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Importance of Extracellular Enzyme Activities in Northern Peatland Biogeochemistry-Possible Coupling with Trace Gas Emission and DOC Dynamics

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A suite of extracellular enzyme activities involved in organic carbon decomposition were determined in three northern peatlands (a bog, a fen, and a swamp) over a 12 month period along with trace gas (CO_2 and N_2O) flux and DOC dynamics in the wetlands. The activities varied 0.008-0.066 μmole g^{-1} min^{-1}, 0.003-0.021 μmole g^{-1} min^{-1}, 0.003-0.016 μmole g^{-1} min^{-1}, 0.004-0.047 μmole g^{-1} min^{-1}, for β-glucosidase, cellobiohydrolase, β-xylosidase, and N-acetylglucosaminidase, respectively. In general, the activities were highest in the forested swamp followed by the fen and the bog. When the data from three wetlands are combined, the enzyme activities exhibited significant positive correlations with trace gas emission and available carbon. Further, the average activity of 4 enzymes explained about 20-40% of the variations of trace gas emssion and available carbon. The results indicate that enzymes related to the mineralization of organic carbon may play an important role in trace gas flux and DOC dynamics in northern peatlands.

Key words : cellulose, organic carbon, peat, soil enzyme, wetland

INTRODUCTION

Wetlands are transitional zones between terrestrial and aquatic ecosystems, having many distinguishing features (Mitsch and Gosselink, 1993). The biogeochemistry of wetlands is highly unique compared to upland ecosystems or aquatic sediments, because diverse redox potential regimes co-exist in a close proximity. In particular, two important aspects of wetland biogeochemistry have been extensively studied. First, wetlands are one of the main sources of methane (CH_4) and nitrous oxide (N_2O), which are much stronger greenhouse gas than carbon dioxide on a molar basis (Rodhe, 1990). The other importance of wetlands is the production and decomposition of dissolved organic carbon (DOC), which is dominant form of organic carbon in many aquatic ecosystems. DOC is an important component of organic energy pathways in ecosystems (Middelboe and Sondergaard, 1993), and hence the amount and the composition of DOC affect substrate availability for heterotrophic bacterial growth (Mann and Wetzel, 1995). Further, several studies have shown that DOC in wetlands would affect various microbial-mediated processes such as trace gas flux (Bianchi *et al*., 1996) and extracellular enzyme activities (Freeman *et al*., 1998).

In the decomposition and nutrient cycling in aquatic or terrestrial ecosystems, extracellular hydrolysis by enzymes has been reported as a critical step for the following reasons. First, other

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sources of nutrients (i.e., weathering of parent rocks and atmospheric deposition) are generally insignificant for the nutrient demand of vegetation and microorganisms. Secondly, almost all microorganisms and plant roots are not permeable to high molecular weight organic matter (Geller, 1985), with which most of the essential nutrients are combined (e.g., cellulose, protein, urea, or phospholipid) (Paul and Clark, 1996). Therefore, extracellular hydrolysis of organic matter is a crucial step prior to nutrient uptake (Chróst, 1991). Finally, the extracellular hydrolysis rate is much lower than the rate of uptake of low molecular weight substrates, which implies the importance of extracellular hydrolysis as a rate-limiting step in nutrient cycles (Hoppe *et al*., 1988).

However, relatively little information is available on characteristics and roles of soil enzymes in wetland ecosystems with few exceptions (Herlihy, 1972; Oshrain and Wiebe, 1979; Speir and Ross, 1990; Vetanovetz and Peterson, 1992; Ivleva *et al*., 1994; Pind *et al*., 1994; Freeman *et al*., 1995; Freeman *et al*., 1996; Freeman *et al*., 1997; Kang and Freeman, 1997; McLatchey and Reddy, 1998; Kang and Freeman, 1999; Shackle *et al*., 2000; Williams *et al*., 2000; Wright and Reddy, 2001; Ravit *et al*., 2003). In contrast, a brief literature search on enzymic study of upland soils (agricultural or forest soils) or sediments reveals more than 100 papers for each system over the same period of time (Science Citation Index, 2005).

The present study aims to fill a gap in our knowledge of this area by determining the significance in wetland biogeochemistry, particularly trace gas emission and dissolved organic carbon (DOC). Specific aims of the study were 1) to compare the activities of 4 enzymes (β-glucosidase, β-xylosidase, cellobiohydrolase and N-acetyl-glucosaminidase) in different types of wetlands and determine possible controlling variables, and 2) to investigate the relationship between the soil enzyme activities and trace gas flux or DOC. We hypothesised that the enzyme activities would be highest in the swamp followed by a fen and a bog. It was also anticipated that trace gas emission (CO_2 and N_2O) and DOC content would closely be related to the enzyme activities.

MATERIALS AND METHODS

1. Site description and physico-chemical variables

The study site was an acidic bog in Migneint (UK grid reference SH 805 458), a calcareous fen in Gors Goch (UK grid reference SH 497 826), and a forest swamp in Cwm-y-Glo (UK grid reference SH 554 626), north Wales, U.K. The bog site is near Ffestiniog in north Wales and covered with *Sphagnum* spp. The fen site is located on Anglesey island, north Wales, and dominated by *Juncus* spp., *Festuca* spp., *Cladium* spp., and *Carex* spp. The swamp site is dominated with *Alnus* spp. and *Salix* spp., which is adjacent to Afon Rhythallt stream. The hydrology of the site is strongly affected by the stream, and rapid change of water Table height was observed. Basic characteristics of the sites are presented in Table 1.

2. Field sampling procedure and measurement

pH and temperature at 10 cm were measured using a pH electrode and a digital thermometer, respectively.

Surface living vegetation was removed and peat was collected to the 10 cm depth from the surface. Approximately 6,000 cm^3 of peat was taken using a knife and a shovel. All the samples were maintained at 4°C until analysis. Five replicate samples collected from each site and all soil enzymes were analysed within a week of the sampling occasion. The number of replicates we employed in this study was to complete an enzyme analysis within 24 hours, but we believe this minimal number would not interfere with an effective statistical comparison.

The gas samples were collected using a closed-chamber technique (Freeman *et al*., 1994). The chambers (4.5 litre) were constructed from polyethylene bottles (Fisons Scientific Apparatus) with the bases removed. These were inserted to a depth of 2 cm and each chamber was sealed with a urea cap containing a septum. After a one-hour collection in the headspace, gas samples were withdrawn into gas-tight syringes (SGE). The increases in the gas concentration over the period were related to background concentrations to give an estimate of flux. A preliminary study showed that the gas accumulation exhibited

linearity up to 2 hours of collection. Five samples were taken from beside each of the water samplers.

Ten mL of water samples were withdrawn using syringe and water sampler (Freeman *et al*., 1994) placed at 10 cm depth. The water sampler is composed of a tube (3 mm in diameter) connected to the tip of a 10 mL syringe packed with glass wool. Water samples were filtered with 0.2 μm filter on the day of the sampling, and kept at 2°C until chemical analysis. Five replicates were taken at each sampling occasion.

3. Laboratory analysis

β-glucosidase, β-xylosidase, cellobiohydrolase, and N-acetylglucosaminidase activities were measured using MUF (methylumbelliferyl) compounds as a model substrate (Freeman *et al*., 1995). In brief, 1 cm^3 of peat was added with 7 mL of 400 μM MUF (methylumbelliferyl) substrate solutions and homogenized in a stomacher (Seward Colworth model 400). The incubation was terminated after 60 minutes. Reaction temperature was maintained at field temperature using either an incubator or water bath with dip cooler. No buffer or pH control was applied because we aimed to determine the natural rates of activities rather then potential activities.

The gas samples were analysed by injecting into an Ai Cambridge model 92 Gas Chromatograph equipped with a Porapak QS column, flame ionisation detector and electron capture detector. The carrier gas was N_2 at a flow rate of 70 cm^3 min^{-1} for N_2O, and 13 cm^3 min^{-1} for CO_2.

Dissolved Organic Carbon (DOC) was determined by the difference between total carbon (TC) and inorganic carbon (IC) in the samples. TC and IC were measured with a TOC meter (Simadzu TOC-500). Phenolic contents were assayed using Folin-Ciocalteau phenol reagent (Box, 1983). Available carbon was defined as the difference between DOC and phenolics, since phenolic materials are a representative recalcitrant fraction of DOC in peatlands.

4. Statistical analysis

A correlation analysis was applied to the data sets of each wetland separately, employing Minitab ver. 11.13. Then, all the data combined and the same correlation analysis was employed. When data were not normally distributed, spearman rank test was used. Since 4 enzyme activities exhibited a significant correlation each other, a mean enzyme activity was calculated by averaging the activities. To prevent differential scalar weighting of enzyme variables, each datum was divided by the mean of the enzyme activity of a kind (Sinsabaugh and Moorhead, 1994). Then, four of such values in each site were averaged (i.e., summed up and then divided by four). A linear regression between the mean enzyme activity and available DOC or trace gas emission was conducted.

RESULTS

1. Enzyme activities

For the β-glucosidase activity, the fen and the swamp sites exhibited similar seasonal variations and magnitude. The activity showed a small peak in early spring and a larger peak over later summer and autumn. The bog site exhibited the least activity and variation. Unlike the other two sites, no decline in activity in May was observed (Fig. 1-a). A similar seasonal trend for cellobiohydrolase activity as β-glucosidase was found in all sites, although the activity was about 30% of the β-glucosidase activity (Fig. 1-a and b). In the swamp and the bog sites, β-xylosidase activity exhibited similar seasonal patterns to β-glucosidase. However, the variation of β-xylosidase activity in the fen was different from the other two enzymes; the activity in early spring was as high as in autumn (Fig. 1-c). Overall, the activity could be ranked as swamp=fen>bog in terms of sites, and autumn>early spring >summer=winter in terms of seasonal variations. The swamp site had the higher N-acetylglucosaminidase than the other sites. The activity was highest over autumn in the swamp, whilst the seasonal variation was less dramatic in the other two sites. The fen site showed a similar trend, namely the highest activity in September. It seems that seasonal variation of N-acetylglucosaminidase activities follows the similar pattern of the three carbon-related enzymes (Fig. 1-d).

2. Gas emissions

The bog site was a sink for CO_2 except in January, whilst up to 6,900 mg m^{-2} day^{-1} (August)

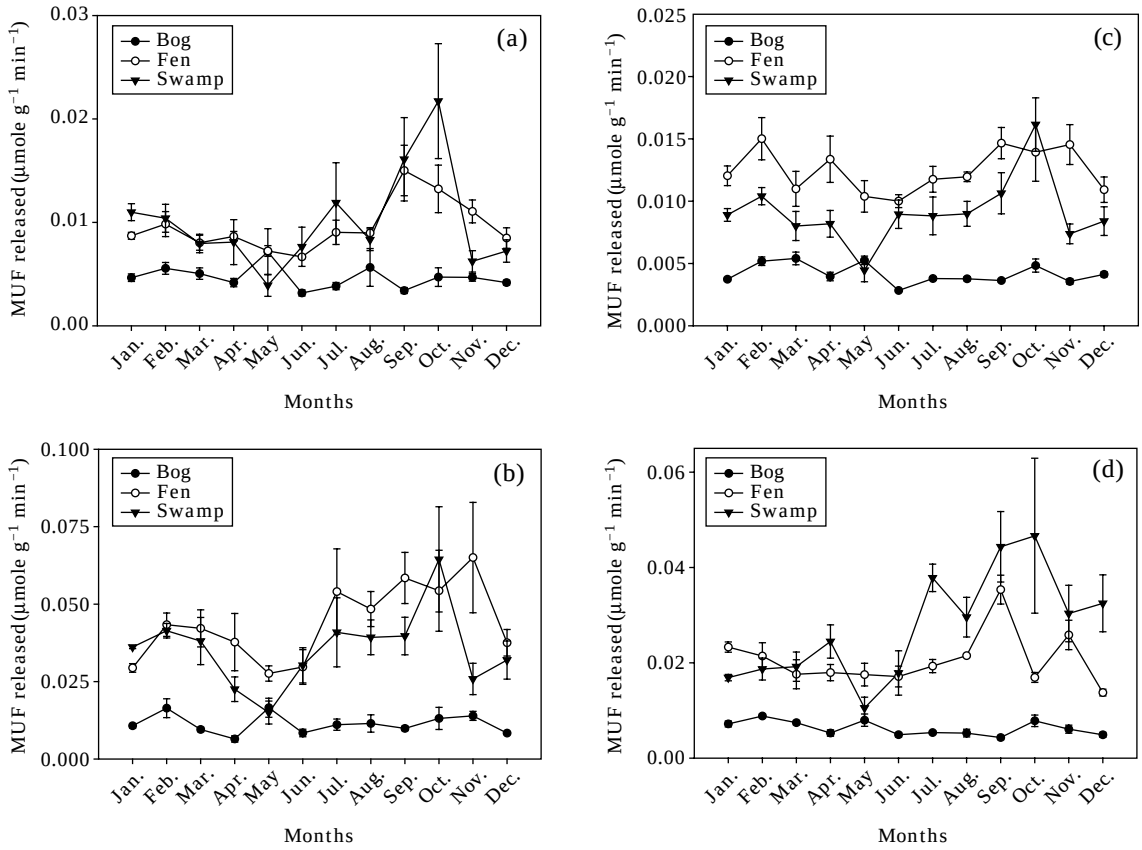

Fig. 1. Variations of β-glucosidase (a), cellobiohydrolase (b), β-xylosidase (c), and N-acetylglucosaminidase (d) in the bog, the fen, and the swamp.

Table 1. The ranges of physico-chemical characteristics and trace gas emissions from the wetlands.

		Bog	Fen	Swamp
Environmental conditions	Soil temperature		2.0-14.5	
	Water table level	−6.5-11	−9-15	−16-45
	Soil organic matter	98.9	87.9	62.3
Water chemistry	DOC (mg L^{-1})	25.5-45.4	29.2-71.4	13.5-87.6
	Phenolics (mg L^{-1})	13.3-48.1	7.6-29.5	4.9-30.8
	Available C (mg L^{-1})	0.0-24.2	11.8-53.4	4.2-66.6
	pH	3.6-4.3	5.7-6.2	5.3-5.7
Gas emissions	CO_2 (mg m^{-2} day^{-1})	−2165-1146	−824-4465	1416-8943
	N_2O (ng m^{-2} day^{-1})	−456-172	−60-322	−20-317

of emission was observed in the fen site. The ranges of CO_2 flux were −1,588-1,146, 824-3,692, and 1,416-8,943 mg m^{-2} day^{-1} for the bog, the fen, and the swamp, respectively (Table 1). In con-trast, N_2O flux varied −0.305-0.127, −0.060-0.323, and −0.020-0.317 mg m^{-2} day^{-1} for the bog, the fen, and the swamp, respectively (Table 1).

3. DOC, phenolics and available carbon

The concentration of dissolved organic carbon in porewater varied 25.5-45.4 (bog), 29.2-71.4 (fen), and 13.5-87.6 (swamp) mg L^{-1} (Table 1). The phenolic concentrations were 13.3-48.1 (bog), 7.6-29.5 (fen), and 4.9-30.8 (swamp) mg L^{-1}

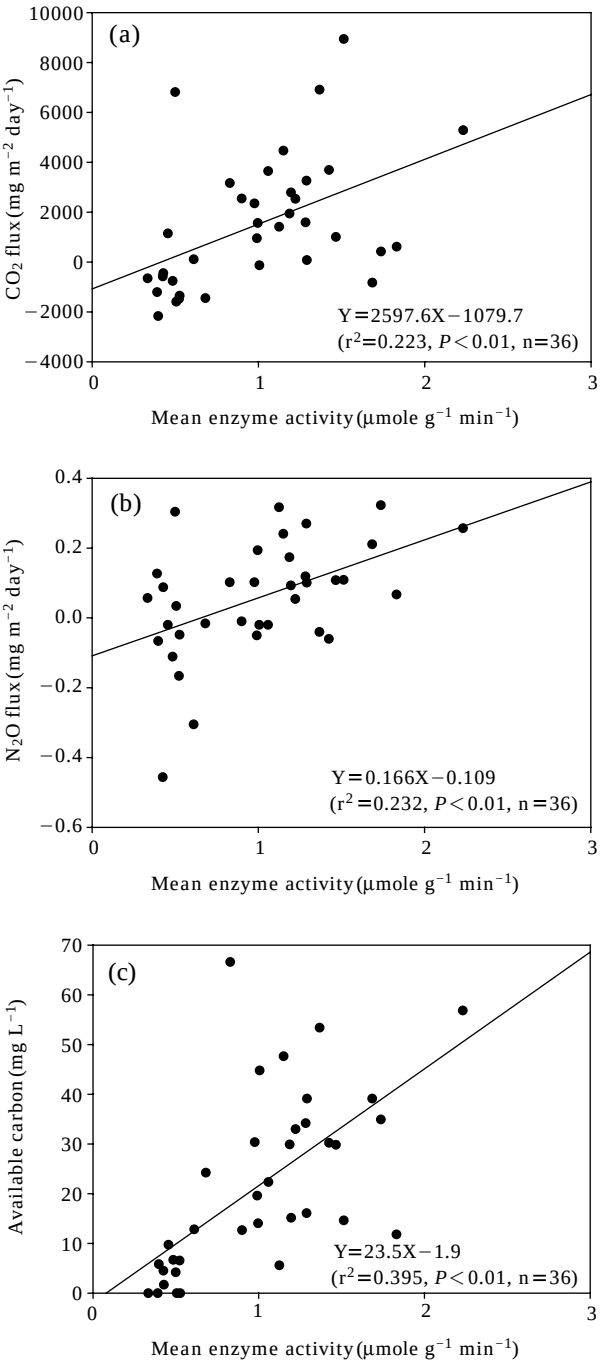

Fig. 2. Regression analysis between the mean enzyme activity and (a) CO_2 flux, (b) N_2O flux, and (c) available carbon.

(Table 1). The differences between DOC concentration and phenolics were defined as available carbon in the present study, of which variations are presented in the Table 1. The ranges were 0.0-24.2 (bog), 11.8-53.4 (fen), and 4.2-66.6 (swamp) mg L^{-1}.

Table 2. Correlation coefficients between enzyme activities and trace gas emission or available carbon. All values are significant at $P<0.01$ (n=36). The analysis was conducted with combined data from three wetlands.

	β-glucosi-dase	Cellobiohy-drolase	β-xylosi-dase	N-acetylglu-cosamini-dase
CO_2	0.457	0.532	0.404	0.619
N_2O	0.491	0.475	0.456	0.454
Available C	0.615	0.456	0.680	0.565

4. Statistical analysis

A simple correlation analysis between enzyme activities and other variables (gas emission, DOC, phenolics, available carbon, water level, and temperature) revealed almost no significant relationship. One exception was negative correlations between phenolic content and β-xylosidase or N-acetylglucosaminidase activities in the bog. However, when all data from three wetlands are combined and the same approach was applied, the enzyme activities exhibited positive correlations with trace gas emission and available carbon content (Table 2).

The results of a simple linear regression are presented in Figure 2. Overall, the mean enzyme activities explained over 20% of the variations in trace gas emission, and around 40% of those in available carbon.

DISCUSSION

1. Variations of soil enzyme activities

Comparing the three sites, the bog site exhibited the lowest enzyme activities in general. This result confirms the low decomposition rates in bogs determined by a litterbag method in many studies (e.g., Reader and Stewart, 1972). Phenolics content seems to inhibit the enzyme activities in the bog, as negative correlations between the phenolic content and β-xylosidase or N-acetylglucosaminidase activities were observed ($r=-0.603$ and $r=-0.616$, both are significant at $P<0.05$). It is feasible that the amount of enzymes are minimal in the bog due to low microbial proliferation (Brock and Bregman, 1989), and

that the enzymes are strongly inhibited by low pH and phenolics (Wetzel, 1992). It is also suggested that growth and death of *Sphagnum* did not affect the enzyme activities significantly. In contrast, litterfall production in the swamp site was concurrent with the higher activities of β-glucosidase, β-xylosidase, cellobiohydrolase, and N-acetylglucosaminidase, which suggests the importance of quality and quantity of substrates in regulating these enzymes.

The fen and the swamp sites generally showed similar magnitude of β-glucosidase and cellobiohydrolase activities. But, the higher β-xylosidase activity was found in the fen than the swamp site. This might be related to the quality of substrate in each site. Both β-glucosidase and cellobiohydrolase are involved in cellulose decomposition, whilst xylosidase plays a key role in xylan decomposition (Eriksson *et al*., 1990). Therefore, the activities might be influenced by characteristics and quality of substrates. It has been known that lignin composition of an angiosperm (e.g., *Alnus*) is different from non-woody vascular plant (e.g., *Juncus*) (Clifford *et al*., 1995). It is speculated that these compositional differences induced different patterns of β-glucosidase and β-xylosidase between the fen and the swamp.

Although Sinsabaugh *et al*. (1993) have measured N-acetylglucosaminidase activity in relation to nitrogen dynamics, our results suggest that the enzyme might be more closely related to carbon cycling than nitrogen cycling. Each site showed higher correlations between N-acetylglucosaminidase and three C-related enzymes than phosphatase or arylsulphatase (Kang and Freeman, 1999). Further, in the swamp site, N-acetylglucosaminidase increased concurrently with the litter production and increases with other three C-related enzymes. However, phosphatase and arylsulphatase did not show this pattern (Kang and Freeman, 1999). Further, we could not find any significant correlations between N-acetylglucosaminidase activity and inorganic nitrogen (NO_3^- or NH_4^+) in pore the water (data not shown).

It is interesting to note that these four enzymes did not show significant correlations with temperature, water table height or pH, whilst two other enzymes (phosphatase and arylsulphatase) exhibited significant correlations in the same sites (Kang and Freeman, 1999). Freeman *et al*. (1998) have also observed that maximum activities of three carbon related enzymes (β-glucosidase, β-xylosidase and esterase) were not concurrent with maximum temperature in a gully-mire. One possible explanation for the results could be found in the substrate quality for the enzyme. Since these enzymes are involved in degradation of plant debris, the input and characteristics of the substrates might be the more important controlling factors as opposed to physico-chemical factors such as temperature, pH, and water table height. For example, in autumn when plants become senescent, the substrate quality and quantity may be optimal for the proliferation of some microorganisms including cellulose degrading fungi or bacteria (Eriksson *et al*., 1990), which in turn yield high enzyme activities. It has been observed that the early stage of decay process of new plant debris is characterized by the rapid disappearance of cellulose and maximum rates of cellulose activity, followed by eventual declining of the enzyme activity (Melillo *et al*., 1989). Therefore, the dominant effects of quality and quantity of substrates in autumn may offset the other controlling variables. When the autumn data were omitted in the correlation analysis, for example, a significant negative correlation ($r=-0.804$, $P<0.01$, $n=10$) between β-glucosidase and water table level was found in the swamp. Detailed chemical fractionation of soil (e.g., humic/fulvic ratio, lignin/cellulose content etc.) would be needed to confirm whether substrate quality affects these enzyme activities.

2. Enzyme activities and gas flux

Trace gas fluxes such as CO_2 or N_2O from wetlands result from complicated reactions. For example, CO_2 could be released by soil microbial respiration, root respiration, or oxidation of CH_4 (Glenn *et al*., 1993). Likewise, N_2O could be produced by denitrification as well as nitrification (Rudaz *et al*., 1991). This would be the reason for the poor correlations between the enzyme activities and trace gas fluxes in each site. However, those fluxes may be driven by a single basic reaction of organic carbon mineralization at a larger scale, which is supported by significant correlations between all enzyme activities and trace gas flux when the data from three wetlands were combined. This finding supports the idea that enzyme activities may play a key role in trace gas flux in wetlands (Freeman *et al*., 1997; Kang *et*

al., 1998).

3. Enzyme activities and DOC dynamics

Dissolved organic carbon (DOC) has been widely used to assess carbon availability in wetlands (Bijay-Singh *et al*., 1988; Swerts *et al*., 1996). This approach might be of limited value in peatlands for several reasons. First, the DOC pool could easily be changed by decomposition and uptake by microorganisms. It has been reported that the generation of readily utilisable products (e.g., monomeric carbon compounds) is slower than its assimilation by microorganisms in aquatic ecosystems (Sinsabaugh *et al*., 1997). Secondly, it has been observed that recalcitrant organic matter (e.g., phenolics) represent a large proportion of the DOC pool in wetlands, and these have been reported to be inhibitory to microorganisms (Wetzel, 1992; Freeman *et al*., 2001). Thus, even under a high concentration of DOC, denitrification or soil respiration could be limited by carbon availability. As such, analysis of carbon-mineralising enzymes would be of great importance to understand peatland biogeochemistry in particular, since peat often contains high organic matter content and DOC concentrations in the pore water while actual carbon availability is low. Our findings-significant correlations between carbon-mineralising enzyme activities and available carbon (i.e., difference between DOC and phenolics)-support this idea.

4. Conclusion

The present study has suggested that extracellular enzyme activities involved in carbon mineralization are closely related to peatland biogeochemistry including DOC dynamics and trace gas emission. Our data suggest that no single variable exerts an overriding influence over the relationship between enzyme activity and the wider biogeochemistry, although it seems significant that available carbon and trace gas emission shows a high degree of correlation with all enzymes as well as mean enzyme activities. Further studies will need to focus on the influence of carbon quality as a regulator of this critical stage in the peatland carbon cycle. In addition, enzymatic couplings should be tested with other temperate wetlands such as marshes and riparian ecosystems to generalise the hypothesis.

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＜국문적요＞

북구 이탄습지의 생지화학적 반응에 있어서 체외효소의 중요성-미량기체 발생량 및 용존유기탄소 동태와의 연관성에 대하여

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세 종류의 이탄습지(bog, fen, swamp)에서 탄수유기물 분해에 관여하는 일군의 체외 효소 활성도, 미량 기체(CO_2와 N_2O), DOC 변화 등을 12개월에 걸쳐 측정하였다. β-glucosidase, cellobiohydrolase, β-xylosidase, N-acetylglucosaminidase 등이 각각 0.008-0.066 μmole g^{-1} min^{-1}, 0.003-0.021 μmole g^{-1} min^{-1}, 0.003-0.016 μmole g^{-1} min^{-1}, 0.004-0.047 μmole g^{-1} min^{-1} 범위의 활성도를 보였다. 전반적으로 swamp에서의 활성도가 가장 높았고, fen과 bog의 순서로 나타났다. 세 종류 습지의 자료를 모두 합쳤을 때, 효소의 활성도는 미량 기체의 발생량이나 가용한 탄소의 양과 유의한 양의 상관관계를 보였다. 또한, 4가지 효소 활성도의 평균값은 미량기체와 가용한 탄소량의 변화에 있어서 20-40% 정도의 변이를 설명할 수 있었다. 이 결과로 비추어, 유기탄소 무기화에 관여하는 효소는 북구 이탄습지에서 미량기체 발생과 DOC 동태에 중요한 역할을 하는 것으로 사료된다.