Front. Earth Sci. China 2010, 4(4): 463–470
DOI 10.1007/s11707-010-0140-3

RESEARCH ARTICLE

Impacts of hydrological conditions on enzyme activities and phenolic concentrations in peatland soil: An experimental simulation

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Abstract Impacts of hydrological conditions on peatland soil enzyme activities and phenolic concentrations were investigated using peat cores from two typical peatlands, the forest swamp and the marsh in North-east China, under water level manipulation in the laboratory. The results indicated varied impacts of dry and waterlogged conditions on soil enzyme activities, depending on the confounding factors including the peatland types and the variation frequency of hydrological conditions. Carbon-related enzyme activities, phenol oxidase and β-glucosidase, were much higher in the marsh than in the forest swamp. On the contrary, phenolic concentration was measured to be much higher in the latter. Soil enzyme activities and phenolic concentrations were found to vary between the two peatlands, much more remarkably than within the individual peatlands caused by the changes in the water level. The negative relationship or inconspicuous correlation between phenolics and phenol oxidase was found to vary with specific soil conditions. These results implied that the enzyme activities and phenolic concentrations might be related to the developmental stages or the types of wetlands more than to hydrological conditions.

Keywords hydrological condition, enzyme, phenolics, peatlands, North-east China

1 Introduction

Peatlands in the northern hemisphere represent about one-third of the global soil carbon sink, but cover only 1% of the global terrestrial area (Gorham, 1991). Besides gaseous exchange with the atmosphere, peatland ecosystems also exchange dissolved organic carbon (DOC) and other materials with the aquatic systems (Pind et al., 1994; Tao, 1998; Freeman et al., 2004). The release of carbon from peatlands is often considered to be largely controlled by water table depth. Particularly, global warming has been expected to cause water table levels to drop substantially, causing more peat to be dry and decomposed. However, the frequency of extreme climate events including both over-drying and extreme precipitation was also predicted to go up in some regions with global climate change (Arnell, 1992; Freeman et al., 1998). There have been increasing evidences that dry-rewet events can greatly influence the biogeochemical processes in peatlands, in which the response of carbon cycling to global climate change might change the balance between peatlands and the atmosphere or aquatic systems (Evans et al., 2005; Shackle et al., 2000).

Enzymes, the important indicators of microbial metabolism, are of great importance in peatland systems (Freeman et al., 1995). β-glucosidase and phosphatase have been widely studied due to their relation with soil carbon and phosphorus cycles (Kang et al., 2005). Phenol oxidase has been found to be one of the scarce enzymes capable of decomposing phenolic compounds, and the activity of phenol oxidase is greatly affected by water level fluctuation (Freeman et al., 2001b). Phenolic compounds, the important part of DOC, were thought to be recalcitrant for decomposition, and could inhibit hydrolase's activities. These natural chemicals might cause great environmental problems if they flow into the water system (Pind et al., 1994; Freeman et al., 2001a). In the context of global climate change, the spatial and temporal variations of precipitation have played a great influence on biogeochemical processes in peatlands, including enzyme

Received March 12, 2010; accepted June 18, 2010

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activities, phenolic concentration and so on. Previous studies indicated that drainage promoted enzyme activities, accelerated organic matter decomposition and lowered phenolic abundance (Freeman et al., 2001b), while the waterlogged condition inhibited enzyme activities and constrained the decomposition (Kang and Freeman, 1999). However, some researches also found increasing enzyme activities in waterlogged conditions (Laiho et al., 2004), especially during the fluctuation between dry and rewet conditions (Williams et al., 2000). On the other hand, the long-term or short-term change in the water level will impact organisms, which in turn could influence enzyme activities and phenolic concentrations indirectly (Jaatinen et al., 2007), and change the carbon release via the exporting of CO_2/CH_4 to the atmosphere or DOC to aquatic systems (Hudson et al., 2003; Freeman et al., 2001b). To date, studies on the effects of dry-rewet conditions on peatlands are still limited, and even controversial in the conclusions. For example, a strong increase in both microbial activity and C/N mineralization was found to occur during the manipulation of dry-rewet conditions (Birth, 1958; Fierer et al., 2003), but absent in other investigations (Degen and Sparling, 1995; Reiche et al., 2009).

Extreme climate events such as prolonged drought and extremely heavy precipitation in North-east China have been confirmed to occur more frequently in recent years (Sun et al., 2007; Zhang et al., 2008). The variation trend of the climate would exert great impacts on peatlands in North-east China. Most of the studies focused on the fluxes of greenhouse gases (CH_4, CO_2 and N_2O) (Zhang et al., 2007; Mu et al., 2009), DOC concentrations (Tao et al., 1997) and enzyme activities (Wan et al., 2009) in the marsh wetland. However, few were conducted concerning dry and waterlogged impacts on phenolics and enzymes in peatlands in North-east China, and our understanding of the impacts of dry-rewet events on the enzyme activities related to soil organic matter decomposition and phenolic concentrations in the peatlands is still very limited. The major objectives of this study were to investigate the impacts of dry and waterlogged conditions on several enzyme activities and phenolic concentrations on the basis of the manipulation of the water level, and to further understand the factors regulating enzyme activities and phenolic concentrations during dry-rewet events.

2 Materials and methods

2.1 Study sites and sampling

Core samples were collected in two typical peatlands (forest swamp and marsh) in Xiaoxing'an Mountains, Heilongjiang province in North-east China. The forest swamp is located in the perennial waterlogged wetland, colonized by several wetland plants including *Larix gmelini*, *Vaccinium uliginosum* and *Sphagnum*. The sampling site is dominated by *Sphagnum* species in the forest swamp. Marsh peatland dominated by *Carex schmidtii* is located in the seasonal waterlogged site.

Nine intact cores (including surface vegetation, 20 cm depth each) were recovered by using PVC pipes (10 cm in diameter and 30 cm long) in the two peatlands, forest swamp (48°19'50.87″ N, 130°34'55.11″E) and marsh (48°21'23.48″ N, 129°10'43.85″ E) in August, 2008. The marsh was dry and the forest swamp was under the lowest water level. The peat soil temperature was in situ measured by a thermometer. The pipes filled with peat samples were sealed and immediately transferred to the laboratory for incubation.

2.2 Peat core incubation

Nine cores for each peatland were incubated under three water level conditions, denoted as high (0±1 cm), medium (−10±1 cm) and low (−18±1 cm) levels, respectively. Corresponding field temperature (20°C) was maintained in the incubation chamber. The cores were incubated for approximately three weeks, during which water was added to ensure the water level remained in the appointed stations.

2.3 Instrumental analysis

At the end of the incubation, the cores were sampled in different horizons (5 cm interval for β-glucosidase and acid phosphatase activity and 3 cm interval for other analyses). Larger roots and stones were removed by hand, and the soils were gently mixed. Phenol oxidase activity, water-soluble phenolic concentration, and organic matter content (OM) were measured according to Xiang et al. (2009a). The pH values were measured using the conventional method of soil chemical analysis. The β-glucosidase and acid phosphatase activities were analyzed according to He et al. (2009). DOC concentrations were determined according to Lin and Tao (1996). Anions (NO^{3-}, SO_4^{2-}) were measured by IC (IC1010). Statistical analyses were conducted using Excel 2003.

3 Results and discussion

3.1 Impacts of dry and waterlogged conditions on enzyme activities

In the forest swamp, phenol oxidase and β-glucosidase activities displayed obvious increases under the dry condition, especially for the low water level condition (Table 1; Figs. 1(a),(b)). As the important indices of peatlands nutrient cycle and the factors on enzyme

Table 1 General features of the forest swamp and the marsh under different water level conditions

	Forest swamp			Marsh		
	H	M	L	H	M	L
PO/(nmol·diqc·g^{-1}·min^{-1})	38.94	45.18	49.64	356.96	411.51	271.36
β-glu/(μg p-Nitrophenol·g^{-1}·h^{-1})	58.7	73.15	236.11	607.55	324.99	435.2
A-pho/(μg p-Nitrophenol·g^{-1}·h^{-1})	502.71	1024.5	994.80	551.76	403.79	979.31
PC/(μg·g^{-1})	191.99	227.52	167.00	48.12	14.69	9.26
DOC/(μg·g^{-1})	1225.26	1381.98	1320.10	1861.37	2055.27	2075.86
PC/DOC/%	15.8	16.4	12.5	2.4	0.7	0.5
NO_3^- /(μg·g^{-1})	0.087	0.12	0.086	0.050	0.051	0.039
SO_4^{2-} /(μg·g^{-1})	0.25	0.36	0.48	0.32	0.3	0.26
pH	6.9	6.3	5.5	6.3	6.2	5.9

Note: H: higher water level = 0±1 cm; M: medium water level = 10±1 cm; L: lower water level = 18±1 cm; PO: Phenol oxidase activity; β-glu:β-glucosidase activity; A-pho: acid phosphatase activity; PC: water soluble phenolics concentration; DOC: dissolved organic carbon; PC/DOC: ratio of PC to DOC; diqc: 2,3-dihydroindole-5,6-quinone-2-carboxylate; g^{-1}: g^{-1} dry organic matter

activities, anions (NO_3^- and SO_4^{2-}) and dissolved organic carbon (DOC) contents also increased when the water level lowered, except for a small decrease in NO_3^- content under the low water level condition (Table 1). The increases in carbon-related enzyme (phenol oxidase and β-glucosidase) activities with the lowered water level indicated the rapid increase in microbial activity and organic matter decomposition, consistent with the conventional knowledge that the water level drawdown increased oxygen supplement and subsequently accelerated C/N mineralization rate (Freeman et al., 2001a,b; Fierer et al., 2003) (Table 1). However, it was found that long-term drought could inhibit microbe activities and carbon loss due to the moisture pressure (Reiche et al., 2009), the deficient input of susceptible fresh litter, and the accumulation of resistant old organic matter (Liski et al., 1999). Here, abrupt increase of β-glucosidase activity under the low water level condition indicated an increasing loss of carbon from the forest swamp.

In the marsh, notable effects on enzyme activities could also be found. However, unlike the dry condition in the forest swamp, the dry-rewet manipulation of the marsh peat in this study brought diverse changes on enzyme activities and other geochemical parameters, such as a notable increase in phenol oxidase activities in the low and medium water levels (Table 1; Fig. 1(d)), but a little decrease in β-glucosidase activity (Table 1; Fig. 1(e)). It is noteworthy that both phenol oxidase and β-glucosidase activities in the upper surface peat are much greater under the high than under the low water level condition. However, Fenner et al. (2005a) found a significant suppression in phenol oxidase activity and a slight increase in β-glucosidase activity under the increased rainfall condition, suggesting that the waterlogged condition inhibited microbe activities and diversity. These differences might arise from the different time duration of dry and wet conditions, i.e., several weeks in our study but a year of manipulation in Fenner et al. (2005a). Fierer and Schimel (2002) pointed out that the effects of varying frequency in dry and wet conditions were different on the transformation of soil carbon and nitrogen. Accordingly, the results of our study might result from the ‘priming effects’ of short-term waterlogged condition after long-term drought (Williams et al., 2000; Xiang and Freeman, 2008). The increased concentrations of available NO_3^- and SO_4^{2-} under the high water level conditions also induced the enhanced microbial activity and the nutrient consumption (Table1).

The fluctuation of phenol oxidase activities in marsh might be remarkably regulated by both oxygen and moisture. Phenol oxidase activity may display a ‘moisture threshold’ in marsh, above which the low oxygenation inhibited the activity and below which the limited moisture played a dominant inhibition (Toberman et al., 2008). The highest activity found in the mid water level was in line with this viewpoint (Fig. 1(e)). Li and Vitt (1995) found that the dominance of *Sphagnum* species also showed the presence of an optimal moisture level. However, this ‘moisture threshold’ was not found in the forest swamp, even though it was dominated by *Sphagnum* species (Fig. 1(a)). This may confirm the conclusion of Kang et al. (2005) that other factors might become effective only when the nutrient limitation was eliminated.

At the peat core surface, β-glucosidase activity showed an abrupt increase under the low water level condition in the forest swamp but under the high water level condition in the marsh. Slim differences were observed between the high and the medium water level condition in the forest swamp or between the medium and the low water level condition in the marsh. These results indicated that β-glucosidase was susceptible to the changes in the extremely dry and waterlogged conditions of the peatlands.

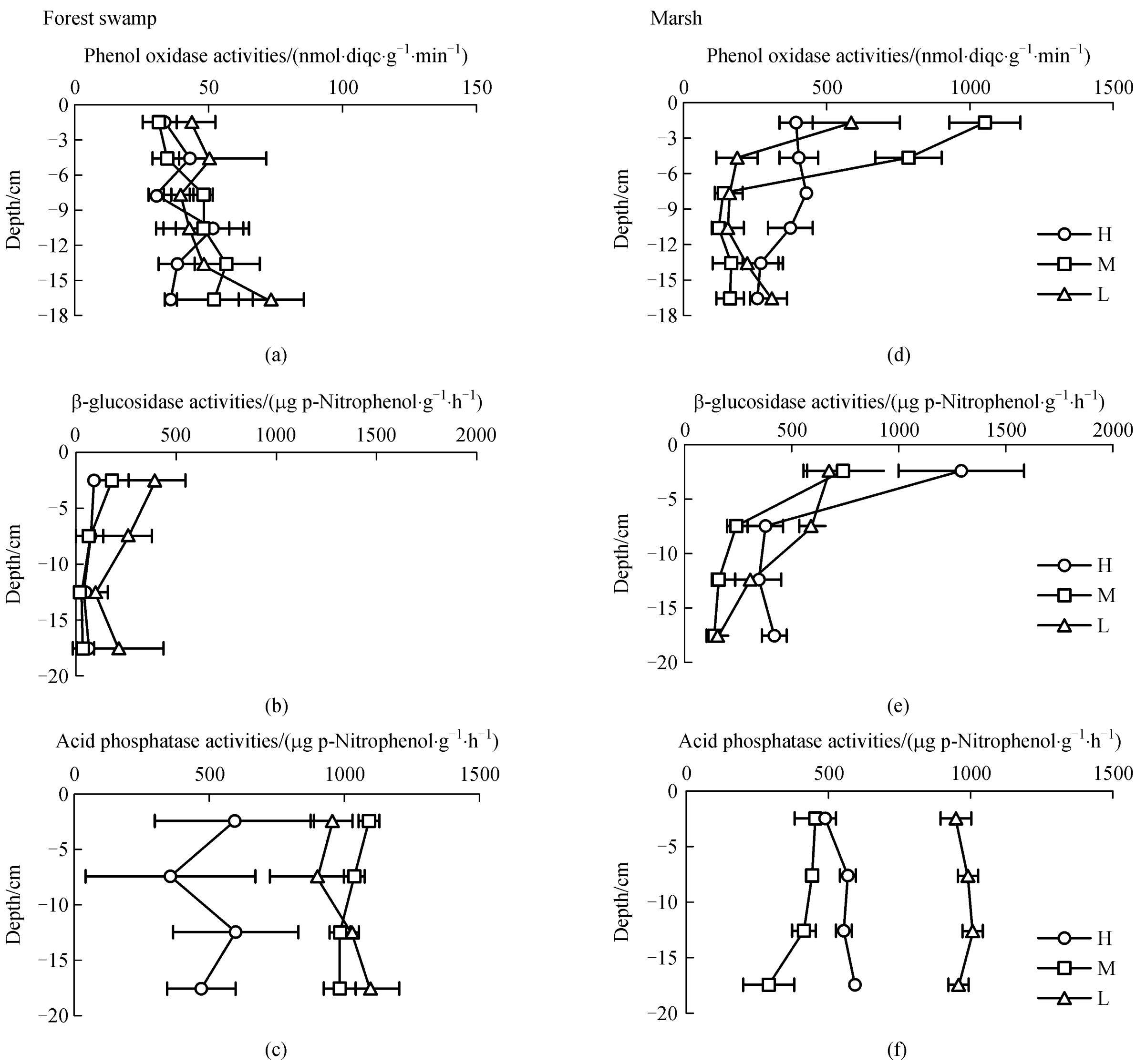

Fig. 1 Impacts of dry and waterlogged conditions on the activities of (a, d) phenol oxidase, (b, e) β-glucosidase, and (c, f) acid phosphatase in the forest swamp (left) and in the marsh (right). H: high water level = 0±1 cm; M: medium water level = 10±1 cm; L: lower water level = 18±1 cm

Acid phosphatase activities decreased in varying degrees in waterlogged peatlands, particularly in the marsh (Fig. 1(f)). However, only a small difference could be found between the medium and the high water level condition in the marsh. The dry condition in the forest swamp brought an increase in acid phosphatase activity, with a small difference being observed between the medium and the low water level condition. It appears that the water level change, if over a certain extent, will not always bring a notable change in the activity of a specific enzyme (Laiho, 2006). The high activity of acid phosphatase under the low water level condition in the two peatlands was consistent with the property of phosphorus, which is immobilized especially in dry conditions. As a result, microorganisms and foliages had to exudate much more phosphatase to get enough phosphorus.

Soil enzyme activities related to carbon and phosphorus biogeochemical processes were observed to show different responses to the dry and wet events in this study. For example, only extremely dry and waterlogged conditions in the peatlands could bring an abrupt increase in β-glucosidase activity, while slightly dry and waterlogged conditions had a great impact on acid phosphatase activity. Differing from β-glucosidase and phosphatase, phenol oxidase showed peak activity under the moderately waterlogged condition (the mid water level condition) in the marsh, but showed only a small change in the forest swamp. Therefore, different dry and waterlogged conditions brought diverse impacts on different enzyme activities. In addition, the notable changes in β-glucosidase and phenol oxidase activities at the marsh surface in comparison with the forest swamp suggested that the peatland types and depth horizons have a great impact on β-glucosidase and phenol oxidase activities.

3.2 Impacts of dry and waterlogged condition on phenolic concentration

In the marsh, the water soluble phenolic concentrations were found to obviously increase in the waterlogged condition, in particular under the high water level condition (Table 1, Fig. 2(b)). This appears to be in line with the previous hypothesis that a poor oxygen supply along with the elevated water level could inhibit hydrolase's activity and enhance phenolic accumulation (Freeman et al., 2001a). However, the higher β-glucosidase activities, as well as the consumption of DOC, appear not to support this point. Therefore, this may be due to the release of part soil organic carbon stored during droughts (Toberman et al., 2008; Xiang and Freeman, 2008b). On the other hand, the absolute or the relative concentration (phenolics/DOC ratio) of phenolics was much less in the marsh than in the forest swamp or in some other studies (Freeman et al. 2001b; Toberman et al., 2008). As He et al. (2009) have already pointed out that the dominant effect on acid phosphatase activity was different in the forest swamp, we presumed that the inhibiting effects of phenolics on enzymes might be offset by some other factors in the marsh, such as the stimulation of elevated CO_2 concentration (Kang et al., 2005).

Compared with those in the marsh wetlands, droughts in the forest swamp created fluctuated phenolic concentrations, with the peak values at the medium water level condition. In addition, a decrease in phenolics/DOC ratio was found under the driest condition, implying the decrease of recalcitrant substrate (Fig. 2(b) (Table 1). However, great care should be taken when predicting that drying would accelerate carbon release from the forest swamp peat to aquatic systems because of the lower water flow under drought conditions (Xiang and Freeman, 2009b).

3.3 Comparison of the impacts on enzyme activities and phenolic concentration between the forest swamp and the marsh

Remarkable differences of carbon-related enzyme (β-glucosidase and phenol oxidase) activities and phenolic concentrations were found between the two contrasting peatlands. Water soluble phenolic concentration was significantly higher in the forest swamp than in the marsh, while β-glucosidase and phenol oxidase activities were dramatically lower in the latter (Table 1; Figs. 1(a)–(d)). Other geochemical parameters also showed significant variations. The concentrations of DOC, organic matter (OM) and anions (NO_3^-, SO_4^{2-}) were significantly greater in the marsh than in the forest swamp (Table 1). These differences between the marsh and the forest swamp might be mainly attributed to the differences in soil types, vegetation, or nutrient conditions. In the *Sphagnum*-dominated forest swamp, the long-term waterlogged condition, as well as the decay-resistance of *Sphagnum*, contributed to the phenolic accumulation. The poor supply of nutrient and energy made microbes less active in *Sphagnum*-dominated peatland than in the nutrient-rich marsh with higher quality substrate supply. The sufficient nutrient supply and the more suitable soil conditions accelerated the decomposition of litters and enzyme activation, which was not beneficial for phenolic accumulation (Verhoeven and Toth, 1995). In addition, the vertical profiles of enzyme activities also showed remarkable differences between the two peatlands. β-glucosidase and phenol oxidase activities in the marsh peat cores were found to dramatically decrease with depth under the three water level conditions, while great variations were present in the forest swamp (Fig. 1(a)–(d)). Apart from the aforementioned factors, the effect of soil physical properties such as hydraulic conductivity or porosity could not be excluded.

Acid phosphatase activity did not show any remarkable difference between the marsh and the forest swamp under

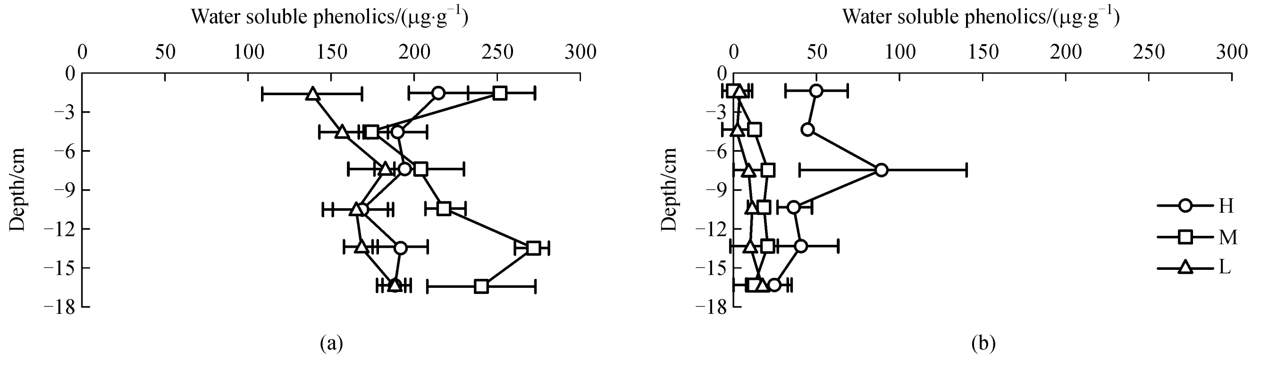

Fig. 2 Impacts of dry and waterlogged conditions on the water soluble phenolic concentration in (a) the forest swamp and in (b) the marsh. H, M, L represent the high, mid and low water level conditions, respectively

the high and the low water level conditions, while a remarkable difference was present under the medium water level condition. The peak activity of the acid phosphatase corresponding with the lowest value of phenolic concentration in the marsh under the low water level condition indicated the inhibition of phenolics on the acid phosphatase (Fig. 1(f)), but this effect was not present in the forest swamp. Both the lowest activity of the acid phosphatase in the upper marsh peat and highest activity in the forest swamp peat appeared under the medium water level condition (Figs. 1(c) and (f); Table 1). A further study on these effects is needed.

Generally, the forest swamp held a lower pH value than the marsh (Verhoeven and Toth, 1995), and acidification inhibited hydrolase's activity (Bonnett et al., 2006). Here, the two peatlands showed a slim difference in pH, and the presence of an acidification trend was found to accompany the water level drawdown (Table 1). Higher acidity under the low water level condition seemed not to induce any noteworthy effects on enzymes and phenolics in this study. Xiang et al. (2009a) pointed out that acidification at the surface might be the main cause of the inhibited responses of phenol oxidase to the increased aeration in the forest swamp. Because the pH value (around 6) of this study was much higher than those in Xiang et al. (2009a) and near the optimal value for phenol oxidase and β-glucosidase (Xie et al., 2008), it might not induce the inhibited effects on phenol oxidase and β-glucosidase activities in this study.

Table 2 Correlations coefficients ($p < 0.05$, $n = 6$) between phenol oxidase and phenolics under different water level conditions in the marsh and in the forest swamp

	Higher water level	Medium water level	Lower water level
Marsh	0.688	−0.866(*)	−0.239
Forest swamp	−0.742(*)	0.402	0.488

Statistical analysis showed a negative relationship or inconspicuous correlation between phenolics and phenol oxidase, which varied with specific soil conditions (Table 2). Freeman et al. (2001a) observed a significant increase of hydrolase's activities with just a little phenolic removal, and found a negative relationship between phenolics and enzymes. However, adjoint increase in phenolic concentration and enzyme activities (Freeman et al., 2001b), as well as a positive relationship (Pind et al., 1994), were also observed. Fenner et al. (2005b) found two peaks in carbon processing of peat, one in the initial and the other in the optimal environmental condition. Though the significantly negative correlation could only be found under the medium water level condition in the marsh and the high water level condition in the forest swamp (Table 2), we could also partly conclude that under the moderated or the initial water level conditions, the negative relationship between phenolics and phenol oxidase still occurred, and this relationship could be used as an indicator of environment stabilization of peatlands.

The variations of carbon-related enzyme activities (β-glucosidase and phenol oxidase) and phenolic concentrations were much notable between the peatlands than within the individual peatlands caused by the water level. As discussed above, we suggested that the difference in enzyme activities and phenolic concentration could be more related to the developmental stages and the types of wetlands.

4 Conclusions

The dry and waterlogged conditions brought diverse impacts on different enzyme activities. The changes of β-glucosidase and phenol oxidase activities were much more remarkable at the marsh peat surface than at the *Sphagnum* peat surface during the dry-rewet event. The differences of carbon-related enzyme activities (β-glucosidase and phenol oxidase) and phenolic concentrations were much notable between the two peatlands than within the individual peatlands caused by the water level. Statistical analysis showed the presence of the negative relationship or inconspicuous correlation between phenolics and phenol oxidase, which varied with specific soil conditions. In addition, the inhibiting effects of phenolics on enzyme activities might be offset by some other factors. Accordingly, we suggested that the differences of enzyme activities and phenolic concentration could be related to the developmental stages and the types of wetlands more than to the hydrological conditions, though the changes in the water level may greatly impact the biogeochemical processes in wetlands.

Acknowledgements This work was financially supported by the National Natural Science Foundation of China (Grant No. 40772205) and the the Scientific Research Foundation for the Returned Overseas Chinese Scholars, State Education Ministry of China.. We thank Wu Y G, Wang H R and Hu X F for assistance with sample measurement.

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