GPP in our study. Therefore, GPP_{max} was modelled as follow:

$$GPP_{max} = (d * Graminoid_{leaf} + e) * e^{-\left(\frac{T_a - f}{g}\right)^2} \quad \text{Eq.IV-7}$$

where d is the rate of electron transport at light saturation (μmol m^{-2} s^{-1}), f is the optimal temperature for photosynthesis (°C), g is a temperature sensitivity factor. T_a is the air temperature (°C). The coefficient e is a fitted parameter.

IV.2.2.3 Models of ecosystem respiration (ER)

In order to identify the parameter which described the variation of ER, measured ER was first correlated to biotic and abiotic parameters, including air and soil temperature at the 3 depths, WTD, number of graminoids leaf and vegetation index (VI; calculated by Eq.III-1) with a linear regression.

The ER was often modelled by temperature with nonlinear regression. Thus here, the equation representing ER with temperature as an explanatory variable was fitted by varying parameters. First, ER was correlated to air or soil temperature at 5, 15 or 30 cm with both exponential and power regression. Then, the residuals of these nonlinear regressions were related to other environmental variables. WTD and the number of graminoids leaves were linearly correlated to the residuals of nonlinear regressions, thus they were included in the model.

The first model of ER was based on the equation of Bortoluzzi et al., (2006) and Leroy et al., (2019), in which ER and temperature were described using power function (second part of the right-hand side of Eq.IV-8), the WTD and number of graminoids leaves were added by a linear function (first part of the right-hand side of Eq.IV-8):

$$ER\_1 = \left(h \times \frac{WTD}{WTD_{ref}} + i \times Graminoid_{leaves}\right) \times \left(\frac{T - T_{min}}{T_{ref} - T_{min}}\right)^j \quad \text{Eq.IV-8}$$

where the reference of water table depth, WTD_{ref}, was also set at -25 cm as mentioned above. T_{min} is the minimum temperature (°C) for positive respiration and T_{ref} is the reference temperature (°C). They were set as -5 and 15 °C, respectively, following Bortoluzzi et al. (2006). T is the measured temperature (°C). The model was fitted with air temperature, soil temperature

at 5, 15 and 30 cm depth. The best fit was found when using soil temperature at 5 cm, thus it was used as T here. The coefficients h, i and j are fitted parameters.

The second model of ER was according to the temperature dependent Arrhenius-type function (Lloyd and Taylor, 1994). As an extension of this method, the linear function of WTD and the number of graminoids leaves was integrated in the model to improve the model fit:

$$ER\_2 = (k \times \frac{WTD}{WTD_{ref}} + l \times Graminoids_{leaves}) \times exp\left[E_0 \times \left(\frac{1}{T_{ref}-T_0} - \frac{1}{T-T_0}\right)\right] \quad \text{Eq.IV-9}$$

where E_0 is an activation energy like parameter (further referred to ecosystem sensitivity to temperature), T_{ref} is the reference temperature and T_0 is the starting temperature constant, which were set as 283.15 and 227.13 K respectively according to Lloyd and Taylor, (1994). T is the mean temperature during the flux measurement. The model was fitted with air temperature, soil temperature at 5, 15 and 30 cm depth and the best fit was found when using soil temperature at 15 cm and it was used as T here. The coefficients k and l are fitted parameters.

IV.2.2.4 Models of CH_4 emission

In order to identify the parameter which described the variation of CH_4 emission, measured CH_4 emission was first correlated to biotic and abiotic parameters, including air and soil temperature at the 3 depths, WTD, number of graminoids leaf and vegetation index (VI; calculated by Eq.III-1) with linear regression.

A strong relationship between CH_4 emissions and temperature/WTD was found with our data. However, the linear relationship between CH_4 emission and WTD was only found when WTD above -9 cm. Following (Schrier-Uijl et al., 2010b), CH_4 emissions data was firstly fitted with soil temperature using nonlinear regression (exponential and power law regression), and both regressions showed similar results. Then the residuals of these nonlinear regressions were related to other environmental variables. WTD was linearly correlated to the residuals of power function when above -9 cm, and the number of graminoids leaves were linearly correlated to the residuals. Thus as an extension of their method, we included these two variables in the models:

$$CH_4\_1 = (m \times \frac{WTD}{WTD_{ref}} + n \times Graminoid_{leaves}) \times (\frac{T_s-T_{min}}{T_{ref}-T_{min}})^p \text{ (WTD>-9cm)} \quad \text{Eq.IV-10}$$

$$CH_4\_2 = \left(q \times \frac{WTD}{WTD_{ref}} + r \times Graminoid_{leaves}\right) \times exp\left[s \times \left(\frac{T_s - T_{min}}{T_{ref} - T_{min}}\right)\right] \text{ (WTD>-9cm)}$$

Eq.IV-11

where T_{min} is minimum temperature (°C) for CH_4 emissions, it was set as 1 °C which was the minimum soil temperature observed at 5 cm depth. T_{ref} is reference temperature (°C), it was set as 20 °C which was the median value of annual soil temperature at 5 cm depth. T_s is the measured soil temperature (°C). The model was fitted with soil temperature at 5, 15 and 30 cm depth. The best fit was found when using soil temperature at 5 cm, thus it was used as T_s here. The coefficients m, n, p and q, r, s are fitted parameters.

IV.2.2.5 Calibration and evaluation of models

Two third (randomly selected) of available data was used to calibrate the model and one third data was used to evaluate the model. The performance of model was evaluated by the adjusted determination coefficient (R_{adj}^2) and the normalized root-mean-square error (NRMSE) of the linear relationship between measured and modelled data:

$$R_{adj}^2 = 1 - \left(1 - \frac{(1-R^2)(n-1)}{n-k-1}\right) \quad \text{Eq.IV-12}$$

where R^2 is traditional R^2, n represent the number of data and k is the number of independent regressors.

$$NRMSE = 100 * \frac{\sqrt{\left(\frac{\sum(y-\hat{y})}{n}\right)}}{\bar{y}} \quad \text{Eq.IV-13}$$

where y is the measured value, $\hat{y}$ is the modelled value, $\bar{y}$ is the mean of measured values and n the number of data.

The parameters of GPP (a, b and c for GPP_1;k, d, e, f and g for GPP_2), ER (h, i and j for ER_1; k, l and E_0 for ER_2) and CH_4 emissions (m, n and p for CH_4_1; q, r and s for CH_4_2) were calibrated by minimizing the NRMSE using the "SANN" method of the optim function in R (R 3.6.3, R Core Team 2020).

IV.2.3 Results and discussion

IV.2.3.1 GPP models

A strong relationship between GPP and temperature, WTD, PAR, number of graminoids leaf and VI was observed (Table IV-3). When the two models with these parameters were compared, GPP_1 showed better performance than GPP_2. The NRMSE and r^2 for the calibration of GPP_1 were 52.8 % and 0.84, respectively, while, they were 74.1 % and 0.44 for GPP_2 (Fig. IV-5a). Evaluation of GPP models confirmed the better representative of GPP_1, with lower NRMSE (43.1 %) and higher r^2 (0.90) compared with the higher NRMSE (81.6 %) and lower r^2 (0.31) of GPP_2 (Fig. IV-5b). Moreover, GPP_1 has more parameters then GPP_1 which lead to a better performance. Thus, GPP_1, which predict better the measured GPP, was selected to model the annual GPP.

The rectangular hyperbola equation was widely used in the modelling of GPP of organic soils in Europe and North America (e.g. Drösler, 2005; Hoffmann et al., 2015; Waddington and Roulet, 1996; Wohlfahrt et al., 2008). Nevertheless, this relationship was not always suitable for all ecosystems with varied vegetation composition. Thus, some studies have attempted to add the effect of vegetation into the light response model. Results showed that the models predict better the GPP when include either ratio vegetation index (RVI) or vascular green area (VGA) when vascular plants exist (Görres et al., 2014; Wilson et al., 2007a). Considering the vegetation composition in our mesocosms (including bryophyte, graminoids and shrubs), both the number of graminoids leaves which represent the effect of these vascular plants ($Graminoid_{leaf}$) and VI which represents the total vegetation were introduced in the rectangular hyperbola equation. The best fit occurred when both parameters were integrated. In addition, Hájek et al., (2009) and Murray et al., (1993) have observed the photo-inhibition of plants, suggesting that in spite of describing GPP by PAR, a temporal change of their relationship should be considered. Some studies introduced a temperature-based factor which values ranged from 0 to 1 into the relationship of GPP and PAR, so that the seasonal change of photosynthetic activity of plants can be represented (Bubier et al., 1999). Therefore, here we added a parameter T_{scale} which represents the temperature sensitivity of photosynthesis and this inclusion improved the performance of the model. GPP was also strongly correlated with WTD (Table IV-3),and thus it was also integrated in the model. Our results highlighted the importance of

integrating the seasonal change of temperature, WTD as well as vegetation community into the light response curve of GPP.

Table IV-3 Linear regression determination coefficient (r^2) of ecosystem respiration (ER), gross primary production (GPP) and methane emissions (CH_4) with air temperature (Ta) and soil temperature (Ts) at 5, 15 and 30 cm depth, water table depth (WTD), photosynthetic active radiation (PAR), the number of graminoids leaf and vegetation index (VI) in control and OTCs plots. Significance levels of correlation are expressed as $^{-/+}p < 0.05$, $^{--/++}p < 0.01$, $^{---/+++}p < 0.001$. $^{-/+}$ represents a negative or positive relationship, respectively.

	Detemination coefficient (r^2)					
	Control			OTCs		
	ER	GPP	CH_4	ER	GPP	CH_4
Ta	0.42^{+++}	0.42^{---}	0.17^{+++}	0.31^{+++}	0.26^{---}	0.18^{+++}
Ts at 5 cm	0.41^{+++}	0.45^{---}	0.24^{+++}	0.34^{+++}	0.31^{---}	0.22^{+++}
Ts at 15 cm	0.46^{+++}	0.49^{---}	0.20^{+++}	0.41^{+++}	0.33^{---}	0.22^{+++}
Ts at 30 cm	0.45^{+++}	0.49^{---}	0.15^{+++}	0.41^{+++}	0.34^{---}	0.22^{+++}
WTD	0.44^{----}	0.42^{---}	0.16^{---a}	0.53^{---}	0.49^{---}	0.15^{---a}
PAR	-	0.28^{---}	-	-	0.35^{---}	-
Graminoids leaf number	0.47^{+++}	0.58^{---}	0.24^{+++}	0.51^{+++}	0.53^{---}	0.28^{+++}
VI	NA	0.05^{-}	NA	0.08^{++}	0.18^{---}	NA

a Data when WTD above -9 cm

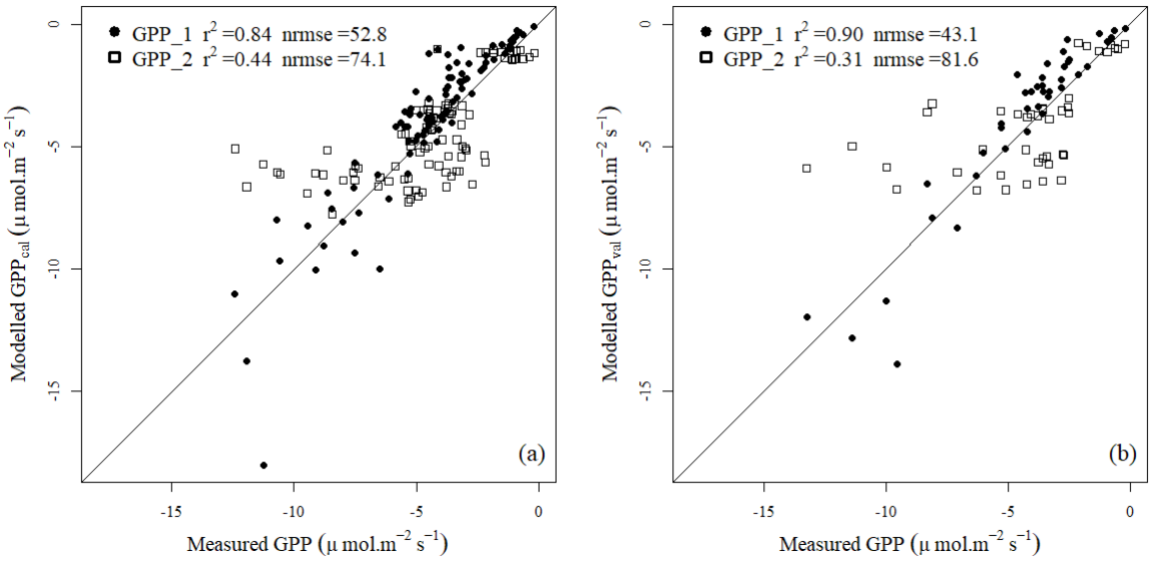

Figure IV-5 Calibration (a) and validation (b) of GPP_1 and GPP_2 by comparison of the simulated and measured gross primary production (GPP). The diagonal lines represent the 1:1.

IV.2.3.2 ER models

In our study, ER was strongly correlated with temperature, WTD and the number of graminoids leaf (Table IV-3), and thus all these parameters were included in the modelling of ER. The calibration of ER models showed same performance of ER_1 and ER_2, with NRMSE of 63 % and r^2 of 0.61 (Fig. IV-6a). Although the differences between ER_1 and ER_2 were low during evaluation, ER_1 yielded to lower NRMSE (NRMSE=42.2 % and 43.2 % for ER_1 and ER_2, respectively) and higher r^2 than ER_2 (r^2=0.82 and 0.81 for ER_1 and ER_2, respectively; Fig. IV-6b). Therefore, ER_1 was selected to calculate the annual ER.

Many previous studies described well the ER with nonlinear regression of temperature (e.g. Drösler, 2005; Elsgaard et al., 2012 and Görres et al., 2014). Furthermore, some research showed that the integration of WTD in the model of ER largely promotes the performance of equation, especially when the seasonal wet-dry cycles have significant effect on ER (e.g. Bortoluzzi et al., 2006; Renou-Wilson et al., 2014). Our study confirmed this result with a satisfactory model when integrate WTD. In addition, the inclusion of the effect of vegetation also improves the model fit to data, and this result was consistent with previous ones (Bortoluzzi et al., 2006; Kandel et al., 2013; Shaver et al., 2013).

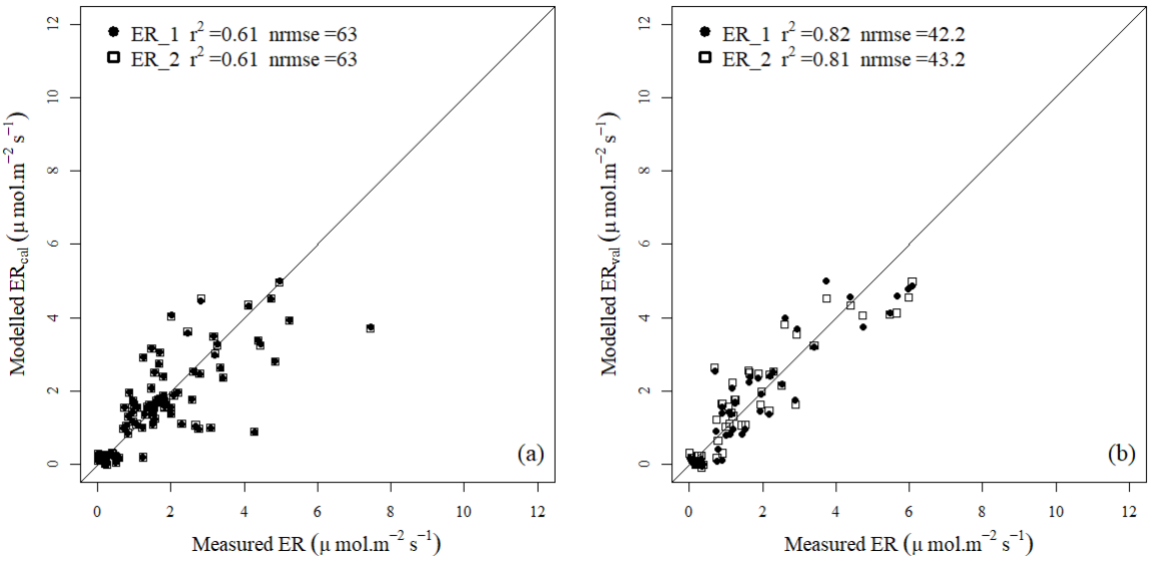

Figure IV-6 Calibration (a) and validation (b) of ER_1 and ER_2 by comparison of the simulated and measured ecosystem respiration (ER). The diagonal lines represent the 1:1.

IV.2.3.3 CH_4 models

The measured CH_4 emission was strongly related to temperature and number of graminoids leaf (Table IV-3), while it only correlated with WTD when above -9 cm. The calibration of CH_4 models showed that the NRMSE for CH_4_1 was slightly lower than CH_4_2 (51.5 vs 53.6 %), and the r^2 for CH_4_1 was slight higher than CH_4_2 (0.75 vs 0.71; Fig. IV-7a). Nevertheless, the evaluation of CH_4_2 led to a slight lower NRMSE than CH_4_1 (74.7 vs 75.1) and a same r^2 (0.41) with CH_4_1 (Fig. IV-7b). Therefore, CH_4_1 model which showed better performance during calibration was chose to estimate the annual CH_4 emission.

In comparison to CO_2 fluxes, the modelling of CH_4 emission with simple models is less reported. Many studies applied the linear interpolation method to construct CH_4 data with high time frequency in order to estimate the time-integrated CH_4 fluxes (e.g. Renou-Wilson et al., 2014; Roulet et al., 2007; Waddington and Roulet, 1996). However, this method required high frequency of measurements to get a more precise estimation, as the variability of CH_4 emissions between day-night or different dates may quiet large. As such, the modelling approach which depends on the environmental parameters was necessary. However, there are a lot of difficulties in constructing simple models for CH_4 emission. The complication was confirmed in our study. First, the CH_4 was only linearly correlated with WTD when WTD above -9 cm. Second, as

mentioned in IV.1.4.1, a temporary increase of CH_4 emission was observed when the WTD drop down (Fig. IV-1d and III-4). The CH_4 emissions dependent on both production rate, oxidation and transportation rate (Limpens et al., 2008), and thus makes it difficult to be model the net effect of all these processes. Additionally, methanogenesis and methanotrophy which occur at different depths of soil showed distinct responses to temperature. Thus using a single temperature at fixes depth cannot estimate the response of these two processes (Baird et al., 2019). Laine et al., (2007) modelled the CH_4 fluxes based on the soil temperature and WTD, with exponential function of temperature and linear function of WTD. Depending on the strong relationship between CH_4 emission and temperature as well as WTD (when above -9 cm), their equation was applied in our study and showed well description of the measured data. However, the modelling of CH_4 emission when WTD below -9 cm remains challenging. Our results emphasized that rather than using the punctual measurement of WTD, the monitoring of dynamic variations of WTD may be required to estimate the CH_4 emission.

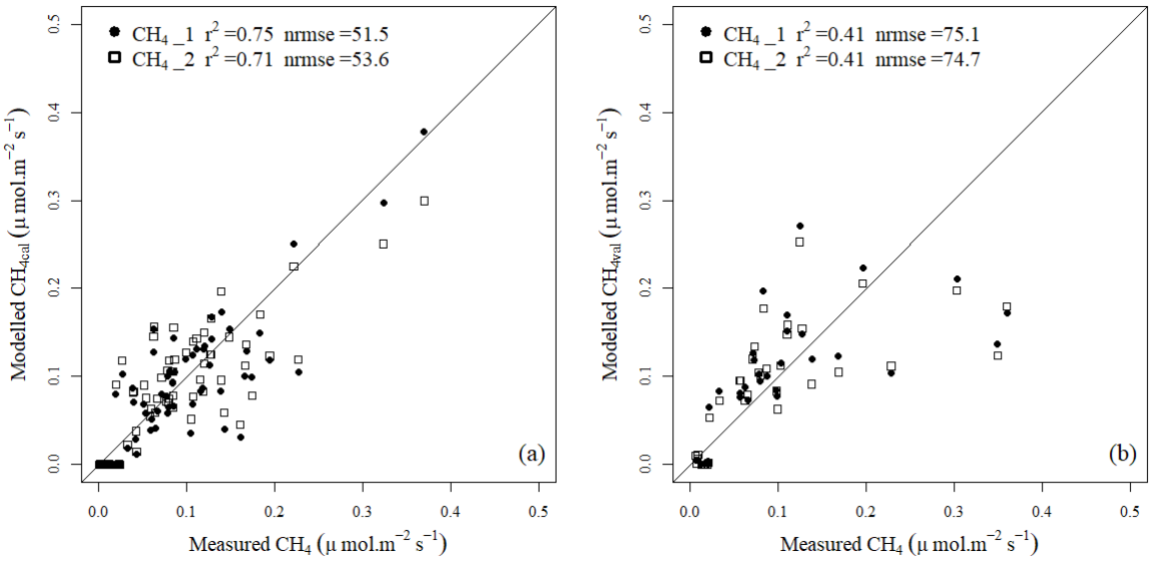

Figure IV-7 Calibration (a) and validation (b) of CH_4_1 and CH_4_2 by comparison of the simulated and measured CH_4 emission. The diagonal lines represent the 1:1.

IV.2.4 Conclusion

In conclusion, in order to estimate the annual C budget, the C fluxes measured with low frequency were related to biotic and abiotic factors, which were monitored with high frequency to construct simple models. Two models were constructed for ER, GPP and CH_4 emission, respectively. The models took into account the effect WTD and vegetation, which improved

the performance of the models. After calibration and evaluation of these models, those that showed better fit with our results were selected: ER_1, GPP_1 and CH_4_1 to model the annual cumulated ER, GPP and CH_4 emissions, respectively. These models were used to calculate the annual C balance in each mesocosm under control and OTCs treatment (see following section).

References

Alm, J., Shurpali, N.J., Tuittila, E.-S., Laurila, T., Maljanen, M., Saarnio, S., Minkkinen, K., 2007. Methods for determining emission factors for the use of peat and peatlands—flux measurements and modelling.

Baird, A.J., Green, S.M., Brown, E., Dooling, G.P., 2019. Modelling time-integrated fluxes of CO2 and CH4 in peatlands: A review. Mires and Peat 24.

Beyer, C., Liebersbach, H., Höper, H., 2015. Multiyear greenhouse gas flux measurements on a temperate fen soil used for cropland or grassland. Journal of Plant Nutrition and Soil Science 178, 99–111. doi:10.1002/jpln.201300396

Bortoluzzi, E., Epron, D., Siegenthaler, A., Gilbert, D., Buttler, A., 2006. Carbon balance of a European mountain bog at contrasting stages of regeneration. New Phytologist 172, 708–718. doi:10.1111/j.1469-8137.2006.01859.x

Bubier, J.L., Frolking, S., Crill, P.M., Linder, E., 1999. . Journal of Geophysical Research: Atmospheres 104, 27683–27692. doi:10.1029/1999JD900219

Burrows, E.H., Bubier, J.L., Mosedale, A., Cobb, G.W., Crill, P.M., 2005. Net Ecosystem Exchange of Carbon dioxide in a Temperate Poor Fen: a Comparison of Automated and Manual Chamber Techniques. Biogeochemistry 76, 21–45. doi:10.1007/s10533-004-6334-6

Drösler, M., 2005. Trace gas exchange and climatic relevance of bog ecosystems, Southern Germany. Technische Universität München.

Elsgaard, L., Görres, C.-M., Hoffmann, C.C., Blicher-Mathiesen, G., Schelde, K., Petersen, S.O., 2012. Net ecosystem exchange of CO2 and carbon balance for eight temperate organic soils under agricultural management. Agriculture, Ecosystems & Environment 162, 52–67. doi:10.1016/j.agee.2012.09.001

Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecological Applications 1, 182–195. doi:10.2307/1941811

Görres, C.-M., Kutzbach, L., Elsgaard, L., 2014. Comparative modeling of annual CO2 flux of temperate peat soils under permanent grassland management. Agriculture, Ecosystems & Environment 186, 64–76. doi:10.1016/j.agee.2014.01.014

Hájek, T., Tuittila, E.-S., Ilomets, M., Laiho, R., 2009. Light responses of mire mosses – a key to survival after water-level drawdown? Oikos 118, 240–250. doi:10.1111/j.1600-0706.2008.16528.x

Hoffmann, M., Jurisch, N., Albiac Borraz, E., Hagemann, U., Drösler, M., Sommer, M., Augustin, J., 2015. Automated modeling of ecosystem CO2 fluxes based on periodic closed chamber measurements: A standardized conceptual and practical approach. Agricultural and Forest Meteorology 200, 30–45. doi:10.1016/j.agrformet.2014.09.005

Johnson, I.R., Thornley, J.H.M., 1984. A model of instantaneous and daily canopy photosynthesis. Journal of Theoretical Biology 107, 531–545.

Johnson, K.A., Goody, R.S., 2011. The Original Michaelis Constant: Translation of the 1913 Michaelis–Menten Paper. Biochemistry 50, 8264–8269. doi:10.1021/bi201284u

June, T., Evans, J.R., Farquhar, G.D., 2004. A simple new equation for the reversible temperature dependence of photosynthetic electron transport: a study on soybean leaf. Functional Plant Biology 31, 275–283. doi:10.1071/fp03250

Kandel, T.P., Elsgaard, L., Lærke, P.E., 2013. Measurement and modelling of CO2 flux from a drained fen peatland cultivated with reed canary grass and spring barley. GCB Bioenergy 5, 548–561. doi:10.1111/gcbb.12020

Laine, A., Wilson, D., Kiely, G., Byrne, K.A., 2007. Methane flux dynamics in an Irish lowland blanket bog. Plant and Soil 299, 181–193. doi:10.1007/s11104-007-9374-6

Laine, A.M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., Minkkinen, K., Fritze, H., Tuittila, E., 2019. Warming impacts on boreal fen CO_2 exchange under wet and dry conditions. Global Change Biology 25, 1995–2008. doi:10.1111/gcb.14617

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., Shuguang, W., Laggoun-Défarge, F., 2019. CO_2 and CH_4 budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*. Biogeosciences 16, 4085–4095. doi:https://doi.org/10.5194/bg-16-4085-2019

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H., Schaepman-Strub, G., 2008. Peatlands and the carbon cycle: from local processes to global implications ? a synthesis. Biogeosciences Discussions 5, 1379–1419.

Lloyd, J., Taylor, J.A., 1994. On the Temperature Dependence of Soil Respiration. Functional Ecology 8, 315–323. doi:10.2307/2389824

Mahadevan, P., Wofsy, S.C., Matross, D.M., Xiao, X., Dunn, A.L., Lin, J.C., Gerbig, C., Munger, J.W., Chow, V.Y., Gottlieb, E.W., 2008. A satellite-based biosphere parameterization for net ecosystem CO2 exchange: Vegetation Photosynthesis and Respiration Model (VPRM). Global Biogeochemical Cycles 22. doi:10.1029/2006GB002735

Murray, K.J., Tenhunen, J.D., Nowak, R.S., 1993. Photoinhibition as a control on photosynthesis and production of Sphagnum mosses. Oecologia 96, 200–207. doi:10.1007/BF00317733

Olson, D.M., Griffis, T.J., Noormets, A., Kolka, R., Chen, J., 2013. Interannual, seasonal, and retrospective analysis of the methane and carbon dioxide budgets of a temperate peatland. Journal of Geophysical Research: Biogeosciences 118, 226–238. doi:10.1002/jgrg.20031

Page, S.E., Baird, A.J., 2016. Peatlands and Global Change: Response and Resilience. Annual Review of Environment and Resources 41, 35–57. doi:10.1146/annurev-environ-110615-085520

Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore, B., Vorosmarty, C.J., 1991. Potential Net Primary Productivity in South America: Application of a Global Model. Ecological Applications: A Publication of the Ecological Society of America 1, 399–429. doi:10.2307/1941899

Renou-Wilson, F., Barry, C., Müller, C., Wilson, D., 2014. The impacts of drainage, nutrient status and management practice on the full carbon balance of grasslands on organic soils in a maritime temperate zone. Biogeosciences 11, 4361–4379. doi:https://doi.org/10.5194/bg-11-4361-2014

Roulet, N.T., Lafleur, P.M., Richard, P.J.H., Moore, T.R., Humphreys, E.R., Bubier, J., 2007. Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. Global Change Biology 13, 397–411. doi:10.1111/j.1365-2486.2006.01292.x

Samaritani, E., Siegenthaler, A., Yli-Petäys, M., Buttler, A., Christin, P.-A., Mitchell, E.A.D., 2011. Seasonal Net Ecosystem Carbon Exchange of a Regenerating Cutaway Bog: How Long Does it Take to Restore the C-Sequestration Function? Restoration Ecology 19, 480–489. doi:10.1111/j.1526-100X.2010.00662.x

Schrier-Uijl, A.P., Kroon, P.S., Leffelaar, P.A., van Huissteden, J.C., Berendse, F., Veenendaal, E.M., 2010a. Methane emissions in two drained peat agro-ecosystems with high and low agricultural intensity. Plant and Soil 329, 509–520. doi:10.1007/s11104-009-0180-1

Schrier-Uijl, A.P., Kroon, P.S., Leffelaar, P.A., van Huissteden, J.C., Berendse, F., Veenendaal, E.M., 2010b. Methane emissions in two drained peat agro-ecosystems with high and low agricultural intensity. Plant and Soil 329, 509–520. doi:10.1007/s11104-009-0180-1

Shaver, G.R., Rastetter, E.B., Salmon, V., Street, L.E., van de Weg, M.J., Rocha, A., van Wijk, M.T., Williams, M., 2013. Pan-Arctic modelling of net ecosystem exchange of CO2. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20120485. doi:10.1098/rstb.2012.0485

Thornley, J.H.M., Johnson, I.R., 1990. Plant and crop modelling: a mathematical approach to plant and crop physiology.

Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Laine, J., 1999. Restored cut-away peatland as a sink for atmospheric CO2. Oecologia 120, 563–574. doi:10.1007/s004420050891

Veenendaal, E.M., Kolle, O., Leffelaar, P.A., Schrier-Uijl, A.P., Van Huissteden, J., Van Walsem, J., Möller, F., Berendse, F., 2007. CO_2 exchange and carbon balance in two grassland sites on eutrophic drained peat soils. Biogeosciences 4, 1027–1040. doi:https://doi.org/10.5194/bg-4-1027-2007

Waddington, J.M., Roulet, N.T., 1996. Atmosphere-wetland carbon exchanges: Scale dependency of CO2 and CH4 exchange on the developmental topography of a peatland. Global Biogeochemical Cycles 10, 233–245. doi:10.1029/95GB03871

Waddington, J.M., Strack, M., Greenwood, M.J., 2010. Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO2 exchange to ecosystem-scale restoration. Journal of Geophysical Research: Biogeosciences 115. doi:10.1029/2009JG001090

Whiting, G.J., 1994. CO2 exchange in the Hudson Bay lowlands: Community characteristics and multispectral reflectance properties. Journal of Geophysical Research: Atmospheres 99, 1519–1528. doi:10.1029/93JD01833

Whiting, G.J., Bartlett, D.S., Fan, S., Bakwin, P.S., Wofsy, S.C., 1992. Biosphere/atmosphere CO2 exchange in tundra ecosystems: Community characteristics and relationships with multispectral surface reflectance. Journal of Geophysical Research: Atmospheres 97, 16671–16680. doi:10.1029/91JD01027

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K.A., Farrell, E.P., Tuittila, E.-S., 2007a. A high resolution green area index for modelling the seasonal dynamics of CO2 exchange in peatland vascular plant communities. Plant Ecology 190, 37–51. doi:10.1007/s11258-006-9189-1

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K.A., Farrell, E.P., Tuittila, E.-S., 2007b. A high resolution green area index for modelling the seasonal dynamics of CO2 exchange in peatland vascular plant communities. Plant Ecology 190, 37–51. doi:10.1007/s11258-006-9189-1

Wohlfahrt, G., Anderson-Dunn, M., Bahn, M., Balzarolo, M., Berninger, F., Campbell, C., Carrara, A., Cescatti, A., Christensen, T., Dore, S., Eugster, W., Friborg, T., Furger, M., Gianelle, D.,

Gimeno, C., Hargreaves, K., Hari, P., Haslwanter, A., Johansson, T., Marcolla, B., Milford, C., Nagy, Z., Nemitz, E., Rogiers, N., Sanz, M.J., Siegwolf, R.T.W., Susiluoto, S., Sutton, M., Tuba, Z., Ugolini, F., Valentini, R., Zorer, R., Cernusca, A., 2008. Biotic, Abiotic, and Management Controls on the Net Ecosystem CO2 Exchange of European Mountain Grassland Ecosystems. Ecosystems 11, 1338–1351. doi:10.1007/s10021-008-9196-2

Yu, Z., Beilman, D.W., Frolking, S., MacDonald, G.M., Roulet, N.T., Camill, P., Charman, D.J., 2011. Peatlands and Their Role in the Global Carbon Cycle. Eos, Transactions American Geophysical Union 92, 97–98. doi:10.1029/2011EO120001

IV.3 Modelled CO_2 and CH_4 fluxes and the C balance of peatlands under experimental warming

NB: This part of work has been accepted by Frontiers in Earth Science:

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IV.3.1 Introduction

Peatlands are important carbon (C) storage terrestrial ecosystems in the world, as they accumulate about 30 % of the world's soil C in only 3 % of the land area (Gorham, 1991; Yu et al., 2010; Jackson et al., 2017). Their C sink function results from the positive small but long-lasting imbalance between the C input from photosynthesis and the C output from decomposition of soil organic matters (OM) (Bragazza et al., 2009). The specific abiotic and biotic conditions in peatlands, such as low temperature, waterlogging, acidity and litter intrinsically recalcitrance to decay (*Sphagnum* litters) limit the microbial decomposition thus lead to the accumulation of OM. Nevertheless, due to the large amount of anthropogenic greenhouse gases (GHGs) emissions to the atmosphere, the earth surface temperature has been observed to increase since the last century, and it is expected to increase 1-3.7 ^oC by the end of the 21st century (IPCC, 2014). As elevated temperature can stimulate the soil decomposition (Dieleman et al., 2016), thus the projected warmer climate may shift the C sink of peatlands to a C source. Furthermore, due to the large C stocks in peatlands, small disturbances in the C cycle processes may lead to marked C release, which will in turn exacerbate the global warming. Therefore, understanding the C balance of peatlands in response to climate warming is of great importance and is a subject of considerable concern.

Temperature controls numerous metabolic processes related to photosynthesis as well as autotrophic and heterotrophic respiration (e.g. Lloyd and Taylor, 1994; Medlyn et al., 2002). Generally, higher temperature could induce more carbon dioxide (CO_2) release by ecosystem respiration (ER; e.g. Chivers et al., 2009; Flanagan and Syed, 2011). For example, Dorrepaal et al. (2009) observed an increase of over 50 % in ER from peat soil induced by a temperature rise of approximately 1^oC. However, the response of photosynthesis to temperature change varies with vegetation types and environmental conditions (Medlyn et al., 2002; Voigt et al.,

2017). Methane (CH_4) emissions from peatlands to the atmosphere depend on the balance of CH_4 production, oxidation and transportation rate. Both CH_4 production by methanogens and oxidation by methanotrophs are strongly correlated with temperature (Segers, 1998). Nevertheless, CH_4 production was reported to be more sensitive to temperature change than CH_4 consumption (Dunfield et al., 1993), thus a warmer climate is expected to increase CH_4 release to the atmosphere. Due to the different responses of these processes, estimating the net response of C in peatlands to climate warming is still challenging.

In addition, climate warming can affect the peatland C cycle indirectly via modifying the vegetation structure. It has been demonstrated that warming could promote the growth of vascular plants, especially ericaceous shrubs and graminoids to the detriment of *Sphagnum* species (Bragazza et al., 2013; Buttler et al., 2015; Dieleman et al., 2015). *Sphagnum* litter is resistant to decay, which is beneficial for the C sequestration in peatlands (AminiTabrizi et al., 2020). However, the presence of vascular plants alters the litter quality in peatlands with an increase of its degradability, which enhances the decomposition (Straková et al., 2011; Leroy et al., 2019). Furthermore, the root exudates from vascular plants are a source of labile C input, which on one hand provide substrate for microbial degradation, and on another hand lead to the priming effect thus stimulate the decomposition of 'old' and so-called recalcitrant OM (Gavazov et al., 2018; Girkin et al., 2018). Nevertheless, this vegetation shift also increases the C input to peatlands because of the higher primary productivity of vascular plants (Gavazov et al., 2018; Leroy et al., 2019).

To date, numerous studies have tried to understand the response of peatlands to global warming. However, most of them focused on northern peatlands in subarctic regions (e.g. Aurela et al., 2004; Chivers et al., 2009; Dieleman et al., 2015; Munir et al., 2015; Voigt et al., 2017; Laine et al., 2019), where the majority of peatlands are located (Strack, 2008). Previous results showed that the effect of warming on the C sequestration of peatlands varied from strengthening to diminishing (e.g. Waddington et al., 1998; Chivers et al., 2009; Ward et al., 2013; Munir et al., 2015; Hanson et al., 2020). Therefore, it is still difficult to draw a conclusion on the precise feedback of peatlands to climate warming. More importantly, there is still a large gap in the understanding of how temperate peatlands will respond to the warming climate. Temperate low-latitude peatlands are already below the temperature which is the projected level of subarctic regions in the future. Furthermore, they have suffered high anthropogenic pressures (e.g. hydrological disturbance; peat cutting or nutrient amendment) and a vegetation shift has occurred (Berendse et al., 2001; Bubier et al., 2007). These disturbances have diminished their

C storage (Dorrepaal et al., 2005; Gogo et al., 2016), thus they have significant potential to act as a C source in the future (Leifeld et al., 2019). Especially under the projected climate warming, it is important to assess how these temperate peatlands will respond to both anthropogenic and climate disturbance.

In order to understand the response to climate warming of a temperate *Sphagnum* peatland which has been invaded by vascular plants (especially *Molinia caerulea*), we conducted a mesocosm experiment. The mesocosms were submitted to two temperature treatments: 1) ambient (control) and 2) moderate experimental warming by open-top chambers (OTCs). The CO_2 and CH_4 fluxes were monitored for 2 years. Then they were modelled by relating to abiotic and biotic factors in order to estimate the annual C budget. We hypothesized that the warming treatment would (1) promote both the C input to peatland through photosynthesis and the C release to the atmosphere through respiration and CH_4 emissions; (2) diminish the C sink function of this ecosystem.

IV.3.2 Materials and methods

IV.3.2.1. Modelling of gross primary production (GPP)

GPP was modelled based on Eq.IV-5 described in IV.2.2:

$$GPP = \frac{GPP_{max} \times PAR}{k+PAR} \times (a \times Graminoid_{leaf} + b \times VI + c \times \frac{WTD}{WTD_{ref}}) \times T_{scale} \quad \text{Eq.IV-14}$$

where GPP_{max} (µmol m^{-2} s^{-1}) is the asymptotic maximum GPP at light saturation, k (µmol photon m^{-2} s^{-1}) is the half-saturation value. These two variables were calculated by the Michaelis-Menten equation (Johnson and Goody, 2011) based on the light response curve of GPP. PAR (mol m^{-2} s^{-1}) is the photosynthetically active radiation. $Graminoid_{leaves}$ is the number of graminoids leaves. VI is the vegetation index (Eq. III-1). WTD is the water table depth (cm), and its reference value, WTD_{ref}, was set at -25 cm, which was the lowest value we observed in the mesocosms. The coefficients a, b and c are fitted empirical parameters. T_{scale} represents the temperature sensitivity of photosynthesis (Raich et al., 1991; Mahadevan et al., 2008):

$$T_{scale} = \frac{(T-T_{min})(T-T_{max})}{(T-T_{min})(T-T_{max})-(T-T_{opt})^2} \quad \text{Eq.IV-15}$$

where T is the measured air temperature (°C). T_{min}, T_{max} and T_{opt} are minimum, maximum and optimum air temperature (°C) for photosynthesis, respectively. Following Leroy et al. (2019), they were set as 0, 20 and 40 °C, respectively.

IV.3.2.2 Modelling of ecosystem respiration (ER)

The ER was modeled based on Eq.IV-8 in IV.2.3:

$$ER = (d \times \frac{WTD}{WTD_{ref}} + e \times Graminoid_{leaf}) \times (\frac{T - T_{min}}{T_{ref} - T_{min}})^f \quad \text{Eq.IV-16}$$

where the reference of water table depth, WTD_{ref}, was also set at -25 cm as mentioned above. T_{min} is the minimum temperature (°C) for positive respiration and T_{ref} is the reference temperature (°C). They were set as -5 and 15 °C, respectively, following Bortoluzzi et al. (2006). T is the measured temperature (°C). The model was fitted with air temperature, soil temperature at 5, 15 and 30 cm depth. The best fit was found when using soil temperature at 5 cm, thus it was used as T here. The coefficients d, e and f are fitted empirical parameters.

IV.3.2.3 Modelling of CH_4 emissions

CH_4 emissions was modelled based on Eq.IV-10 in IV.2.4:

$$CH_4 = \left(g \times \frac{WTD}{WTD_{ref}} + h \times Graminoid_{leaves}\right) \times \left(\frac{T_s - T_{min}}{T_{ref} - T_{min}}\right)^i \text{ (WTD>-9cm)} \quad \text{Eq.IV-17}$$

where T_{min} is minimum temperature (°C) for CH_4 emissions, it was set as 1 °C which was the minimum soil temperature observed at 5 cm depth. T_{ref} is reference temperature (°C), it was set as 20 °C which was the median value of annual soil temperature at 5 cm depth. T_s is the measured soil temperature (°C). The model was fitted with soil temperature at 5, 15 and 30 cm depth. The best fit was found when using soil temperature at 5 cm, thus it was used as T_s here. The coefficients g, h and i are fitted empirical parameters.

There were 74 WTD data points measured below WTD of -9 cm, i.e. 28.6 % of the total of 259 measured data. When WTD was below -9 cm, CH_4 emissions were independent of temperature and WTD. Thus, the CH_4 emissions were not modelled by Eq.IV-17, but they were linearly interpolated in this case.

IV.3.2.4 Calibration and evaluation of models

Two thirds (randomly selected) of the available data from each treatment were used to calibrate the model and another one third of the data were used to evaluate the model. The quality of model was evaluated by the adjusted determination coefficient (R_{adj}^2) and the normalized root-mean-square error (NRMSE; %) of the linear relationship between measured and modelled data:

$$R_{adj}^2 = 1 - \left(1 - \frac{(1-R^2)(n-1)}{n-k-1}\right) \quad \text{Eq.IV-12}$$

where R^2 is the coefficient of determination, n represent the number of data and k is the number of independent regressors.

$$NRMSE = 100 * \frac{\sqrt{\left(\frac{\sum(y-\hat{y})}{n}\right)}}{\bar{y}} \quad \text{Eq.IV-13}$$

where y is the measured value, $\hat{y}$ is the modelled value, $\bar{y}$ is the mean of measured values and n the number of data.

The fitted parameters of GPP model (a, b and c), ER model (d, e and f) and CH_4 emissions model (g, h and i) were calibrated by minimizing the NRMSE using the "SANN" method of the optimum function in R (R 3.6.3, R Core Team 2020).

IV.3.2.5 Calculation of annual C fluxes and C budget

After calibration and evaluation of the C fluxes models, the models were parameterized for each mesocosm under both treatments individually. All the variables used in the models were interpolated to set a 1 h dataset. To do so, PAR, air and soil temperature at 3 depths which were monitored with high frequency (5 min) were averaged over a 1 h time step. The others variables which were measured with low frequency (WTD, number of graminoids leaves and VI) were linearly interpolated between the punctual measurements to set a 1 h dataset. Then, the GPP, ER and CH_4 emissions were calculated at a 1 h time step using the relationships between C fluxes and environmental variables constructed above. Due to the technical problems in August 2018 and the lockdown because of Covid-19 from March 2020, the environmental variables data recorded by weather stations were not complete during these periods. Thus, the modelled GPP, ER and CH_4 emissions at a 1 h time step were only calculated from September

2018 to September 2019. Then, the annual cumulated GPP, ER and CH_4 emissions (gC m^{-2} yr^{-1}) during this period were calculated as the sum of values at a 1 h time step.

The annual greenhouse gas C budget (GGCB; gC m^{-2} yr^{-1}) indicates the net gaseous C accumulation/release rate of the ecosystem. It was calculated for each mesocosm under both treatments as follow:

$$GGCB = -GPP + ER + F_{CH_4} \quad \text{Eq.IV-18}$$

where GPP is the annual cumulated gross primary production (gC m^{-2} yr^{-1}), ER is the annual cumulated ecosystem respiration (gC m^{-2} yr^{-1}), F_{CH4} is the annual cumulated emission of CH_4 (gC m^{-2} yr^{-1}).

IV.3.2.6 Statistics

The differences of the calculated GPP_{max} between the two treatments at different dates were analyzed by one-way ANOVA. The significant differences in the modelled annual cumulated GPP, ER, CH_4 emission, NEE and GGCB between the two treatments were assessed by one-way ANOVA. Before statistical analysis, the normality of distribution and the homogeneity of variance of the data were tested. All the statistics were performed in OriginPro 2019 (OriginLab, USA).

IV.3.3 Results

IV.3.3.1 Modelled C fluxes

The GPP, ER and CH_4 models were calibrated and evaluated for the two treatments separately. Calibration of the models showed that the modelled data were in good agreements of the measured data, with high R^2_{adj} (>0.5) and low NRMSE (<70 %). Meanwhile, the evaluation results also suggested the good representative of the models to the measured data, with R^2_{adj} higher than 0.8 and NRMSE lower than 42 % (except for the CH_4 model which showed a $R^2_{adj} < 0.4$ and an NRMSE > 70 %; Table IV-4).

Table IV-4 R^2_{adj} and normalized root-mean-square errors (NRMSE; %) for calibration and evaluation of ecosystem respiration (ER), gross primary production (GPP) and CH_4 emissions models under control and OTC treatments.

	Calibration				Evaluation			
	Control		OTCs		Control		OTCs	
	r^2_{adj}	NRMSE	r^2_{adj}	NRMSE	r^2_{adj}	NRMSE	r^2_{adj}	NRMSE
GPP	0.88	40.9	0.84	55.8	0.89	39.3	0.93	38.5
ER	0.66	59.3	0.59	63	0.82	40.4	0.82	41.4
CH_4	0.71	52.7	0.80	44.5	0.83	40.4	0.38	74.8

IV.3.3.1.1 GPP

The GPP_{max}, which was calculated using the Michaelis-Menten equation based on the photosynthesis-irradiation curve, exhibited obvious seasonal trends. It ranged from -1.60 to -15.61 μmol m^{-2} s^{-1} for control and from -1.96 to -20.26 μmol m^{-2} s^{-1} for OTC plots, with higher photosynthetic capacity during summer and lower during winter (Fig. IV-8a). GPP_{max} was enhanced by OTC treatment in September 2018 and September 2019. A linear relationship between GPP_{max} and the number of graminoids leaves was observed for both treatments (Fig. IV-8b).

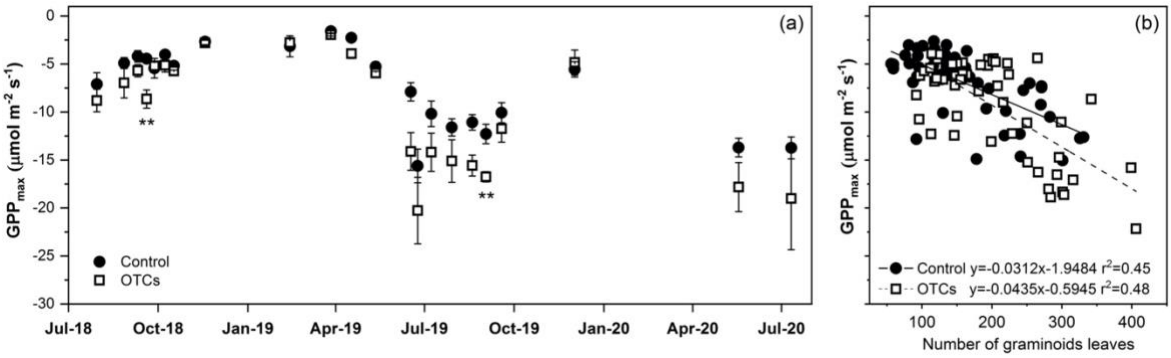


Figure IV-8 The maximum rate of photosynthesis (GPP_{max}) calculated from the photosynthesis-irradiance curve from July 2018 to July 2020 (a) and the linear relationship between GPP_{max} and the number of graminoids leaves (b). Significant differences of ANOVA are expressed as $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

The GPP model was parameterized for each replicate under the two treatments individually. The results showed that the R^2_{adj} of mesocosms ranged from 0.81 to 0.99, and the NRMSE values ranged from 6.0 to 45.3 % (Supplimentary Table IV-1). Therefore, this model represented the measured GPP well (Supplementary Figure IV-1a and b). The model parameters

a and b, which represent sensitivity to vegetation change, and parameter c which represents sensitivity to WTD change, showed similar values between the two treatments (-0.001 ± 0.002 and -0.001 ± 0.001 of a; 2.61 ± 1.21 and 2.53 ± 0.47 of b; 0.10 ± 0.40 and -0.14 ± 0.27 of c for the control and OTC treatment respectively; Supplimentary Table IV-1).

The annual cumulated GPP during September 2018 to September 2019 ranged from -449 to -640 gC m^{-2} yr^{-1} for control plots and from -523 to -719 gC m^{-2} yr^{-1} for OTC plots (Supplimentary Table IV-1). Comparing the two treatments, it was significant higher in OTC plots compared with control (602 ± 73 vs. 501 ± 70 gC m^{-2} yr^{-1}; p=0.036; Table IV-5). This result suggested that experimental warming increased the CO_2 input through photosynthesis. In particular, the enhancement of warming on the GPP mainly occurred during April-May 2019 (Fig. IV-9a), corresponding to the higher graminoids leaf number under OTC treatment in this period (Figure III-5d).

IV.3.3.1.2 ER

The results of parameterizing the ER model for each mesocosm showed that, the R^2_{adj} values ranged from 0.58 to 0.95, with the exception of R6 under OTC treatment (R^2_{adj}=0.06). The NRMSE values ranged from 23.8 to 70.2 %, except for R6 under OTC treatment (NRMSE=104.1 %; Supplimentary Table IV-1). These model quality indicators suggested the good agreements between modelled and measured ER values (Supplementary Figure IV-1c and d). The model parameters d, e and f, which represent sensitivity to WTD, vegetation and temperature change, respectively, were similar between the two treatments (1.65 ± 1.70 and 1.62 ± 2.10 of d; 0.005 ± 0.003 and 0.006 ± 0.003 of e; 2.03 ± 0.46 and 1.54 ± 0.97 of f for control and OTC treatment respectively; Supplimentary Table IV-1).

The annual cumulated ER during September 2018 to September 2019 was 500 ± 102 gC m^{-2} yr^{-1} in control plots (ranging from 354 to 641 gC m^{-2} yr^{-1}) and 615 ± 171 gC m^{-2} yr^{-1} in OTC plots (ranging from 382 to 840 gC m^{-2} yr^{-1}; Table IV-5 and Supplimentary Table IV-1), but the difference was not significant (p=0.19; Fig. IV-9a).

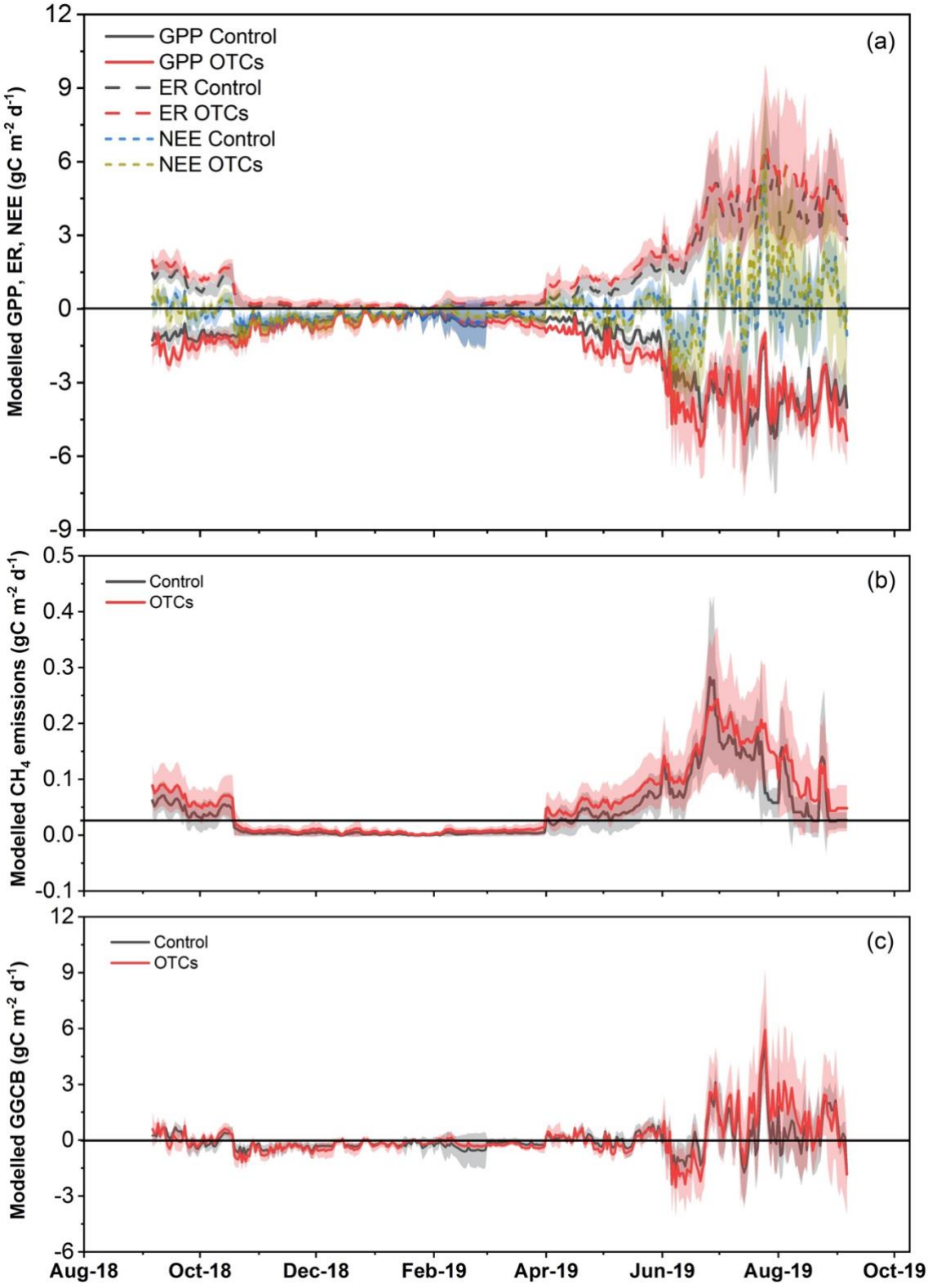


Figure IV-9 Modelled daily cumulated GPP (solid lines), ER (dash lines), NEE (short dash lines; gC m^{-2} d^{-1}; a), CH_4 emissions (gC m^{-2} d^{-1}; b) and greenhouse gas C budget (GGCB; gC m^{-2} d^{-1}; c) from September 2018 to September 2019 in control and OTCs plots. Lines indicate the mean values of replicates and colored shading indicates the error bars of standard deviation.

IV.3.3.1.3 CH_4

After parameterizing the CH_4 model for each replicate, we found that the R^2_{adj} ranged from 0.82 to 0.97, except R3 under OTC (R^2_{adj}=0.44). The NRMSE values ranged between 18.3 and 41.7 % with the exception of R3 under OTC (NRMSE=66.7 %; Supplimentary Table IV-1). Thus, this model represented the measured CH_4 well (Supplementary Figure IV-1E and F). The model parameters g, h and i, which represent sensitivity to WTD, vegetation and temperature, respectively, were similar between the two treatments (0.06 ± 0.05 and 0.06 ± 0.08 of g; 0.0004 ± 0.0002 and 0.0004 ± 0.0002 of h; 2.15 ± 1.72 and 1.24 ± 0.89 of i for control and OTC treatment respectively; Supplimentary Table IV-1).

The modelled annual CH_4 emission ranged from 11 to 22 gC m^{-2} yr^{-1} under control and from 11 to 33 gC m^{-2} yr^{-1} under OTC treatment (Supplimentary Table IV-1), with an average of 16 ± 5 and 21 ± 9 gC m^{-2} yr^{-1} in control and OTC plots, respectively (Table IV-5). However, the warming treatment had no significant effect on the annual CH_4 emission (p=0.83; Fig. IV-9b).

IV.3.3.2 NEE and GGCB

The annual NEE of the control plots showed a slight input of CO_2 (-2 ± 83 gC m^{-2} yr^{-1}) but that of OTC plots exhibited a slight output of CO_2 (13 ± 136 gC m^{-2} yr^{-1}; Table IV-5). While no significant difference between the two treatments was found (p=0.83). The annual GGCB showed a release of 14 ± 82 and 34 ± 137 gC m^{-2} yr^{-1} for control and OTC treatment, respectively (Table IV-5). However, the difference was not significant (p=0.77). Thus, mesocosms under both treatments acted as C source. Particularly, a strong net C source was found during July-August 2019 for both treatments (Fig. IV-9c), corresponding to the low WTD in this period (Figure III-4). This strong net C source mainly resulted from the net CO_2 source, as NEE showed similar values as GGCB during this period (Fig. IV-9a), while CH_4 emissions only accounted for 0.9-2.2% in the total C fluxes.

Table IV-5 Modeled annual cumulated gross primary production (GPP; gC m^{-2} yr^{-1}), ecosystem respiration (ER; gC m^{-2} yr^{-1}), CH_4 emissions (CH_4; gC m^{-2} yr^{-1}), net ecosystem exchange (NEE; gC m^{-2} yr^{-1}) and greenhouse gases carbon budget (GGCB; gC m^{-2} yr^{-1}) from September 2018 to September 2019 in control and OTC plots. Data are presented as mean ± SD, n=6.

	GPP	ER	CH_4	NEE	GGCB
Control	-501 ± 70	500 ± 102	16 ± 5	-2 ± 83	14 ± 82
OTCs	-602 ± 73	615 ± 171	21± 9	13 ± 136	34 ± 137

IV.3.4 Discussion

IV.3.4.1 Climate regime and vegetation control on the CO_2 fluxes

On the whole, the annual GPP (~450 to 720 gC m^{-2} yr^{-1}) and ER (~350 to 840 gC m^{-2} yr^{-1}; Supplimentary Table IV-1) in the present study were higher than those from boreal peatlands, which showed the GPP and ER fluxes between 100 and 500 gC m^{-2} yr^{-1} (e.g. Cliche Trudeau et al., 2014; Peichl et al., 2014). This may be caused by the differences in climate regime, particularly the higher annual temperature in our study site compared to sites at higher latitudes. While when compared to studies conducted under the same climate condition, our values were lower. In the same site (La Guette peatland) where our mesocosms were collected, D'Angelo et al. (2021) reported the GPP and ER were all above 1000 gC m^{-2} yr^{-1} with *in situ* measurements. In addition, Leroy et al. (2019) estimated an annual GPP of 1300 gC m^{-2} yr^{-1} and ER of 1000 gC m^{-2} yr^{-1} in mesocosms dominated by *Molinia caerulea* collected from La Guette peatland. This could be attributed to the differences in vegetation. La Guette peatland was almost entirely invaded by *Molinia caerulea* (Gogo et al., 2011), thus the percentage cover of *Molinia* in both field and *Molinia* dominated mesocosms were higher than our mesocosms. The GPP of graminoids was higher than that of shrubs and bryophytes, and the GPP of graminoids dominated peatlands was similar with those of temperate grasslands (Rydin and Jeglum, 2013; Leroy et al., 2019). Therefore, compared with the results of D'Angelo et al. (2021) and Leroy et al., (2019), the lower GPP observed in our study could be attributed to the lower abundance of graminoids. This was supported by the fact that mesocosms with only *Sphagnum* had lower GPP and ER (400 and 380 gC m^{-2} yr^{-1}, respectively; Leroy et al., 2019) than our study. In addition, the positive relationship between GPP_{max} and the number of

graminoids leaves also confirmed the strong effect of graminoids abundance on GPP (Fig. IV-8b). The lower ER observed in our study also can be attributed to the lower abundance of graminoids. *Molinia caerulea* has extensive root system, which is larger than other species. Thus the lower abundance of this species compared with previous studies could induce lower root and leaf respiration in our mesocosms.

IV.3.4.2 Stimulation of OTCs on the GPP

In previous studies, the effect of temperature rise on GPP varied from increasing (e.g. Chivers et al., 2009) to decreasing (e.g. Voigt et al., 2017) or no effect (e.g. Johnson et al., 2013; Laine et al., 2019), depending on the peatland type and initial vegetation composition. In our research, the warming treatment significantly increased the annual cumulated GPP of mesocosms from 500 to 615 gC m^{-2} yr^{-1}. The enhancement mainly occurred during April-May 2019 (Fig. IV-9a), when the number of graminoids leaves was higher under warming treatment than control (Figure III-5d). Experimental warming facilitated the growth of graminoids, thus increase the plant biomass (evidenced by the higher leaves number). The increase of plant biomass in turn increased the capacity of vegetation to withdraw CO_2 from the atmosphere (higher GPP). Our result of a significant correlation between GPP_{max} and graminoids leaves number (Fig. IV-8b) confirmed this statement. In addition, Tuittila et al. (2004) found that the GPP of *Sphagnum* increased with water content. In our study, the *Sphagnum* at 5 cm depth was wetter under OTC treatment than control during summer (Fig. III-3), probably caused by the less wind presence and lower wind speed in OTCs compared with ambient environment which reduced the evapotranspiration. Thus, the higher water content of *Sphagnum* in OTC plots may also contributed to the higher GPP under warming treatment.

IV.3.4.3 WTD modulate the ER response to warming

The warming treatment had no significant effect on the annual cumulated ER in our research. This result was inconsistent with previous studies which reported an increase of ER with temperature (e.g. Updegraff et al., 2001; Chivers et al., 2009; Voigt et al., 2017; Samson et al., 2018). Laine et al. (2019) found a low temperature sensitivity of ER under wet condition. In their study, warming had no significant effect on ER under ambient wet condition, while ER was significantly increased by moderate warming under dry condition. The low temperature sensitivity of ER under wet condition may be attributed to the low temperature sensitivity of

soil respiration, as it was reported to be less sensitive to temperature change under anaerobic than aerobic condition (Szafranek-Nakonieczna and Stepniewska (2014). Meanwhile, Chen et al. (2018) found a positive relationship between the temperature sensitivity (Q_{10}) of soil respiration and the soil redox potential, which confirmed this result. In our study, the mean WTD throughout the monitoring were -6.80 and -6.68 cm for control and OTC treatment, respectively (Table III-1). The WTD was mostly above -5 cm except during summer (Fig. III-4), suggesting a dominant anaerobic condition in our mesocosms. Therefore, the water saturated condition may lead to a low temperature sensitivity of soil respiration and thus a similar ER under both treatments.

IV.3.4.4 WTD dependence of CH_4 emission

The annual cumulated CH_4 emission in our results was lower than the 33 gC m^{-2} yr^{-1} found by Leroy et al. (2019) with mesocosms collected from the same peatland. This was caused by the lower WTD in our mesocosms (Fig. III-4) compared with them. During our monitoring, WTD reached to a level below -15 cm during July-September 2019, while it remained above -10 cm most of time in their experiment (data in Leroy et al., 2017). WTD has been reported to be a stronger regulator on CH_4 emissions than temperature (Roulet et al., 1992; Turetsky et al., 2008). When the WTD decreased, the amount of water-saturated (i.e. anaerobic) peat declined and the aerobic layer increased, thus the oxidation of CH_4 was promoted. In our study, the correlation between CH_4 emissions and temperature was only found when WTD ranged between 0 and -9 cm. However, when WTD dropped below -9 cm, CH_4 emissions were independent of temperature (Fig. IV-1d). This result confirmed the controlling of WTD on CH_4 emissions. In our results of the measured CH_4 emissions, the enhancement of CH_4 emission by warming treatment was only found when WTD initially reached the lowest level (Fig. IV-1d and Fig. III-4). Thus warming alone may have only slight effect on the CH_4 emissions, while if warming interacted with WTD dropdown, their interaction could have significant effect on the CH_4 emissions (Munir and Strack, 2014).

IV.3.4.5 Temperature and WTD modulated peatlands functioning

Previous research showed that the peatlands varied from C sink (e.g. Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007) to C source (e.g. Waddington and Roulet, 2000; Voigt et al., 2017). In our study, the C balance of individual mesocosm showed large variations

ranging from gaseous C sink to source, with an average of 14 and 34 gC m^{-2} yr^{-1} output of C under control and OTC treatment respectively (Table IV-5). The La Guette peatland also acted as a C source with an output of 220 gC m^{-2} yr^{-1} during 2013 and 2014. The stronger C source in the field than our mesocosms was linked to the repeated droughts in the previous years (D'Angelo et al., 2021). However, in the study of Leroy et al. (2019), both *Sphagnum* and *Molinia caerulea* dominated mesocosms collected from this peatland acted as gaseous C sink. This difference may be caused by the low WTD in our mesocosms during summer (Fig. III-4). We found that the mesocosms under both treatments showed high positive NEE values during July-September 2019 (Fig. IV-9a), suggesting a strong CO_2 source. This strong CO_2 source corresponded to the low WTD in this period (Fig. III-4). The low WTD induced a higher respiration under aerobic condition, thus the ER exceeded GPP and led to a net CO_2 release. The CH_4 emissions decreased following the decline of WTD, while it only accounted for 0.9-2.2% of the total C fluxes. Therefore, the net C losses in our study were mainly driven by the net CO_2 output. The controlling of WTD on the CO_2 exchange was in accordance with Laine et al. (2019), who observed a decreasing CO_2 uptake with low WTD due to the increase of CO_2 release as a result of the increased OM decomposition.

Hanson et al. (2020) have found that an air temperature increase of 2.25-9 ^oC enhanced the net C source of peatland during 3 years monitoring. Bridgham et al. (2008) conducted a 7-years monitoring and the results showed that a soil warming of 1.6-4.1 ^oC significantly reduced the C accumulation of peatland. Bragazza et al. (2016) also observed a reduction of peatland C accumulation with 5 ^oC air temperature increase during 3 years. Compared with our study, these studies which found an impact of warming on the C budget of peatlands always have stronger temperature increases than us (0.9 ^oC increase in air temperature; 1.35 and 0.95 ^oC increase in soil temperature at 5 and 15 cm depth, respectively), or longer time warming treatment. With a moderate warming (+0.7 ^oC soil warming at 2 cm depth) for 2 years like our study, Chivers et al. (2009) found that warming did not modify the C balance of peatland. In addition, there was other research found that the C sink of peatland can be enhanced by manipulated warming (about 1 ^oC air temperature increase; Munir et al., 2015). This was caused by the enhanced growth of shrubs by warming in their treed bog. It has been demonstrated that the response of GHG emissions to warming largely depended on the vegetation composition and environmental conditions of the study site, as well as the warming methods, the warming rate and the duration of the experiment (Gong et al., 2020). Any difference in these factors could lead to contrasting results. In our study, we found that a temperate peatland which has suffered a vegetation shift

from *Sphagnum*- to vascular plant-dominance remained stable in response to short-term moderate warming. However, as the vascular plants could benefit more from warming than *Sphagnum* (Bragazza et al., 2013; Buttler et al., 2015; Dieleman et al., 2015), a vegetation structure change under long-term warming is expected, which may lead to a modification of C balance in the future.

IV.3.5 Conclusion

In our study, the CO_2 and CH_4 fluxes of mesocosms collected from a temperate peatland were monitored and modelled using abiotic and biotic factors, including temperature, WTD and vegetation. Models based on these variables described the measured data well. The modelled results showed that the experimental warming significantly enhanced the annual CO_2 uptake through photosynthesis, but had no effect on the ER and CH_4 emissions. The increase of photosynthesis was attributed to the faster growth of graminoids under warming treatment during the early growing season. The mesocosms under both treatments acted as gaseous C source and it was caused by the net CO_2 release during low WTD period in summer. The gaseous C balance remained stable under the 2 years of moderate warming. Our study demonstrated the strong effect of moderate warming on the gaseous C fluxes of temperate peatlands. Moreover, we emphasized the necessity of integrating the WTD and vegetation change along with warming to determine the effect of their interactions on the peatland C fluxes. Further studies of long-term monitoring with a consideration of climate induced both abiotic and biotic factors will be needed to better estimate the feedback of peatlands to global changes as well as its magnitude.

References

AminiTabrizi, R., Wilson, R. M., Fudyma, J. D., Hodgkins, S. B., Heyman, H. M., Rich, V. I., et al. (2020). Controls on soil organic matter degradation and subsequent greenhouse gas emissions across a permafrost thaw gradient in Northern Sweden. *Front. Earth Sci.* 8. doi:10.3389/feart.2020.557961.

Aronson, E. L., and McNulty, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agric. For. Meteorol.* 149, 1791–1799. doi:10.1016/j.agrformet.2009.06.007.

Aurela, M., Laurila, T., and Tuovinen, J.-P. (2004). The timing of snow melt controls the annual CO_2 balance in a subarctic fen. *Geophys. Res. Lett.* 31. doi:10.1029/2004GL020315.

Berendse, F., Breemen, N. V., Rydin, Hå., Buttler, A., Heijmans, M., Hoosbeek, M. R., et al. (2001). Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. *Glob. Change Biol.* 7, 591–598. doi:10.1046/j.1365-2486.2001.00433.x.

Bortoluzzi, E., Epron, D., Siegenthaler, A., Gilbert, D., and Buttler, A. (2006). Carbon balance of a European mountain bog at contrasting stages of regeneration. *New Phytol.* 172, 708–718. doi:10.1111/j.1469-8137.2006.01859.x.

Bragazza, L., Buttler, A., Robroek, B. J. M., Albrecht, R., Zaccone, C., Jassey, V. E. J., et al. (2016). Persistent high temperature and low precipitation reduce peat carbon accumulation. *Glob. Change Biol.* 22, 4114–4123. doi:https://doi.org/10.1111/gcb.13319.

Bragazza, L., Buttler, A., Siegenthaler, A., and Mitchell, E. A. D. (2009). Plant litter decomposition and nutrient release in peatlands. *GMS* 184, 99–110. doi:10.1029/2008GM000815.

Bragazza, L., Parisod, J., Buttler, A., and Bardgett, R. D. (2013). Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. *Nat. Clim. Change* 3, 273–277. doi:10.1038/nclimate1781.

Bridgham, S. D., Pastor, J., Dewey, B., Weltzin, J. F., and Updegraff, K. (2008). Rapid carbon response of peatlands to climate change. *Ecology* 89, 3041–3048. doi:https://doi.org/10.1890/08-0279.1.

Bubier, J. L., Moore, T. R., and Bledzki, L. A. (2007). Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Glob. Change Biol.* 13, 1168–1186. doi:10.1111/j.1365-2486.2007.01346.x.

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., et al. (2015). Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *J. Veg. Sci.* 26, 964–974. doi:10.1111/jvs.12296.

Chen, H., Zou, J., Cui, J., Nie, M., and Fang, C. (2018). Wetland drying increases the temperature sensitivity of soil respiration. *Soil Biol. Biochem.* 120, 24–27. doi:10.1016/j.soilbio.2018.01.035.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan rich fen. *Ecosystems* 12, 1329–1342. doi:10.1007/s10021-009-9292-y.

Cliche Trudeau, N., Garneau, M., and Pelletier, L. (2014). Interannual variability in the CO_2 balance of a boreal patterned fen, James Bay, Canada. *Biogeochemistry* 118, 371–387. doi:10.1007/s10533-013-9939-9.

D'Angelo, B., Leroy, F., Guimbaud, C., Jacotot, A., Zocatelli, R., Gogo, S., et al. (2021). Carbon balance and spatial variability of CO_2 and CH_4 fluxes in a *Sphagnum*-dominated peatland in a temperate climate. *Wetlands* 41, 5. doi:10.1007/s13157-021-01411-y.

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Glob. Change Biol.* 21, 388–395. doi:10.1111/gcb.12643.

Dieleman, C. M., Lindo, Z., McLaughlin, J. W., Craig, A. E., and Branfireun, B. A. (2016). Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry* 128, 385–396. doi:10.1007/s10533-016-0214-8.

Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., and Logtestijn, R. S. P. V. (2005). Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *J. Ecol.* 93, 817–828. doi:10.1111/j.1365-2745.2005.01024.x.

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., et al. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* 460, 616–619. doi:10.1038/nature08216.

Dunfield, P., Dumont, R., and Moore, T. R. (1993). Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biol. Biochem.* 25, 321–326.

Flanagan, L. B., and Syed, K. H. (2011). Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Glob. Change Biol.* 17, 2271–2287. doi:10.1111/j.1365-2486.2010.02378.x.

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., et al. (2018). Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. *Glob. Change Biol.* 24, 3911–3921. doi:10.1111/gcb.14140.

Girkin, N. T., Turner, B. L., Ostle, N., Craigon, J., and Sjögersten, S. (2018). Root exudate analogues accelerate CO_2 and CH_4 production in tropical peat. *Soil Biol. Biochem.* 117, 48–55. doi:10.1016/j.soilbio.2017.11.008.

Gogo, S., Laggoun-Défarge, F., Delarue, F., and Lottier, N. (2011). Invasion of a *Sphagnum*-peatland by *Betula spp* and *Molinia caerulea* impacts organic matter biochemistry. Implications for carbon and nutrient cycling. *Biogeochemistry* 106, 53–69. doi:10.1007/s10533-010-9433-6.

Gogo, S., Laggoun-Défarge, F., Merzouki, F., Mounier, S., Guirimand-Dufour, A., Jozja, N., et al. (2016). In situ and laboratory non-additive litter mixture effect on C dynamics of *Sphagnum rubellum* and *Molinia caerulea* litters. *J. Soils Sediments* 16, 13–27. doi:10.1007/s11368-015-1178-3.

Gong, Y., Wu, J., Vogt, J., and Ma, W. (2020). Greenhouse gas emissions from peatlands under manipulated warming, nitrogen addition, and vegetation composition change: a review and data synthesis. *Environ. Rev.* doi:10.1139/er-2019-0064.

Gorham, E. (1991). Northern Peatlands: Role in the carbon cycle and probable responses to climatic warming. *Ecol. Appl.* 1, 182–195. doi:10.2307/1941811.

Hanson, P. J., Griffiths, N. A., Iversen, C. M., Norby, R. J., Sebestyen, S. D., Phillips, J. R., et al. (2020). Rapid net carbon loss from a whole-ecosystem warmed peatland. *AGU Adv.* 1, e2020AV000163. doi:https://doi.org/10.1029/2020AV000163.

IPCC (2014). Climate Change 2014: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. *Cambridge University Press*.

Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., and Piñeiro, G. (2017). The ecology of soil carbon pools, vulnerabilities, and biotic and abiotic controls. *Annu. Rev. Ecol. Evol. Syst.* 48, 419–445. doi:10.1146/annurev-ecolsys-112414-054234.

Johnson, C. P., Pypker, T. G., Hribljan, J. A., and Chimner, R. A. (2013). Open top chambers and infrared lamps: A comparison of heating efficacy and CO_2/CH_4 dynamics in a Northern Michigan peatland. *Ecosystems* 16, 736–748. doi:10.1007/s10021-013-9646-3.

Johnson, K. A., and Goody, R. S. (2011). The original Michaelis constant: Translation of the 1913 Michaelis–Menten Paper. *Biochemistry* 50, 8264–8269. doi:10.1021/bi201284u.

Kandel, T. P., Elsgaard, L., and Lærke, P. E. (2013). Measurement and modelling of CO_2 flux from a drained fen peatland cultivated with reed canary grass and spring barley. *GCB Bioenergy* 5, 548–561. doi:10.1111/gcbb.12020.

Koehler, A.-K., Sottocornola, M., and Kiely, G. (2011). How strong is the current carbon sequestration of an Atlantic blanket bog? *Glob. Change Biol.* 17, 309–319. doi:10.1111/j.1365-2486.2010.02180.x.

Laine, A. M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., et al. (2019). Warming impacts on boreal fen CO_2 exchange under wet and dry conditions. *Glob. Change Biol.* 25, 1995–2008. doi:10.1111/gcb.14617.

Laine, A., Wilson, D., Kiely, G., and Byrne, K. A. (2007). Methane flux dynamics in an Irish lowland blanket bog. *Plant Soil* 299, 181–193. doi:10.1007/s11104-007-9374-6.

Leifeld, J., Wüst-Galley, C., and Page, S. (2019). Intact and managed peatland soils as a source and sink of GHGs from 1850 to 2100. *Nat. Clim. Change* 9, 945–947. doi:10.1038/s41558-019-0615-5.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., and Laggoun-Défarge, F. (2017). Vegetation composition controls temperature sensitivity of CO_2 and CH_4 emissions and DOC concentration in peatlands. *Soil Biol. Biochem.* 107, 164–167. doi:10.1016/j.soilbio.2017.01.005.

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., et al. (2019). CO_2 and CH_4 budgets and global warming potential modifications in *Sphagnum*-dominated peat mesocosms invaded by *Molinia caerulea*. *Biogeosciences* 16, 4085–4095. doi:https://doi.org/10.5194/bg-16-4085-2019.

Lloyd, J., and Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323. doi:10.2307/2389824.

Mahadevan, P., Wofsy, S. C., Matross, D. M., Xiao, X., Dunn, A. L., Lin, J. C., et al. (2008). A satellite-based biosphere parameterization for net ecosystem CO_2 exchange: Vegetation photosynthesis and respiration model (VPRM). *Glob. Biogeochem. Cycles* 22. doi:10.1029/2006GB002735.

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., et al. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol.* 3, 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x.

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., et al. (2002). Temperature response of parameters of a biochemically based model of photosynthesis.

II. A review of experimental data. *Plant Cell Environ.* 25, 1167–1179. doi:10.1046/j.1365-3040.2002.00891.x.

Munir, T. M., Perkins, M., Kaing, E., and Strack, M. (2015). Carbon dioxide flux and net primary production of a boreal treed bog: Responses to warming and water-table-lowering simulations of climate change. *Biogeosciences* 12, 1091–1111. doi:https://doi.org/10.5194/bg-12-1091-2015.

Munir, T. M., and Strack, M. (2014). Methane flux influenced by experimental water table drawdown and soil warming in a dry boreal continental bog. *Ecosystems* 17, 1271–1285. doi:10.1007/s10021-014-9795-z.

Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., et al. (2008). Contemporary carbon accumulation in a boreal oligotrophic minerogenic mire – a significant sink after accounting for all C-fluxes. *Glob. Change Biol.* 14, 2317–2332. doi:10.1111/j.1365-2486.2008.01654.x.

Peichl, M., Öquist, M., Löfvenius, M. O., Ilstedt, U., Sagerfors, J., Grelle, A., et al. (2014). A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide exchange in a boreal fen. *Environ. Res. Lett.* 9, 055006. doi:10.1088/1748-9326/9/5/055006.

Raich, J. W., Rastetter, E. B., Melillo, J. M., Kicklighter, D. W., Steudler, P. A., Peterson, B. J., et al. (1991). Potential net primary productivity in South America: Application of a global model. *Ecol. Appl. Publ. Ecol. Soc. Am.* 1, 399–429. doi:10.2307/1941899.

Roulet, N., Moore, T., Bubier, J., and Lafleur, P. (1992). Northern fens: methane flux and climatic change. *Tellus B* 44, 100–105. doi:10.1034/j.1600-0889.1992.t01-1-00002.x.

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R., and Bubier, J. (2007). Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Glob. Change Biol.* 13, 397–411. doi:10.1111/j.1365-2486.2006.01292.x.

Rydin, H., and Jeglum, J. K. (2013). *The Biology of Peatlands, 2e*. OUP Oxford.

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., et al. (2018). The Impact of experimental temperature and water level manipulation on carbon dioxide release in a poor fen in Northern Poland. *Wetlands* 38, 551–563. doi:10.1007/s13157-018-0999-4.

Segers, R. (1998). Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry* 41, 23–51. doi:10.1023/A:1005929032764.

Strack, M. (2008). *Peatlands and climate change*. IPS, International Peat Society.

Straková, P., Niemi, R. M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., et al. (2011). Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Available at: https://jukuri.luke.fi/handle/10024/516544 [Accessed July 23, 2020].

Szafranek-Nakonieczna, A., and Stepniewska, Z. (2014). Aerobic and anaerobic respiration in profiles of Polesie Lubelskie peatlands. *Int. Agrophysics* 28. Available at: http://yadda.icm.edu.pl/yadda/element/bwmeta1.element.agro-9a68ce86-a247-40f5-ae04-41017c4101d4 [Accessed May 31, 2020].

Thornley, J. H. M., and Johnson, I. R. (1990). Plant and crop modelling: a mathematical approach to plant and crop physiology. Available at: https://agris.fao.org/agris-search/search.do?recordID=XF2016001523 [Accessed August 3, 2020].

Tuittila, E.-S., Vasander, H., and Laine, J. (2004). Sensitivity of C sequestration in reintroduced *Sphagnum* to water-level variation in a cutaway Peatland. *Restor. Ecol.* 12, 483–493. doi:10.1111/j.1061-2971.2004.00280.x.

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *J. Geophys. Res. Biogeosciences* 113. doi:10.1029/2007JG000496.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., and Harth, C. (2001). Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecol. Appl.* 11, 311–326. doi:10.1890/1051-0761(2001)011[0311:ROCACE]2.0.CO;2.

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of subarctic tundra increases emissions of all three important greenhouse gases – carbon dioxide, methane, and nitrous oxide. *Glob. Change Biol.* 23, 3121–3138. doi:10.1111/gcb.13563.

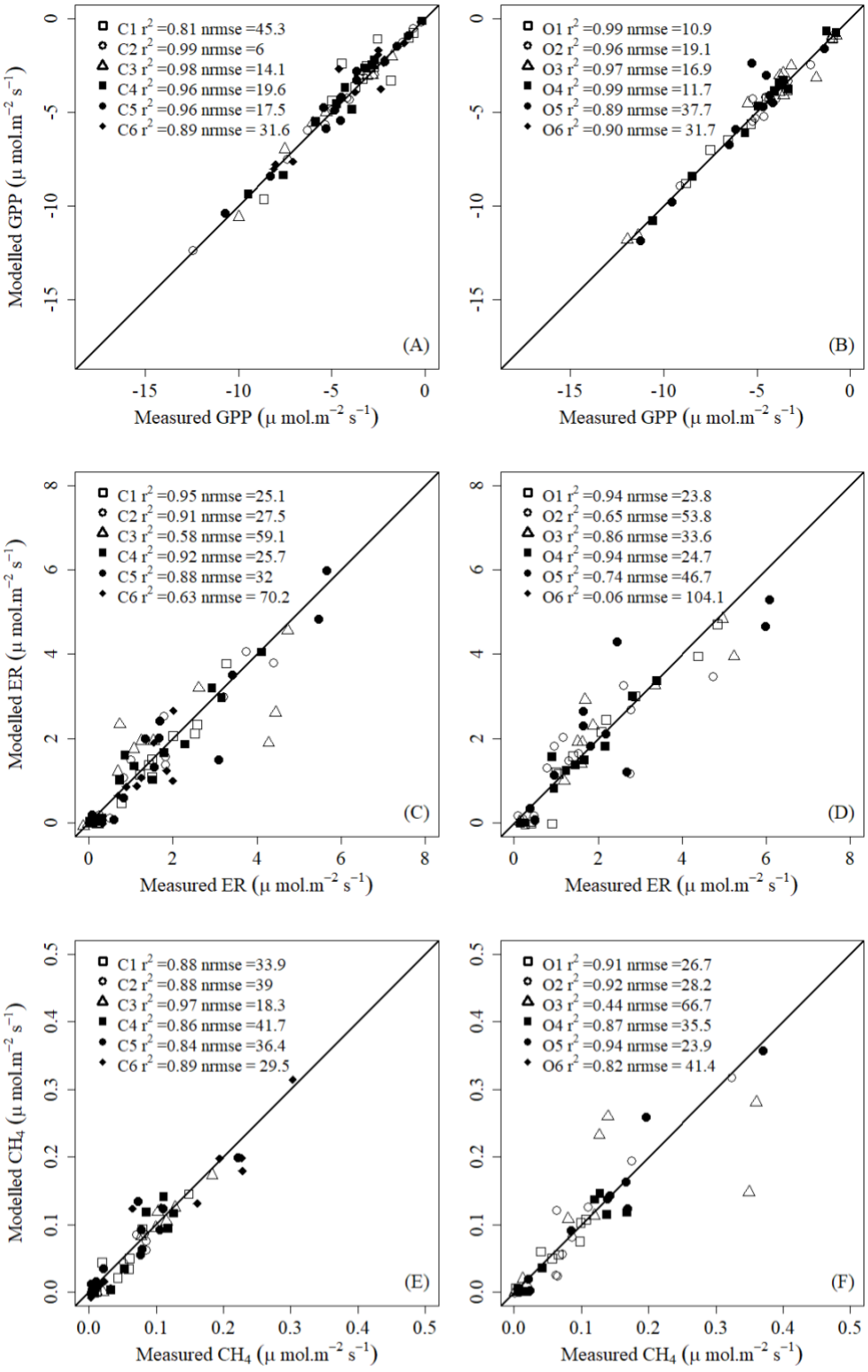
Waddington, J. M., Griffis, T. J., and Rouse, W. R. (1998). Northern Canadian wetlands: net ecosystem CO_2 exchange and climatic change. *Clim. Change* 40, 267–275. doi:10.1023/A:1005468920206.

Waddington, J. M., and Roulet, N. T. (2000). Carbon balance of a boreal patterned peatland. *Glob. Change Biol.* 6, 87–97. doi:10.1046/j.1365-2486.2000.00283.x.

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., and Bardgett, R. D. (2013). Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition. *Ecol. Lett.* 16, 1285–1293. doi:10.1111/ele.12167.

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., and Hunt, S. J. (2010). Global peatland dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* 37. doi:10.1029/2010GL043584.

Supplementary materials



Supplimentary Figure IV-1 Comparison of the measured and modelled GPP (A and B), ER (C and D) and CH_4 emissions (E and F) for 6 replicates (C1-C6) under control and 6 replicates (O1-O6) under OTCs treatments.

Supplimentary Table IV-1 R^2_{adj}, normalized root mean square errors (NRMSE; %), adjusted model parameters (a, b and c for ER; d, e and f for GPP; g, h and i for CH_4) and annual cumulated fluxes (average±SD; gC m^{-2} y^{-1}) for calibration of ecosystem respiration (ER), gross primary production (GPP) and CH_4 emissions (CH_4) for each mesocosm under control and OTCs treatments.

			a	**b**	**c**	**R^2_{adj}**	**NRMSE**	**Annual fluxes**
GPP	Control	R1	-0.0041	4.99	0.51	0.81	45.3	-492
		R2	0.0002	1.68	-0.86	0.99	6	-449
		R3	0.0004	2.07	-0.55	0.98	14.1	-472
		R4	0.0002	1.92	0.50	0.96	19.6	-457
		R5	-0.00004	2.33	0.03	0.96	17.5	-640
		R6	-0.0023	2.64	0.20	0.89	31.6	-499
		Mean	-0.001 ± 0.002	2.61 ± 1.21	0.10 ± 0.40			-501±70
	OTCs	R1	-0.0013	2.57	-0.09	0.99	10.9	-523
		R2	-0.00002	2.06	-0.30	0.96	19.1	-590
		R3	-0.0010	2.88	-0.38	0.97	16.9	-657
		R4	-0.0009	3.06	-0.08	0.99	11.7	-577
		R5	-0.0014	1.89	-0.33	0.89	37.7	-719
		R6	-0.0017	2.76	0.35	0.90	31.7	-547
		Mean	-0.001 ± 0.001	2.53 ± 0.47	-0.14 ± 0.27			-602±73
			d	**e**	**f**	**R^2_{adj}**	**NRMSE**	**Annual fluxes**
ER	Control	R1	2.27	0.0053	2.52	0.95	25.1	512
		R2	2.82	0.0038	1.61	0.91	27.5	490
		R3	-1.34	0.0108	2.13	0.58	59.1	575
		R4	1.79	0.0043	1.59	0.92	25.7	426
		R5	3.40	0.0033	2.57	0.88	32	641
		R6	0.92	0.0045	1.75	0.63	70.2	354
		Mean	1.65 ± 1.70	0.005 ± 0.003	2.03 ± 0.46			500±102
	OTCs	R1	-1.01	0.0120	2.75	0.94	23.8	691
		R2	1.60	0.0081	0.65	0.65	53.8	542
		R3	1.92	0.0042	2.54	0.86	33.6	741
		R4	-0.56	0.0057	1.63	0.94	24.7	382
		R5	3.62	0.0050	1.26	0.74	46.7	840
		R6	4.12	0.0031	0.37	0.06	104.1	493
		Mean	1.62 ± 2.10	0.006 ± 0.003	1.54 ± 0.97			615±171
CH_4			**g**	**h**	**i**	**R^2_{adj}**	**NRMSE**	**Annual fluxes**

Control	R1	0.0033	0.0006	1.50	0.88	33.9	11
	R2	0.0747	0.0002	4.31	0.88	39	15
	R3	0.0084	0.0006	1.46	0.97	18.3	20
	R4	0.0373	0.0003	4.32	0.86	41.7	12
	R5	0.0971	0.0002	0.75	0.84	36.4	12
	R6	0.1165	0.0007	0.55	0.89	29.5	22
	Mean	0.06 ± 0.05	0.0004 ± 0.0002	2.15 ± 1.72			16±5
OTCs	R1	0.0499	0.0003	1.42	0.91	26.7	12
	R2	-0.0481	0.0007	2.62	0.92	28.2	25
	R3	0.1722	0.0004	0.65	0.44	66.7	33
	R4	0.0165	0.0004	1.82	0.87	35.5	20
	R5	0.1196	0.0005	0.68	0.94	23.9	26
	R6	0.0715	0.0001	0.24	0.82	41.4	11
	Mean	0.06 ± 0.08	0.0004 ± 0.0002	1.24 ± 0.89			21±9

V. *Quantity and quality of belowground dissolved organic carbon (DOC) under experimental warming*

V.1 Introduction

Northern peatlands play a vital role in the global carbon cycle by storing approximately one third of earth's terrestrial carbon (C) in 3 % of the world's land area (Gorham, 1991). They mainly exist in high latitude where low temperature and the water-saturated condition are offered. Benefit from the cold, acidic and anoxic conditions which inhibit the microbial decomposition, C is effectively accumulated as peat in this ecosystem (Rydin and Jeglum, 2013; van Breemen, 1995). However, due to the anticipated global climate warming, a shift of peatlands functioning from C sink to C source is expected (Wieder, 2001). Much attempts have been made to understand the feedback of peatlands to climate warming by assessing the C fluxes between peatlands and atmosphere, while less attention was payed to the changes of belowground dissolved organic matter (DOC) pool. Actually, in this C rich ecosystems, DOC export has been estimated to represent up to 20 % of total C loss (Koehler et al., 2011). Therefore, understanding the response of DOC pool to climate warming is essential to predict the functioning of peat C reservoirs.

DOC of peatlands is produced through the decomposition of peat and plant remains, plants root exudates and microbial secretions (e.g. extracellular enzymes; Kalbitz et al., 2000). All these production pathways are controlled by environmental parameters such as temperature, which is a central control on microbial processes (Moore and Dalva, 2001). Several studies have reported an increase of DOC concentration with elevated temperature due to the enhancement of decomposition rate, litter input or root exudates (e.g. Dieleman et al., 2016; Fenner et al., 2007a; C. Freeman et al., 2001; Kane et al., 2014; Lou et al., 2014). While the DOC concentration depends on the balance between DOC production and consumption, the DOC mineralization also could be stimulated by increasing temperature, and its efficiency depends on the quality of DOC (Moore et al., 2008; Wickland et al., 2007). The vegetation composition is also a strong regulator on the dynamics of DOC pool as it influences the decomposition processes. As the builder of boreal peatlands, *Sphagnum* mosses can inhibit the decomposition by generating decay-resistance litters (Straková et al., 2011), and thus lead to the formation of peatlands. However, the invasion of vascular plants brings easily degradable litter as well as labile root exudates, which stimulate and prime the microbial decomposition (Girkin et al., 2018; Kuzyakov et al., 2000; Straková et al., 2010). The warming climate is expected to promote the growth of vascular plants, especially ericaceous shrubs and graminoid plants at the detriment of *Sphagnum* species (Bragazza et al., 2013; Buttler et al., 2015;

Dieleman et al., 2015). Thus, the temperature increase is likely to alter the dynamics of DOC pool via modifying plants communities.

DOC of peatlands consist of diverse compounds with different molecular weight: labile DOC with low molecular weight and simple structure (such as carbohydrates, amino acids and fatty acid) and less readily decomposable DOC with high molecular weight and complex structure (such as phenolic, lignin and fulvic acids; Fenner et al., 2001; Kalbitz et al., 2003). It has been reported that the DOC in peatlands is dominated by high molecular C compounds, because the labile DOC is easily consumed by microbes (Biester et al., 2014; Kiikkilä et al., 2014). The quality of DOC in terms of the proportion of labile or more decomposed organic carbon (OC) (refers to high or low quality respectively) played an important role in the C cycle processes，as it determines the microbial decomposition rate. Dieleman et al., (2016) reported an increase of both lability and recalcitrance under warming treatment. Fenner et al., (2007), Kane et al., (2014), Lou et al., (2014) and Dieleman et al., (2016) found a decrease of aromaticity of porewater DOC under warming treatment. The inconsistent results from previous research exhibited the difficulties to determine the quality of DOC pool in response to changing climate. Therefore, specific experiments concerning the response of DOC to temperature increase in specific study site are necessary to evaluate the C losses from peatlands in a future climate.

Here, in order to examine the effect of warming on the DOC pool of a temperate *Sphagnum* peatland which has been invaded by vascular plants (especially *Molinia caerulea*), a mesocosm experiment with experimental warming induced by open-top chambers (OTCs) was conducted. The quantity and quality of DOC at 3 depths corresponding to litter/rhizosphere of mosses/vascular plants as well as out of rhizosphere were measured. We hypothesized that 1) the DOC concentration will increase due to higher vegetation input under warming treatment, especially at surface and subsurface layer where an increase of soil temperature was prevailing; 2) the lability of DOC pool will increase due to the enhancement of plant derived root exudates, especially at the depth of vascular plants roots.

V.2 Materials and method

V.2.1 Analysis of quantity and quality of Dissolved organic matter (DOM)

Porewater samples was collected from 3 depths (5, 15 and 30 cm) of each mesocosm through the rhizons by connecting syringes and making vacuum in them. All samples were

filtered with 0.45 μm filter then stored at 4 °C before analysis. The DOC and TN concentrations of samples were determined with a Shimadzu TOC-5000. The samples were acidified to reach a pH below 2 with hydrochloric acid, in order to convert the inorganic carbon into CO_2. The CO_2 was purged to leave only the non-purgeable organic carbon. A precise volume of sample was injected into an oven at 720 °C where the organic carbon is oxidized and released in the form of CO_2. CO_2 concentration was measured by an infrared detector and the carbon concentration of the sample can be calculated via the calibration curve. When a sample was introduced into the combustion tube and heated to 720 °C, the total nitrogen in the sample was decomposed to nitrogen monoxide. The carrier gas, which contains nitrogen monoxide, is cooled and dehumidified by the dehumidifier and then enters a chemiluminescence gas analyzer where nitrogen monoxide was detected. $SUVA_{254}$ was determined by UV absorbance of samples measured at λ=254 nm at room temperature using a UV spectrophotometer (Thermo Evolution 220). $SUVA_{254}$ was calculated as absorbance divided by DOC concentration: $SUVA_{254} = Absorbance_{254}/DOC$, and it is expressed in L cm^{-1} mg^{-1}.

The fluorescence excitation-emission matrices (EEMs) of DOC in porewater was characterized at room temperature using spectrofluorometer (HITACHI F-7000) with a xenon lamp. EEMs were measured with excitation wavelengths ranging from 220 to 450 nm and emission wavelengths ranging from 250 to 550 nm. The scanning speed was 150 nm/min with a fixed increments of 10 nm for excitation and 1 nm for emission. Different groups of compounds were identified by PARAFAC modelling through decomposing EEMs data and grouping various fluorophores according to their fluorescence properties. The core consistency diagnostic (CORCONDIA) was used to determine the appropriate model complexity and the number of fluorescence components (Bro and Kiers, 2003). Fluorescence indices: FI which is the fluorescence index (Cory and McKnight, 2005; McKnight et al., 2001) and HIX which is the humidification index (Ohno, 2002) were determined by PARAFAC modelling (Fellman et al., 2010; Huguet et al., 2009). Three components were identified within the fluorescence EEMs of our samples (CORCONDIA= **73.569**; Table V-1; Fig V-1). The type (Fellman et al., 2010), denomination (Coble et al., 2014) and properties (Fellman et al., 2010) of these three components were identified and summarized in Table V-1 The ratio of concentration of M component and sum of C and C^+ component (M/C) was calculated to represent the proportion of recently produced DOM.

Table V-1 Characteristic of different components identified by the PARAFAC model

Component	Excitation/ Emission (nm)	Denomination	Type of component	Description
1	350/432	C	UVC humic like	High molecular weight humic compounds origin from vascular
2	370/488	C^+	UVC humic-like	Terrestrial humic compounds (frequent in soils and waters near OM sources)
3	290/422	M	UVA humic-like	Low molecular weight humic compounds

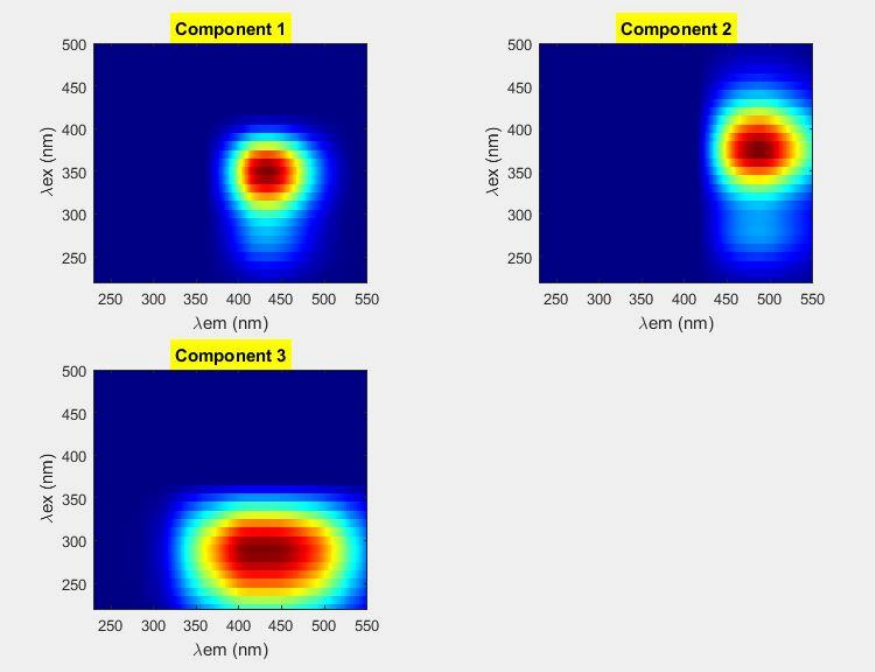


Figure V-1 Three components identified by the PARAFAC model.

V.2.2 Statistics

The effect of time, treatments, depths and their interactions on the DOC concentration, $SUVA_{254}$, and fluorescence indices (FI, HIX_{EM} and M/C ratio) were determined by three-way ANOVAs (Origin 2019).

V.3 Results

V.3.1 DOC concentration and aromaticity

Statistic results showed that depth has significant effect on DOC concentration (depth: $p<0.001$), and the pattern of DOC concentration over time differed among depths (time × depth: $p<0.001$; Table V-2). However, no significant difference was found between the two treatments (Table V-2). The initial DOC concentration of pore water was higher at 5 and 15 cm of mesocosms than at 30 cm depth (Fig. V-2a, b and c), suggesting that the vegetation input and/or microbial decomposition were stronger at these two layers in La Guette peatland. After setting up, DOC concentration at 5 cm under both treatments showed significant seasonal variation, with high values in summer and low values in winter (Fig. V-2a). At 5 cm depth, it showed a positive relationship with soil temperature and a negative relationship with pH (Fig. V-2a and b). While the DOC concentration at 15 and 30 cm did not exhibit seasonal dependence. The DOC concentration at 15 cm decreased from July to December 2018, then it increased in winter 2019. In the growing season of 2019, it showed an increase first then a steady decline (Fig. V-2b). DOC concentration at 30 cm increased from July to October 2018 followed by a stabilization until spring 2019. Similar trend at 15 cm was observed during growing season of 2019 (Fig. V-2c).

Table V-2 Effect of Time, treatment, depth and their interactions on the DOC concentration, $SUVA_{254}$, FI, HIX_{EM} and M/C ratio. Significant effect is tested by three-way ANOVAs and are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$ (n=6).

	DOC	$SUVA_{254}$	FI	HIX_{EM}	M/C
Time	***	***	***	***	NA
Treatment	NA	NA	*	NA	NA
Depth	***	NA	***	NA	***
Time × Treatment	NA	NA	NA	NA	NA
Time × Depth	***	**	*	***	***
Treatment × Depth	NA	NA	NA	NA	NA
Time × Treatment × Depth	NA	NA	NA	NA	NA

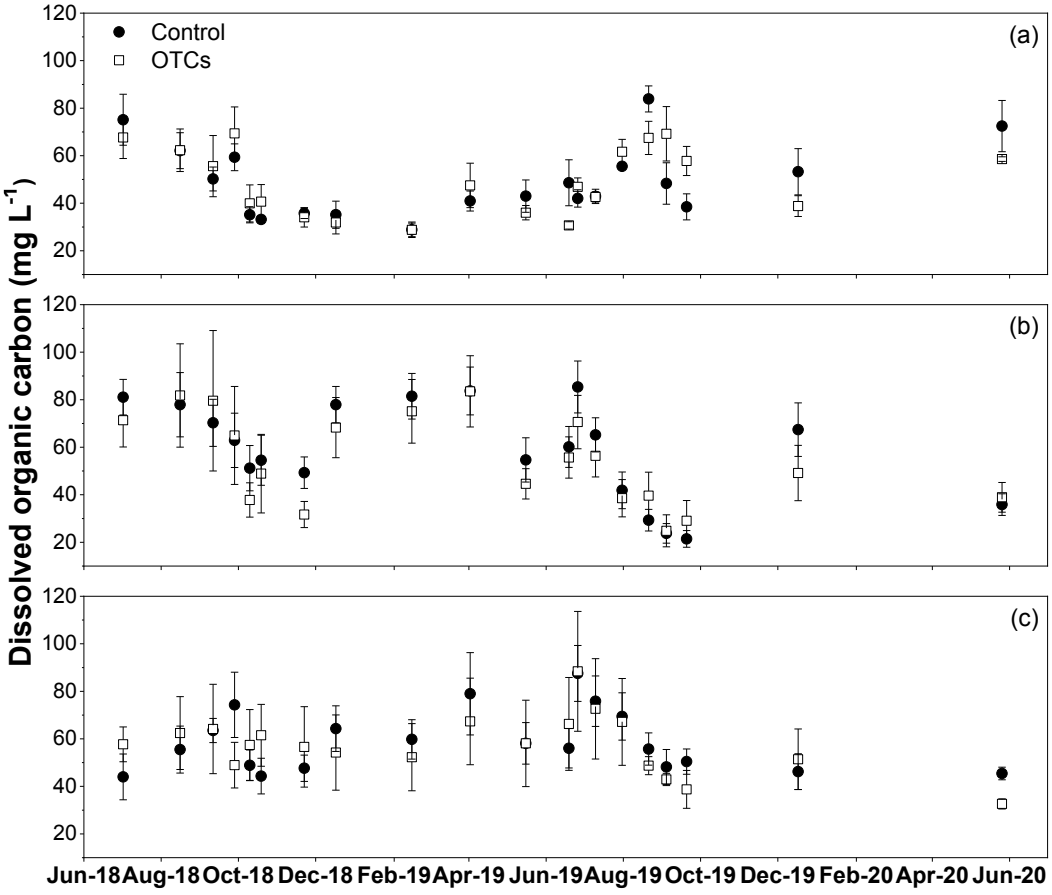


Figure V-2 Dissolved organic carbon (DOC) concentration (mg L^{-1}) at 5, 15 and 30 cm depth in mesocosms from July 2018 to June 2020 for control and OTCs plots. Error bar represents standard error mean (SEM).

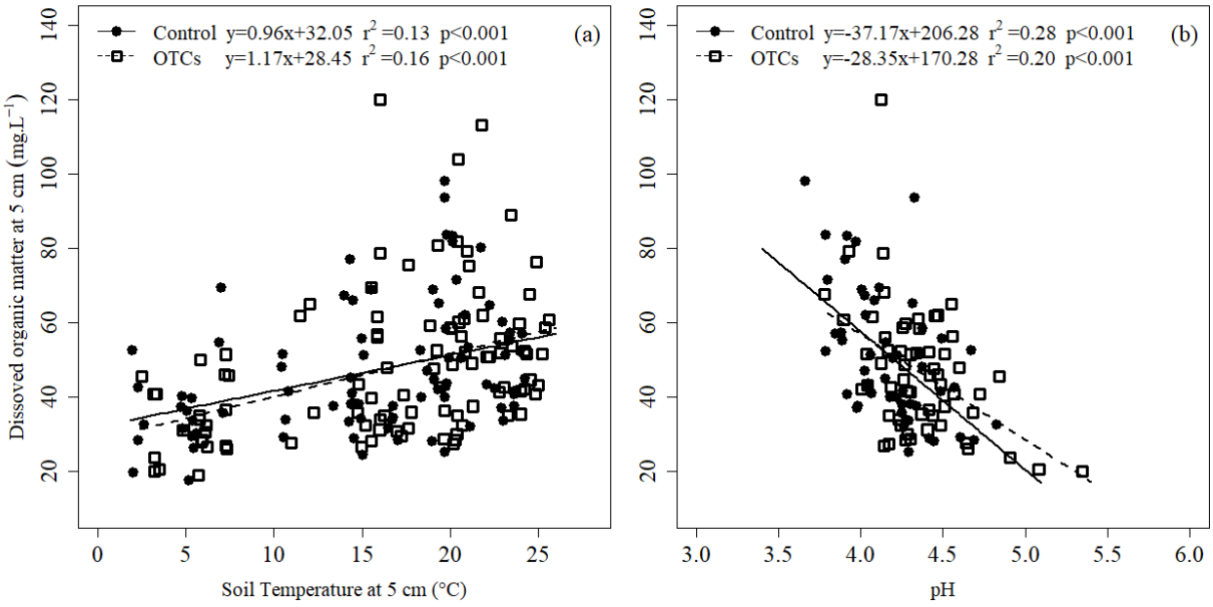


Figure V-3 Relationship at 5 cm depth between dissolved organic carbon (DOC) concentration (mg L^{-1}) and soil temperature (a) and pH (b) for control and OTCs plots. Error bar represents standard error mean (SEM).

There are no significant difference of $SUVA_{254}$ between control and OTCs plots, as well as between the 3 depths, while the effect of time on $SUVA_{254}$ was significant (time: $p<0.001$; Table V-2). Moreover, the pattern of $SUVA_{254}$ over time differed among depths (time × depth: $p<0.01$; Table V-2). The initial value of $SUVA_{254}$ gradually decreased with depth (Fig. V-4). $SUVA_{254}$ at the 3 depths of mesocosms maintained constant from July 2018 to February 2019 with some small shifts under both treatments. However, at the beginning of growing season 2019 (April), $SUVA_{254}$ showed low values at all depths, then it increased but decreased again in July, followed by an increase from August to September 2019. In winter 2019 and May 2020, it exhibited stable with the level at the end of growing season 2019 (Fig. V-4).

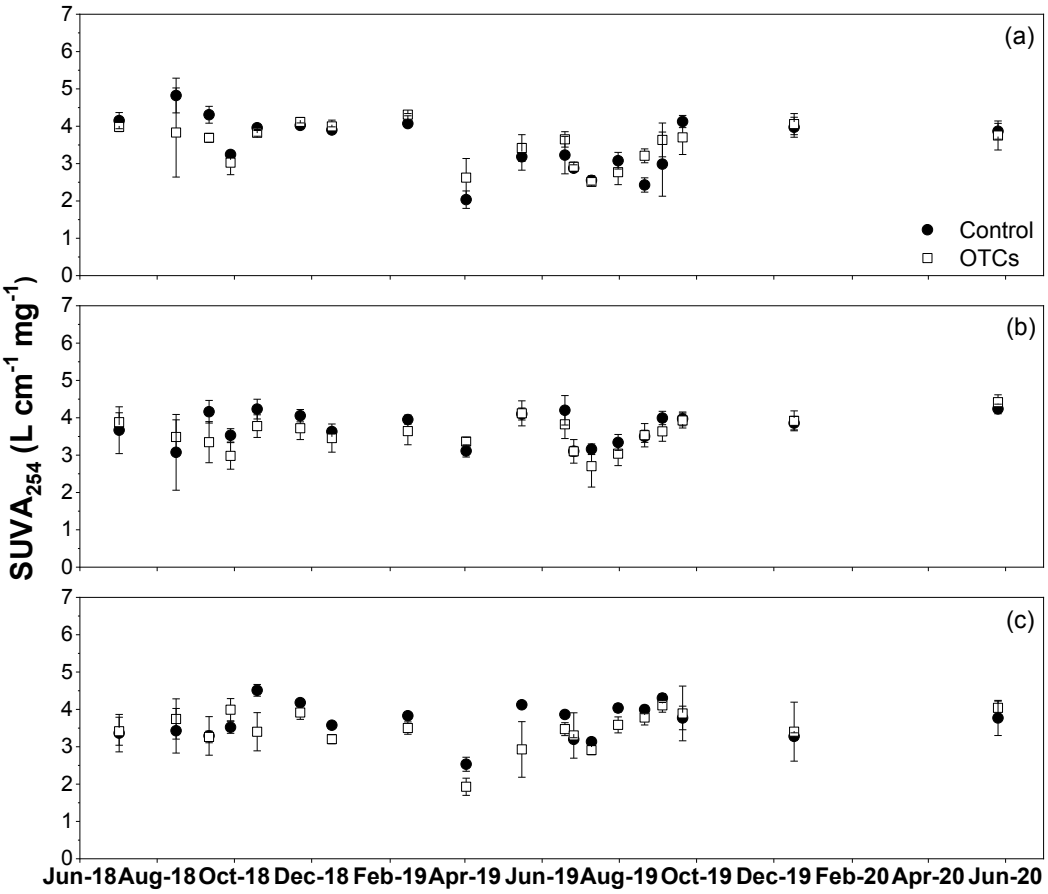


Figure V-4 Specific ultraviolet absorbance at the wavelength 254 nm $SUVA_{254}$ (L cm^{-1} mg^{-1}) at 5, 15 and 30 cm depth in mesocosms from July 2018 to June 2020 in control and OTCs plots. Error bar represents standard error mean (SEM).

V.3.2 Fluorescence indexes of DOC

Before the monitoring, the fluorescence indexes (FI) which indicate the source of OM was similar at 5 and 15 cm (between 1 to 1.2) while it was higher at 30 cm (1.29 ± 0.04 for control and 1.41 ± 0.05), indicating more terrestrial derived OM rather than microbial produced at 5 and 15 cm than deep layer. After setting up the experiment, FI increased at all depth, which suggests more proportion of microbial sourced OM (Fig. V-5). Time, warming treatment and depth all have significant difference effect on FI (time: p<0.001; treatment: p<0.05; depth: p<0.001), and its pattern over time depends on the depth (time × depth: P<0.05; Table V-2).

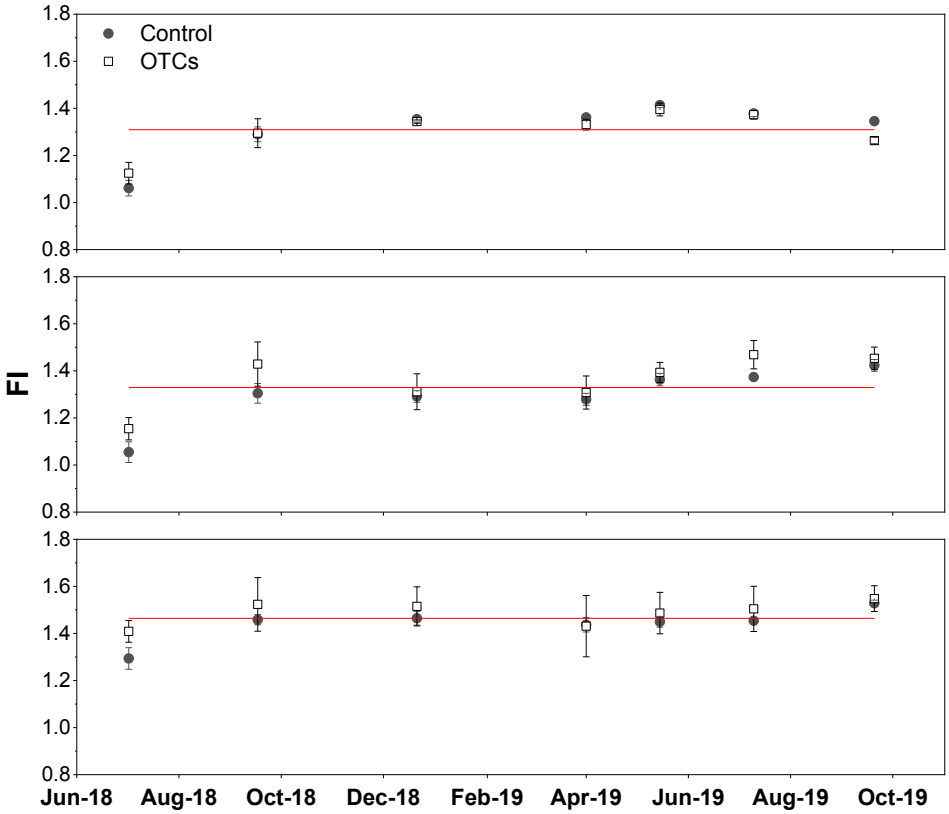


Figure V-5 The fluorescence index FI of pore water at 5, 15 and 30 cm in mesocosms from July 2018 to September 2019 for control and OTCs plots. Error bar represents standard error mean (SEM) and red line represents the mean value at each depths.

HIX_{EM} indicates the humification degree of OM, with higher value of more degraded OM and lower values of more labile OM. In the whole monitoring period, lower values of HIX_{EM} were observed during May and July 2019 at all three depths (Fig. V-6), suggesting higher input of labile OM from plants during growing season. A high value was found at -15 cm in December 2018, which means more proportion of decomposed OM (Fig. V-6). HIX_{EM} was significantly different among seasons ($P<0.001$) and time interacted with depth which impacted the HIX_{EM} value ($P<0.001$; Table V-2). The warming treatment had no significant effect on this index.

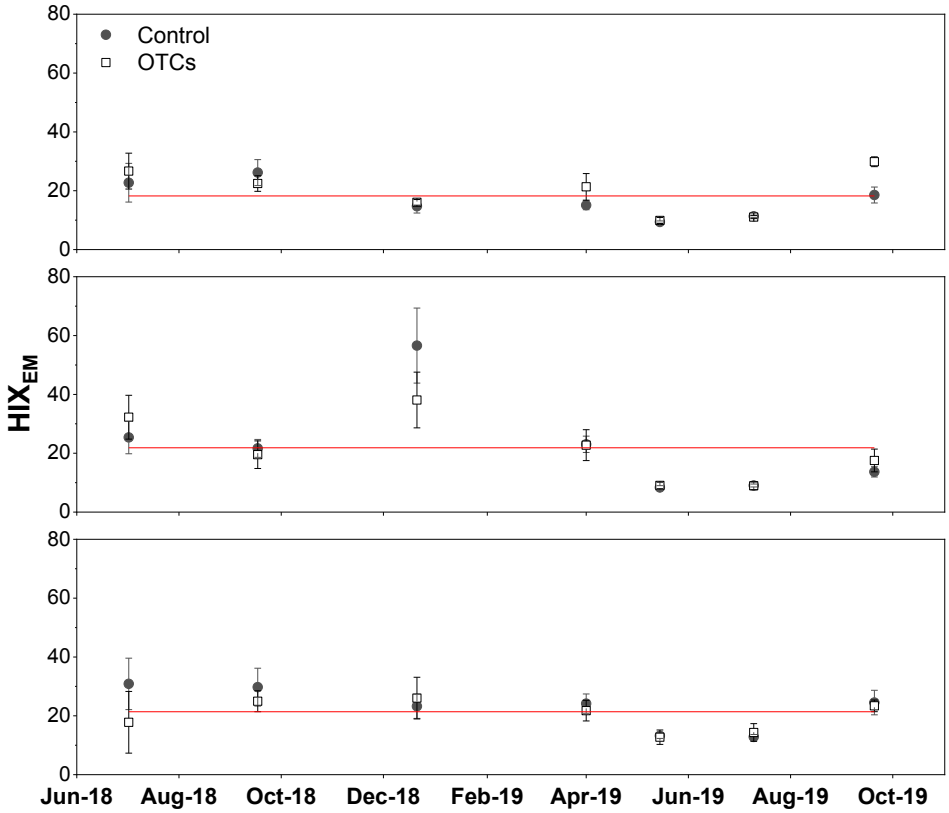


Figure V-6 The fluorescence index HIX_{EM} of pore water at 5, 15 and 30 cm in mesocosms from July 2018 to September 2019 for control and OTCs plots. Red line represent the mean value at each depths.

Ratio of M and C components concentration (M/C) represents the proportion of recently produced labile DOC. M/C ratio decreased with depth (depth: $P<0.001$; Fig. V-7; Table V-2), which obviously means that OM in deep layer is more degraded and recalcitrant than in subsurface layer. No significant difference was found between the two treatments.

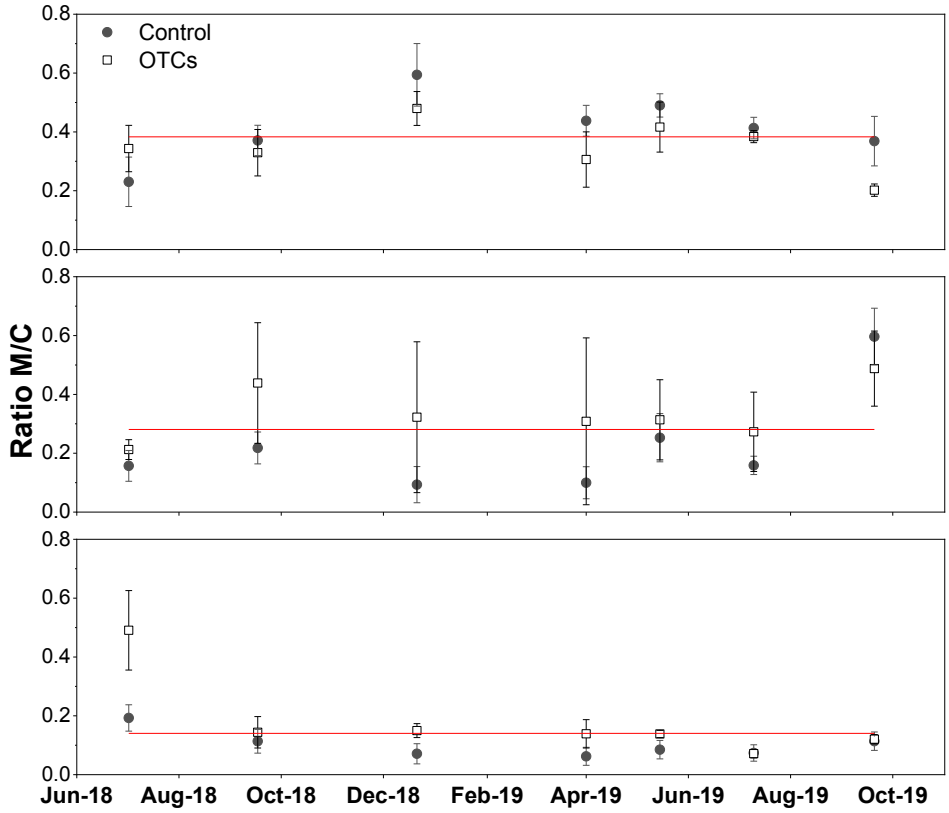


Figure V-7 The ratio of concentration of M and C components (M/C) of pore water at 5, 15 and 30 cm in mesocosms from July 2018 to September 2019 for control and OTCs plots. Error bar represents SEM and red line represents the mean value at each depths.

V.4 Discussion

V.4.1 Vegetation effect on the seasonal variation of DOC concentration

The increased DOC concentration under elevated temperature has been observed in some previous studies (Dieleman et al., 2016; C. Freeman et al., 2001; Lou et al., 2014). While in this study, under the higher peat temperature (1.35 and 0.92 ^{o}C higher in OTCs plots compared with control at 5 and 15 cm, respectively), DOC concentration showed no significant differences than that in control plots. This may be caused by the small soil temperature increase induced by OTCs, which was lower than that found in previous studies. For example, Dieleman et al., (2016) observed an increase of DOC concentration under 4 and 8 ^{o}C elevation of soil temperature. Thus in our study, the absence of DOC concentration change may be due to the relatively small temperature increase in the short-term warming duration (2 years).

Nevertheless, a significant effect of seasonal variation on DOC concentration was observed (Table V-2), which was consistent with previous research reporting that the seasonal

change of temperature and plant/microbial activities affects the quantity of DOC (Kane et al., 2014; Scott et al., 1998). Furthermore, the seasonal variation of DOC concentration varied with depth (Table V-2). This result may result from the effect of vegetation and its rhizosphere in the dynamics of DOC pool as the 3 depths corresponded to the effect of different plants. In addition, the decreasing substrate quality with depth also may impact on the DOC pool as it determined the decomposition rate (Davidson and Janssens, 2006). The DOC concentration at 5 cm depth showed clear season change, with positive relationship with temperature (Fig. V-2a and V-3a). This could be attributed to the temperature enhanced decomposition of *Sphagnum* litter as this depth was in the zone of *Sphagnum* litter. In addition, *Sphagnum* contains phenolic compounds, which make its litter resistant to decay (Chris Freeman et al., 2001). However, during summer when WTD drop down, the phenol oxidase activity was stimulated under aerobic condition, thus lead to a decreased concentration of phenolic compounds which favor the decay of OM (Fenner and Freeman, 2011). A negative relationship between DOC concentration and pH at 5 cm depth was found in our study (Fig. V-3b). Nevertheless, previous study reported that higher pH could increase the solubility of DOC through increasing the amount of negatively charged groups on the humus colloids (Bonnett et al., 2006). Therefore, the temperature may be a dominant factor controlling DOC concentration at 5 cm than pH in our study. The depth at 15 cm was close to the rhizosphere of vascular plants, and as such, the DOC at this depth could be affected by the root exudates of vascular plants. Especially, *Molinia caerulea*, which is the dominant vascular plants invading in our site, has extensive roots systems compared with other species. Root exudates from graminoids was shown to be an important source of labile C to the DOC pool (Dieleman et al., 2017; Robroek et al., 2016). The gradually decline of DOC concentration from July to September 2019 at 15 cm depth corresponded to the low WTD (around or less than 15 cm) in this period (Fig. III-4). It has been reported that wet condition promotes the graminoids production. Therefore, the decrease of DOC concentration at 15 cm depth under low WTD may result from the reduction of roots exudates because of the decreasing production of graminoids. This result suggested that the WTD could affect the plant physiology and further the DOC pool. The DOC concentration at 30 cm depth showed similar trend with 15 cm depth, suggesting that the quantity of DOC in this layer was influenced by the rhizosphere of vascular plants because of the downward diffusion of porewater.

V.4.2 Effect of vegetation on the quality of DOC

Although previous studies observed a decrease of $SUVA_{254}$ under warming (Dieleman et al., 2016; Kane et al., 2014), the aromaticity of DOC was not significantly impacted by

experimental warming in the 3 depths in our study. However, $SUVA_{254}$ varied with time and its pattern over time varied with depths. The decrease of aromaticity at the beginning of growing season 2019 may result from the higher labile C input when the plants physiology recovered. Corresponding to the low WTD during July to September 2019, $SUVA_{254}$ showed a trend of increase. As mentioned above, the DOC concentration decreased during drought condition as vegetation input of labile C was declined, thus leading to an increasing aromaticity. In addition, the lowered WTD, which results in the oxygen presence in the subsurface layer of peat, enhanced the microbial decomposition and thus more aromatic decomposition products.

$HIX_{EM,}$ which indicate the humification level of OM, only varied with time but did not show significant difference between treatments and depths. Furthermore, its variation along time differed within depths (Table V-2**)**. This result indicated that the humification level within the 3 depths were similar. The low values of HIX_{EM} during May and July 2019 in the 3 depths suggested more labile C from vegetation input in this period, which corresponds to the higher GPP in this period (Fig. IV-1a). The high level of HIX_{EM} during winter 2018 at 15 cm depth may result from the less root exudates of graminoids in winter which leads to more proportion of decomposed DOC.

The ratio M/C only showed significant depth differences, while no difference was observed between treatments and seasons (Table V-2**)**. The M/C ratio at 30 cm was significantly lower than at 5 and 15 cm. This suggested that the fresher DOC production was associated to the litter/rhizosphere of plants. Furthermore, this result was consistent with the observed FI, which showed higher values at 30 cm. Higher FI indicated that the DOC was more microbial derived and in contrary, lower FI represented more plants derived. Therefore, the higher FI in the deepest layer suggested that the DOC in deep layer contained more decomposed compounds derived from microbial activity compared with surface and subsurface layer. These results implied the DOC quality variability in the vertical profile. DOC at surface and subsurface layer (5 and 15 cm) received more fresh C derived from the vegetation, while DOC at deep layer is dominant by the highly decomposed compounds.

V.5 Conclusion

In this study, both quantity and quality of DOC at 3 depths were determined under the effect of experimental warming. We found that the mean daily soil temperature increase of 1.35 and 0.92 ^{o}C at 5 and 15 cm, respectively, did not induce a change of DOC pool during the 2 years monitoring. The DOC concentration at the 3 depths showed different seasonal variations.

At 5 cm it showed clear seasonal trend positively varying with temperature. However, it was affected by the interactions between WTD and vascular plants physiology during growing season at 15 cm, with a gradually decrease of concentration under drought. In addition, the vegetation effect on the quality of DOC was identified. The DOC at 5 and 15 cm comprises of more freshly labile compounds due to the input of plants. While at 30 cm there was more decomposed C from microbial source. The humification level of DOC in the 3 depths was similar while it varied with seasons, with a lower humification degree during growing season. Our study highlighted the slight soil temperature increase in short term may not have significant effect on the belowground DOC pool. Whereas plants communities or their rhizosphere play an important role in determining the dynamic of DOC pool. Thus, the potentially shift of plant composition to warming climate and accompanied drought in long-term may lead to a change of belowground DOC chemistry.

Reference

Biester, H., Knorr, K.-H., Schellekens, J., Basler, A., Hermanns, Y.-M., 2014. Comparison of different methods to determine the degree of peat decomposition in peat bogs. Biogeosciences 11, 2691–2707. doi:https://doi.org/10.5194/bg-11-2691-2014

Bonnett, S.A.F., Ostle, N., Freeman, C., 2006. Seasonal variations in decomposition processes in a valley-bottom riparian peatland. Science of The Total Environment 370, 561–573. doi:10.1016/j.scitotenv.2006.08.032

Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant–soil microbe feedback in response to climate warming in peatlands. Nature Climate Change 3, 273–277. doi:10.1038/nclimate1781

Bro, R., Kiers, H.A.L., 2003. A new efficient method for determining the number of components in PARAFAC models. Journal of Chemometrics 17, 274–286. doi:10.1002/cem.801

Buttler, A., Robroek, B.J.M., Laggoun-Défarge, F., Jassey, V.E.J., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A.D., Bragazza, L., 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. Journal of Vegetation Science 26, 964–974. doi:10.1111/jvs.12296

Coble, P.G., Lead, J., Baker, A., Reynolds, D.M., Spencer, R.G.M., 2014. Aquatic Organic Matter Fluorescence. Cambridge University Press.

Cory, R.M., McKnight, D.M., 2005. Fluorescence spectroscopy reveals ubiquitous presence of oxidized and reduced quinones in dissolved organic matter. Environmental Science & Technology 39, 8142–8149. doi:10.1021/es0506962

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. doi:10.1038/nature04514

Dieleman, C.M., Branfireun, B.A., Lindo, Z., 2017. Northern peatland carbon dynamics driven by plant growth form — the role of graminoids. Plant and Soil 415, 25–35. doi:10.1007/s11104-016-3099-3

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., Lindo, Z., 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. Global Change Biology 21, 388–395. doi:10.1111/gcb.12643

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., Craig, A.E., Branfireun, B.A., 2016. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. Biogeochemistry 128, 385–396. doi:10.1007/s10533-016-0214-8

Fellman, J.B., Hood, E., Spencer, R.G.M., 2010. Fluorescence spectroscopy opens new windows into dissolved organic matter dynamics in freshwater ecosystems: A review. Limnology and Oceanography 55, 2452–2462. doi:10.4319/lo.2010.55.6.2452

Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nature Geoscience 4, 895–900. doi:10.1038/ngeo1323

Fenner, N., Freeman, C., Hughes, S., Reynolds, B., 2001. Molecular weight spectra of dissolved organic carbon in a rewetted Welsh peatland and possible implications for water quality. Soil Use and Management 17, 106–112. doi:10.1111/j.1475-2743.2001.tb00015.x

Fenner, N., Freeman, C., Lock, M.A., Harmens, H., Reynolds, B., Sparks, T., 2007. Interactions between Elevated CO2 and Warming Could Amplify DOC Exports from Peatland Catchments. Environmental Science & Technology 41, 3146–3152. doi:10.1021/es061765v

Freeman, C., Evans, C.D., Monteith, D.T., Reynolds, B., Fenner, N., 2001. Export of organic carbon from peat soils. Nature 412, 785–785. doi:10.1038/35090628

Freeman, Chris, Ostle, N., Kang, H., 2001. An enzymic "latch" on a global carbon store. Nature 409, 149–149. doi:10.1038/35051650

Girkin, N.T., Turner, B.L., Ostle, N., Craigon, J., Sjögersten, S., 2018. Root exudate analogues accelerate CO2 and CH4 production in tropical peat. Soil Biology and Biochemistry 117, 48–55. doi:10.1016/j.soilbio.2017.11.008

Gorham, E., 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecological Applications 1, 182–195. doi:10.2307/1941811

Huguet, A., Vacher, L., Relexans, S., Saubusse, S., Froidefond, J.M., Parlanti, E., 2009. Properties of fluorescent dissolved organic matter in the Gironde Estuary. Organic Geochemistry 40, 706–719. doi:10.1016/j.orggeochem.2009.03.002

Kalbitz, K., Schmerwitz, J., Schwesig, D., Matzner, E., 2003. Biodegradation of soil-derived dissolved organic matter as related to its properties. Geoderma, Ecological aspects of dissolved organic matter in soils 113, 273–291. doi:10.1016/S0016-7061(02)00365-8

Kalbitz, K., Solinger, S., Park, J.-H., Michalzik, B., Matzner, E., 2000. Controls on the dynamics of dissolved organic matter in soils: a review. Soil Science 165, 277–304.

Kane, E.S., Mazzoleni, L.R., Kratz, C.J., Hribljan, J.A., Johnson, C.P., Pypker, T.G., Chimner, R., 2014. Peat porewater dissolved organic carbon concentration and lability increase with warming: a field temperature manipulation experiment in a poor-fen. Biogeochemistry 119, 161–178. doi:10.1007/s10533-014-9955-4

Kiikkilä, O., Smolander, A., Ukonmaanaho, L., 2014. Properties of Dissolved Organic Matter in Peatland: Implications for Water Quality after Harvest. Vadose Zone Journal 13, vzj2013.08.0155. doi:10.2136/vzj2013.08.0155

Koehler, A.-K., Sottocornola, M., Kiely, G., 2011. How strong is the current carbon sequestration of an Atlantic blanket bog? Global Change Biology 17, 309–319. doi:10.1111/j.1365-2486.2010.02180.x

Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry 32, 1485–1498. doi:10.1016/S0038-0717(00)00084-5

Lou, X.-D., Zhai, S.-Q., Kang, B., Hu, Y.-L., Hu, L.-L., 2014. Rapid response of hydrological loss of DOC to water table drawdown and warming in Zoige Peatland: Results from a Mesocosm Experiment. PLOS ONE 9, e109861. doi:10.1371/journal.pone.0109861

McKnight, D.M., Boyer, E.W., Westerhoff, P.K., Doran, P.T., Kulbe, T., Andersen, D.T., 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. Limnology and Oceanography 46, 38–48. doi:10.4319/lo.2001.46.1.0038

Moore, T.R., Dalva, M., 2001. Some controls on the release of dissolved organic carbon by plant tissues and soils. Soil Science 166, 38–47.

Moore, T.R., Paré, D., Boutin, R., 2008. Production of dissolved organic carbon in Canadian forest soils. Ecosystems 11, 740–751. doi:10.1007/s10021-008-9156-x

Ohno, T., 2002. Fluorescence inner-filtering correction for determining the humification index of dissolved organic matter. Environmental Science & Technology 36, 742–746. doi:10.1021/es0155276

Robroek, B.J.M., Albrecht, R.J.H., Hamard, S., Pulgarin, A., Bragazza, L., Buttler, A., Jassey, V.E., 2016. Peatland vascular plant functional types affect dissolved organic matter chemistry. Plant and Soil 407, 135–143. doi:10.1007/s11104-015-2710-3

Rydin, H., Jeglum, J.K., 2013. The Biology of Peatlands, 2e. OUP Oxford.

Scott, M.J., Jones, M.N., Woof, C., Tipping, E., 1998. Concentrations and fluxes of dissolved organic carbon in drainage water from an upland peat system. Environment International, Humus as an Environmental Factor 24, 537–546. doi:10.1016/S0160-4120(98)00043-9

Straková, P., Anttila, J., Spetz, P., Kitunen, V., Tapanila, T., Laiho, R., 2010. Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. Plant and Soil 335, 501–520. doi:10.1007/s11104-010-0447-6

Straková, P., Niemi, R.M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R., 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes.

van Breemen, N., 1995. How Sphagnum bogs down other plants. Trends in Ecology & Evolution 10, 270–275. doi:10.1016/0169-5347(95)90007-1

Wickland, K.P., Neff, J.C., Aiken, G.R., 2007. Dissolved organic carbon in Alaskan boreal forest: sources, chemical characteristics, and biodegradability. Ecosystems 10, 1323–1340. doi:10.1007/s10021-007-9101-4

Wieder, R.K., 2001. Past, Pesent, and future peatland carbon balance: an empirical model based on 210Pb-dated cores. Ecological Applications 11, 327–342. doi:10.1890/1051-0761(2001)011[0327:PPAFPC]2.0.CO;2

VI. *Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change*

NB: This part of work has been published in Soil Biology and Biochemistry:

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VI.1 Introduction

Peatlands play a crucial role in global carbon cycle, with a storage of about 30 % of global soil carbon (C) in 3 % of the earth's land surface (Gorham, 1991). However, global climate change may alter the cold and wet conditions which favorable to their C sink function (Waddington and Roulet, 1996; Page and Baird, 2016). Soil respiration, being an important efflux of carbon dioxide (CO_2) from peatlands to the atmosphere, is largely controlled by abiotic factors: temperature, soil moisture and O_2 availability (Wang et al., 2010; Szafranek-Nakonieczna and Stepniewska, 2014). In addition, soil organic matter (OM) quality in terms of the proportion of labile or complex C compounds (referred to high and poor quality respectively; Dieleman et al., 2016), also affects respiration and temperature sensitivity. These factors vary in vertical peat profile with temperature variability, O_2 availability and OM quality decreasing with depth. Thus, in the context of climate change, it is crucial to understand the response of soil respiration in different depths to realistic and expected changes in temperature and water table depth (WTD) that determines O_2 availability. The quality of OM is a key factor in the response of ecosystems to increase temperature. Poor-quality OM decomposes slowly, resulting in lower CO_2 production, while it has been reported to be more sensitive to temperature change (Davidson and Janssens, 2006; Conant et al., 2008b). Effects of abiotic factors on CO_2 production in peat was frequently studied (e.g. Hilasvuori et al., 2013; Leifeld et al., 2012; Treat et al., 2014), while as the soil respiration was regulated by the biological processes, the constrains are both abiotic, biotic and interactive. To address this gap, we conducted a short-term incubation of peat from a site presenting a sharp decrease of OM quality with depth to examine soil respiration under various environmental conditions. Our objectives were to (1) determine the effect of temperature, O_2 availability, OM quality and microbial biomass (MB) in regulating soil respiration; (2) investigate the temperature sensitivity of peat decomposition at two different degradation states.

VI.2 Materials and methods

Peat samples were taken from a near soil surface layer (5-10 cm) and a subsurface layer (35-40 cm) at four different *Sphagnum* locations about 20 m apart under *Sphagnum rubellum* hummocks on April 2019 in La Guette peatland (a *Sphagnum* acidic fen in France, Gogo et al., 2011). The samples from these four locations were used as replicates. The two layers corresponded to less and more decomposed peat respectively as the older and deeper litters has been exposed to decay for longer time (properties described in Table VI-1; Hilasvuori et al.,

2013). Eight collected samples were homogenized separately and stored at 4 °C for two weeks before incubation. Subsamples of 10g from 5-10 cm depth and 30 g from 35-40 cm depth were transferred into 250 mL jars, sealed and vacuumed, then flushed with pure nitrogen (N_2) or air for anaerobic and aerobic incubation (16 for each condition including 2 replicates for each of the 8 collected samples), respectively. The jars were incubated at constant temperature in FitoClima 1200 incubator (Aralab) for 7 days. Each day, 5 mL gas was collected and CO_2 concentration was analyzed by LGR Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, Inc. CA) and replaced by same volume of N_2/air to maintain pressure. These processes were reproduced every week under 7 temperatures between 4 and 28 °C, in 4 °C step. The CO_2 production rate was calculated by the linear regression of CO_2 concentration versus time.

The exponential fitting of CO_2 production rate and temperature was described as (Eq.VI-1):

$$R_s = ae^{bT} \quad \text{Eq.VI-1}$$

where R_s is the soil respiration rate; T is temperature (°C); and a and b are fitting parameters. The temperature sensitivity indicator Q_{10}, which is the factor by which soil respiration increases by a 10°C increase in temperature was calculated by Eq. VI-2 (Lloyd and Taylor, 1994):

$$Q_{10} = e^{10b} \quad \text{Eq. VI-2}$$

Total carbon and nitrogen contents (TC, TN) of the eight collected samples were measured by an elemental analyzer (Thermo-126 FLASH 2000 CHNS/O Analyzer). Microbial biomass of the eight collected samples and samples after incubation was determined by the chloroform fumigation extraction method (Jenkinson and Powlson, 1976). Water extractable organic carbon (WEOC) corresponded to the organic carbon concentration of non-fumigated samples. Normality of distribution, homogeneity of variance of data were tested, three-way ANOVA was used to determine effect of the temperature, O_2 availability and OM quality on the CO_2 production rate. One-way ANOVA was used to determine the difference of soil properties and Q_{10}.

VI.3 Results and discussion

VI.3.1 Temperature and O_2 availability effect on soil respiration

CO_2 production rate/gram dry peat continuously increased with increasing temperature (Fig VI-1a and b). Whereas CO_2 production rate/gram MB increased with elevated temperature until 24 °C, then declined at 28 °C (Fig. VI-1c and d), suggesting an optimum temperature between these two temperatures. The contrary trend observed at 28 °C could be attributed to the higher amount of MB at 28 ^oC than at 24 ^oC (43.3 % and 197.2 % higher in 5-10 cm, 186.6 % and 99.2 % higher in 35-40 cm under aerobic and anaerobic, respectively). Therefore, temperature increased the microbial respiratory activity and thus the soil respiration rate, but there is an optimum temperature between 24 and 28 ^oC. When above this threshold temperature, the increasing soil respiration could be attributed to the larger MB amount.

Low O_2 availability restricts microbial activities (Yavitt et al., 1997). Our study confirmed that aerobic condition enhanced soil respiration and this effect depends on temperature (Fig. VI-2; Table VI-2). At 28 ^oC, anaerobic incubation reduced CO_2 production rate compared with aerobic conditions (decrease of 25.5 % and 35.5 % for 5-10 and 35-40 cm, respectively), while significant difference was only observed in 35-40 cm (p<0.001). No significant effect of O_2 availability was found at 4 ^oC.

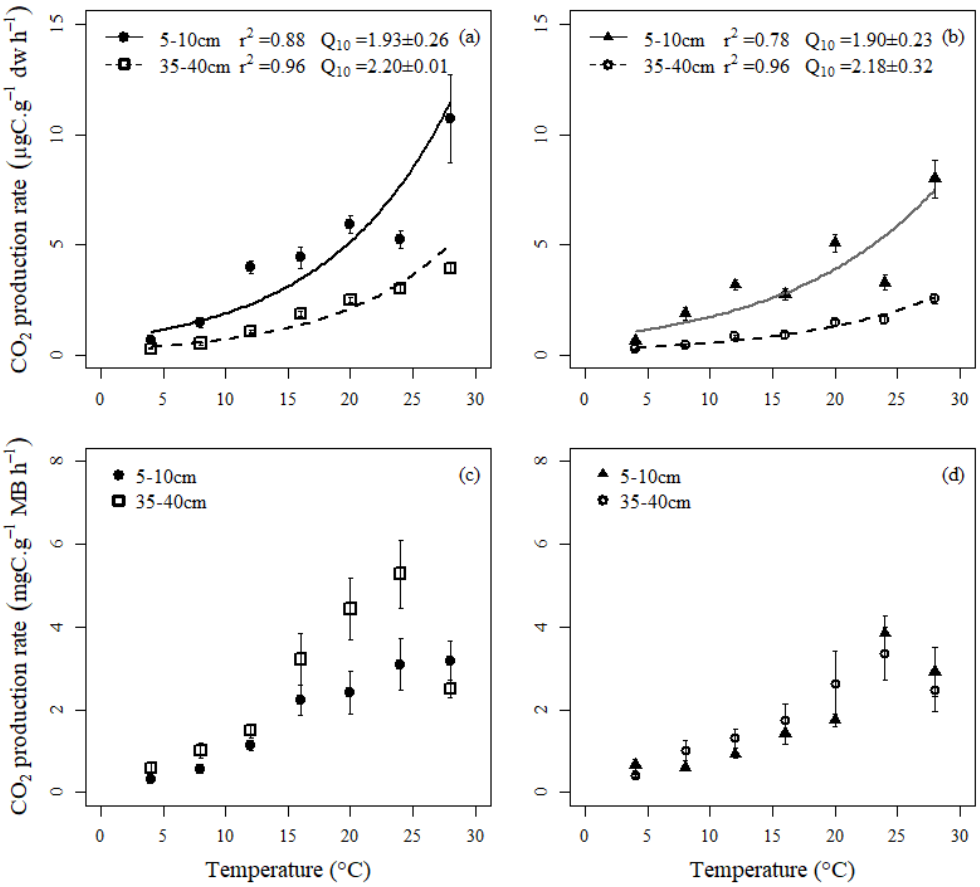


Figure VI-1 CO_2 production rate (µgC g^{-1} dw h^{-1}) under (a) aerobic and (b) anaerobic conditions; and CO_2 production per gram microbial biomass (mgC g^{-1} MB h^{-1}) under (c) aerobic and (d) anaerobic conditions as a function of temperature for peat from 5-10 cm and 35-40 cm layer. The lines in panels a and b correspond to the model fitted to the measurements. Error bars represent the standard deviation (SD).

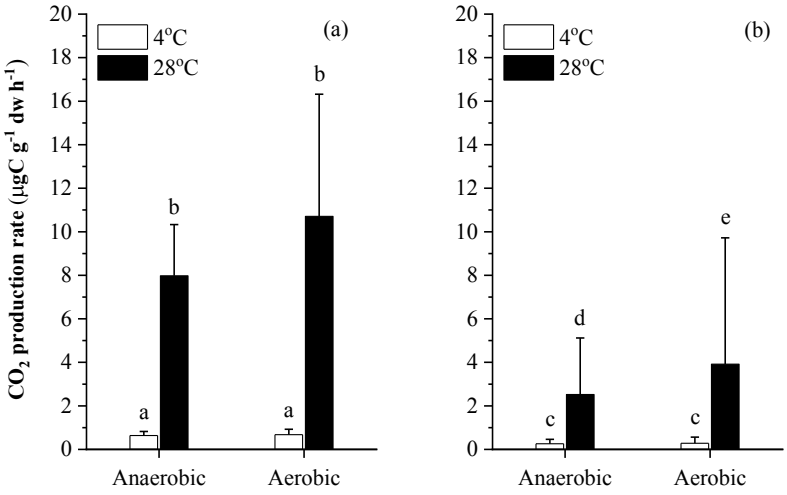


Figure VI-2 CO_2 production rate (μgC g^{-1} dw h^{-1}) of peat from (a) 5-10 cm layer and (b) 35-40 cm layer incubated at 4 and 28°C during 7 days incubation under anaerobic and aerobic conditions. Different letters represent significant differences by ANOVA in each panel and error bars represent the standard deviation (SD).

VI.3.2 OM quality regulate the soil respiration rate and Q_{10}

The decreasing C:N with depth (Table VI-1) suggested an increased decomposition degree, as microbes consume C-rich OM while recycle N, resulting in higher relative N concentration in more decomposed soil (Biester et al., 2014; Broder et al., 2012; Kuhry and Vitt, 1996). Additionally, WEOC also declined with depth (Table VI-1), suggesting a decreased availability of labile substrates (Kalbitz and Geyer, 2002; Biester et al., 2006). These results showed that the gradient of decomposition degree is steep in our site. CO_2 production rate/gram MB was higher for 35-40 cm than 5-10 cm at 16-24 °C under aerobic, while it was similar under anaerobic incubation (Fig VI-1 c and d). This could be related to the decline of fungi to bacteria ratio with peat depth found by Zocatelli et al (article in preparation) of our samples and in other studies (Sjögersten et al., 2016). Each unit cell mass of fungi release less CO_2 than bacteria due to the lower surface-to-volume ratio. Thus the lower relative abundance of fungi in 35-40 cm leads to higher respiration rate/gram MB (Blagodatskaya and Anderson, 1998). However, a lower MB was observed in 35-40 cm compared to 5-10 cm both before (Table VI-1; p=0.08) and after incubation (average of all incubation conditions: 0.80 ± 0.51 vs. 2.70 ± 1.41 mgC g^{-1}dw; p <0.001). Therefore, these results suggested that the decreasing CO_2 production rate with

depth (Fig. VI-1a and b) was linked to the lower available labile C substrate and less MB, but not the microbial respiratory activity.

Table VI-1 Physical, chemical and biological properties of peat from 5-10 cm and 35-40 cm layer (n=4, mean ± SD). Significance levels of one-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

	5-10 cm	35-40 cm	*p*
Water content (%)	85.17 ± 3.00	86.09 ±3 .10	
C:N	97.44 ± 13.29	21.94 ± 1.29	***
WEOC (mg C g^{-1} dw)	1.02 ± 0.14	0.54 ± 0.09	**
Microbial biomass C (mg C g^{-1} dw)	2.97 ±1.36	1.39 ± 0.70	

The Q_{10} increased with depth in aerobic conditions, (Fig. VI-1a and b, p=0.014) but not in anaerobic condition (p=0.072). These results indicated that the more decomposed OM is more sensitive to temperature change than labile ones, confirming previously reported results (Conant et al., 2008b, 2008a; Davidson and Janssens, 2006). These results showed that the combination of higher temperature and increase frequency of drought would generate most favorable conditions for CO_2 production. This would stimulate soil respiration in subsurface layer with more decomposed peat, especially this layer was only 40 cm apart from surface. Such a stimulation of old peat decomposition could significantly increase the CO_2 emission to the atmosphere with an increasing possibility of transforming this ecosystem into a net C source.

Calculation of Q_{10} with a limited temperature range or insufficient points affects the exponential fit and could cause large variations of results (e.g. Chen et al., 2010; McKenzie et al., 1998; Waddington et al., 2001). In our study, a large temperature range (4-28 ^{o}C) with reduced step (4 ^{o}C) was applied to get more reliable results. Our results were in the range of those from different studies that showed Q_{10} of CO_2 production mostly ranged between 1-2.5 (65.9 %; Supplimentary Table VI-1 and Supplimentary Figure VI-1). A linear increase of Q_{10} with peat depth was observed (Supplimentary Figure VI-2, R^2=0.66; p=0.004 without outliers). This relationship allows Q_{10} to be more finely adjusted in models instead of using a constant value.

Table VI-2 Effect of the organic matter (OM) quality, temperature, Aerobic/anaerobic condition and their interactions on CO_2 production rate ($\mu gC\ g^{-1}\ dw\ h^{-1}$). Significance levels of three-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$ (n=8).

	CO_2 production rate ($\mu gC\ g^{-1}\ dw\ h^{-1}$)
OM quality	***
Temperature	***
Aerobic/anaerobic condition	***
OM quality *Temperature	***
OM quality* Aerobic/anaerobic condition	
Temperature* Aerobic/anaerobic condition	*
OM quality* Temperature* Aerobic/anaerobic condition	

VI.4 Conclusion

In conclusion, the effect of temperature, O_2 availability, substrate quality and their interactions on soil respiration were identified (Table VI-2). Raised temperature, aerobic condition and high OM quality significantly increased the release of CO_2. These factors regulate the respiratory activity or amount of MB with implications for peat decomposition. Our study emphasized the importance of integrating environmental parameters, substrate quality, and MB when evaluating the response of soil respiration to climate change. Q_{10} of soil respiration was higher in more decomposed peat and showed a vertical variation. As an important parameter in modeling carbon cycle of peatlands under global warming, the vertical heterogeneity of Q_{10} should be taken into account to improve the estimation of CO_2 production in peat profiles.

References

Biester, H., Knorr, K.-H., Schellekens, J., Basler, A., and Hermanns, Y.-M. (2014). Comparison of different methods to determine the degree of peat decomposition in peat bogs. *Biogeosciences* 11, 2691–2707. doi:https://doi.org/10.5194/bg-11-2691-2014.

Biester, H., Selimović, D., Hemmerich, S., and Petri, M. (2006). Halogens in pore water of peat bogs – the role of peat decomposition and dissolved organic matter. *Biogeosciences* 3, 53–64. doi:https://doi.org/10.5194/bg-3-53-2006.

Blagodatskaya, E. V., and Anderson, T.-H. (1998). Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO2 of microbial communities in forest soils. *Soil Biol. Biochem.* 30, 1269–1274. doi:10.1016/S0038-0717(98)00050-9.

Bosatta, E., and Ågren, G. I. (1999). Soil organic matter quality interpreted thermodynamically. *Soil Biol. Biochem.* 31, 1889–1891. doi:10.1016/S0038-0717(99)00105-4.

Broder, T., Blodau, C., Biester, H., and Knorr, K. H. (2012). Peat decomposition records in three pristine ombrotrophic bogs in southern Patagonia. *Biogeosciences* 9, 1479–1491. doi:https://doi.org/10.5194/bg-9-1479-2012.

Chen, X., Tang, J., Jiang, L., Li, B., Chen, J., and Fang, C. (2010). Evaluating the impacts of incubation procedures on estimated Q10 values of soil respiration. *Soil Biol. Biochem.* 42, 2282–2288. doi:10.1016/j.soilbio.2010.08.030.

Conant, R. T., Drijber, R. A., Haddix, M. L., Parton, W. J., Paul, E. A., Plante, A. F., et al. (2008a). Sensitivity of organic matter decomposition to warming varies with its quality. *Glob. Change Biol.* 14, 868–877. doi:10.1111/j.1365-2486.2008.01541.x.

Conant, R. T., Steinweg, J. M., Haddix, M. L., Paul, E. A., Plante, A. F., and Six, J. (2008b). Experimental Warming Shows That Decomposition Temperature Sensitivity Increases with Soil Organic Matter Recalcitrance. *Ecology* 89, 2384–2391. doi:10.1890/08-0137.1.

Davidson, E. A., and Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173. doi:10.1038/nature04514.

Dieleman, C. M., Lindo, Z., McLaughlin, J. W., Craig, A. E., and Branfireun, B. A. (2016). Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry* 128, 385–396. doi:10.1007/s10533-016-0214-8.

Gogo, S., Laggoun-Défarge, F., Delarue, F., and Lottier, N. (2011). Invasion of a Sphagnum-peatland by Betula spp and Molinia caerulea impacts organic matter biochemistry. Implications for carbon and nutrient cycling. *Biogeochemistry* 106, 53–69. doi:10.1007/s10533-010-9433-6.

Gorham, E. (1991). Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecol. Appl.* 1, 182–195. doi:10.2307/1941811.

Hilasvuori, E., Akujärvi, A., Fritze, H., Karhu, K., Laiho, R., Mäkiranta, P., et al. (2013). Temperature sensitivity of decomposition in a peat profile. *Soil Biol. Biochem.* 67, 47–54. doi:10.1016/j.soilbio.2013.08.009.

Hornibrook, E. R. C., Longstaffe, F. J., Fyfe, W. S., and Bloom, Y. (2000). Carbon-isotope ratios and carbon, nitrogen and sulfur abundances in flora and soil organic matter from a temperate-zone bog and marsh. *Geochem. J.* 34, 237–245. doi:10.2343/geochemj.34.237.

Jenkinson, D. S., and Powlson, D. S. (1976). The effects of biocidal treatments on metabolism in soil—V: A method for measuring soil biomass. *Soil Biol. Biochem.* 8, 209–213. doi:10.1016/0038-0717(76)90005-5.

Kalbitz, K., and Geyer, S. (2002). Different effects of peat degradation on dissolved organic carbon and nitrogen. *Org. Geochem.* 33, 319–326. doi:10.1016/S0146-6380(01)00163-2.

Kuhry, P., and Vitt, D. H. (1996). Fossil Carbon/Nitrogen Ratios as a Measure of Peat Decomposition. *Ecology* 77, 271–275. doi:10.2307/2265676.

Leifeld, J., Steffens, M., and Galego-Sala, A. (2012). Sensitivity of peatland carbon loss to organic matter quality. *Geophys. Res. Lett.* 39. doi:10.1029/2012GL051856.

Lloyd, J., and Taylor, J. A. (1994). On the Temperature Dependence of Soil Respiration. *Funct. Ecol.* 8, 315–323. doi:10.2307/2389824.

McKenzie, C., Schiff, S., Aravena, R., Kelly, C., and St. Louis, V. (1998). Effect of temperature on production of CH4 and CO2 from Peat in a Natural and Flooded Boreal Forest Wetland. *Clim. Change* 40, 247–266. doi:10.1023/A:1005416903368.

Page, S. E., and Baird, A. J. (2016). Peatlands and Global Change: Response and Resilience. *Annu. Rev. Environ. Resour.* 41, 35–57. doi:10.1146/annurev-environ-110615-085520.

Sjögersten, S., Caul, S., Daniell, T. J., Jurd, A. P. S., O'Sullivan, O. S., Stapleton, C. S., et al. (2016). Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. *Soil Biol. Biochem.* 98, 42–53. doi:10.1016/j.soilbio.2016.03.016.

Szafranek-Nakonieczna, A., and Stepniewska, Z. (2014). Aerobic and anaerobic respiration in profiles of Polesie Lubelskie peatlands. *Int. Agrophysics* 28. Available at: http://yadda.icm.edu.pl/yadda/element/bwmeta1.element.agro-9a68ce86-a247-40f5-ae04-41017c4101d4 [Accessed May 30, 2020].

Treat, C. C., Wollheim, W. M., Varner, R. K., Grandy, A. S., Talbot, J., and Frolking, S. (2014). Temperature and peat type control CO2 and CH4 production in Alaskan permafrost peats. *Glob. Change Biol.* 20, 2674–2686. doi:10.1111/gcb.12572.

Waddington, J. M., Rotenberg, P. A., and Warren, F. J. (2001). Peat CO2 production in a natural and cutover peatland: Implications for restoration. *Biogeochemistry* 54, 115–130. doi:10.1023/A:1010617207537.

Waddington, J. M., and Roulet, N. T. (1996). Atmosphere-wetland carbon exchanges: Scale dependency of CO2 and CH4 exchange on the developmental topography of a peatland. *Glob. Biogeochem. Cycles* 10, 233–245. doi:10.1029/95GB03871.

Wang, X., Li, X., Hu, Y., Lv, J., Sun, J., Li, Z., et al. (2010). Effect of temperature and moisture on soil organic carbon mineralization of predominantly permafrost peatland in the Great Hing'an Mountains, Northeastern China. *J. Environ. Sci.* 22, 1057–1066. doi:10.1016/S1001-0742(09)60217-5.

Yavitt, J. B., Williams, C. J., and Wieder, R. K. (1997). Production of methane and carbon dioxide in peatland ecosystems across North America: Effects of temperature, aeration, and organic chemistry of peat. *Geomicrobiol. J.* 14, 299–316. doi:10.1080/01490459709378054.

Supplementary materials

Supplimentary Table VI-1 Summary of Q_{10} of CO_2 production of peat from this study and literature results.

Reference	Q_{10}	Sampling depth (cm)	Property of peat	Nature of the peat
This study	1.93	7.5	WC* 80-90%	Poor fen
	1.90	7.5	WC 80-91%	Poor fen
	2.20	40	WC 80-92%	Poor fen
	2.18	40	WC 80-93%	Poor fen
Waddington et al., 2001	1.09	0		Plateau bog
	1.77	0		Plateau bog
	1.12	5		Plateau bog
	1.68	5		Plateau bog
	1.15	10		Plateau bog
	1.92	10		Plateau bog
	2.33	75		Plateau bog
	2.43	75		Plateau bog
McKenzie et al., 1998	2.87	10		Boreal forest peatland
	1.69	10		Boreal forest peatland
	2.10	10		Boreal forest peatland
	2.41	10		Boreal forest peatland
	2.88	10		Boreal forest peatland
	1.77	10		Boreal forest peatland
	2.37	25		Boreal forest peatland
	1.92	25		Boreal forest peatland
	3.39	25		Boreal forest peatland
	2.54	25		Boreal forest peatland
	3.91	25		Boreal forest peatland
	2.69	25		Boreal forest peatland
	2.85	50		Boreal forest peatland
	3.40	50		Boreal forest peatland

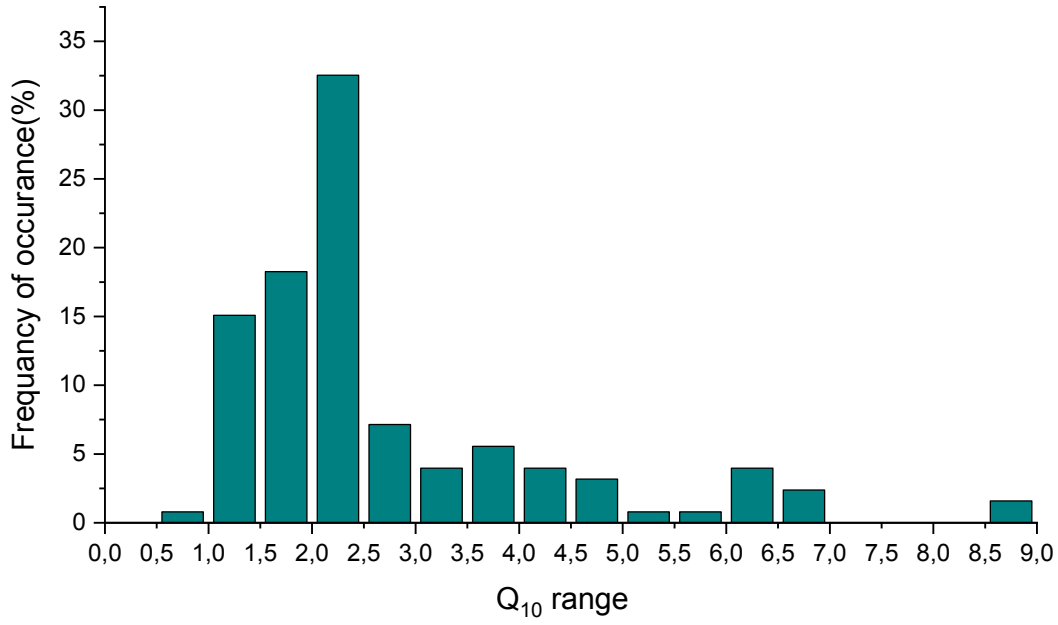
	2.58	50		Boreal forest peatland
	3.12	50		Boreal forest peatland
	1.76	50		Boreal forest peatland
	2.66	10		Boreal forest peatland
	3.54	10		Boreal forest peatland
	2.28	10		Boreal forest peatland
	2.86	10		Boreal forest peatland
	2.38	10		Boreal forest peatland
	1.52	10		Boreal forest peatland
	3.06	25		Boreal forest peatland
	2.48	25		Boreal forest peatland
	3.67	25		Boreal forest peatland
	2.26	25		Boreal forest peatland
	0.62	25		Boreal forest peatland
	1.12	25		Boreal forest peatland
	5.80	50		Boreal forest peatland
	2.80	50		Boreal forest peatland
Hilasvuori et al., 2013	1.98	10		
	2.20	23		
	2.38	30		
	2.08	34		
	2.06	40		
Hardie et al., 2011	3.3	5	WC 100%	Temperate peatland
	3.9	15	WC 100%	Temperate peatland
	3.8	25	WC 100%	Temperate peatland
	4.2	5	WC 50%	Temperate peatland
	5.3	15	WC 50%	Temperate peatland
	8.7	25	WC 50%	Temperate peatland
Wang et al., 2010	2.08	15	WC 0%	Permafrost
	2.01	15	WC 30%	Permafrost
	2.14	15	WC 60%	Permafrost
	2.01	15	WC 100%	Permafrost

	2.1	15	Complete saturation	Permafrost
	2.05	25	WC 0%	Permafrost
	1.95	25	WC 30%	Permafrost
	2.14	25	WC 60%	Permafrost
	2.03	25	WC 100%	Permafrost
	2.10	25	Complete saturation	Permafrost
	2.16	15	WC 0%	Permafrost
	2.08	15	WC 30%	Permafrost
	2.27	15	WC 60%	Permafrost
	2.12	15	WC 100%	Permafrost
	2.14	15	Complete saturation	Permafrost
	2.14	25	WC 0%	Permafrost
	2.14	25	WC 30%	Permafrost
	2.27	25	WC 60%	Permafrost
	2.23	25	WC 100%	Permafrost
	2.25	25	Complete saturation	Permafrost
	1.40	2.5		Bog
	1.20	2.5		Bog
	1.20	2.5		Bog
	1.60	2.5		Bog
	1.20	2.5		Bog
	1.30	2.5		Bog
	1.60	2.5		Bog
Joseph B.	1.30	2.5		Bog
Yavitt, 2000	1.30	2.5		Bog
	1.40	2.5		Bog
	1.40	2.5		Bog
	1.40	2.5		Bog
	1.40	2.5		Bog
	1.30	2.5		Bog
	1.40	2.5		Bog
	1.60	2.5		Bog

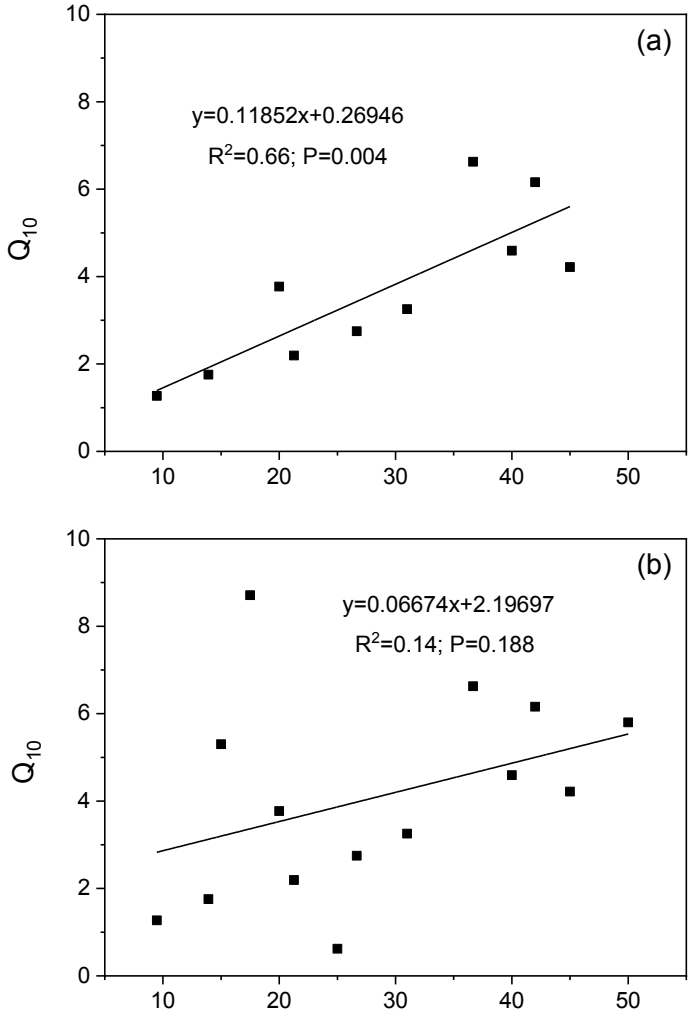
	1.60	2.5	Bog
	1.50	2.5	Bog
	1.30	37.5	Bog
Koch et al., 2007	1.70	2.5	Transitional fen
	1.90	2.5	
	2.00	2.5	Wet fen
	2.10	2.5	Transitional fen
	2.00	2.5	
	2.30	2.5	Wet fen
	2.20	2.5	Transitional fen
	1.80	2.5	
	2.10	2.5	Wet fen
Szafranek-Nakonieczna and Stepniewska, 2014	8.72	10	Low moor peatland
	6.73	30	Low moor peatland
	6.08	50	Low moor peatland
	4.15	70	Low moor peatland
	6.42	10	Transition peatlands
	4.49	30	Transition peatlands
	4.19	50	Transition peatlands
	6.00	70	Transition peatlands
	4.67	10	High peatlands
	6.02	30	High peatlands
	6.62	50	High peatlands
	4.53	70	High peatlands
	2.44	10	Low moor peatland
	1.68	30	Low moor peatland
	1.73	50	Low moor peatland
	4.54	70	Low moor peatland
	3.95	10	Transition peatlands
	3.63	30	Transition peatlands
	1.83	50	Transition peatlands
	1.17	70	Transition peatlands

4.63	10	High peatlands
6.53	30	High peatlands
6.28	50	High peatlands
4.06	70	High peatlands

*WC repersent water content in %



Supplimentary Figure VI-1 Range of Q_{10} summarized in Supplimentary Table VI-1 and their frequency.



Supplimentary Figure VI-2 Relationship between Q_{10} of CO_2 production rate and soil depth (cm) without (a) and with (b) outliers (frequency of occurrence < 2 %) based on data summarized in Supplementary Table VI-1.

VII. ***General conclusions and perspectives***

VII.1 Introduction

Peatlands are major C storage ecosystems in the world. They efficiently accumulated large quantities of organic carbon as peat due to the specific environmental conditions (cold, wet and acidic) and characteristic vegetation (*Sphagnum* spp.). However, the present and future climate change may diminish their C sink function, or even shift them to a C source. If this ecosystem is disturbed by climate warming, it has large potentials for massive CO_2 and CH_4 release to atmosphere, which will in turn exacerbate the global warming. Therefore, it is crucial to understand the feedback of peatlands to atmosphere under the context of global climate warming.

Temperature controls many metabolic processes related to photosynthesis, respiration and CH_4 emission. Thus the climate warming could accelerate the microbial decomposition or plant activities and lead to an increase of CO_2 and CH_4 emissions to atmosphere or the export of DOC. Most of research focused on the subarctic peatlands in the northern hemisphere where majority of peatlands are located and the climate warming is expected to be greater. It is still uncertain how temperate peatlands respond to global warming, especially those located in lower latitude where limited peatlands exist and vegetation change has been occurred with different species due to the past anthropogenic disturbance. Thus, in order to estimate the functioning of a temperate *Sphagnum* peatland which has been invaded by vascular plants under global change (climate warming and hydrological disturbances), we conducted a mesocosms experiment with manipulated experimental warming. We focused on the effect of warming on 1) the feedback of greenhouse gas emission peatlands to atmosphere, 2) belowground DOC release, and 3) key regulators of these processes.

VII.2 General conclusions

VII.2.1 CO_2, CH_4 fluxes and C balance under warming and the controlling factors on soil respiration

The CO_2 and CH_4 fluxes of mesocosms under control and OTCs treatment were monitored for 2 years. Results showed that under the effect of mean air temperature increase of 0.9 °C, soil temperature increases of 1.35 °C at 5 cm and of 0.92 °C at 15 cm depth, and an enhancement of GPP, ER and NEE were observed. While it only occurred during early or late stage of growing season, no warming effect was found in the peak of growing season. In early

growing season, the increase of all GPP, ER and NEE was related to the faster growth of graminoids under warming treatment. A temporary increase of CH_4 emission corresponded to the initial WTD drop down was found. This was caused by the higher transportation rate of stored CH_4 in aerobic condition. The strong effect of OTCs on CH_4 emission was only observed when WTD dramatically drop down, suggesting the regulation of interactions between temperature and WTD on CH_4 emission was stronger than solely temperature. The temperature sensitivity (Q_{10}) of GPP, ER and CH_4 emission decreased in response to warming, implying that the processes linked to these C fluxes acclimated to the increasing temperature. Thus, although an enhancement of gaseous C fluxes was observed by warming, this effect in long term may be overestimated due to the decreasing temperature sensitivity under increasing temperature. The decreasing Q_{10} under warming could be applied in the modelling of C fluxes to improve the accuracy of prediction.

In order to understand the feedback of peatlands to atmosphere under warming treatment, we estimated the annual gaseous C balance by constructing models for CO_2 and CH_4 fluxes. To construct these models, the measured GPP, ER and CH_4 fluxes were related to the biotic and abiotic factors by linear or nonlinear regressions. The models with integration of temperature as well as effect of WTD and vegetation were the most performant to represent the measured values. The modelled annual GPP was significantly increased by experimental warming, with an absorption of -602.03 ± 73.27 compared with -501.39±70.44 gC m^{-2} y^{-1} for control plots (Fig. VII-1**)**. The higher GPP was associated with the higher aboveground biomass (especially graminoids and ericaceous shrub) observed under warming treatment. In addition, this also was linked to the stronger GPP of *Sphagnum* with higher water content in OTCs plots in summer, as OTCs give a shelter against the wind and thus reduce evapotranspiration. The experimental warming showed no significant difference on ER and CH_4 emission (an output of 499.89 ± 102.42 and 614.84 ± 171.16 gC m^{-2} y^{-1} for ER; 15.56 ± 4.60 and 21.10 ± 8.54 gC m^{-2} y^{-1} for CH_4 emission under OTCs treatment and control, respectively; Fig. VII-1). The net gaseous C exchange of mesocosms was not significantly affected by warming treatment, with 14.06 ± 82.02 and 33.91 ± 136.86 gC m^{-2} yr^{-1} output under control and OTCs treatment respectively (Fig. VII-1**)**. The gaseous C source of mesocosms under both treatments was result from the strong net CO_2 release during summer drought. The contribution of CH_4 emissions in the total C fluxes only accounted for 0.9-2.2%, and thus the C source function was mainly driven by the net CO_2 release. However, as the global warming potential (GWP_{100}) of CH_4 is 34 times than that of CO_2. The GWP_{100} showed an increasing tendency under the effect of

simulated warming (699.92 ± 321.14 vs. 1003.40 ± 622.84 gCO_2 eq m^{-2} y^{-1} in control and OTCs plots, respectively; Fig. VII-1). These results emphasized the gaseous C exchange components rapidly responded to the moderate warming, while the net C exchange remained stable.

Through the incubation of peat with different degradation level (from 5-10 cm and 35-40 cm layer), we found that temperature, O_2 availability, substrate quality and their interactions all significant affected on soil respiration. Raised temperature increased the soil respiration rate through promoting the microbial respiratory activity (CO_2 production rate/gram microbial biomass), while there is a temperature threshold between 24 and 28 ^oC. Aerobic condition enhanced soil respiration and its effect depends on temperature. The more decomposed peat at 35-40 cm layer showed a lower CO_2 production rate due to less labile carbon and lower microbial biomass, but its temperature sensitivity was higher than more labile peat at 5-10 cm peat layer under aerobic condition (2.20 ± 0.01 vs. 1.93 ± 0.26; Fig. VII-1). Our results indicated that combination of higher temperature and increase frequency of drought would stimulate soil respiration, especially the subsurface layer with more decomposed peat which is only 40 cm apart from surface. This stimulation could increase the CO_2 emission and thus increase the possibility of a positive feedback of this ecosystem to atmosphere.

VII.2.2 Dynamics of belowground DOC

The concentration and quality of DOC at 3 depths (5, 15 and 30 cm) was not affected by soil temperature increase of 1.35 and 0.92 ^oC at 5 and 15 cm, respectively (Fig. VII-1). However, a significant effect of depth was observed on the seasonal variations of DOC concentration. DOC concentration at 5 cm which is in the zone of *Sphagnum* litter showed clear seasonal trend with positive relationship with temperature. The temperature enhanced decomposition of *Sphagnum* litter and low WTD induced higher phenol oxidase activity that all contributed to the higher DOC concentration in summer compared with winter. However, at 15 cm it gradually declined following the decrease of WTD. This may be attributed to the decreasing productivity of graminoids under dry condition and thus as root exudates under dry condition. The DOC concentration at 30 cm was influenced by processes occurring at 15 cm depth and thus showed similar trend.

Furthermore, the quality of DOC varied with depth. DOC at 5 and 15 cm contained more freshly labile compounds due to the input of plants. While there were more decomposed C compounds from microbial source at 30 cm. Lower humification degree were found during growing season. This could be linked with the higher GPP in this period and thus more labile

C from vegetation input. Our study highlighted that the plants-soil interaction play an important role in determining the dynamic of DOC pool. Thus, the potentially shift of plant composition and elevated temperature and accompanied drought in long-term may lead to a change of belowground DOC chemistry, with implications of C cycle processes under warming climate.

VII.3 Perspectives

The moderate increase of temperature for 2 years induced a change of CO_2 and CH_4 fluxes between peatland ecosystems and atmosphere as well as their temperature sensitivity, while had no effect on the DOC pool. The cumulated annual CO_2 uptake by photosynthesis was increased, while annual CO_2 and CH_4 release was not changed. The mesocosms under both showed gaseous C source and their functioning remained stable in response to warming treatment. Temperature as well as its interactions with O_2 availability and substrate quality controls the CO_2 production from peat. Thus, the C cycle in peatlands was modified by warming in a short time basis. Our study suggested that peatland ecosystems responded rapidly to the temperature increase, confirmed that they are vulnerable in face of climate warming.

There has been preliminary results emerged from our study which is necessary to be studied deeply:

1) The modelling of CH_4 emission need to be improved. As discussed in chapter IV.1, the complicated processes involved in the net CH_4 emission makes it difficult to model with simple variables. Furthermore, the CH_4 emission always shows a “delay response” to the WTD fluctuations. Therefore, the modelling of CH_4 emission with fixed temperature and WTD did not take into account the dynamic fluctuations of CH_4 emission following the change of environmental parameters. Baird et al., (2019) proposed to use a variable which describe the change of WTD rather than a fixed value in the model of CH_4 emission. Therefore, to better examine the CH_4 emission in response to the dynamics of WTD, a continuous monitoring of lowering/raising WTD combined with measurements of CH_4 emission was needed.

2) The characterization of the vegetation abundance and composition in response to long term warming is necessary, although no significant difference of vegetation composition was observed in our short-term experimental warming. Faster growth of graminoids in early growing season under the warming treatment was found, and it was responsible for the lower NEE (stronger net CO_2 adsorption). In spite of this, the vertical heterogeneity

of the quantity and quality of DOC implied the role of different vegetation communities in determining the DOC pool. Thus, the examination of C fluxes and DOC pool under the interactive effect of temperature and vegetation modification is essential to estimate the peatlands structure and functioning stability. The interactions between biotic and abiotic factors are complex, and it depends on the initial type of plants and climate regimes. Thus the determination of plant-climate, plant-soil and plant-plant interactions of specific sites in long term is necessary to estimate peatland functioning.

3) The microbial community composition in the vertical profile needs to be identified. Moreover, the microbial activities of different groups under soil warming also need to be investigated. The vertical variability of microbial structure was found and it was driven by the substrate quality and environmental conditions (Sjögersten et al., 2016). Different microbial groups may respond differentially to the soil warming. Thus their activities may have implication on the quantity and quality of DOC. In particular, with the enhancement of aboveground plant abundance induced by warming in early growing season which was observed in our study, the above- and below-ground interactions between plants and microorganisms are also likely lead to a shift of microbial communities in the same period. The measurement of microbial community, activity, aboveground plant community and DOC could bring us more insights into the dynamics of DOC pool.

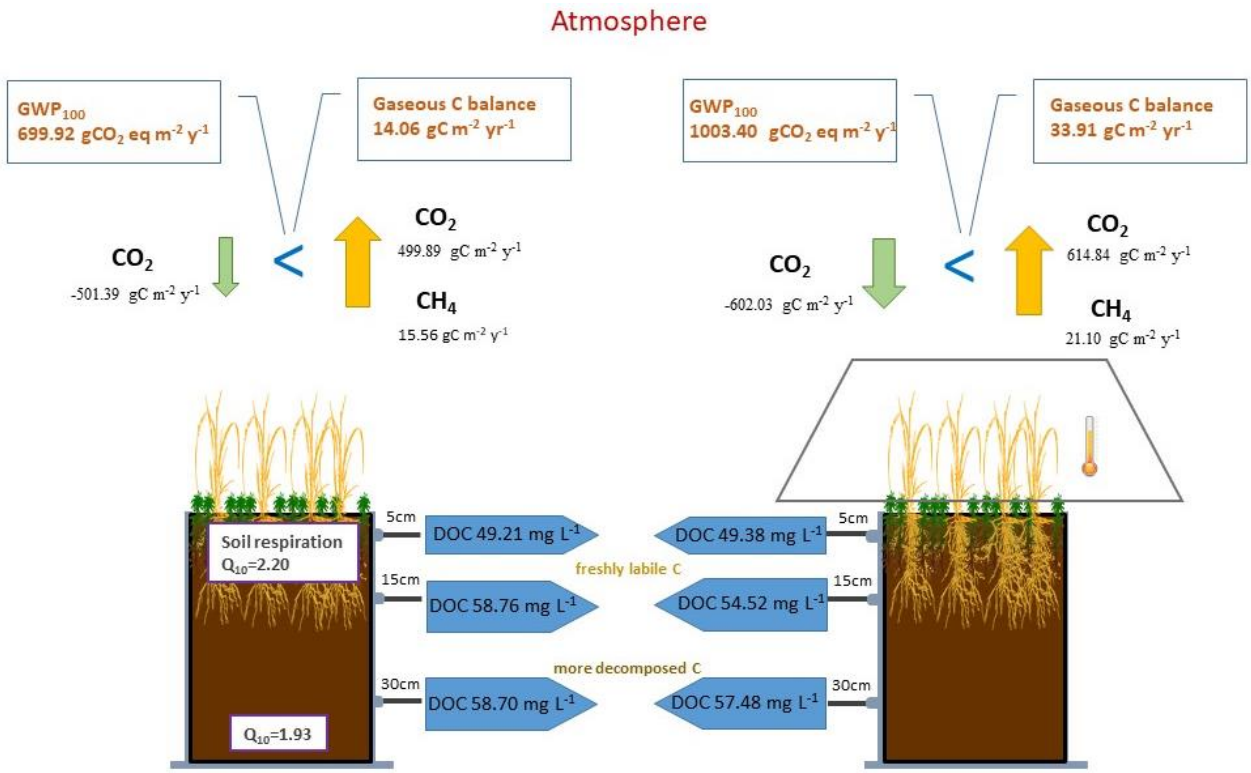


Figure VII-1 Summary of results from our study: CO_2, CH_4 fluxes, gaseous C balance, global warming potential (GWP_{100}), dissolved organic carbon (DOC) concentration at 5, 15 and 30 cm depth of mesocosm under control and OTCs treatment. Temperature sensitivity (Q_{10}) of soil respiration from peat at 5-10 cm and 35-40 cm layer.

References

Baird, A.J., Green, S.M., Brown, E., Dooling, G.P., 2019. Modelling time-integrated fluxes of CO2 and CH4 in peatlands: A review. Mires and Peat 24.

Sjögersten, S., Caul, S., Daniell, T.J., Jurd, A.P.S., O'Sullivan, O.S., Stapleton, C.S., Titman, J.J., 2016. Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. Soil Biology and Biochemistry 98, 42–53. doi:10.1016/j.soilbio.2016.03.016

VIII. ***Annex***

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Short Communication

Abiotic and biotic drivers of microbial respiration in peat and its sensitivity to temperature change

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Peatland

ABSTRACT

The effect of climate change on peatlands is of great importance due to their large carbon stocks. In this study, we examined microbial biomass and effect of temperature and O_2 availability on soil respiration of surface and subsurface *Sphagnum* peat. The interactive effect of biotic and abiotic factors significantly affects soil respiration. Increasing temperature enhanced the microbial respiratory activity and thus the soil respiration, while there is a temperature threshold. The more decomposed subsurface peat showed a lower CO_2 production due to less labile carbon and lower microbial biomass, but a higher temperature sensitivity. Q_{10} of aerobic respiration increased from 1.93 ± 0.26 in surface to 2.20 ± 0.01 in subsurface peat. The linear relationship between Q_{10} and depth in the uppermost 50 cm peat section can be used to improve the estimation of CO_2 production in peat profiles.

Peatlands play a crucial role in global carbon cycle, with a storage of about 30 % of global soil carbon (C) in 3 % of the earth's land surface (Gorham, 1991). However, global climate change may alter the cold and wet conditions which favorable to their C sink function (Page and Baird, 2016; Waddington and Roulet, 1996). Soil respiration, being an important efflux of carbon dioxide (CO_2) from peatlands to the atmosphere, is largely controlled by abiotic factors: temperature, soil moisture and O_2 availability (Szafranek-Nakonieczna and Stepniewska, 2014; Wang et al., 2010). In addition, soil organic matter (OM) quality in terms of the proportion of labile or complex C compounds (referred to high and poor quality respectively; Dieleman et al., 2016), also affects respiration and temperature sensitivity. These factors vary in vertical peat profile with temperature variability, O_2 availability and OM quality decreasing with depth. Thus, in the context of climate change, it is crucial to understand the response of soil respiration in different depths to realistic and expected changes in temperature and water table depth (WTD) that determines O_2 availability. The OM quality is a key factor in the response of ecosystems to the increasing temperature. Poor-quality OM decomposes slowly, resulting in lower CO_2 production, while it has been reported to be more sensitive to temperature change (Conant et al., 2008b; Davidson and Janssens, 2006). Effects of abiotic factors on CO_2 production in peat was frequently studied (e.g. Hilasvuori et al., 2013; Leifeld et al., 2012; Treat et al., 2014), while as the soil respiration was regulated by the biological processes, the constrains are both abiotic, biotic and interactive. To address this gap, we conducted a short-term incubation of peat from a site presenting a sharp decrease of OM quality with depth to examine soil respiration under various environmental conditions. Our objectives were to (1) determine the effect of temperature, O_2 availability, OM quality and microbial biomass (MB) in regulating soil respiration; (2) investigate the temperature sensitivity of peat decomposition at two different degradation states.

Peat samples were taken from a near soil surface layer (5–10 cm) and a subsurface layer (35–40 cm) at four different *Sphagnum* locations about 20 m apart under *Sphagnum rubellum* hummocks on April 2019 in La Guette peatland (a *Sphagnum* acidic fen in France, Gogo et al., 2011). The samples from these four locations were used as replicates. The two layers corresponded to less and more decomposed peat respectively as the older and deeper litters has been exposed to decay for longer time (properties described in Table 2; Hilasvuori et al., 2013). Eight collected samples were homogenized separately and stored at 4 °C for two weeks before incubation. Subsamples of 10 g from 5–10 cm depth and 30 g from 35–40 cm depth were transferred into 250 mL jars, sealed and vacuumed, then flushed with pure nitrogen (N_2) or air for anaerobic and aerobic incubation (16 for each condition including 2 replicates for each of the 8 collected samples), respectively. The jars were incubated at constant temperature in FitoClima 1200 incubator (Aralab) for 7 days.

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Table 1
Effect of the organic matter (OM) quality, temperature, aerobic/anaerobic condition and their interactions on CO_2 production rate (μgC g^{-1} dw h^{-1}). Significance levels of three-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

	CO_2 production rate (μgC g^{-1} dw h^{-1})
OM quality	***
Temperature	***
Aerobic/anaerobic condition	***
OM quality *Temperature	***
OM quality* Aerobic/anaerobic condition	
Temperature* Aerobic/anaerobic condition	*
OM quality* Temperature* Aerobic/anaerobic condition	

Table 2
Physical, chemical and biological properties of peat from 5-10 cm and 5-20 cm layer (n = 4, mean ± SD). Significance levels of one-way ANOVA are expressed as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

	5–10 cm	35–40 cm	*p*
Water content (%)	85.17 ± 3.00	86.09 ± 3.10	
C:N	97.44 ± 13.29	21.94 ± 1.29	***
WEOC (mgC g^{-1} dw)	1.02 ± 0.14	0.54 ± 0.09	**
Microbial biomass C (mgC g^{-1} dw)	2.97 ± 1.36	1.39 ± 0.70	

Each day, 5 mL gas was collected and CO_2 concentration was analyzed by LGR Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, Inc. CA) and replaced by same volume of N_2/air to maintain pressure. These processes were reproduced every week under 7 temperatures between 4 and 28 °C, in 4 °C step. The CO_2 production rate was calculated by the linear regression of CO_2 concentration versus time. Temperature sensitivity (Q_{10}) of CO_2 production was determined following Lloyd and Taylor (1994).

Total carbon and nitrogen contents (TC, TN) of the eight collected samples were measured by an elemental analyzer (Thermo-126 FLASH, 2000 CHNS/O Analyzer). Microbial biomass of the eight collected samples and samples after incubation was determined by the chloroform fumigation extraction method (Jenkinson and Powlson, 1976). Water extractable organic carbon (WEOC) corresponded to the organic carbon concentration of non-fumigated samples. Normality of distribution, homogeneity of variance of data were tested, three-way ANOVA was used to determine effect of the temperature, O_2 availability and OM quality on the CO_2 production rate. One-way ANOVA was used to determine the difference of soil properties and Q_{10}.

CO_2 production rate/gram dry peat continuously increased with increasing temperature (Fig. 1a and b). Whereas CO_2 production rate/gram MB increased with elevated temperature until 24 °C, then declined at 28 °C (Fig. 1c and d), suggesting an optimum temperature between these two temperatures. The contrary trend observed at 28 °C could be attributed to the higher amount of MB at 28 °C than at 24 °C (43.3% and 197.2% higher in 5–10 cm, 186.6% and 99.2% higher in 35–40 cm

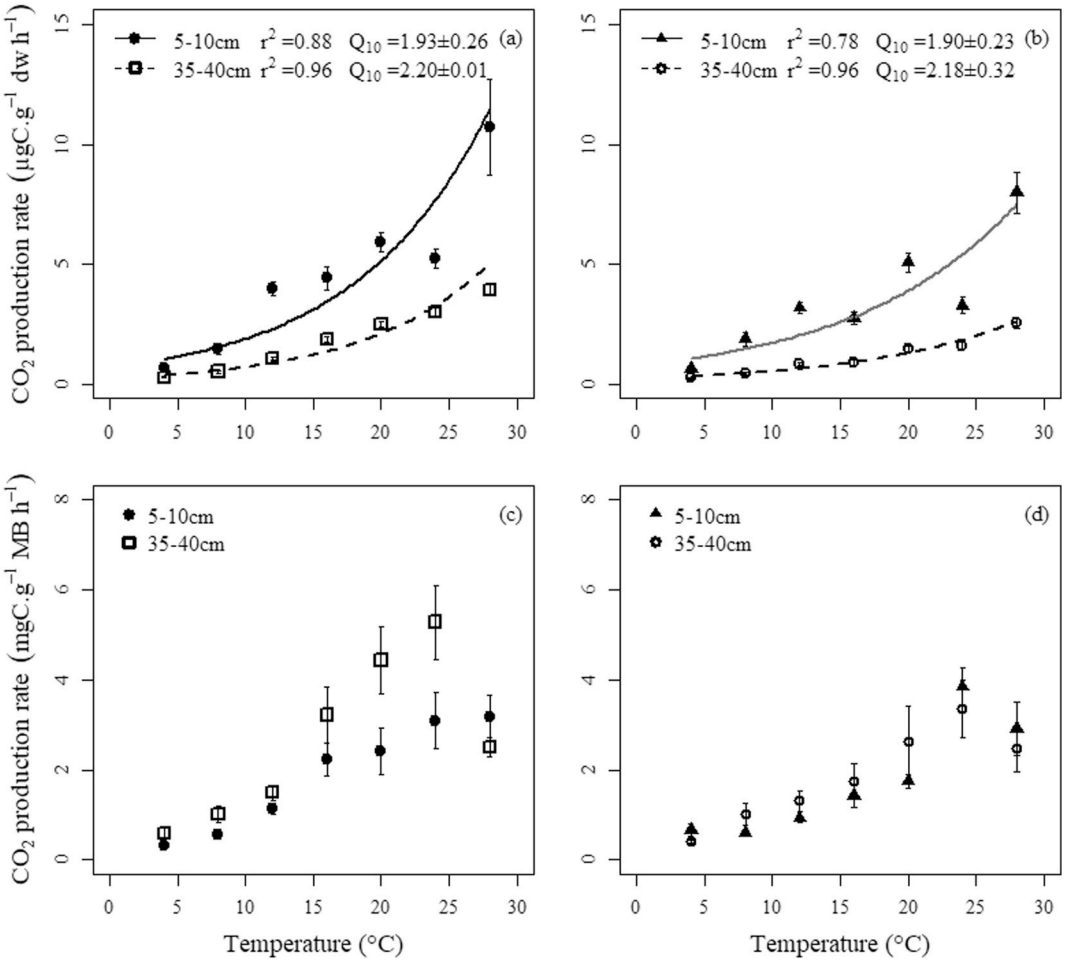

Fig. 1. CO_2 production rate (μgC g^{-1} dw h^{-1}) under (a) aerobic and (b) anaerobic conditions; and CO_2 production rate per gram microbial biomass (mgC g^{-1} MB h^{-1}) under (c) aerobic and (d) anaerobic conditions as a function of temperature for peat from 5–10 cm and 35–40 cm layer. The lines in panels a and b correspond to the model fitted to the measurements.

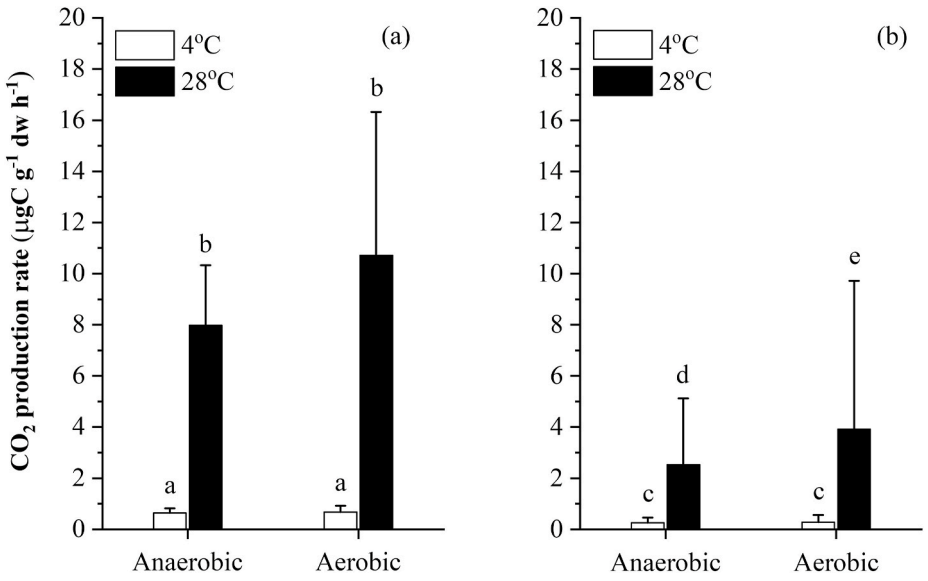

Fig. 2. CO_2 production rate (μgC g^{-1} dw h^{-1}) of peat from (a) 5–10 cm layer and (b) 35–40 cm layer incubated at 4 and 28 °C during 7 days incubation under anaerobic and aerobic conditions. Different letters represent significant differences by ANOVA in each panel and error bars represent the standard error.

under aerobic and anaerobic, respectively). Therefore, temperature increased the microbial respiratory activity and thus the soil respiration rate, but there is an optimum temperature between 24 and 28 °C. When above this threshold temperature, the increasing soil respiration could be attributed to the larger MB amount.

Low O_2 availability restricts microbial activities (Yavitt et al., 1997). Our study confirmed that aerobic condition enhanced soil respiration and this effect depends on temperature (Fig. 2; Table 1). At 28°C, anaerobic incubation reduced CO_2 production rate compared with aerobic conditions (decrease of 25.5% and 35.5% for 5–10 and 35–40 cm, respectively), while significant difference was only observed in 35–40 cm ($p < 0.001$). No significant effect of O_2 availability was found at 4 °C

The decreasing C:N with depth (Table 2) suggested an increased decomposition degree, as microbes consume C-rich OM while recycle N, resulting in higher relative N concentration in more decomposed soil (Biester et al., 2014; Broder et al., 2012; Kuhry and Vitt, 1996). Additionally, WEOC also declined with depth (Table 2), suggesting a decreased availability of labile substrates (Biester et al., 2006; Kalbitz and Geyer, 2002). These results showed that the gradient of decomposition degree is steep in our site. CO_2 production rate/gram MB was higher for 35–40 cm than 5–10 cm at 16–24 °C under aerobic, while it was similar under anaerobic incubation (Fig. 1 c and d). This could be related to the decline of fungi to bacteria ratio with peat depth found by Zocatelli et al. (in preparation) of our samples and in other studies (Sjögersten et al., 2016). Each unit cell mass of fungi release less CO_2 than bacteria due to the lower surface-to-volume ratio. Thus the lower relative abundance of fungi in 35–40 cm lead to higher respiration rate/gram MB (Blagodatskaya and Anderson, 1998). However, a lower MB was observed in 35–40 cm compared to 5–10 cm both before (Table 2; $p = 0.08$) and after incubation (average of all incubation conditions: 0.80 ± 0.51 vs. 2.70 ± 1.41 mgC g^{-1}dw; $p < 0.001$). Therefore, these results suggested that the decreasing CO_2 production rate with depth (Fig. 1a and b) was linked to the lower available labile C substrate and less MB, but not the microbial respiratory activity.

The Q_{10} increased with depth in aerobic condition (Fig. 1a and b, $p = 0.014$), but not in anaerobic condition ($p = 0.072$). This result indicated that the more decomposed OM is more sensitive to temperature change than labile ones, confirming previously reported results (Conant et al, 2008a, 2008b; Davidson and Janssens, 2006). These results showed that the combination of higher temperature and increase frequency of drought would generate most favorable conditions for CO_2 production. This would stimulate soil respiration in subsurface layer with more decomposed peat, especially this layer was only 40 cm apart from surface. Such a stimulation of old peat decomposition could significantly increase the CO_2 emission to the atmosphere with an increasing possibility of transforming this ecosystem into a net C source.

Calculation of Q_{10} with a limited temperature range or insufficient points affects the exponential fit and could cause large variations of results (e.g. Chen et al., 2010; McKenzie et al., 1998; Waddington et al., 2001). In our study, a large temperature range (4–28 °C) with reduced step (4 °C) was applied to get more reliable results. Our results were in the range of those from different studies that showed Q_{10} of CO_2 production mostly ranged between 1 and 2.5 (65.9%; Table S1 and Fig. S1). A linear increase of Q_{10} with peat depth was observed (Fig. S2, $R^2 = 0.66$; $p = 0.004$ without outliers). This relationship allows Q_{10} to be more finely adjusted in models instead of using a constant value.

In conclusion, the effect of temperature, O_2 availability, substrate quality and their interactions on soil respiration were identified (Table 1). Raised temperature, aerobic condition and high OM quality significantly increased the release of CO_2. These factors regulate the respiratory activity or amount of MB with implications for peat decomposition. Our study emphasized the importance of integrating environmental parameters, substrate quality, and MB when evaluating the response of soil respiration to climate change. Q_{10} of soil respiration was higher in more decomposed peat and showed a vertical variation. As an important parameter in modeling C cycle of peatlands under global warming, the vertical heterogeneity of Q_{10} should be taken into account to improve the estimation of CO_2 production in peat profiles.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.108077.

References

Biester, H., Knorr, K.-H., Schellekens, J., Basler, A., Hermanns, Y.-M., 2014. Comparison of different methods to determine the degree of peat decomposition in peat bogs. Biogeosciences 11, 2691–2707.

Biester, H., Selimović, D., Hemmerich, S., Petri, M., 2006. Halogens in pore water of peat bogs – the role of peat decomposition and dissolved organic matter. Biogeosciences 3, 53–64.

Blagodatskaya, E.V., Anderson, T.-H., 1998. Interactive effects of pH and substrate quality on the fungal-to-bacterial ratio and qCO_2 of microbial communities in forest soils. Soil Biology and Biochemistry 30, 1269–1274.

Broder, T., Blodau, C., Biester, H., Knorr, K.H., 2012. Peat decomposition records in three pristine ombrotrophic bogs in southern Patagonia. Biogeosciences 9, 1479–1491.

Chen, X., Tang, J., Jiang, L., Li, B., Chen, J., Fang, C., 2010. Evaluating the impacts of incubation procedures on estimated Q_{10} values of soil respiration. Soil Biology and Biochemistry 42, 2282–2288.

Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., Six, J., Steinweg, J.M., 2008a. Sensitivity of organic matter decomposition to warming varies with its quality. Global Change Biology 14, 868–877.

Conant, R.T., Steinweg, J.M., Haddix, M.L., Paul, E.A., Plante, A.F., Six, J., 2008b. Experimental warming shows that decomposition temperature sensitivity increases with soil organic matter recalcitrance. Ecology 89, 2384–2391.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173.

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., Craig, A.E., Branfireun, B.A., 2016. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. Biogeochemistry 128, 385–396.

Gogo, S., Laggoun-Défarge, F., Delarue, F., Lottier, N., 2011. Invasion of a *Sphagnum*-peatland by *Betula spp* and *Molinia caerulea* impacts organic matter biochemistry. Implications for carbon and nutrient cycling. Biogeochemistry 106, 53–69.

Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1, 182–195.

Hilasvuori, E., Akujärvi, A., Fritze, H., Karhu, K., Laiho, R., Mäkiranta, P., Oinonen, M., Palonen, V., Vanhala, P., Liski, J., 2013. Temperature sensitivity of decomposition in a peat profile. Soil Biology and Biochemistry 67, 47–54.

Jenkinson, D.S., Powlson, D.S., 1976. The effects of biocidal treatments on metabolism in soil—V: a method for measuring soil biomass. Soil Biology and Biochemistry 8, 209–213.

Kalbitz, K., Geyer, S., 2002. Different effects of peat degradation on dissolved organic carbon and nitrogen. Organic Geochemistry 33, 319–326.

Kuhry, P., Vitt, D.H., 1996. Fossil carbon/nitrogen ratios as a measure of peat decomposition. Ecology 77, 271–275.

Leifeld, J., Steffens, M., Galego-Sala, A., 2012. Sensitivity of peatland carbon loss to organic matter quality. Geophysical Research Letters 39.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315–323.

McKenzie, C., Schiff, S., Aravena, R., Kelly, C., St Louis, V., 1998. Effect of temperature on production of CH_4 and CO_2 from peat in a natural and flooded boreal forest wetland. Climatic Change 40, 247–266.

Page, S.E., Baird, A.J., 2016. Peatlands and global change: response and resilience. Annual Review of Environment and Resources 41, 35–57.

Sjögersten, S., Caul, S., Daniell, T.J., Jurd, A.P.S., O'Sullivan, O.S., Stapleton, C.S., Titman, J.J., 2016. Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. Soil Biology and Biochemistry 98, 42–53.

Szafranek-Nakonieczna, A., Stepniewska, Z., 2014. Aerobic and anaerobic respiration in profiles of Polesie Lubelskie peatlands. International Agrophysics 28.

Treat, C.C., Wollheim, W.M., Varner, R.K., Grandy, A.S., Talbot, J., Frolking, S., 2014. Temperature and peat type control CO_2 and CH_4 production in Alaskan permafrost peats. Global Change Biology 20, 2674–2686.

Waddington, J.M., Rotenberg, P.A., Warren, F.J., 2001. Peat CO_2 production in a natural and cutover peatland: implications for restoration. Biogeochemistry 54, 115–130.

Waddington, J.M., Roulet, N.T., 1996. Atmosphere-wetland carbon exchanges: scale dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland. Global Biogeochemical Cycles 10, 233–245.

Wang, X., Li, X., Hu, Y., Lv, J., Sun, J., Li, Z., Wu, Z., 2010. Effect of temperature and moisture on soil organic carbon mineralization of predominantly permafrost peatland in the Great Hing'an Mountains, Northeastern China. Journal of Environmental Sciences 22, 1057–1066.

Yavitt, J.B., Williams, C.J., Wieder, R.K., 1997. Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. Geomicrobiology Journal 14, 299–316.

Zocatelli, et al. (in preparation). Sensitivity to Temperature and Oxygen Availability of Microbial Communities in Peat Revealed by PLFA Analysis – an Incubation Study.

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Response of Peatland CO_2 and CH_4 Fluxes to Experimental Warming and the Carbon Balance

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The function of peatlands as a large carbon (C) reservoir results from the net C uptake under cold, wet, and acid environments. However, in the context of global warming, the balance between C input and release is expected to change, which may further alter the C sink of peatlands. To examine the response to climate warming of a temperate *Sphagnum* peatland which has been invaded by vascular plants, a mesocosm experiment was conducted with open top chambers (OTCs) to simulate a moderate temperature increase. Gross primary production (GPP), ecosystem respiration (ER), and methane (CH_4) emissions were monitored for 2 years. The CO_2 and CH_4 fluxes were modeled by relating to abiotic and biotic factors, including temperature, water table depth (WTD), and vegetation, in order to calculate the annual C budget. Results showed that the annual cumulated GPP was significantly enhanced by the simulated warming (–602 compared to –501 gC m^{-2} yr^{-1} in OTC and control plots, respectively), mainly due to the increase of graminoid biomass by warming, while experimental warming had no significant effect on the annual ER and CH_4 emissions (an output of 615 and 500 gC m^{-2} yr^{-1} for ER; 21 and 16 gC m^{-2} yr^{-1} for CH_4 emissions in OTC and control plots, respectively). The annual NEE and C budget were not affected by the short-term experimental warming. The mesocosms under both treatments acted as a gaseous C source with 34 and 14 gC m^{-2} yr^{-1} output under OTC and control treatment, respectively. This C source was driven by the strong net carbon dioxide (CO_2) release during a low WTD period in summer, as CH_4 emissions only accounted for 0.9–2.2% of the total C fluxes. Our study identified the effect of moderate warming on the C fluxes, even on a short-term basis. Also, our findings highlighted that the response of C fluxes to warming largely depends on the WTD and vegetation composition. Thus, long-term monitoring of hydrology and vegetation change under climate warming is essential to examine their interactions in determining the C fluxes in peatlands.

Keywords: CO_2 fluxes, methane emissions, carbon budget, climate warming, peatland

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INTRODUCTION

Peatlands are important carbon (C) storage terrestrial ecosystems in the world as they accumulate about 30% of the world's soil C in only 3% of the land area (Gorham, 1991; Yu et al., 2010; Jackson et al., 2017). Their C sink function results from the positive small but long-lasting imbalance between the C input from photosynthesis and the C output from decomposition of soil organic matters (OMs) (Bragazza et al., 2009). The specific abiotic and biotic conditions in peatlands, such as low temperature, waterlogging, acidity, and litter intrinsically recalcitrance to decay (*Sphagnum* litters) limit the microbial decomposition, thus leading to the accumulation of OMs. Nevertheless, due to the large amount of anthropogenic greenhouse gas (GHG) emissions into the atmosphere, the earth surface temperature has been observed to be increasing since the last century, and it is expected to increase 1–3.7°C by the end of the 21st century (Intergovernmental Panel on Climate Change, 2014). As elevated temperature can stimulate the soil decomposition (Dieleman et al., 2016), the projected warmer climate may shift the C sink of peatlands to a C source. Furthermore, due to the large C stocks in peatlands, small disturbances in the C cycle processes may lead to marked C release, which will in turn exacerbate the global warming. Therefore, understanding the C balance of peatlands in response to climate warming is of great importance and is a subject of considerable concern.

Temperature controls numerous metabolic processes related to photosynthesis as well as autotrophic and heterotrophic respiration (e.g., Lloyd and Taylor, 1994; Medlyn et al., 2002). Generally, higher temperature could induce more carbon dioxide (CO_2) release by ecosystem respiration (ER; e.g., Chivers et al., 2009; Flanagan and Syed, 2011). For example, Dorrepaal et al. (2009) observed an increase of over 50% in ER from peat soil induced by a temperature rise of approximately 1°C. However, the response of photosynthesis to temperature change varies with vegetation types and environmental conditions (Medlyn et al., 2002; Voigt et al., 2017). Methane (CH_4) emissions from peatlands to the atmosphere depend on the balance of CH_4 production, oxidation, and transportation rate. Both CH_4 production by methanogens and oxidation by methanotrophs are strongly correlated with temperature (Segers, 1998). Nevertheless, CH_4 production was reported to be more sensitive to temperature change than CH_4 consumption (Dunfield et al., 1993). Thus, a warmer climate is expected to increase CH_4 release into the atmosphere. Due to the different responses of these processes, estimating the net response of C in peatlands to climate warming is still challenging.

In addition, climate warming can affect the peatland C cycle indirectly *via* modifying the vegetation structure. It has been demonstrated that warming could promote the growth of vascular plants, especially ericaceous shrubs and graminoids, to the detriment of *Sphagnum* species (Bragazza et al., 2013; Buttler et al., 2015; Dieleman et al., 2015). *Sphagnum* litter is resistant to decay, which is beneficial for the C sequestration in peatlands (AminiTabrizi et al., 2020). However, the presence of vascular plants alters the litter quality in peatlands with an increase of its degradability, which enhances the decomposition (Straková et al., 2011; Leroy et al., 2019). Furthermore, the root exudates from vascular plants are a source of labile C input, which on the one hand provide substrate for microbial degradation and on the other hand lead to the priming effect, thus stimulating the decomposition of "old" and the so-called recalcitrant OMs (Gavazov et al., 2018; Girkin et al., 2018). Nevertheless, this vegetation shift also increases the C input to peatlands because of the higher primary productivity of vascular plants (Gavazov et al., 2018; Leroy et al., 2019).

To date, numerous studies have tried to understand the response of peatlands to global warming. However, most of them focused on northern peatlands in subarctic regions (e.g., Aurela et al., 2004; Chivers et al., 2009; Dieleman et al., 2015; Munir et al., 2015; Voigt et al., 2017; Laine et al., 2019), where the majority of peatlands are located (Strack, 2008). Previous results showed that the effect of warming on the C sequestration of peatlands varied from strengthening to diminishing (e.g., Waddington et al., 1998; Chivers et al., 2009; Ward et al., 2013; Munir et al., 2015; Hanson et al., 2020). Therefore, it is still difficult to draw a conclusion on the precise feedback of peatlands to climate warming. More importantly, there is still a large gap in the understanding of how temperate peatlands will respond to the warming climate. Temperate low-latitude peatlands are already below the temperature which is the projected level of subarctic regions in the future. Furthermore, they have suffered high anthropogenic pressures (e.g., hydrological disturbance, peat cutting, or nutrient amendment), and a vegetation shift has occurred (Berendse et al., 2001; Bubier et al., 2007). These disturbances have diminished their C storage (Dorrepaal et al., 2005; Gogo et al., 2016). Thus, they have significant potential to act as a C source in the future (Leifeld et al., 2019). Especially under the projected climate warming, it is important to assess how these temperate peatlands will respond to both anthropogenic and climatic disturbances.

In order to understand the response to climate warming of a temperate *Sphagnum* peatland which has been invaded by vascular plants (especially *Molinia caerulea*), we conducted a mesocosm experiment. The mesocosms were submitted to two temperature treatments: 1) ambient (control) and 2) moderate experimental warming by open top chambers (OTCs). The CO_2 and CH_4 fluxes were monitored for two years. Then, they were modeled by relating to abiotic and biotic factors in order to estimate the annual C budget. We hypothesized that the warming treatment would 1) promote both the C input to peatland through photosynthesis and the C release to the atmosphere through respiration and CH_4 emissions and 2) diminish the C sink function of this ecosystem.

MATERIALS AND METHODS

Mesocosm Experiment

Sample Preparation and Monitored Variables

Twelve mesocosms (intact cylindrical peat monoliths, 30 cm in diameter, and 40 cm in depth; **Supplementary Figure S1A**) were collected from La Guette peatland (France) in June 2018. This site is a transitional acid fen with typical species including *Sphagnum* mosses (*Sphagnum cuspidatum* and *Sphagnum rubellum*) and ericaceous shrubs (*Erica tetralix* and *Calluna vulgaris*). However, this site has been invaded by vascular plants (mainly *Molinia caerulea* and *Betula* spp.) for 30 years, and the invasion was accelerated in recent decades due to the hydrological disturbance (Gogo et al., 2011). The sampling

locations were selected to ensure that all the mesocosms contained a representative species assemblage, including mosses, vascular plants, and ericaceous shrubs. The mesocosms were sealed at the bottom and placed in the holes dug into the ground outside the Institut des Sciences de la Terre d'Orléans (ISTO) laboratory in July 2018 (**Supplementary Figure S1B**). They were separated into two treatments: six for warming treatment equipped with passive warming OTCs (called "OTC" plots) designed following the International Tundra Experiment (ITEX) protocol (Marion et al., 1997; Aronson and McNulty, 2009; **Supplementary Figure S1C**), and another six without OTCs were used as control (called "control" plots).

The air temperature at 10 cm above the soil surface, and the soil temperature at 5, 15, and 30 cm depths of the mesocosms were monitored with temperature probes (Campbell Scientific T107, United States). The water content of surface *Sphagnum* peat at 5 cm depth was monitored with soil moisture probes inserted vertically into the soil (Decagon EC-5, METER group United States). The temperature and relative humidity of the ambient air were monitored by temperature and relative humidity probes (Campbell Scientific CS215, United States), the solar radiation of the ambient environment was monitored by a SP-LITE pyranometer (Campbell Scientific, United States), the precipitation was monitored by a tipping bucket rain gauge (Campbell Scientific AGR100), the wind speed and direction of the ambient environment were monitored by a wind monitor (Campbell Scientific 05103, United States), and the atmospheric pressure of the ambient environment was monitored by a barometric pressure sensor (Campbell Scientific CS100, United States). These probes were connected to dataloggers (Campbell Scientific CR800, United States) in the weather stations installed near the study site (**Supplementary Figure S1D**), and the data were recorded every 5 min.

The water supply of mesocosms was mainly from natural precipitation. However, in order to maintain a similar WTD in all the mesocosms during the summer drought period, water collected from the drainage ditch near La Guette peatland was added to mesocosms when necessary. The WTD was measured manually by piezometers installed in mesocosms.

The vegetation communities in mesocosms were separated into three groups: bryophytes (*Sphagnum* spp.), graminoids (*Molinia caerulea* and *Eriophorum angustifolium*), and ericaceous shrubs (*Erica tetralix* and *Calluna vulgaris*). Each group was regarded as a distinct plant stratum, and the percentage cover of each stratum could reach 100%. The percentage cover of each species in their stratum and the number of graminoid leaves were measured after gas flux measurement. A vegetation index (VI), representing the amount of vegetation present, was calculated by summing the percentage cover of the three groups and dividing it by the total potential maximum cover (**Eq. 1**; D'Angelo et al., 2021):

$$\mathrm{VI} = \frac{\mathrm{BS} + \mathrm{GS} + \mathrm{SS}}{\mathrm{TC}}, \quad (1)$$

where BS, GS, and SS represent the percentage cover of bryophytes, graminoids, and ericaceous shrubs, respectively. TC is the total potential maximum cover calculated as $n \times 100\%$, in which n is the number of plant strata.

CO_2 and CH_4 Fluxes Measurements

The measurements of CO_2 and CH_4 fluxes were carried out by the static chamber method (e.g., Leroy et al., 2019) from August 2018 to July 2020. The transparent PVC chamber was equipped with a low-speed battery-operated fan to circulate the air inside the chamber during measurements. Between measurements, the chamber was air-flushed to equilibrate the headspace concentration with that of the ambient air. The CO_2 measurements were performed using a CO_2 sensor (Vaisala Carbocap GMP343, Finland) inserted into the chamber. The transparent chamber was used to measure the net ecosystem exchange (NEE), which is the difference between ecosystem respiration (ER) and gross primary production (GPP). ER was measured by covering the chamber with an opaque cover to prevent the photosynthesis. The NEE was measured under different light conditions which were artificially modulated by adding different numbers of plastic nets above the mesocosms. In this case, the light response of GPP was assessed, and it was used to calculate the GPP modeling parameters (see *Gross primary production*). During the measurement, CO_2 concentration (ppm) was recorded every 5 s. The measurements always lasted until a clear linear slope of CO_2 concentration vs. time was obtained, but for a maximum of 5 min. During the CO_2 measurements, the air temperature and humidity inside the chamber were also measured with a temperature and humidity meter (Vaisala Humicap HM70, Finland) inserted into the chamber. Photosynthetically active radiation (PAR; mol m^{-2} s^{-1}), which is measured as the photosynthetic photon flux density (PPFD), was measured by placing a PAR sensor (SDEC JYP 1000, France) on the top of chamber. PAR was measured at the beginning and at the end of each CO_2 measurement, and their mean was used to represent PAR during this measurement. CH_4 emissions were measured using a LGR Ultraportable Greenhouse Gas Analyzer (Los Gatos Research, United States) connected to the transparent chamber. The measurement of CH_4 concentration (ppm) also lasted until a clear linear slope of CH_4 concentration vs. time was obtained, but for a maximum of 5 min. The CO_2 and CH_4 concentrations measured during the first 30 s of measurement were always excluded to remove the fluctuation caused by the placement of the chamber (e.g., ebullition). If saturation occurred at the end of the measurement, the data were also excluded to keep only the linear slope. If ebullition occurred during the CH_4 measurement, the measurement was repeated to include only the diffusive emissions of CH_4. Atmosphere was regarded as the reference for C fluxes. Thus, positive values of CO_2/CH_4 fluxes indicated an emission into atmosphere and negative values indicated an uptake by the ecosystem.

The flux of CO_2/CH_4 (μmol m^{-2} s^{-1}) was calculated by **Eq. 2**

$$F_{\mathrm{CO_2/CH_4}} = \frac{(V/A) \times (d_c/d_t) \times \mathrm{Pat_m}}{R \times (T + 273.15)}, \quad (2)$$

where R is the gas constant at 273.15 K (8.314 m^3 Pa K^{-1} mol^{-1}), T is the temperature inside the chamber (°C), V is the volume of the chamber (m^3), A is the surface area of the chamber (m^2), $\mathrm{Pat_m}$ is the atmospheric pressure (Pa), and d_c/d_t is the CO_2/CH_4

concentration change against time (ppm s^{-1}) calculated using linear regression.

Modeling of CO_2 and CH_4 Fluxes

Gross Primary Production

The relationship between GPP and PPFD was often described by a rectangular hyperbolic saturation curve (Thornley and Johnson, 1990):

$$\mathrm{GPP} = \frac{\mathrm{GPP_{max}} \times \mathrm{PAR}}{k + \mathrm{PAR}}, \tag{3}$$

where $\mathrm{GPP_{max}}$ (μmol m^{-2} s^{-1}) is the asymptotic maximum GPP at light saturation and k (μmol photon m^{-2} s^{-1}) is the half-saturation value. These two variables were calculated by the Michaelis–Menten equation (Johnson and Goody, 2011) based on the light response curve of GPP (methods described above). PAR (mol m^{-2} s^{-1}) is the photosynthetically active radiation.

This approach was modified by Kandel et al. (2013) who introduced the effect of temperature and vegetation into the light response model. Here, we modeled GPP following their equation, while a simple VI (**Eq. 1**) was used instead of the ratio vegetation index (RVI) in their equation. The model performance was improved when the number of graminoid leaves and WTD were incorporated with the linear function:

$$\mathrm{GPP} = \frac{\mathrm{GPP_{max}} \times \mathrm{PAR}}{k + \mathrm{PAR}} \times \left(a \times \mathrm{Graminoid_{leaves}} + b \times \mathrm{VI} + c \times \frac{\mathrm{WTD}}{\mathrm{WTD_{ref}}} \right) \times T_{\mathrm{scale}}, \tag{4}$$

where $\mathrm{Graminoid_{leaves}}$ is the number of graminoid leaves, VI is the vegetation index (**Eq. 1**), and WTD is the water table depth (cm), and its reference value, $\mathrm{WTD_{ref}}$, was set at −25 cm, which was the lowest value we observed in the mesocosms. The coefficients a, b, and c are fitted empirical parameters. T_{scale} represents the temperature sensitivity of photosynthesis (Raich et al., 1991; Mahadevan et al., 2008):

$$T_{\mathrm{scale}} = \frac{(T - T_{\mathrm{min}})(T - T_{\mathrm{max}})}{(T - T_{\mathrm{min}})(T - T_{\mathrm{max}}) - \left(T - T_{\mathrm{opt}}\right)^2}, \tag{5}$$

where T is the measured air temperature (°C). T_{min}, T_{max}, and T_{opt} are the minimum, maximum, and optimum air temperatures (°C) for photosynthesis, respectively. Following Leroy et al. (2019), they were set as 0, 20, and 40°C, respectively.

Ecosystem Respiration

ER was modeled based on the equation of Bortoluzzi et al. (2006) and Leroy et al. (2019). The measured ER data were fitted with temperature using nonlinear power regression. Then, the residuals of this power regression were related to other abiotic and biotic variables. WTD and the number of graminoid leaves were linearly correlated to the residuals of the power regression. Thus, they were included in the model by a linear function:

$$\mathrm{ER} = \left(d \times \frac{\mathrm{WTD}}{\mathrm{WTD_{ref}}} + e \times \mathrm{Graminoid_{leaves}} \right) \times \left(\frac{T - T_{\mathrm{min}}}{T_{\mathrm{ref}} - T_{\mathrm{min}}} \right)^f, \tag{6}$$

where the reference of water table depth, $\mathrm{WTD_{ref}}$, was also set at −25 cm as mentioned above. T_{min} is the minimum temperature (°C) for positive respiration and T_{ref} is the reference temperature (°C). They were set as −5 and 15°C, respectively, following the study of Bortoluzzi et al. (2006). T is the measured temperature (°C). The model was fitted with air temperature and soil temperature at 5, 15, and 30 cm depths. The best fit was found when using the soil temperature at 5 cm. Thus, it was used as T here. The coefficients d, e, and f are fitted empirical parameters.

CH_4 Emissions

In accordance with Laine et al. (2007), data of CH_4 emissions were fitted with soil temperature using nonlinear regression, and then the residuals of the nonlinear regression were related to other variables. WTD was linearly correlated to the residuals when values were above 9 cm, and the number of graminoid leaves was also linearly correlated to the residuals. Thus, they were included in the model as follows:

$$\mathrm{CH_4} = \left(g \times \frac{\mathrm{WTD}}{\mathrm{WTD_{ref}}} + h \times \mathrm{Graminoid_{leaves}} \right) \times \left(\frac{T_s - T_{\mathrm{min}}}{T_{\mathrm{ref}} - T_{\mathrm{min}}} \right)^i (\mathrm{WTD} > -9\,cm). \tag{7}$$

where T_{min} is the minimum temperature (°C) for CH_4 emissions; it was set as 1°C, which was the minimum soil temperature observed at 5 cm depth. T_{ref} is the reference temperature (°C); it was set as 20°C which was the median value of annual soil temperature at 5 cm depth. T_s is the measured soil temperature (°C). The model was fitted with soil temperature at 5, 15, and 30 cm depths. The best fit was found when using the soil temperature at 5 cm. Thus, it was used as T_s here. The coefficients g, h, and i are fitted empirical parameters.

There were 74 WTD data points measured below WTD of −9 cm, that is, 28.6% of the total of 259 measured data. When WTD was below 9 cm, CH_4 emissions were independent of temperature and WTD. Thus, the CH_4 emissions were not modeled by **Eq. 7**, but they were linearly interpolated in this case.

Calibration and Evaluation of Models

Two-thirds (randomly selected) of the available data from each treatment were used to calibrate the model, and another one-third of the data were used to evaluate the model. The quality of model was evaluated by the adjusted determination coefficient R^2_{adj} and the normalized root-mean-square error (NRMSE; %) of the linear relationship between measured and modeled data:

$$R^2_{\mathrm{adj}} = 1 - \left(1 - \frac{(1 - R^2)(n - 1)}{n - k - 1} \right), \tag{8}$$

where R^2 is the coefficient of determination, n represents the number of data, and k is the number of independent regressors.

$$\mathrm{NRMSE} = 100 * \frac{\sqrt{\left(\frac{\sum (y-\hat{y})}{n}\right)}}{\overline{y}}, \quad (9)$$

where y is the measured value, $\hat{y}$ is the modeled value, $\overline{y}$ is the mean of measured values, and n is the number of data.

The fitted parameters of the GPP model (a, b, and c), ER model (d, e, and f), and the CH_4 emission model (g, h, and i) were calibrated by minimizing the NRMSE using the "SANN" method of the optimum function in *R* (version 3.6.3, R Core Team, 2020).

Calculation of Annual C Fluxes and C Budget

After calibration and evaluation of the C flux models, the models were parameterized for each mesocosm under both treatments individually. All the variables used in the models were interpolated to set a 1-h dataset. To do so, PAR, air, and soil temperature at 3 depths, which were monitored with a high frequency (5 min), were averaged over a 1-h time step. The other variables which were measured with a low frequency (WTD, number of graminoid leaves, and VI) were linearly interpolated between the punctual measurements to set a 1-h dataset. Then, the GPP, ER, and CH_4 emissions were calculated at a 1-h time step using the relationships between C fluxes and environmental variables constructed above (**Eq. 6**, **Eq. 7**, and **Eq. 8**). Due to the technical problems in August 2018 and the lockdown because of COVID-19 from March 2020, the environmental variable data recorded by weather stations were not complete during these periods. Thus, the modeled GPP, ER, and CH_4 emissions at a 1-h time step were only calculated from September 2018 to September 2019. Then, the annual cumulated GPP, ER, and CH_4 emissions ($gC\,m^{-2}\,yr^{-1}$) during this period were calculated as the sum of values at a 1-h time step.

The annual greenhouse gas C budget (GGCB; $gC\,m^{-2}\,yr^{-1}$) indicates the net gaseous C accumulation/release rate of the ecosystem. It was calculated for each mesocosm under both treatments as follows:

$$\mathrm{GGCB} = -\mathrm{GPP} + \mathrm{ER} + F_{CH_4}. \quad (10)$$

where GPP is the annual cumulated gross primary production ($gC\,m^{-2}\,yr^{-1}$), ER is the annual cumulated ecosystem respiration ($gC\,m^{-2}\,yr^{-1}$), and FCH_4 is the annual cumulated emission of CH_4 ($gC\,m^{-2}\,yr^{-1}$).

Statistics

The significant differences in the annual mean of air temperature (T_a) and soil temperature (T_s) at 5, 15, and 30 cm depths, and the WTD and water content of surface *Sphagnum* peat between control and OTC treatment were assessed by one-way ANOVA. The effects of experimental warming and time on the percentage cover of vegetation species, number of graminoid leaves, and vegetation index (VI) were analyzed by two-way repeated measure ANOVA using time as the repeated-measure factor and treatment as the between-group factor. The differences of the measured GPP, ER, NEE, and CH_4 emissions between control and OTC plots at different periods of the growing season [early growing season (EG; April–May), middle growing season (MG: June–August), late growing season (LG: September), and the whole growing season (WG: April–September)] were analyzed by two-way repeated measure ANOVA using time as the repeated-measure factor and treatment as the between-group factor. The differences of the calculated GPP_{max} between the two treatments at different dates were analyzed by one-way ANOVA. The significant differences in the modeled annual cumulated GPP, ER, CH_4 emission, NEE, and GGCB between the two treatments were assessed by one-way ANOVA. Before statistical analysis, the normality of distribution and the homogeneity of variance of the data were tested. All the statistics were performed in OriginPro 2019 (OriginLab, United States).

TABLE 1 | Mean value of air temperature (T_a) and soil temperature (T_s) at 5, 15, and 30 cm depths of mesocosms, water table depth (WTD), and water content of *Sphagnum* at 5 cm depth from August 2018 to July 2020. Significant differences of ANOVA are expressed as $^*p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$. Data are presented as mean ± SD, $n = 6$.

	Mean		Significance
	Control	OTCs	
T_a (°C)	14.01 ± 0.07	14.91 ± 0.14	***
T_s at 5 cm (°C)	13.85 ± 0.42	15.20 ± 0.32	**
T_s at 15 cm (°C)	14.38 ± 0.17	15.30 ± 0.33	**
T_s at 30 cm (°C)	14.77 ± 0.10	14.94 ± 0.32	
WTD (cm)	−6.80 ± 0.47	−6.68 ± 1.08	
Water content (%)	65.87 ± 3.53	70.71 ± 7.51	

RESULTS

Environmental Variables

The air temperature and soil temperature at 5 and 15 cm depths increased significantly under OTC treatment. The mean air temperature was 0.9°C higher in OTC plots than in control during the 2 years of monitoring (**Table 1**). The mean soil temperature at 5 cm depth was increased by 1.35°C, and at 15 cm depth, it was increased by 0.92°C with OTC treatment. However, the mean soil temperature at 30 cm was not significantly affected by OTC treatment (**Table 1**). The mean WTD and water content of surface peat throughout the monitoring were similar between the two treatments (**Table 1**). During the 2 years of monitoring, the WTD ranged from −0.4 to −23.5 cm for control plots and from −0.5 to −18 cm for OTC plots (**Supplementary Figure S2A**), with higher levels in winter and lower levels in summer. The water content of surface *Sphagnum* peat showed similar seasonal variations to the WTD. However, significant differences between the two treatments were found during July–September 2019 and April–May 2020, with higher values in OTC plots than in control plots (**Supplementary Figure S2B**). The percentage cover of *Sphagnum* increased significantly with time ($p < 0.05$; **Figure 1A**), while that of graminoids and shrubs remained constant (**Figures 1B,C**),

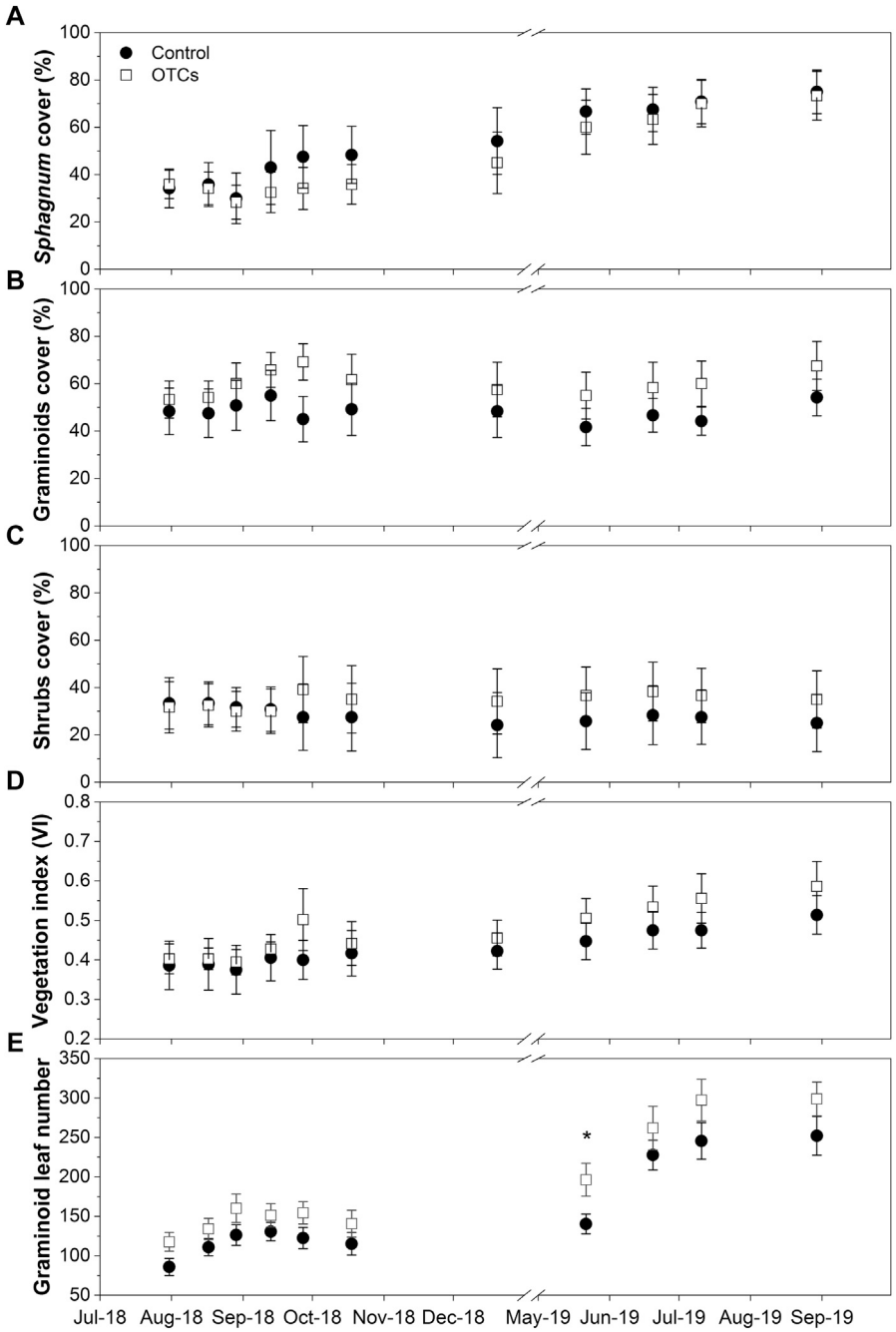

FIGURE 1 | Percentage cover (%) of **(A)** bryophytes (*Sphagnum*), **(B)** graminoids (*Molinia caerulea* and *Eriophorum angustifolium*), and **(C)** ericaceous shrubs (*Erica tetralix* and *Calluna vulgaris* and **(D)** vegetation index (VI) and **(E)** the number of graminoid leaves from August 2018 to September 2019. Significant differences are expressed as $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$.

resulting in an increase of the vegetation index (VI) with time ($p < 0.05$; **Figure 1D**). However, the differences between the two treatments were not significant. The number of graminoid leaves increased significantly with time ($p < 0.05$), and it was significantly higher in OTC plots than in control plots in May 2019 ($p < 0.05$; **Figure 1E**).

Measured CO_2 and CH_4 Fluxes

The GPP, ER, and NEE showed clear seasonal variations with high absolute values during summer and low absolute values during winter (**Figures 2A–C**). Comparing the two treatments, GPP was increased by OTC treatment during EG ($p < 0.001$) and LG ($p < 0.05$) in 2019, while no significant differences were

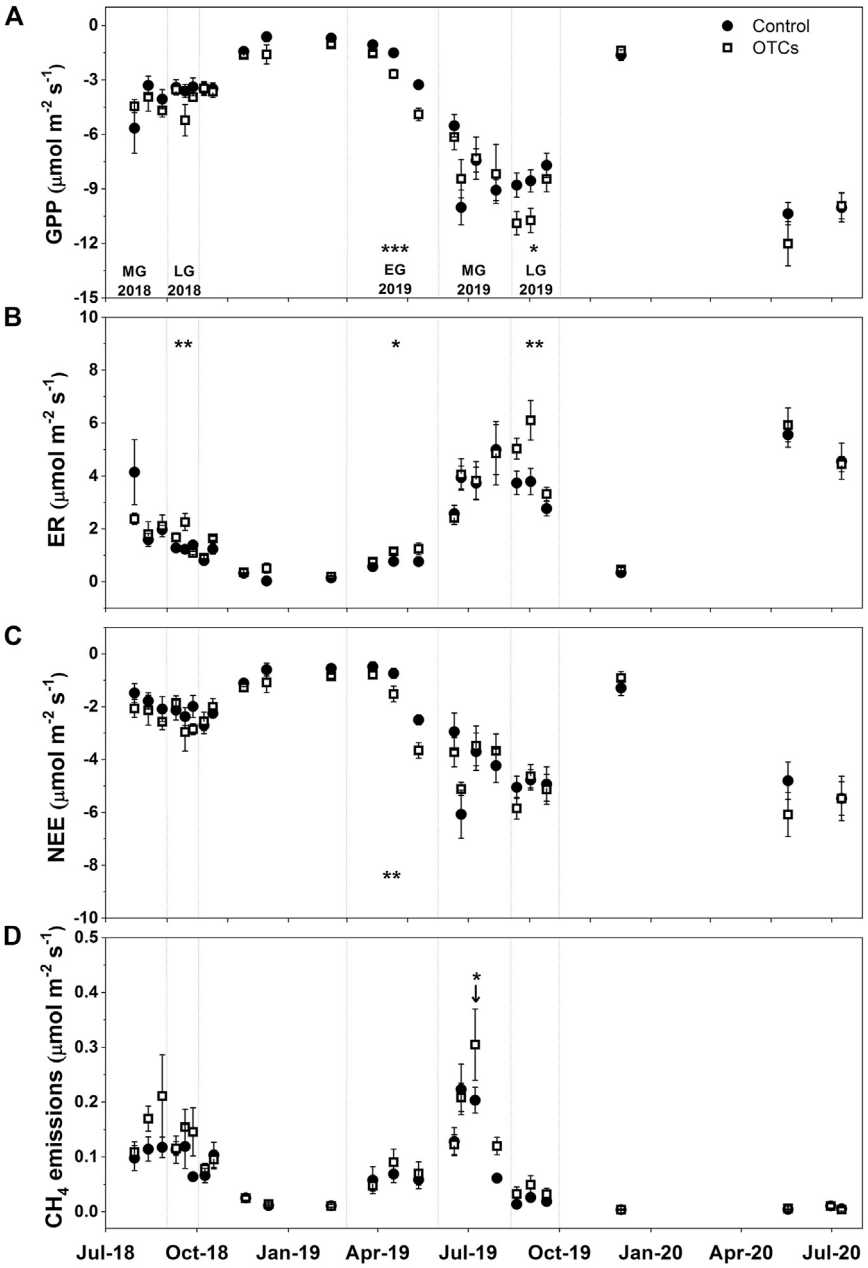

FIGURE 2 | Measured **(A)** GPP (μmol m^{-2} s^{-1}), **(B)** ER (μmol m^{-2} s^{-1}), **(C)** NEE (μmol m^{-2} s^{-}), and **(D)** CH_4 emissions (μmol m^{-2} s^{-1}) from August 2018 to July 2020 in control and OTC plots. Significant differences are expressed as $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$. Letters indicate different periods of growing season (EG = early growing season, MG = middle growing season, and LG = late growing season).

observed in 2018 ($p = 0.41$), and during MG ($p = 0.60$) and WG in 2019 ($p = 0.21$; **Figure 2A**). ER was increased during LG in 2018 ($p < 0.01$), and EG ($p < 0.05$) and LG in 2019 ($p < 0.01$; **Figure 2B**). NEE was enhanced only during EG in 2019 ($p < 0.01$; **Figure 2C**). CH_4 emissions also showed high values in summer and low values in winter (**Figure 2D**). Nevertheless, low values were also observed during August–September 2019 and May–July 2020 corresponding to the low WTD (below −10 cm; **Supplementary Figure S2A**) in these periods. CH_4 emissions were not significantly affected by warming treatment during any period of growing season (**Figure 2D**), while a significant difference between the two treatments was found when the WTD initially reached to the lowest level, with higher values under OTC treatment than in control ($p < 0.05$; **Figure 2D**).

Modeled CO_2 and CH_4 Fluxes

The GPP, ER, and CH_4 models were calibrated and evaluated for the two treatments separately. Calibration of the models showed

TABLE 2 | Modeled annual cumulated gross primary production (GPP; gC m^{-2} yr^{-1}), ecosystem respiration (ER; gC m^{-2} yr^{-1}), CH_4 emissions (CH_4; gC m^{-2} yr^{-1}), net ecosystem exchange (NEE; gC m^{-2} yr^{-1}), and greenhouse gases carbon budget (GGCB; gC m^{-2} yr^{-1}) from September 2018 to September 2019 in control and OTC plots. Data are presented as mean ± SD, n = 6.

	GPP	ER	CH_4	NEE	GGCB
Control	−501 ± 70	500 ± 102	16 ± 5	−2 ± 83	14 ± 82
OTCs	−602 ± 73	615 ± 171	21 ± 9	13 ± 136	34 ± 137

that the modeled data were in good agreement with the measured data, with high R^2_{adj} (>0.5) and low NRMSE (<70%). Meanwhile, the evaluation results also suggested the good representative of the models to the measured data, with R^2_{adj} higher than 0.8 and NRMSE lower than 42% (except for the CH_4 model which showed an R^2_{adj} < 0.4 and an NRMSE >70%; **Supplementary Table S1**).

Modeled Gross Primary Production

The GPP_{max}, which was calculated using the Michaelis–Menten equation based on the photosynthesis-irradiation curve, exhibited obvious seasonal trends. It ranged from −1.60 to −15.61 μmol m^{-2} s^{-1} for control plots and from −1.96 to −20.26 μmol m^{-2} s^{-1} for OTC plots, with higher photosynthetic capacity during summer and lower during winter (**Supplementary Figure S3A**). GPP_{max} was enhanced

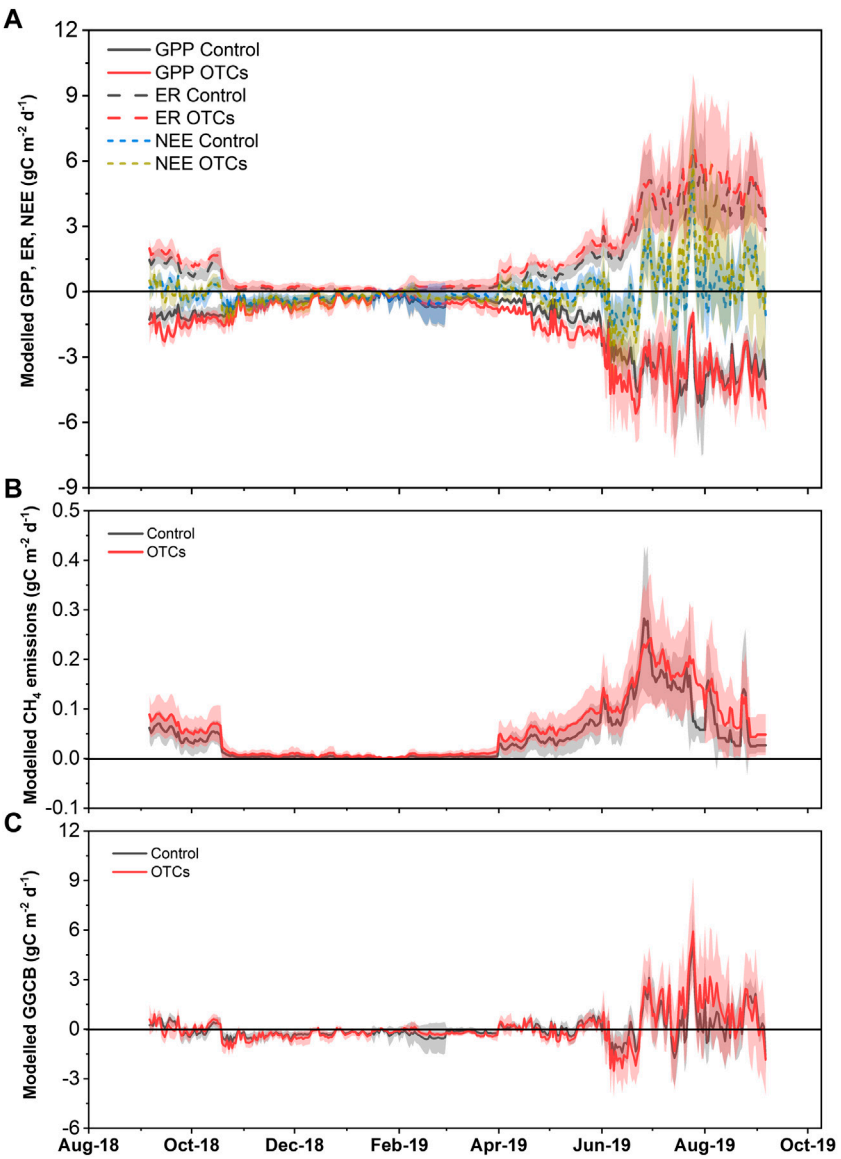

FIGURE 3 | Modeled daily cumulated **(A)** GPP (gC m^{-2} d^{-1}; solid lines), ER (gC m^{-2} d^{-1}; dash lines), NEE (gC m^{-2} d^{-1}; short dash lines), **(B)** CH_4 emissions (gC m^{-2} d^{-1}), and **(C)** greenhouse gas carbon budget (GGCB; gC m^{-2} d^{-1}) from September 2018 to September 2019 in control and OTC plots. Lines indicate the mean values of replicates, and colored shading indicates the error bars of standard deviation.

by OTC treatment in September 2018 and September 2019 (**Supplementary Figure S3A**). A linear relationship between GPP_{max} and the number of graminoid leaves was observed for both treatments (**Supplementary Figure S3B**).

The GPP model was parameterized for each replicate under the two treatments individually. The results showed that the R^2_{adj} of mesocosms ranged from 0.81 to 0.99, and the NRMSE values ranged from 6.0 to 45.3% (**Supplementary Table S2**). Therefore, this model represented the measured GPP well (**Supplementary Figures S4A,B**). The model parameters a and b which represent the sensitivity to vegetation change, and the parameter c which represents the sensitivity to WTD change, all showed similar values between the two treatments (**Supplementary Table S2**). The annual cumulated GPP during September 2018 to September 2019 ranged from −449 to −640 gC m^{-2} yr^{-1} for control plots and from −523 to −719 gC m^{-2} yr^{-1} for OTC plots (**Supplementary Table S2**). Comparing the two treatments, it was significantly higher in OTC plots than in control plots (602 ± 73 vs. 501 ± 70 gC m^{-2} yr^{-1}; p = 0.036; **Table 2**). This result suggested that experimental warming increased the CO_2 input through photosynthesis. In particular, the enhancement of warming on the GPP mainly occurred during April–May 2019 (**Figure 3A**), corresponding to the higher graminoid leaf number under OTC treatment in this period (**Figure 1E**).

Modeled Ecosystem Respiration

The results of parameterizing the ER model for each mesocosm showed that the R^2_{adj} values ranged from 0.58 to 0.95, with the exception of R6 under OTC treatment (R^2_{adj} = 0.06). The NRMSE values ranged from 23.8 to 70.2%, except for R6 under OTC treatment (NRMSE = 104.1%; **Supplementary Table S2**). These results suggested the good agreements between modeled and measured ER values (**Supplementary Figures S4C, D**). The model parameters d, e, and f (represent the sensitivity to WTD, vegetation, and temperature change, respectively) were similar between the two treatments (**Supplementary Table S2**). The annual cumulated ER from September 2018 to September 2019 was 500 ± 102 gC m^{-2} yr^{-1} in control plots (ranging from 354 to 641 gC m^{-2} yr^{-1}) and 615 ± 171 gC m^{-2} yr^{-1} in OTC plots (ranging from 382 to 840 gC m^{-2} yr^{-1}; **Table 2** and **Supplementary Table S2**), but the difference was not significant (p = 0.19; **Figure 3A**).

Modeled CH_4 Emissions

After parameterizing the CH_4 model for each replicate, we found that the R^2_{adj} ranged from 0.82 to 0.97, except R3 under OTCs (R^2_{adj} = 0.44). The NRMSE values ranged between 18.3 and 41.7%, with the exception of R3 under OTCs (NRMSE = 66.7%; **Supplementary Table S2**). Thus, this model represented the measured CH_4 emissions well (**Supplementary Figures S4E, F**). The model parameters g, h, and i (represent the sensitivity to WTD, vegetation, and temperature, respectively) were similar between the two treatments (**Supplementary Table S2**). The modeled annual CH_4 emission ranged from 11 to 22 gC m^{-2} yr^{-1} under control and from 11 to 33 gC m^{-2} yr^{-1} under OTC treatment (**Supplementary Table S2**), with an average of 16 ± 5 and 21 ± 9 gC m^{-2} yr^{-1} in control and OTC plots, respectively (**Table 2**). However, the warming treatment had no significant effect on the annual CH_4 emission (p = 0.83; **Figure 3B**).

Modeled Net Ecosystem Exchange and Greenhouse Gas C Budget

The annual NEE of the control plots showed a slight input of CO_2 (−2 ± 83 gC m^{-2} yr^{-1}) but that of OTC plots exhibited a slight output of CO_2 (13 ± 136 gC m^{-2} yr^{-1}; **Table 2**); however, no significant difference between the two treatments was found (p = 0.83). The annual GGCB showed a release of 14 ± 82 and 34 ± 137 gC m^{-2} yr^{-1} for control and OTC treatment, respectively (**Table 2**). However, the difference was not significant (p = 0.77). Thus, mesocosms under both treatments acted as a C source. Particularly, a strong net C source was found during July–August 2019 for both treatments (**Figure 3C**), corresponding to the low WTD in this period (**Supplementary Figure S2A**). This strong net C source mainly resulted from the net CO_2 source, as NEE showed similar values as GGCB during this period (**Figure 3A**), while CH_4 emissions only accounted for 0.9–2.2% in the total C fluxes.

DISCUSSION

Climate Regime and Vegetation Control on the CO_2 Fluxes

On the whole, the annual GPP (~450–720 gC m^{-2} yr^{-1}) and ER (~350–840 gC m^{-2} yr^{-1}; **Supplementary Table S2**) in the present study were higher than those from boreal peatlands, which showed the GPP and ER fluxes between 100 and 500 gC m^{-2} yr^{-1} (e.g., Cliche Trudeau et al., 2014; Peichl et al., 2014). This may be caused by the differences in climate regime, particularly by the higher annual temperature in our study site than in sites at higher latitudes. While when compared to studies conducted under the same climatic condition, our values were lower. In the same site (La Guette peatland) where our mesocosms were collected, D'Angelo et al. (2021) reported the GPP and ER were all above 1,000 gC m^{-2} yr^{-1} with *in situ* measurements. In addition, Leroy et al. (2019) estimated an annual GPP of 1,300 gC m^{-2} yr^{-1} and ER of 1,000 gC m^{-2} yr^{-1} in mesocosms dominated by *Molinia caerulea* collected from La Guette peatland. This could be attributed to the differences in vegetation. La Guette peatland was almost entirely invaded by *Molinia caerulea* (Gogo et al., 2011). Thus, the percentage cover of *Molinia* in both field and *Molinia*-dominated mesocosms was higher than that of our mesocosms. The GPP of graminoids was higher than that of shrubs and bryophytes, and the GPP of graminoid-dominated peatlands was similar with those of temperate grasslands (Rydin and Jeglum, 2013; Leroy et al., 2019). Therefore, compared with the results of D'Angelo et al. (2021) and Leroy et al. (2019), the lower GPP observed in our study could be attributed to the lower abundance of graminoids. This was supported by the fact that mesocosms with only *Sphagnum* had a lower GPP and ER (400 and 380 gC m^{-2} yr^{-1}, respectively, Leroy et al., 2019) than those in our study. In addition, the positive relationship between GPP_{max} and the number of graminoid leaves also confirmed the strong effect of graminoid abundance on GPP (**Supplementary Figure S3B**). The lower ER observed in our study can also be attributed to the

lower abundance of graminoids. *Molinia caerulea* has an extensive root system, which is larger than that of other species. Thus, the lower abundance of this species compared with previous studies could induce lower root and leaf respiration in our mesocosms.

Stimulation of Experimental Warming on the Gross Primary Production

In previous studies, the effect of temperature rise on GPP varied from increasing (e.g., Chivers et al., 2009) to decreasing (e.g., Voigt et al., 2017) or no effect (e.g., Johnson et al., 2013; Laine et al., 2019), depending on the peatland type and initial vegetation composition. In our research, the warming treatment significantly increased the annual cumulated GPP of mesocosms from 500 to 615 $gC\,m^{-2}\,yr^{-1}$ (**Table 2**). The enhancement mainly occurred during April–May 2019 (**Figure 3A**), when the number of graminoid leaves was higher under warming treatment than that in control (**Figure 1E**). Experimental warming facilitated the growth of graminoids, thus increasing the plant biomass (evidenced by the higher leaf number). The increase of plant biomass in turn increased the capacity of vegetation to withdraw CO_2 from the atmosphere (higher GPP). Our result of a significant correlation between GPP_{max} and graminoid leaf number (**Supplementary Figure S3B**) confirmed this statement. In addition, Tuittila et al. (2004) found that the GPP of *Sphagnum* increased with the water content. In our study, the *Sphagnum* at 5 cm depth was wetter under OTC treatment than that under control during summer (**Supplementary Figure S2B**), probably caused by the lower wind presence and speed in OTCs than in ambient environment, which reduced the evapotranspiration. Thus, the higher water content of *Sphagnum* in OTC plots may also have contributed to the higher GPP under warming treatment.

Water Table Depth Modulates the Ecosystem Respiration Response to Warming

The warming treatment had no significant effect on the annual cumulated ER in our research. This result was inconsistent with previous studies which reported an increase of ER with temperature (e.g., Updegraff et al., 2001; Chivers et al., 2009; Voigt et al., 2017; Samson et al., 2018). Laine et al. (2019) found a low temperature sensitivity of ER under the wet condition. In their study, warming had no significant effect on ER under the ambient wet condition, while ER was significantly increased by moderate warming under the dry condition. The low temperature sensitivity of ER under the wet condition may be attributed to the low temperature sensitivity of soil respiration as it was reported to be less sensitive to temperature change under the anaerobic than aerobic condition (Szafranek-Nakonieczna and Stepniewska, 2014). Meanwhile, Chen et al. (2018) found a positive relationship between the temperature sensitivity (Q_{10}) of soil respiration and the soil redox potential, which confirmed this result. In our study, the mean WTD throughout the monitoring was −6.80 and −6.68 cm for control and OTC treatment, respectively (**Table 1**). The WTD was mostly above −5 cm except during summer (**Supplementary Figure S2A**), suggesting a dominant anaerobic condition in our mesocosms. Therefore, the water saturated condition may lead to a low temperature sensitivity of soil respiration and thus a similar ER under both treatments.

Water Table Depth Dependence of CH_4 Emissions

The annual cumulated CH_4 emission in our results was lower than 33 $gC\,m^{-2}\,yr^{-1}$ found by Leroy et al. (2019), with mesocosms collected from the same peatland. This was caused by the lower WTD in our mesocosms (**Supplementary Figure S2A**) than in their experiment. During our monitoring, WTD reached to a level below −15 cm during July–September 2019, while it remained above −10 cm most of the time in their experiment (data in Leroy et al., 2017). WTD has been reported to be a stronger regulator on CH_4 emissions than temperature (Roulet et al., 1992; Turetsky et al., 2008). When the WTD decreased, the amount of water-saturated (i.e., anaerobic) peat decreased and the aerobic layer increased. Thus, the oxidation of CH_4 was promoted. In our study, the correlation between CH_4 emissions and temperature was only found when WTD ranged between 0 and −9 cm. However, when WTD dropped below −9 cm, CH_4 emissions were independent of temperature (**Figure 2D**). This result confirmed the controlling of WTD on CH_4 emissions. In our results of the measured CH_4 emissions, the enhancement of CH_4 emission by warming treatment was only found when WTD initially reached the lowest level (**Figure 2D**). Thus, warming alone may have only a slight effect on the CH_4 emissions, while if warming interacted with WTD dropdown, their interaction could have a significant effect on the CH_4 emissions (Munir and Strack, 2014).

Temperature and Water Table Depth Modulate the Peatland Functioning

Previous research showed that the peatlands varied from C sink (e.g., Koehler et al., 2011; Nilsson et al., 2008; Roulet et al., 2007) to C source (e.g., Waddington and Roulet, 2000; Voigt et al., 2017). In our study, the C balance of individual mesocosm showed large variations ranging from gaseous C sink to the source, with an average of 14 and 34 $gC\,m^{-2}\,yr^{-1}$ output of C under control and OTC treatment, respectively (**Table 2**). The La Guette peatland also acted as a C source with an output of 220 $gC\,m^{-2}\,yr^{-1}$ between 2013 and 2014. The stronger C source in the field than our mesocosms was linked to the repeated droughts in the previous years (D'Angelo et al., 2021). However, in the study of Leroy et al. (2019), both *Sphagnum* and *Molinia caerulea* dominated mesocosms collected from this peatland acted as gaseous C sink. This difference may be caused by the low WTD in our mesocosms during summer (**Supplementary Figure S2A**). We found that the mesocosms under both treatments showed high positive NEE

values during July–September 2019 (**Figure 3A**), suggesting a strong CO_2 source. This strong CO_2 source corresponded to the low WTD in this period (**Supplementary Figure S2A**). The low WTD induced a higher respiration under the aerobic condition. Thus, the ER exceeded GPP and led to a net CO_2 release. The CH_4 emissions decreased following the decline of WTD, while it only accounted for 0.9–2.2% of the total C fluxes. Therefore, the net C losses in our study were mainly driven by the net CO_2 output. The controlling of WTD on the CO_2 exchange was in accordance with the findings of Laine et al. (2019), who observed a decreasing CO_2 uptake with low WTD due to the increase of CO_2 release as a result of the increased OM decomposition.

Hanson et al. (2020) have found that an air temperature increase of 2.25–9°C enhanced the net C source of peatland during 3 years of monitoring. Bridgham et al. (2008) conducted a 7-year monitoring, and the results showed that a soil warming of 1.6–4.1°C significantly reduced the C accumulation of peatland. Bragazza et al. (2016) also observed a reduction of peatland C accumulation with 5°C air temperature increase during 3 years. Compared with our study, these studies which found an impact of warming on the C budget of peatlands always have a stronger temperature increase than our study (0.9°C increase in air temperature; 1.35 and 0.95°C increase in soil temperature at 5 and 15 cm depths, respectively) or longer time warming treatment. With moderate warming (+0.7°C soil warming at 2 cm depth) for 2 years like in our study, Chivers et al. (2009) found that warming did not modify the C balance of peatland. In addition, there was another research that found the C sink of peatland can be enhanced by manipulated warming (about 1°C air temperature increase; Munir et al., 2015). This was caused by the enhanced growth of shrubs by warming in their treed bog. It has been demonstrated that the response of GHG emissions to warming largely depended on the vegetation composition and environmental conditions of the study site, as well as the warming methods, the warming rate, and the duration of the experiment (Gong et al., 2020). Any difference in these factors could lead to contrasting results. In our study, we found that a temperate peatland which has suffered a vegetation shift from *Sphagnum* to vascular plants dominance remained stable in response to short-term moderate warming. However, as the vascular plants could benefit more from warming than *Sphagnum* (Bragazza et al., 2013; Buttler et al., 2015; Dieleman et al., 2015), a vegetation structure change under long-term warming is expected, which may lead to a modification of C balance in the future.

CONCLUSION

In our study, the CO_2 and CH_4 fluxes of mesocosms collected from a temperate peatland were monitored and modeled using abiotic and biotic factors, including temperature, WTD, and vegetation. Models based on these variables described the measured data well. The modeled results showed that the experimental warming significantly enhanced the annual CO_2 uptake through photosynthesis but had no effect on the ER and CH_4 emissions. The increase of photosynthesis was attributed to the faster growth of graminoids under warming treatment during the early growing season. The mesocosms under both treatments acted as a gaseous C source, and it was caused by the net CO_2 release during a low WTD period in summer. The gaseous C balance remained stable under the 2 years of moderate warming. Our study demonstrated the strong effect of moderate warming on the gaseous C fluxes of temperate peatlands. Moreover, we emphasized the necessity of integrating the WTD and vegetation change along with warming to determine the effect of their interactions on the peatland C fluxes. Further studies of long-term monitoring with a consideration of climate induced both abiotic and biotic factors will be needed to better estimate the feedback of peatlands to global changes as well as its magnitude.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

QL, SG, and FL-D designed and prepared the experiment. QL collected data. CG helped on the CH_4 measurements. QL, SG, and FL performed the data treatment and modeling. QL wrote the article with the help of all coauthors.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2021.631368/full#supplementary-material

REFERENCES

AminiTabrizi, R., Wilson, R. M., Fudyma, J. D., Hodgkins, S. B., Heyman, H. M., Rich, V. I., et al. (2020). Controls on Soil Organic Matter Degradation and Subsequent Greenhouse Gas Emissions across a Permafrost Thaw Gradient in Northern Sweden. *Front. Earth Sci.* 8, 381. doi:10.3389/feart.2020.557961

Aronson, E. L., and McNulty, S. G. (2009). Appropriate Experimental Ecosystem Warming Methods by Ecosystem, Objective, and Practicality. *Agric. For. Meteorology* 149, 1791–1799. doi:10.1016/j.agrformet.2009.06.007

Aurela, M., Laurila, T., and Tuovinen, J.-P. (2004). The Timing of Snow Melt Controls the Annual CO2balance in a Subarctic Fen. *Geophys. Res. Lett.* 31, L16119. doi:10.1029/2004GL020315

Berendse, F., Van Breemen, N., Rydin, H., Buttler, A., Heijmans, M., Hoosbeek, M. R., et al. (2001). Raised Atmospheric CO2 Levels and Increased N Deposition Cause Shifts in Plant Species Composition and Production in Sphagnum Bogs. *Glob. Change Biol.* 7, 591–598. doi:10.1046/j.1365-2486.2001.00433.x

Bortoluzzi, E., Epron, D., Siegenthaler, A., Gilbert, D., and Buttler, A. (2006). Carbon Balance of a European Mountain Bog at Contrasting Stages of Regeneration. *New Phytol.* 172, 708–718. doi:10.1111/j.1469-8137.2006.01859.x

Bragazza, L., Buttler, A., Robroek, B. J. M., Albrecht, R., Zaccone, C., Jassey, V. E. J., et al. (2016). Persistent High Temperature and Low Precipitation Reduce Peat Carbon Accumulation. *Glob. Change Biol.* 22, 4114–4123. doi:10.1111/gcb.13319

Bragazza, L., Buttler, A., Siegenthaler, A., and Mitchell, E. A. D. (2009). Plant Litter Decomposition and Nutrient Release in Peatlands. *GMS* 184, 99–110. doi:10.1029/2008GM000815

Bragazza, L., Parisod, J., Buttler, A., and Bardgett, R. D. (2013). Biogeochemical Plant-Soil Microbe Feedback in Response to Climate Warming in Peatlands. *Nat. Clim Change* 3, 273–277. doi:10.1038/nclimate1781

Bridgham, S. D., Pastor, J., Dewey, B., Weltzin, J. F., and Updegraff, K. (2008). Rapid Carbon Response of Peatlands to Climate Change. *Ecology* 89, 3041–3048. doi:10.1890/08-0279.1

Bubier, J. L., Moore, T. R., and Bledzki, L. A. (2007). Effects of Nutrient Addition on Vegetation and Carbon Cycling in an Ombrotrophic Bog. *Glob. Change Biol.* 13, 1168–1186. doi:10.1111/j.1365-2486.2007.01346.x

Buttler, A., Robroek, B. J. M., Laggoun-Défarge, F., Jassey, V. E. J., Pochelon, C., Bernard, G., et al. (2015). Experimental Warming Interacts with Soil Moisture to Discriminate Plant Responses in an Ombrotrophic Peatland. *J. Veg. Sci.* 26, 964–974. doi:10.1111/jvs.12296

Chen, H., Zou, J., Cui, J., Nie, M., and Fang, C. (2018). Wetland Drying Increases the Temperature Sensitivity of Soil Respiration. *Soil Biol. Biochem.* 120, 24–27. doi:10.1016/j.soilbio.2018.01.035

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2009). Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO2 Fluxes in an Alaskan Rich Fen. *Ecosystems* 12, 1329–1342. doi:10.1007/s10021-009-9292-y

Cliche Trudeau, N., Garneau, M., and Pelletier, L. (2014). Interannual Variability in the CO2 Balance of a Boreal Patterned Fen, James Bay, Canada. *Biogeochemistry* 118, 371–387. doi:10.1007/s10533-013-9939-9

D'Angelo, B., Leroy, F., Guimbaud, C., Jacotot, A., Zocatelli, R., Gogo, S., et al. (2021). Carbon Balance and Spatial Variability of CO_2 and CH_4 Fluxes in a *Sphagnum*-Dominated Peatland in a Temperate Climate. *Wetlands* 41, 5. doi:10.1007/s13157-021-01411-y

Dieleman, C. M., Branfireun, B. A., McLaughlin, J. W., and Lindo, Z. (2015). Climate Change Drives a Shift in Peatland Ecosystem Plant Community: Implications for Ecosystem Function and Stability. *Glob. Change Biol.* 21, 388–395. doi:10.1111/gcb.12643

Dieleman, C. M., Lindo, Z., McLaughlin, J. W., Craig, A. E., and Branfireun, B. A. (2016). Climate Change Effects on Peatland Decomposition and Porewater Dissolved Organic Carbon Biogeochemistry. *Biogeochemistry* 128, 385–396. doi:10.1007/s10533-016-0214-8

Dorrepaal, E., Cornelissen, J. H. C., Aerts, R., Wallén, B., and Van Logtestijn, R. S. P. (2005). Are Growth Forms Consistent Predictors of Leaf Litter Quality and Decomposability across Peatlands along a Latitudinal Gradient?. *J. Ecol.* 93, 817–828. doi:10.1111/j.1365-2745.2005.01024.x

Dorrepaal, E., Toet, S., van Logtestijn, R. S. P., Swart, E., van de Weg, M. J., Callaghan, T. V., et al. (2009). Carbon Respiration from Subsurface Peat Accelerated by Climate Warming in the Subarctic. *Nature* 460, 616–619. doi:10.1038/nature08216

Dunfield, P., Knowles, R., Dumont, R., and Moore, T. (1993). Methane Production and Consumption in Temperate and Subarctic Peat Soils: Response to Temperature and pH. *Soil Biol. Biochem.* 25, 321–326. doi:10.1016/0038-0717(93)90130-4

Flanagan, L. B., and Syed, K. H. (2011). Stimulation of Both Photosynthesis and Respiration in Response to Warmer and Drier Conditions in a Boreal Peatland Ecosystem. *Glob. Change Biol.* 17, 2271–2287. doi:10.1111/j.1365-2486.2010.02378.x

Gavazov, K., Albrecht, R., Buttler, A., Dorrepaal, E., Garnett, M. H., Gogo, S., et al. (2018). Vascular Plant-Mediated Controls on Atmospheric Carbon Assimilation and Peat Carbon Decomposition under Climate Change. *Glob. Change Biol.* 24, 3911–3921. doi:10.1111/gcb.14140

Girkin, N. T., Turner, B. L., Ostle, N., Craigon, J., and Sjögersten, S. (2018). Root Exudate Analogues Accelerate CO2 and CH4 Production in Tropical Peat. *Soil Biol. Biochem.* 117, 48–55. doi:10.1016/j.soilbio.2017.11.008

Gogo, S., Laggoun-Défarge, F., Delarue, F., and Lottier, N. (2011). Invasion of a *Sphagnum*-Peatland by *Betula Spp* and *Molinia Caerulea* Impacts Organic Matter Biochemistry. Implications for Carbon and Nutrient Cycling. *Biogeochemistry* 106, 53–69. doi:10.1007/s10533-010-9433-6

Gogo, S., Laggoun-Défarge, F., Merzouki, F., Mounier, S., Guirimand-Dufour, A., Jozja, N., et al. (2016). *In Situ* and Laboratory Non-additive Litter Mixture Effect on C Dynamics of *Sphagnum Rubellum* and *Molinia Caerulea* Litters. *J. Soils Sediments* 16, 13–27. doi:10.1007/s11368-015-1178-3

Gong, Y., Wu, J., Vogt, J., and Ma, W. (2020). Greenhouse Gas Emissions from Peatlands under Manipulated Warming, Nitrogen Addition, and Vegetation Composition Change: a Review and Data Synthesis. *Environ. Rev.* 28, 428–437. doi:10.1139/er-2019-0064

Gorham, E. (1991). Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecol. Appl.* 1, 182–195. doi:10.2307/1941811

Hanson, P. J., Griffiths, N. A., Iversen, C. M., Norby, R. J., Sebestyen, S. D., Phillips, J. R., et al. (2020). Rapid Net Carbon Loss from a Whole-Ecosystem Warmed Peatland. *AGU Adv.* 1, e2020AV000163. doi:10.1029/2020AV000163

Intergovernmental Panel on Climate Change (2014). *Climate Change 2014: The Physical Science Basis: Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., and Piñeiro, G. (2017). The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls. *Annu. Rev. Ecol. Evol. Syst.* 48, 419–445. doi:10.1146/annurev-ecolsys-112414-054234

Johnson, C. P., Pypker, T. G., Hribljan, J. A., and Chimner, R. A. (2013). Open Top Chambers and Infrared Lamps: A Comparison of Heating Efficacy and CO2/CH4 Dynamics in a Northern Michigan Peatland. *Ecosystems* 16, 736–748. doi:10.1007/s10021-013-9646-3

Johnson, K. A., and Goody, R. S. (2011). The Original Michaelis Constant: Translation of the 1913 Michaelis-Menten Paper. *Biochemistry* 50, 8264–8269. doi:10.1021/bi201284u

Kandel, T. P., Elsgaard, L., and Laerke, P. E. (2013). Measurement and Modelling of CO2flux from a Drained Fen Peatland Cultivated with Reed Canary Grass and spring Barley. *GCB Bioenergy* 5, 548–561. doi:10.1111/gcbb.12020

Koehler, A.-K., Sottocornola, M., and Kiely, G. (2011). How strong Is the Current Carbon Sequestration of an Atlantic Blanket Bog?. *Glob. Change Biol.* 17, 309–319. doi:10.1111/j.1365-2486.2010.02180.x

Laine, A., Wilson, D., Kiely, G., and Byrne, K. A. (2007). Methane Flux Dynamics in an Irish lowland Blanket Bog. *Plant Soil* 299, 181–193. doi:10.1007/s11104-007-9374-6

Laine, A. M., Mäkiranta, P., Laiho, R., Mehtätalo, L., Penttilä, T., Korrensalo, A., et al. (2019). Warming Impacts on Boreal Fen CO 2 Exchange under Wet and Dry Conditions. *Glob. Change Biol.* 25, 1995–2008. doi:10.1111/gcb.14617

Leifeld, J., Wüst-Galley, C., and Page, S. (2019). Intact and Managed Peatland Soils as a Source and Sink of GHGs from 1850 to 2100. *Nat. Clim. Change* 9, 945–947. doi:10.1038/s41558-019-0615-5

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Hu, Z., and Laggoun-Défarge, F. (2017). Vegetation Composition Controls Temperature Sensitivity

of CO2 and CH4 Emissions and DOC Concentration in Peatlands. *Soil Biol. Biochem.* 107, 164–167. doi:10.1016/j.soilbio.2017.01.005

Leroy, F., Gogo, S., Guimbaud, C., Bernard-Jannin, L., Yin, X., Belot, G., et al. (2019). CO2 and CH4 Budgets and Global Warming Potential Modifications in Sphagnum-Dominated Peat Mesocosms Invaded by Molinia Caerulea. *Biogeosciences* 16, 4085–4095. doi:10.5194/bg-16-4085-2019

Lloyd, J., and Taylor, J. A. (1994). On the Temperature Dependence of Soil Respiration. *Funct. Ecol.* 8, 315–323. doi:10.2307/2389824

Mahadevan, P., Wofsy, S. C., Matross, D. M., Xiao, X., Dunn, A. L., Lin, J. C., et al. (2008). A Satellite-Based Biosphere Parameterization for Net Ecosystem CO2exchange: Vegetation Photosynthesis and Respiration Model (VPRM). *Glob. Biogeochem. Cycles* 22, GB2005. doi:10.1029/2006GB002735

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., et al. (1997). Open-top Designs for Manipulating Field Temperature in High-Latitude Ecosystems. *Glob. Change Biol.* 3, 20–32. doi:10.1111/j.1365-2486.1997.gcb136.x

Medlyn, B. E., Dreyer, E., Ellsworth, D., Forstreuter, M., Harley, P. C., Kirschbaum, M. U. F., et al. (2002). Temperature Response of Parameters of a Biochemically Based Model of Photosynthesis. II. A Review of Experimental Data. *Plant Cell Environ* 25, 1167–1179. doi:10.1046/j.1365-3040.2002.00891.x

Munir, T. M., Perkins, M., Kaing, E., and Strack, M. (2015). Carbon Dioxide Flux and Net Primary Production of a Boreal Treed Bog: Responses to Warming and Water-Table-Lowering Simulations of Climate Change. *Biogeosciences* 12, 1091–1111. doi:10.5194/bg-12-1091-2015

Munir, T. M., and Strack, M. (2014). Methane Flux Influenced by Experimental Water Table Drawdown and Soil Warming in a Dry Boreal continental Bog. *Ecosystems* 17, 1271–1285. doi:10.1007/s10021-014-9795-z

Nilsson, M., Sagerfors, J., Buffam, I., Laudon, H., Eriksson, T., Grelle, A., et al. (2008). Contemporary Carbon Accumulation in a Boreal Oligotrophic Minerogenic Mire - a Significant Sink after Accounting for All C-Fluxes. *Glob. Change Biol.* 14, 2317–2332. doi:10.1111/j.1365-2486.2008.01654.x

Peichl, M., Öquist, M., Ottosson Löfvenius, M., Ilstedt, U., Sagerfors, J., Grelle, A., et al. (2014). A 12-year Record Reveals Pre-growing Season Temperature and Water Table Level Threshold Effects on the Net Carbon Dioxide Exchange in a Boreal Fen. *Environ. Res. Lett.* 9, 055006. doi:10.1088/1748-9326/9/5/055006

Raich, J. W., Rastetter, E. B., Melillo, J. M., Kicklighter, D. W., Steudler, P. A., Peterson, B. J., et al. (1991). Potential Net Primary Productivity in South America: Application of a Global Model. *Ecol. Appl. Publ. Ecol. Soc. Am.* 1, 399–429. doi:10.2307/1941899

Roulet, N., Moore, T., Bubier, J., and Lafleur, P. (1992). Northern Fens: Methane Flux and Climatic Change. *Tellus B* 44, 100–105. doi:10.1034/j.1600-0889.1992.t01-1-00002.x

Roulet, N. T., Lafleur, P. M., Richard, P. J. H., Moore, T. R., Humphreys, E. R., and Bubier, J. (2007). Contemporary Carbon Balance and Late Holocene Carbon Accumulation in a Northern Peatland. *Glob. Change Biol.* 13, 397–411. doi:10.1111/j.1365-2486.2006.01292.x

R Core Team (2020). *A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rydin, H., and Jeglum, J. K. (2013). *The Biology of Peatlands*. 2e. Oxford: Oxford University Press.

Samson, M., Słowińska, S., Słowiński, M., Lamentowicz, M., Barabach, J., Harenda, K., et al. (2018). The Impact of Experimental Temperature and Water Level Manipulation on Carbon Dioxide Release in a Poor Fen in Northern Poland. *Wetlands* 38, 551–563. doi:10.1007/s13157-018-0999-4

Segers, R. (1998). Methane Production and Methane Consumption: a Review of Processes Underlying Wetland Methane Fluxes. *Biogeochemistry* 41, 23–51. doi:10.1023/A:1005929032764

Strack, M. (2008). *Peatlands and Climate Change*. Saarijärvi, Finland: International Peat Society, Saarijärven Offset Oy.

Straková, P., Niemi, R. M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., et al. (2011). Litter Type Affects the Activity of Aerobic Decomposers in a Boreal Peatland More Than Site Nutrient and Water Table Regimes. Available at: https://jukuri.luke.fi/handle/10024/516544 ((Accessed July 23, 2020).

Szafranek-Nakonieczna, A., and Stepniewska, Z. (2014). Aerobic and Anaerobic Respiration in Profiles of Polesie Lubelskie Peatlands. Int. Agrophysics 28. , 2014 Available at: http://yadda.icm.edu.pl/yadda/element/bwmeta1.element.agro-9a68ce86-a247-40f5-ae04-41017c4101d4 (Accessed May 31, 2020).

Thornley, J. H. M., and Johnson, I. R. (1990). Plant and Crop Modelling: a Mathematical Approach to Plant and Crop Physiology. Available at: https://agris.fao.org/agris-search/search.do?recordID=XF2016001523 (Accessed August 3, 2020).

Tuittila, E.-S., Vasander, H., and Laine, J. (2004). Sensitivity of C Sequestration in Reintroduced *Sphagnum* to Water-Level Variation in a Cutaway Peatland. *Restor Ecol.* 12, 483–493. doi:10.1111/j.1061-2971.2004.00280.x

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., and McGuire, A. D. (2008). Short-term Response of Methane Fluxes and Methanogen Activity to Water Table and Soil Warming Manipulations in an Alaskan Peatland. *J. Geophys. Res.* 113, G00A10. doi:10.1029/2007JG000496

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., and Harth, C. (2001). Response of CO 2 and CH 4 Emissions from Peatlands to Warming and Water Table Manipulation. *Ecol. Appl.* 11, 311–326. doi:10.2307/3060891

Voigt, C., Lamprecht, R. E., Marushchak, M. E., Lind, S. E., Novakovskiy, A., Aurela, M., et al. (2017). Warming of Subarctic Tundra Increases Emissions of All Three Important Greenhouse Gases - Carbon Dioxide, Methane, and Nitrous Oxide. *Glob. Change Biol.* 23, 3121–3138. doi:10.1111/gcb.13563

Waddington, J. M., Griffis, T. J., and Rouse, W. R. (1998). Northern Canadian Wetlands: Net Ecosystem CO_2 Exchange and Climatic Change. *Clim. Change* 40, 267–275. doi:10.1023/A:1005468920206

Waddington, J. M., and Roulet, N. T. (2000). Carbon Balance of a Boreal Patterned Peatland. *Glob. Change Biol.* 6, 87–97. doi:10.1046/j.1365-2486.2000.00283.x

Ward, S. E., Ostle, N. J., Oakley, S., Quirk, H., Henrys, P. A., and Bardgett, R. D. (2013). Warming Effects on Greenhouse Gas Fluxes in Peatlands Are Modulated by Vegetation Composition. *Ecol. Lett.* 16, 1285–1293. doi:10.1111/ele.12167

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., and Hunt, S. J. (2010). Global Peatland Dynamics since the Last Glacial Maximum. *Geophys. Res. Lett.* 37, L13402. doi:10.1029/2010GL043584

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Qian LI

Effet du réchauffement climatique sur le cycle du carbone dans les tourbières - approche expérimentale

Les tourbières sont des zones humides qui ont stocké environ 30 % de carbone (C) des sols mondiaux dans seulement 3 % de la superficie terrestre et ce, grâce à des conditions favorables (faible température, engorgement et acidité). Cependant, le changement climatique pourrait modifier significativement les processus du cycle du C et la fonction puits de C des tourbières en les transformant en un système source émetteur de C. L'objectif de ce travail est d'étudier l'effet du réchauffement climatique simulé (par open top chambers; OTCs) sur les processus du cycle du C d'une tourbière à sphaignes tempérée qui a été envahie par des plantes vasculaires et d'évaluer les facteurs clés qui contrôlent ces processus. Les travaux ont porté principalement sur des flux de C gazeux à l'interface écosystème-atmosphère et de la dynamique du carbone organique dissous (COD) dans des mésocosmes de tourbe de 40 cm d'épaisseur. Les résultats montrent une augmentation de la photosynthèse et de la respiration de l'écosystème sous l'effet des OTCs en début et en fin de saison de végétation. L'augmentation des émissions de CH_4 par les OTCs n'a été observée que lorsque le niveau d'eau dans les mésocosmes a fortement diminué. En revanche, la sensibilité à la température (Q_{10}) des flux de CO_2 et de CH_4 ont tous diminué en réponse au réchauffement. La photosynthèse annuelle modélisée a été sensiblement augmentée par le réchauffement, mais le bilan de C gazeux et le potentiel de réchauffement climatique n'ont pas été affectés de manière significative. Au cours des deux années de suivi, bien que la concentration et la qualité du COD n'ont pas été affectées par le réchauffement, nous avons constaté que des températures élevées et des conditions aérobies augmentaient la respiration du sol. La tourbe profonde ayant un fort taux de décomposition a montré un taux de production de CO_2 plus faible mais a révélé une sensibilité à la température (Q_{10}) plus élevée que celle de la tourbe de surface. L'augmentation du Q_{10} avec la profondeur devrait être utiliser pour améliorer les estimations de production de CO_2 dans les profils de tourbe.

Mots clés: Réchauffement climatique, Flux de CO_2 et CH_4, Bilan de carbone, Carbone organique dissous, Tourbières

Effect of climate warming on the carbon cycle of peatlands - experimental approach

Peatlands are wetlands that have stored about 30 % of global soil carbon (C) in only 3% of the earth land surface, thanks to favorable conditions (low temperature, waterlogging and acidity). However, climate change could significantly modify the C cycle processes in peatlands and thus swift their functioning from C sink to C source. The aim of this work is to study the effect of simulated warming (by open top chambers; OTCs) on the C cycle processes of a temperate *Sphagnum* peatland which has been invaded by vascular plants and to assess the key factors controlling these processes. The work mainly focused on the gaseous C fluxes at the ecosystem-atmosphere interface and the dynamics of belowground dissolved organic carbon (DOC) in peat mesocosms of 40cm thick. The results show that OTCs significantly enhanced the photosynthesis and ecosystem respiration during early and late growing season. The increase of CH_4 emission by OTCs was only observed when water table depth sharply declines in the mesocosms. However, the temperature sensitivity (Q_{10}) of CO_2 and CH_4 fluxes declined in response to warming. The modelled annual photosynthesis was significantly enhanced by warming, while the gaseous C budget and global warming potential were not significantly affected. During the 2 years monitoring, although DOC concentration and quality were not affected by warming, we found that higher temperatures and aerobic conditions increased the soil respiration. Deep peat showed a lower CO_2 production rate, but higher Q_{10} than that of surface peat. The increasing Q_{10} with depth in the uppermost peat section could be used to improve the estimation of CO_2 production in peat profiles.

Keywords: Climate warming; CO_2 and CH_4 fluxes; Carbon balance; Dissolved organic carbon; Peatlands

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