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Title: Shift in plant-soil interactions along a lakeshore hydrological gradient

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Abstract

Wetlands occupy the transitional zone between aquatic and terrestrial systems. Hydrological conditions have significant influence on wetland plant communities and soil biogeochemistry. However, our knowledge about plant-soil interactions in wetlands along hydrological gradients is still limited, although it is crucial to guide wetland management decisions and to adapt, whenever possible, hydrological conditions to the different plant communities. To this aim, we related vegetation composition, plant functional traits, soil physicochemical properties, soil microbial biomass, and soil enzymatic activities in wetlands on the southeastern shore of Neuchâtel lake, Switzerland, a lake whose level is partly regulated. Aboveground and belowground plant biomass and correspondent C, N and P concentrations remained constant or decreased moving from the vegetation community subjected to more frequent flooding events to the community with almost no flooding. The soil organic layer exhibited always higher nutrient concentrations and greater enzymatic activities than the organo-mineral and mineral layers. The chemical and biological characteristics of the soil organic layer showed decreasing values for most of the parameters along the hydrological gradient from lakeshore to upland wetland communities. On the basis of nutrient stoichiometry, plant-soil system in the plant community with most flooding events had no-nutrient limitation, while there was a N limitation in the transitional community. In the upland plant community where there was no flooding effect, the plant-soil system was characterized by N and P co-limitation. These findings are important because they provide a threshold for flooding regime by the lake in the context of optimization of lake level regulation under various stakeholders needs.

Keywords: wetland; flooding; plant biomass; biogeochemistry; nutrient stoichiometry

1. Introduction

Wetlands are important ecosystems supporting biodiversity by providing habitats for numerous plants and animals (Neckles et al., 1990; Gibbs, 2000). Furthermore, they ensure several key ecosystem services such as flood control, groundwater replenishment, water purification, carbon (C) sequestration and they provide livelihoods for local populations (Ramsar, 2013). Extreme climate events such as flooding and drought, as well as anthropogenic activities such as sand mining and agriculture intensification (Lai et al., 2014; Xu et al., 2019) are likely to change the hydrological conditions of wetlands (Hingray et al., 2007; Sarneel et al., 2019) and their habitats (Dawson et al., 2003). In particular, variation in frequency and duration of soil flooding and dryness can profoundly affect biogeochemical cycles of C, nitrogen (N) and phosphorous (P) with cascading effects on wetland plant community composition (Baldwin and Mitchell, 2000; Wang et al., 2015b; Swanson et al., 2017).

Flooding regime affects soil organic C and nutrient content and availability by controlling microbial mineralization (Wolf et al., 2013; Wang et al., 2015a; Swanson et al., 2017). Accumulation of degraded organic compounds in water saturated soils and under oxygen deficiency (Hopkinson, 1992; Swanson et al., 2017) leads to increasing dissolved soil organic carbon (DOC) and nutrients, resulting partly from C, N and P leaching from leaf litter under rewetting conditions (Baldwin and Mitchell, 2000; Shrestha et al., 2014). Extracellular degrading enzymes are produced by microorganisms in response to environmental signals or through cell lysis (Sinsabaugh et al., 2009; Cui et al., 2018). It has been proved that their higher activities in wet conditions can accelerate organic C, N and P mineralization rates by breaking down large organic molecules for microbial consumption (Wilson et al., 2011; Heuck et al., 2015). Soil organic carbon (SOC) and nutrient concentrations were shown to be relatively higher in the wetter as compared to the drier part in both river and lake wetlands (Bai et al., 2005; Wang et al., 2016) and this increase of nutrient pool promoted microbial activity and

75 nutrient cycling (Baldwin and Mitchell, 2000; Heuck et al., 2015). Thus, microbial biomass is
76 both a source and a sink for nutrients and participates to nutrient transformation (Gil-Sotres et
77 al., 2005). However, drying of formerly inundated wetlands may cause a severe C limitation
78 and consequently a decrease in the rate of nutrient cycling because of C being lost (Baldwin
79 and Mitchell, 2000) and microbial die-off (Qiu and McComb, 1995).

80 Hydrological conditions in wetlands can have strong impact on plant-soil interactions (Fu
81 et al., 2018; Wang et al., 2018) through changing both organic matter accumulation and
82 mineralization processes (Wilson et al., 2011; Swanson et al., 2017). Plant C, N, P
83 concentrations and their stoichiometric ratios may reflect nutrient availability from substrate
84 and plant nutrient uptake (Demars and Edwards, 2007; Agren, 2008; Elser et al., 2010),
85 Furthermore, the above- and belowground nutrient content and stoichiometry are tightly linked
86 (Bell et al., 2014) and therefore represent important indicators of ecosystem structure and
87 nutrient cycling (Zechmeister-Boltenstern et al., 2015; Sardans et al., 2017). Plant nutrient
88 content and stoichiometry have been studied to detect tissue nutrient allocation (Wang et al.,
89 2015b; Hu et al., 2018), seasonal nutrient variation (Fu et al., 2018), nutrient limitation (Bedford
90 et al., 1999; Demars and Edwards, 2007) or variation between plant functional types (Wang
91 and Moore, 2014; Hu et al., 2018). For example, Li et al. (2017) and Li et al. (2018b) showed
92 that soil nutrient content and stoichiometry are changing along hydrological gradients, and that
93 plant nutrient content and stoichiometry are regulated rather by flooding duration than by soil
94 nutrient content.

95 Different plant species and their abundances can also cause variation in soil and microbial
96 nutrient stoichiometry (De Graaff et al., 2010; Bell et al., 2014) and modulate ecosystem
97 functions through ecological processes affecting microbial and enzymatic activities (Bever et
98 al., 2010; Kardol et al., 2010). There are ample evidences of the close relationships among plant
99 species and soil stoichiometry (Hobbie et al., 2006; Bell et al., 2014; Wang et al., 2018). Pattern

of nutrient availability varies among plant species (Bedford et al., 1999; Güsewell and Koerselman, 2002) and conversely, plants apply some control over nutrient availability by driving soil microbial and enzymatic activities (Richardson et al., 2009; Sardans and Peñuelas, 2012; Bragazza et al., 2015). Along hydrological gradients, the relationship between plant functional traits and soil properties has been explored in wetlands, revealing potential plant-soil relationships (Liu et al., 2015; Wang et al., 2015b; Hu et al., 2018).

In the present study, we investigated soil physico-chemical characteristics (including C, N, P stock and availability), soil microbial biomass nutrients (C, N, P), soil enzymatic activities, and nutrient content in plant and moss biomass (C, N, P) in three plant communities along a hydrological gradient from lakeshore to upland. Investigations took place at the beginning and at peak of the growing season in a wetland along the southern shore of Lake Neuchâtel, Switzerland. We hypothesized that: (i) soil nutrient content, microbial biomass and enzymatic activities, and plant nutrient content are higher in the flooded areas near the lakeshore as compared to the upland area; (ii) the nutrient stoichiometry of plant and soil components can reveal contrasted ecosystem functioning along the hydrological gradient, with a N and P limitation for plant communities of the upland area, as opposed to no N and P limitation for the plant communities close to the lakeshore subjected to flooding.

2. Materials and methods

2.1 Study site

The study was conducted in the wetlands along the southern shore of Lake Neuchâtel (46°54'28"N, 6°52'02"E) in Switzerland, which is the Ramsar site called "Grande Cariçaie". The climate is defined as pluvial sub-oceanic (Buttler, 1990) with a mean annual temperature of 9.4 °C and mean annual precipitation of 891 mm (MeteoSuisse,

<https://www.meteosuisse.admin.ch> - Payerne, period 1981-2010). Five main plant communities, respectively dominated by *Molinia caerulea* (L.) Moench, *Schoenus nigricans* L., *Carex panicea* L., *Carex elata* All. and *Phragmites australis* (Ca.) Steud. can be found moving from the upland wetland to the lake shoreline (Buttler et al., 1985; Buttler and Gallandat, 1989; Buttler and Muhlhauser, 1994). These plant communities experience an annual flooding regime depending on the lake water level, which is partly regulated and is on average low in winter, high in spring and intermediate in summer and autumn (<https://www.hydrodaten.admin.ch/fr/2149.html>). Thus, flooding by the intrusion of the lake into the wetland occurs mainly in spring and early summer time, and relates to the snowmelt in the Alps. Heavy rain can recharge the soil water rapidly in autumn, which translates into superficial flooding's event in the upland wetlands which are not influenced by the lake water (Buttler, 1987).

2.2. Sampling design

Distinct plant communities distributed along an elevation gradient (i.e. transects from lakeshore to upland) were selected, a method frequently used in wetland ecosystem studies (e.g. Li et al., 2017; Fu et al., 2018). The three plant communities dominated by *C. elata*, *C. panicea* and *S. nigricans* were selected for this study because they represent the interface between the vegetation influenced by the lake intrusion into the wetland, e.g. *Caricetum elatae* W. Koch 26, variant with *Phalaris arundinaceae*, the transitional vegetation, e.g. *Caricetum elatae* W. Koch 26, variant with *Carex panicea* and the vegetation not reached by the lake, e.g. *Orchio-Schoenetum nigricantis* Oberd. 57, variant with *Galium palustre* (Buttler and Gallandat, 1989). Along this gradient, which is topographically characterized by a gentle slope with about 30-60 cm increase of soil level towards the upland wetland, soils show a marked hydromorphic feature:

histic humaquept (*C. elatae* community), wet typic haplaquoll (*C. panicea* community) and dry typic haplaquoll (*S. nigricans* community) (Buttler and Gobat, 1991).

Four transects at least 1 km apart were established from the upland to the shoreline (Supplementary Fig. S1). In each of the three plant communities crossed by these transects, one 10 m × 10 m plot was randomly selected, leading to a total of 12 plots (4 transects × 3 plant communities). The different botanical compositions in different plots are given in the Supplementary Table S1. One piezometer was installed in each plot to monitor the soil water level (Supplementary Fig. S2). *Carex elata* community was mostly flooded with decreasing water levels during the study period, *C. panicea* community experienced wet conditions with soil saturated in spring and a subsequent drop of water level below -35 cm in August, and *S. nigricans* community, typically never flooded with water level decreasing from -4 to -70 cm during the measurement period. Data loggers (Onset HOBO Water Temp Pro v2) were also installed in the soil at 5 cm depth to monitor the soil temperature (Supplementary Fig. S3). Overall, from March to August, the top-soil temperature increased regularly from 5 °C to more than 20 °C, with the soil in *C. elata* community being always slightly colder than that in *C. panicea* and *S. nigricans* communities, which had very similar temperatures.

2.3. Plant and soil collection

Plant and soil samples were collected in all plots at the beginning of the plant growing season (April 2018) and at the peak of plant biomass (July 2018) (Supplementary Fig. S4). In addition to the groundwater level measured with the piezometers, the soil volumetric water content was measured at 0-10 cm depth in each plot and at each sampling time using a portable TDR (FieldScout TDR100, UK).

Aboveground vascular plant biomass (AGB), moss biomass (MB) and plant litter (L) were collected in all plots using a 50 cm × 50 cm quadrat in *S. nigricans* and *C. panicea*

communities, and a 100 cm × 100 cm quadrat in *C. elata* community. Vascular plants were clipped at the ground level, while litter and mosses were picked up carefully to avoid soil particles. All the aboveground material was placed in separated bags, transported to the laboratory, and then oven-dried at 65 °C for 4 days. Once oven-dried, this plant material was weighted in order to estimate the dry mass (DM) per square meter for each plot and kept for further analysis.

Three soil cores (5.6 cm diameter × 30 cm depth) per plot were randomly collected (in-between the tussocks for *C. elata* and *S. nigricans* communities) for belowground biomass (BGB - roots and rhizomes) sampling. The same layers as for soil sampling (see below) were used and pooled so as to have a composite sample for each layer. Roots and rhizomes were carefully collected by gentle washing in water. As for the aboveground material, the belowground biomass was oven-dried at 65 °C during 4 days and weighted in order to estimate the dry mass (DM) per square meter for each plot and kept for further analysis.

Three other soil cores (5.6 cm diameter × 30 cm depth) per plot were collected in a similar way for the soil sampling as for the belowground biomass. Based on the soil color and texture, each soil core was divided into three parts: organic layer (OL), organo-mineral layer (OML), and mineral layer (ML) ([Supplementary Figs. S4 and S5](#)). The top 5 cm of the organic layers from the three soil cores were collected and pooled in one composite sample. For the organo-mineral layer, the 5 cm immediately below the entire organic layer were taken and pooled. For the mineral layer, the upper 2 cm of this layer was removed to avoid irregular transition and the following 5 cm below were collected, which again were pooled in one composite sample. These samples were placed in polyethylene bags, transported to the laboratory and stored at 4 °C until being further processed.

In order to determine the soil bulk density (BD), a last soil core was sampled and an intact piece (5.6 cm diameter × 5 cm depth) was taken for each soil layer and oven-dried at 105 °C

for 48 h and weighted. Bulk density was calculated by dividing the mass of the oven-dried soil sample by its volume and expressed as g.cm^{-3} .

2.4. Plant and moss C, N and P analyses

A subsample of dry plant material was washed and dried again, then ground to a fine powder using a ball mill before chemical analysis. Total organic carbon (C) and total nitrogen (N) concentrations were determined by thermal combustion using an elemental analyzer (CE Instruments model NA2500 Nitrogen Carbon Analyzer) and expressed as percent of dry weight. Total phosphorus (P) concentration was determined by the molybdenum blue method after $\text{HClO}_4\text{-H}_2\text{SO}_4$ digestion using a continuous flow autoanalyser (FlowSys, Systea, Anagni, Italy) and expressed as percent of dry weight. Finally, C:N, C:P and N:P stoichiometric ratios were calculated for aboveground and belowground plant biomass, plant litter and moss biomass ([Supplementary Fig. S4](#)).

2.5. Soil chemical analyses

For chemical analyses, any visible coarse plant material in the soil samples was removed by hand-sorting. Soil samples were divided into two subsamples: i) a subsample was oven-dried at 65 °C for 4 days and ground to a fine powder using a ball mill in order to determine total organic C (TOC), N (TN) and P (TP) concentrations, and ii) a fresh subsample was stored at 4 °C in order to determine soil pH, nitrate (N-NO_3^-) and ammonium (N-NH_4^+) concentrations, dissolved organic C (DOC), N (DN) and P (DP) concentrations, soil microbial biomass and soil enzymatic activities. For the determination of soil water content (SWC) and in order to quantify all the measured parameters per g of dry soil weight, 10 g of fresh soil samples for each replicate were oven-dried at 105 °C for 48 h. In addition, these oven-dried samples were burned at 550 °C for 6 h in order to determine the soil organic matter content by loss of ignition (LOI).

TOC, TN and TP were determined for each replicate following the same methods as for plant and moss material and expressed as percent of dry soil weight. Soil pH was measured in 1:5 (w/v) soil water suspension with a portable pH meter (WTW multi 3430, Weilheim, Germany) after stirring the mixture for 2 h. N-NH_4^+ and N-NO_3^- concentrations were determined after extraction of 5 g of fresh soil with 30 ml of 1 M KCl extraction and filtration through 0.45 μm filter using a continuous flow autoanalyzer (SEAL Analytical, Germany) and the results were expressed as mg.kg^{-1} oven dry soil.

Microbial biomass carbon (MBC), nitrogen (MBN) and phosphorus (MBP) were measured using the chloroform fumigation extraction method (Brookes et al., 1985). Three pairs of about 5 g of fresh soil (3 g for MBP) were weighed for each replicate. One sample from each pair was stored at 4 °C while the other sample was put in a vacuum desiccator and subjected to chloroform vapor. After 24 h of fumigation in the dark at ambient temperature, the fumigated soil samples and the corresponding ones kept unfumigated in the fridge were extracted with a 25 ml of 0.5 M K_2SO_4 for MBC and MBN and with 40 ml of 0.5 M NaHCO_3 for MBP. All solutions were filtered through a 0.45 μm filter before analysis. Organic C and N concentrations in the solutions from both fumigated and unfumigated samples were determined using a TOC/TN analyzer (Shimadzu TOC-V), while P concentration was determined by colorimetry using a spectrophotometer at 890 nm (Olsen et al., 1954). Soil DOC, DN and DP were determined as the concentrations obtained from the unfumigated samples. The soil MBC, MBN and MBP values were estimated as the differences between fumigated and unfumigated samples using an extractability factor of 0.45 for C (Vance et al., 1987), 0.54 for N (Brookes et al., 1985) and 0.40 for P (Brookes et al., 1982) and expressed as mg.kg^{-1} oven dry soil.

In order to measure the soil enzymatic activities, 1 g of fresh soil was mixed with 10 ml of water, stirred for 1 h, and the supernatant was collected after centrifugation. The activities of extracellular hydrolase enzymes were measured by adding 50 μl of 4-methylumbelliferyl- β -

D-glucoside for the activity of β -glucosidase (BG), 4-MUF-N-acetyl- β -D-glucosaminide for the activity of β -1, 4-N-acetylglucosaminidase (NAG), L-leucine-7-amido-4-methylcoumarin hydrochloride for the activity of leucine aminopeptidase (LAP) and 4-MUF-phosphate for the activity of phosphatase (PHO) to 250 μ l of the soil extract. After 2 h of incubation, the fluorescence was measured on a microplate reader (BioTek SynergyMX) at 450 nm emission and 330 nm excitation wavelength. To quantify product release and account for quenching effects, a set of standards was prepared using methylumbelliferone (MUF) and 7-amino-4-methylcoumarin (MUC) mixed with soil extract. Enzymatic activities were expressed as μ mol of substrate (MUF and MUC) converted per min and per g (dry weight) of soil (Freeman et al., 2004).

The C:N, C:P and N:P stoichiometric ratios were calculated for bulk soil and its dissolved fraction and for microbial biomass.

2.6. Data analysis

Statistical analyses were performed with the R software 3.2.3 (R. Core Team, 2017). When necessary, data were log or square root transformed, and the normality and homoscedasticity of the distribution of residuals of models were visually verified.

We used a linear mixed effects model approach (“nlme” package, Pinheiro et al., 2020), followed by Tukey HSD tests for post hoc comparisons, to test the effects of vegetation type (*C. elata*, *C. panicea* or *S. nigricans* community), growing season (beginning or peak of the growing season), and their interactions on plant and moss parameters. To consider the fact that we had three plots per transect, the random part of the model indicated that the plots were nested within transects.

For what concerns the soil physico-chemical, microbial and enzymatic parameters, we used a linear mixed-effects model approach followed by Tukey HSD tests for post hoc

comparisons in order to test the effects of soil layers (organic, organo-mineral or mineral layer), vegetation type (*C. elata*, *C. panicea* or *S. nigricans* community), growing season (beginning or peak of the growing season), and their interactions, specifying soil layers nested into plots nested into transects as random factor.

A redundancy analysis (RDA) was used to link the plant chemical characteristics of the three vegetation types taken at two sampling times (C, N and P contents and their stoichiometry in above- and belowground plant biomass, moss biomass and plant litter) as a response to the soil characteristics (chemical and biological variables – see [Supplementary Tables S2 and S3](#)).

Finally, a principal component analysis (PCA) was used to determine the correlations between stoichiometry of C, N and P in the plant material, in the bulk soil and in its dissolved fraction, and in the microbial biomass.

3. Results

3.1 Plant and moss parameters

Litter mass and belowground biomass were between 2.4 and 3.5 times higher in *C. elata* community compared to *C. panicea* and *S. nigricans* communities ([Table 1 and 2](#); [Supplementary Table S2](#)), while differences in aboveground and moss biomass among the three plant communities were dependent on the sampling time during the growing season (significant vegetation type $\times$ growing season interaction, [Table 1](#)). At the beginning of the growing season, aboveground biomass of *C. elata* community was lower than that of *C. panicea* and *S. nigricans* communities, while aboveground biomass of *C. elata* community was higher than that of *C. panicea* at the peak of growing season ([Fig. 1a](#)). Concerning moss biomass, there was no difference among plant communities at the beginning of growing season, while moss biomass of *C. elata* community was 5 times higher than that of the two other plant communities at the

peak of growing season (Fig. 1b). When summing all plant and moss materials, the organic matter stock was approximately 2.5-time higher in *C. elata* community (10'063 g.m⁻²) as compared to *C. panicea* (4'037 g.m⁻²) and *S. nigricans* (3'803 g.m⁻²) communities. The aboveground biomass increased more than 8 times during the growing season, while litter mass was 30% lower (Table 2; Supplementary Table S2). Belowground biomass decreased by 32% from the beginning to the peak of biomass period, while moss biomass increased 1.6-times, although these trends were not significant (Tables 1 and 2; Supplementary Table S2).

Carbon content in belowground biomass and litter were higher in *C. elata* community compared to *S. nigricans* community (Table 1; Supplementary Table S2). Nitrogen content in aboveground biomass of *C. panicea* community was similar to that of the *C. elata* community and higher than that of *S. nigricans* community at the beginning of the growing season, while it was similar to that of *S. nigricans* community and lower than that of *C. elata* community at the peak of the growing season (significant vegetation type × growing season interaction, Table 1; Fig. 1c). Phosphorus content in aboveground biomass showed a trend of decrease according to the gradient *C. elata* > *C. panicea* > *S. nigricans*, i.e. from lakeshore to upland communities (Table 1; Supplementary Table S2). The decrease in P content in aboveground biomass during the growing season was dependent on the plant community (significant vegetation type × growing season interaction, Table 1), since the P content decreased only in the *C. elata* and *C. panicea* communities (Fig. 1d).

Nitrogen and P content in moss biomass was also higher in *C. elata* compared to *S. nigricans* community (Table 1; Supplementary Table S2). In litter, C content increased, while N content decreased during the growing season, and in belowground biomass both N and P contents decreased during the growing season (Tables 1 and 2; Supplementary Table S2).

3.2 Soil physico-chemical parameters

Bulk density and pH increased according to the gradient organic > organo-mineral > mineral layers (i.e. soil depth) while, in the opposite, all other physico-chemical parameters decreased according to soil depth (Tables 3 and 4; Supplementary Table S3). Moreover, bulk density and pH increased from lakeshore to upland plant communities while, in the opposite, all other physico-chemical parameters decreased according to this vegetation gradient (Tables 3 and 4; Supplementary Table S3). Overall, more physico-chemical parameters were significantly different between *C. elata* and *C. panicea* communities than between *C. panicea* and *S. nigricans* communities (Supplementary Table S3).

Except for soil pH and nitrate, the differences among the three plant communities were dependent on the soil layer (significant soil layer $\times$ vegetation type interaction, Table 3), with decreasing differences among plant communities according to increasing soil depth. For example, while we observed marked differences for soil total P (TP) and available P (DP) in organic layer among plant communities, the values of mineral layer were much less marked or similar between plant communities (Fig. 2a and b). The differences in soil available C (DOC) and nitrate contents among the 3 plant communities were also dependent on the growing season (significant vegetation type $\times$ growing season interaction, Table 3). Soil DOC values were similar between the 3 plant communities at the beginning of the growing season, while DOC was higher in *C. elata* compared to the two other communities at the peak of growing season (Fig. 3a). Soil nitrate was higher in *C. elata* and *C. panicea* communities compared to *S. nigricans* community at the beginning of the growing season, while similar values between the three plant communities were observed at the peak of growing season (Fig. 3b).

Only few soil physico-chemical parameters varied across the growing season (Table 3). Soil pH and DN increased while, on the opposite, nitrate decreased between the beginning and the peak of the growing season (Tables 3 and 4; Supplementary Table S3). The increase in soil available N (DN) across the growing season was higher in the organic and organo-mineral

layers compared to the mineral layer (significant soil layer $\times$ growing season interaction, Table 3; Fig. 4a), while ammonium content increased only in the organic layer (significant soil layer $\times$ growing season interaction, Table 3; Fig. 4b).

3.3 Soil microbial biomass and enzyme activity

Soil microbial biomass and enzymatic parameters decreased according to soil depth and according to the vegetation gradient from lakeshore to upland (Tables 3 and 4; Supplementary Table S3). Contrary to microbial biomass, the four enzymatic activities varied across the growing season (Table 3), with higher values reported at the peak compared to the beginning of growing season (Table 4; Supplementary Table S3).

Except for leucine aminopeptidase activity, the differences in microbial biomass and enzymatic parameters among the three plant communities were dependent on the soil layer considered (significant soil layer $\times$ vegetation type interaction, Table 3), with decreasing differences according to increasing soil depth (Fig. 2c and d). Finally, the differences in enzymatic parameters among plant communities or among soil layers were stronger at the peak compared to the beginning of growing season (significant soil layers $\times$ growing season and vegetation type $\times$ growing season interactions, Table 3).

3.4 Plant-soil interactions

The redundancy analysis model (RDA) provides a synthetic view on the relationship between plant chemical characteristics as a response to soil characteristics in the upper organic layer at two sampling periods, April and July (Supplementary Fig. S6). *C. elata* community samples are strongly linked, along axis 1, to high values of N and P in aboveground biomass, moss biomass and plant litter, while belowground biomass samples vary mostly along axis 2, with higher P and N values in April.

The relationships among stoichiometry of C, N and P in all sampled compartments (plant, moss, soil and microbial biomass) in April and July are given in the principal component analysis (PCA) of the Fig. 5. *C. elata* community samples are mostly positively correlated to soil dissolved C:N ratio and strongly negatively correlated to C:P and N:P in microbial biomass. Samples of *C. panicea* community are mostly positively correlated to C:N ratios in belowground biomass, in bulk soil and also weakly in microbial biomass, and strongly negatively correlated to C:P and N:P ratios in bulk soil and in belowground biomass, as well as in soil dissolved C:P. Finally, samples of *S. nigricans* community are positively correlated to several ratios, in particular to C:P and N:P ratios in microbial biomass, to soil dissolved N:P, to bulk soil C:N ratio and to C:N, C:P and N:P ratios in aboveground biomass, moss and litter.

4. Discussion

4.1 Plant biomass and its nutrients content reflect the hydrological gradient induced by the lake flooding

The seasonal pattern of aboveground biomass was different among the three vegetation types. In spring, before the vegetation started to grow, *C. elata* had the lowest aboveground biomass, but later in the season, at the peak of biomass period, the trend reversed and *C. elata* community developed more biomass compared to *C. panicea* and *S. nigricans* communities (in this later case the difference was only marginal). This reflects in the litter accumulation, which was higher in *C. elata* community. Mosses also developed more during the vegetation period in *C. elata* community due to the very favorable microclimatic conditions resulting from high soil moisture and shading conditions under the tussocks. The total plant biomass reflects well the hydrological gradient, with highest values in *C. elata* community and lowest in *S. nigricans* community. Li et al. (2017) found opposite results for biomass distribution along an elevation

gradient in Dongting Lake wetland (China), with increasing aboveground biomass with decreasing soil water content. This can be explained by the different hydrological conditions in these two wetlands. In Dongting Lake wetland, the upland plant community still experiences an annual flooding event, similarly to the community close to the lake shoreline and therefore its ecological functioning cannot be assimilated to a conservative nutrient poor biogeochemical cycle as in the *S. nigricans* community investigated in the present study.

As we hypothesized, plant nutrient content generally decreased along the hydrological gradient, with higher values in *C. elata* community, which is under the influence of the lake flooding. This was particularly true for N and P content in plant aboveground and moss biomasses. The concentrations of these two elements in aboveground biomass also showed the intermediate status of *C. panicea* community, as exemplified by its N content which was similar to *C. elata* in spring, when both vegetation types were flooded by the lake, and similar to *S. nigricans* later in the dryer season (Fig. 1c). Nutrients provided by the lake water are important sources for wetland plants, and indeed, in *C. elata* community, and to some extent also in *C. panicea* community, vascular plants and mosses could absorb more nutrients than in *S. nigricans* community, which contributed to the higher biomass accumulation. Furthermore, C and nutrients from the litter leachates (Demars and Edwards, 2007; Shrestha et al., 2014) and organic matter accumulation (Wilson et al., 2011; Swanson et al., 2017) under flooding conditions are also beneficial for the plant nutrient absorption and growth.

We assessed the nutrient content in aboveground and moss biomass by pooling the plant species, since each plant community was dominated by only a few species (Buttler, 1987, see also Supplementary Table S1). Nevertheless, plant nutrients can show a high interspecific variability and low phenotypic response to nutrient supply (Demars and Edwards, 2007; Li et al., 2017; Hu et al., 2018). Plants have lower nutrient resorption proficiency in nutrient-rich environment (Hopkinson, 1992; Mao et al., 2016), while under extremely low nutrient

availability, they can adapt by maintaining small nutrient concentrations in photosynthetically active tissues (Wang and Moore, 2014). In *S. nigricans* community, we can speculate that plants could transfer and store more nutrients into the living roots. It was also observed that shoots remain partly green over winter, which can contribute to the storage of nutrients, while all the aboveground biomass dies out in *C. elata* vegetation (*personal observations*). As a consequence, in *S. nigricans* community these nutrients could be mobilized during the growing season and allow for relatively high aboveground biomass production as compared to *C. elata* community (Fig. 1a, no statistical difference between CE and SN at the peak of biomass). Nutrient translocation was the reason why litter quality was increased with nutrient enrichment in N-limited wetlands (Mao et al., 2016). We did not detect any vegetation type $\times$ growing season cross effect for accumulated litter and its quality (Table 1), so that we assume that the existing litter became similar in the different vegetation types during winter decomposition already. Litter decomposition was mostly related to leaf N content (de Neiff et al., 2006) and flooding can accelerate decomposition through increasing soil moisture (Shrestha et al., 2014; Heuck et al., 2015) and nutrient leaching (Baldwin and Mitchell, 2000; Shrestha et al., 2014). This could explain why, despite initial nutrient concentration differences in early senescent biomass and distinct nutrient translocation capacity in the three communities, there was no significant differences in litter N and P contents. However, C content in litter decreased along the hydrological gradient, with highest values in *C. elata* and lowest in *S. nigricans* communities. This difference of litter C content potentially provides more energy for microorganisms in the *C. elata* community.

From a stoichiometric perspective, in aboveground and moss biomass, C:N, C:P and N:P ratios were significantly lower in *C. elata* and higher in *S. nigricans* communities (Supplementary Table S4). Even if this trend is still visible in the litter, differences were non-significant, which could advocate for similar decomposition rates. In litter bags decomposition

experiments, [Buttler \(1987\)](#) found that k decomposition rates were 0.229, 0.224 and 0.253 for *C. elata*, *C. panicea* and *S. nigricans* communities, respectively, thus a higher decomposability for the litter in *S. nigricans* community was measured. This discrepancy can be explained by the quality of the litter used. Because of the plant morphology, fresh litter can easily be collected on *S. nigricans* tussocks at the end of the growing season as standing senescent leaves, while for *Carex* species, these senescent leaves tend to fall down and mix with older leaves on the ground, so that litter samples might be more heterogeneous and comprise leaves in a more advanced decomposition stage.

4.2 Soil organic matter quantity and quality reflects the flooding regimes

Under intensive flooding, as happened in *C. elata* community near the lakeshore, there was more than double the amount of organic matter accumulated in the ecosystem, as compared to *C. panicea* and *S. nigricans* communities. With respect to the belowground biomass, which was also highest in *C. elata* community, it cannot be concluded on higher root growth as it was not possible to distinguish between living and dead roots, but lower soil bulk density can indicate higher organic matter content in relation to higher root productivity ([Rokosch et al., 2009](#)). As for litter, the strong decrease of belowground biomass during the growing season points to the degradation of dead organic matter. In the belowground biomass, there was no difference in plant N and P concentrations among the three communities, despite different soil nutrient conditions ([Table 4](#)). Like for the N:P ratio of above-ground biomass and mosses, the N:P ratio of belowground biomass was higher in the *S. nigricans* community where there is no flooding than in the other two communities. This result is contrary to the finding in [Wang et al. \(2018\)](#) where N:P ratio of belowground biomass was increased with flooding intensity. These opposed results might be explained by distinct nutrient limitation in the two study areas. Below-ground biomass C content decreased along the hydrological gradient, with highest values in *C.*

elata and lowest in *S. nigricans* communities, which mirrors in the trend for higher below-ground biomass C:N and C:P ratios in *C. elata* community. This reflected the humus types, which were marked differently by hydromorphic features: peaty anmoor, anmoor-hydromull and hydromull in *C. elata*, *C. panicea* and *S. nigricans* communities, respectively (Buttler and Gobat, 1991). This is consistent with the decrease of soil organic matter and C contents along the vegetation gradient, as well as in the increase of bulk density and pH (Table 4 and Supplementary Table S3).

4.3 High organic matter in wetter soils triggers enzyme activity, which in turn accelerates nutrient mineralization

The soils in the three plant communities differed in their chemical and biological characteristics of their surface organic layer, which showed, as hypothesized, decreasing values for most of the parameters along the hydrological gradient, from *C. elata* to *S. nigricans* communities. Thus, higher soil fertility near the lakeshore also allowed higher microbial biomass. Along the growing season, DOC increased markedly in *C. elata* community, as a result of intense organic matter decomposition of the accumulated litter under high soil biological activity. Thus, higher organic matter contributed to the enzyme activity, which in turn could accelerate nutrient mineralization (Wilson et al., 2011; Heuck et al., 2015). Conversely, nitrate was higher at the beginning of the vegetation period, but decreased thereafter because it was used readily for the high biomass production, and consequently the soils could not be differentiated anymore by their nitrate content at the peak of biomass. Enzyme activity was affected not only by the availability of organic matter, but was also promoted by temperature increase during the growing season (Sinsabaugh et al., 2008; Manzoni et al., 2012).

4.4 Plant-soil interaction and nutrient limitation in different hydrological conditions

The three studied vegetation types are characterized by different nutrient requirements and, according to our hypothesis, this translates into different nutrient limitation and stoichiometric ratios in the plant material, soil and microbial pools. In *C. elata* community, N and P are not limiting because of the regular input of nutrients by lake water. With respect to NO_3 , values were on a yearly average 1.7 mg.L^{-1} in the lake water, as opposed to 0.1 mg.L^{-1} in the soil solution of the organic layer in the considered soils, while values for PO_4 were indifferently 0.1 mg.L^{-1} in both the lake water and the upper horizon of these soils, but undetectable in the deeper horizons (Buttler, 1992). This shows that despite the inflow of nutrients from the lake in the wettest plant communities, the nutrient content in the soil does not discriminate the plant communities, despite obvious differences in biomass production and associated nutrient content (this study and Buttler, 1992). This is explained by the immediate uptake of nutrients for biomass production and its feedback effect onto the soil during the vegetation period in wetlands (Dykyjová and Úlehlová, 1978; Bayley et al., 1985). Indeed, hydrological differences among the various vegetation communities can affect soil organic matter accumulation and mineralization processes (Wilson et al., 2011; Swanson et al., 2017), as well as plant nutrient resorption (Wang et al., 2015a). Finally, losses of nutrients from soil organic matter and litter decomposition are important for the eutrophic vegetation influenced by the lake and contribute to a high C:N ratio in the soil dissolved fraction. It has been reported that dissolved organic carbon was higher under flooding than non-flooding condition in floodplain vegetation (Shrestha et al., 2014) and it was increased by flooding duration (Blodau and Moore, 2003; Kim et al., 2014). Therefore, for vegetation under the influence of lake inundation and high nutrient inputs, there is a rapid turnover of nutrients. Conversely, in the upland wetland vegetation characterized by *S. nigicans*, which is never affected by lake flooding, N and P are limiting, which translates in high N:P ratios in the soil dissolved fraction

as well as high C:N, C:P and N:P ratios in aboveground biomass, mosses and litter, as well as high C:P and N:P ratios in the microbial biomass. Under such low nutrient availability, nutrient translocation from senescing tissues is a strategy for plants to retard nutrient loss (Hopkinson, 1992; Aldous, 2002). This translocation process of nutrients to roots by species such as *S. nigricans* (also *Molinia caerulea* and *M. arundinacea*, both present in *S. nigricans* community) is specific to a conservative biogeochemical cycle. In *C. panicea* community, which has an intermediate position along the vegetation gradient, only N is limiting, which translates into high C:N ratios in bulk soil, below-ground biomass and microbial biomass, and low C:P and N:P ratios in bulk soil and below-ground biomass, as well as low C:P ratio in the soil dissolved fraction.

5. Conclusion

High nutrient concentrations in plant leaves tend to be associated with the “live-fast/die young” end of the leaf economics spectrum (Wright et al., 2004; Kazakou et al., 2007), a characteristic which holds for the lakeshore vegetation under the influence of the lake flooding, as opposed to the upland wetland vegetation, which is never reached by lake flooding (Bueche et al., 1994). Our findings have strong implication for wetland management. The wetland hydrodynamic depends strongly on the lake level regulation at the outlet of the lake Neuchâtel, where a dam has been built (Buttler et al., 1995). It is a request to the hydraulic managers to consider the various stakeholders needs for setting the water level curve along the year. Constraints are given by the electricity power plants on the Aar river, navigation on the Rhin river, agriculture in the floodplains around the lake, fisheries and nature conservancy on the south shore of lake Neuchâtel which has become a Ramsar site. In this respect, the wetland vegetation and their soils are sensitive to lake flooding regime, as it was shown in this study. It is therefore important that the water level of the lake is set to optimize the flooding regime in

the wetland, more specifically that most of the vegetation of the type of *C. elata* along the lakeshore (but also the *Phragmites communis* belt near the lakeshore and ponds) can be flooded in spring, and the least possible vegetation of the type of *S. nigricans* (and neighboring *Molinia coearulea* vegetation) is reached by lake water (Buttler et al., 1995). These findings are important because they provide a threshold for flooding regime by the lake in the context of optimization of lake level regulation under various stakeholders needs. An inadequate water management would affect soil sustainability with a loss of C from the highly organic soils if they would be less flooded. In the opposite, dryer soils would also trigger shrub encroachments and lead to a loss of the most valuable habitats in connection with the lake, which are crucial for many organisms, as for example for fish and bird reproduction. Finally, a general flooding would suppress in the upland wetlands some plant and animal species of high naturalistic importance such as orchids or tree frog.

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References

573 Agren, G.I., 2008. Stoichiometry and Nutrition of Plant Growth in Natural Communities.
574 Annual Review of Ecology Evolution and Systematics 39, 153-170.

575 Aldous, A.R., 2002. Nitrogen translocation in Sphagnum mosses: effects of atmospheric
576 nitrogen deposition. New Phytologist 156, 241-253.

577 Bai, J.H., Ouyang, H., Deng, W., Zhu, Y.M., Zhang, X.L., Wang, Q.G., 2005. Spatial
578 distribution characteristics of organic matter and total nitrogen of marsh soils in river
579 marginal wetlands. Geoderma 124, 181-192.

580 Baldwin, D.S., Mitchell, A.M., 2000. The effects of drying and re-flooding on the sediment and
581 soil nutrient dynamics of lowland river-floodplain systems: A synthesis. Regulated Rivers-
582 Research & Management 16, 457-467.

583 Bayley, S.E., Zoltek, J.J., Hermann, A.J., Dolan, T.J., Tortora, L., 1985. Experimental
584 manipulation of nutrients and water in a freshwater marsh: effects on biomass,
585 decomposition, and nutrient accumulation. Limnology and Oceanography 30, 500-512.

586 Bedford, B.L., Walbridge, M.R., Aldous, A., 1999. Patterns in nutrient availability and plant
587 diversity of temperate North American wetlands. Ecology 80, 2151-2169.

588 Bell, C., Carrillo, Y., Boot, C.M., Rocca, J.D., Pendall, E., Wallenstein, M.D., 2014.
589 Rhizosphere stoichiometry: are C:N:P ratios of plants, soils, and enzymes conserved at the
590 plant species-level? New Phytologist 201, 505-517.

591 Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C.,
592 Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in
593 microbial interactions. Trends in Ecology & Evolution 25, 468-478.

594 Blodau, C., Moore, T.R., 2003. Experimental response of peatland carbon dynamics to a water
595 table fluctuation. Aquatic Sciences 65, 47-62.

596 Bragazza, L., Bardgett, R.D., Mitchell, E.A.D., Buttler, A., 2015. Linking soil microbial
597 communities to vascular plant abundance along a climate gradient. *New Phytologist* 205,
598 1175-1182.

599 Bragazza, L., Parisod, J., Buttler, A., Bardgett, R.D., 2013. Biogeochemical plant–soil microbe
600 feedback in response to climate warming in peatlands. *Nature Climate Change* 3, 273-277.

601 Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform Fumigation and
602 the Release of Soil-Nitrogen - a Rapid Direct Extraction Method to Measure Microbial
603 Biomass Nitrogen in Soil. *Soil Biology & Biochemistry* 17, 837-842.

604 Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of Microbial Biomass
605 Phosphorus in Soil. *Soil Biology & Biochemistry* 14, 319-329.

606 Bueche, M., Buttler, A., Cornali, Ph., Perrochet, P., 1994. Effects of water level regulation of
607 lake Neuchâtel (Switzerland) on the shore wetlands: mathematical modelling of
608 groundwater-lakewater interactions. *Proceedings of the International Symposium*
609 "Conservation and Management of Fens", 6th-10th June 1994, Poland, International Peat
610 Society - Agricultural University Warsaw, pp. 201-212.

611 Buttler, A. Quelques aspects climatiques dans les marais non boisés de la rive sud du lac de
612 Neuchâtel (Suisse). *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 113, 217-
613 230.

614 Buttler, A., 1987. Etude écosystémique des marais non boisés de la rive sud du lac de Neuchâtel
615 (Suisse): phytosociologie, pédologie, hydrodynamique et hydrochimie, production végétale,
616 cycles biogéochimiques et influence du fauchage sur la végétation. Thèse de doctorat,
617 Université de Neuchâtel (Suisse), pp. 284.

618 Buttler, A., 1992. Hydrochimie des nappes des prairies humides de la rive sud du lac de
619 Neuchâtel. *Bulletin d'Écologie* 23, 35-47.

620 Buttler, A., Bueche, M., Cornali, Ph., Gobat, J.M., 1985. Historischer und ökologischer

621 Ueberblick über das Südostufer des Neuenburger Sees. *Telma* (Hannover) 15, 31-42.

622 Buttler, A., Cornali, P., Bueche, M., 1995. Etude des effets de la régulation des lacs
623 subjurassiens sur la végétation et le milieu. Rapport Université de Neuchâtel, sur mandat de
624 l'Office fédéral de l'environnement, des forêts et du paysage (OFEFP), 154, + annexes.

625 Buttler, A., G. Mulhauser, G., 1994. The result of a century of hydrological control - the
626 fenlands of La Grande Caricaie, in: Gruenig, A. (ed.). *Mires and Man. Mire Conservation in*
627 *a Densely Populated Country - the Swiss Experience. Excursion Guide and Symposium*
628 *Proceedings of the 5th Field Symposium of the International Mire Conservation Group*
629 *(IMCG) to Switzerland 1992.* Birmensdorf, Swiss Federal Institute for Forest, Snow and
630 *Landscape Research*, 173-180.

631 Buttler, A., Gallandat, J.D., 1989. Phytosociologie des prairies humides de la rive sud du lac de
632 Neuchâtel (Suisse) et modèle de succession autogène. *Phytocoenologia* 18, 129-158.

633 Buttler, A., Gobat, J.M., 1991. Les sols hydromorphes des prairies humides de la rive sud du
634 lac de Neuchâtel (Suisse). *Bulletin d'Écologie* 22, 405-418.

635 Cui, Y.X., Fang, L.C., Guo, X.B., Wang, X., Zhang, Y.J., Li, P.F., Zhang, X.C., 2018.
636 Ecoenzymatic stoichiometry and microbial nutrient limitation in rhizosphere soil in the arid
637 area of the northern Loess Plateau, China. *Soil Biology & Biochemistry* 116, 11-21.

638 Dawson, T.P., Berry, P.M., Kampa, E., 2003. Climate change impacts on freshwater wetland
639 habitats. *Journal for Nature Conservation* 11, 25-30.

640 De Graaff, M.A., Classen, A.T., Castro, H.F., Schadt, C.W., 2010. Labile soil carbon inputs
641 mediate the soil microbial community composition and plant residue decomposition rates.
642 *New Phytologist* 188, 1055-1064.

643 De Neiff, A.P., Neiff, J.J., Casco, S.L., 2006. Leaf litter decomposition in three wetland types
644 of the Paraná River floodplain. *Wetlands* 26, 558-566.

645 Demars, B.O.L., Edwards, A.C., 2007. Tissue nutrient concentrations in freshwater aquatic
646 macrophytes: high inter-taxon differences and low phenotypic response to nutrient supply.
647 Freshwater Biology 52, 2073-2086.

648 Dykyjová, D., Úlehlová, B., 1978. Structure and chemistry of the fishpond bottom, Pond
649 Littoral Ecosystems. Springer, Berlin, pp. 141-156.

650 Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G., Enquist, B.J., 2010. Biological
651 stoichiometry of plant production: metabolism, scaling and ecological response to global
652 change. New Phytologist 186, 593-608.

653 Freeman, C., Ostle, N.J., Fenner, N., Kang, H., 2004. A regulatory role for phenol oxidase
654 during decomposition in peatlands. Soil Biology & Biochemistry 36, 1663-1667.

655 Fu, X.H., Li, F., Zhu, L.L., Xie, Y.H., Hu, C., Chen, X.S., Deng, Z.M., 2018. Change in
656 ecological stoichiometry of *Carex brevicuspis* in response to seasonal dynamics and
657 elevation in Dongting Lake, China. Nordic Journal of Botany 36, e01821.

658 Gibbs, J.P., 2000. Wetland loss and biodiversity conservation. Conservation Biology 14, 314-
659 317.

660 Gil-Sotres, F., Trasar-Cepeda, C., Leirós, M., Seoane, S., 2005. Different approaches to
661 evaluating soil quality using biochemical properties. Soil Biology and Biochemistry 37, 877-
662 887.

663 Güsewell, S., Koerselman, W., 2002. Variation in nitrogen and phosphorus concentrations of
664 wetland plants. Perspectives in Plant Ecology, Evolution and Systematics 5, 37-61.

665 Heuck, C., Weig, A., Spohn, M., 2015. Soil microbial biomass C:N:P stoichiometry and
666 microbial use of organic phosphorus. Soil Biology & Biochemistry 85, 119-129.

667 Hingray, B., Mouhous, N., Mezghani, A., Bogner, K., Schaefli, B., Musy, A., 2007. Accounting
668 for global-mean warming and scaling uncertainties in climate change impact studies:
669 application to a regulated lake system. Hydrology and Earth System Sciences 11, 1207-1226.

670 Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytowskiak, R., Hale, C., Karolewski, P.,
671 2006. Tree species effects on decomposition and forest floor dynamics in a common garden.
672 *Ecology* 87, 2288-2297.

673 Hopkinson, C.S., 1992. A comparison of ecosystem dynamics in freshwater wetlands. *Estuaries*
674 15, 549-562.

675 Hu, M.J., Penuelas, J., Sardans, J., Sun, Z.G., Wilson, B., Huang, J.F., Zhu, Q.L., Tong, C.,
676 2018. Stoichiometry patterns of plant organ N and P in coastal herbaceous wetlands along
677 the East China Sea: implications for biogeochemical niche. *Plant and Soil* 431, 273-288.

678 Kardol, P., Cregger, M.A., Campeny, C.E., Classen, A.T., 2010. Soil ecosystem functioning
679 under climate change: plant species and community effects. *Ecology* 91, 767-781.

680 Kazakou, E., Garnier, E., Navas, M.L., Roumet, C., Collin, C., Laurent, G., 2007. Components
681 of nutrient residence time and the leaf economics spectrum in species from Mediterranean
682 old-fields differing in successional status. *Functional Ecology* 21, 235-245.

683 Kim, Y., Ullah, S., Moore, T.R., Roulet, N.T., 2014. Dissolved organic carbon and total
684 dissolved nitrogen production by boreal soils and litter: the role of flooding, oxygen
685 concentration, and temperature. *Biogeochemistry* 118, 35-48.

686 Lai, X., Shankman, D., Huber, C., Yesou, H., Huang, Q., Jiang, J., 2014. Sand mining and
687 increasing Poyang Lake's discharge ability: A reassessment of causes for lake decline in
688 China. *Journal of Hydrology* 519, 1698-1706.

689 Li, F., Gao, H., Zhu, L.L., Xie, Y.H., Yang, G.S., Hu, C., Chen, X.S., Deng, Z.M., 2017. Foliar
690 nitrogen and phosphorus stoichiometry of three wetland plants distributed along an elevation
691 gradient in Dongting Lake, China. *Scientific Reports* 7, 2820.

692 Li, F., Hu, C., Xie, Y.H., Liu, W.Z., Chen, X.S., Deng, Z.M., Hou, Z.Y., 2018. Influence of
693 Differ P Enrichment Frequency on Plant Growth and Plant C:N:P in a P-Limited Subtropical
694 Lake Wetland, China. *Frontiers in Plant Science* 9, 1608.

695 Liu, F.D., Liu, Y.H., Wang, G.M., Song, Y., Liu, Q., Li, D.S., Mao, P.L., Zhang, H., 2015.
 696 Seasonal Variations of C: N: P Stoichiometry and Their Trade-Offs in Different Organs of
 697 *Suaeda salsa* in Coastal Wetland of Yellow River Delta, China. Plos One 10, e0138169.
 698 Manzoni, S., Taylor, P., Richter, A., Porporato, A., Ågren, G.I., 2012. Environmental and
 699 stoichiometric controls on microbial carbon-use efficiency in soils. New Phytologist 196,
 700 79-91.
 701 Mao, R., Chen, H.M., Zhang, X.H., Shi, F.X., Song, C.C., 2016. Effects of P addition on plant
 702 C:N:P stoichiometry in an N-limited temperate wetland of Northeast China. Science of the
 703 Total Environment 559, 1-6.
 704 Neckles, H.A., Neill, C., 1994. Hydrologic Control of Litter Decomposition in Seasonally
 705 Flooded Prairie Marshes. Hydrobiologia 286, 155-165.
 706 Olsen, S., Cole, C., Watanabe, F., Dean, L., 1954. Estimation of available phosphorus in soils
 707 by extraction with sodium bicarbonate. USDA Circular Nr 939, US Gov. Print. Office,
 708 Washington, D.C.
 709 Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological
 710 systems. Ecology 44, 322-331.
 711 Qiu, S., McComb, A.J., 1995. Planktonic and microbial contributions to phosphorus release
 712 from fresh and air-dried sediments. Marine and Freshwater Research 46, 1039-1045.
 713 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2020. nlme: Linear and Nonlinear Mixed Effects
 714 Models. R package version 3.1-147, <https://CRAN.R-project.org/package=nlme>. Ramsar,
 715 2013. The Ramsar Manual. 6th ed. Ramsar Convention Secretariat, Switzerland, pp. 110.
 716 Richardson, A.E., Barea, J.-M., McNeill, A.M., Prigent-Combaret, C., 2009. Acquisition of
 717 phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms.
 718 Plant and Soil 321, 305-339.

719 Rokosch, A.E., Bouchard, V., Fennessy, S., Dick, R., 2009. The use of soil parameters as
720 indicators of quality in forested depressional wetlands. *Wetlands* 29, 666-677.

721 Sardans, J., Bartrons, M., Margalef, O., Gargallo-Garriga, A., Janssens, I.A., Ciais, P.,
722 Obersteiner, M., Sigurdsson, B.D., Chen, H.Y.H., Peñuelas, J., 2017. Plant invasion is
723 associated with higher plant-soil nutrient concentrations in nutrient-poor environments.
724 *Global Change Biology* 23, 1282-1291.

725 Sardans, J., Peñuelas, J., 2012. The Role of Plants in the Effects of Global Change on Nutrient
726 Availability and Stoichiometry in the Plant-Soil System. *Plant Physiology* 160, 1741-1761.

727 Sarneel, J.M., Hefting, M.M., Kowalchuk, G.A., Nilsson, C., Van der Velden, M., Visser, E.J.,
728 Voosenek, L.A., Jansson, R., 2019. Alternative transient states and slow plant community
729 responses after changed flooding regimes. *Global Change Biology* 25, 1358-1367.

730 Shrestha, J., Niklaus, P.A., Pasquale, N., Huber, B., Barnard, R.L., Frossard, E., Schleppi, P.,
731 Tockner, K., Luster, J., 2014. Flood pulses control soil nitrogen cycling in a dynamic river
732 floodplain. *Geoderma* 228, 14-24.

733 Sinsabaugh, R.L., Hill, B.H., Shah, J.J.F., 2009. Eoenzymatic stoichiometry of microbial
734 organic nutrient acquisition in soil and sediment. *Nature* 462, 795-798.

735 Sinsabaugh, R.L., Lauber, C.L., Weintraub, M.N., Ahmed, B., Allison, S.D., Crenshaw, C.,
736 Contosta, A.R., Cusack, D., Frey, S., Gallo, M.E., Gartner, T.B., Hobbie, S.E., Holland, K.,
737 Keeler, B.L., Powers, J.S., Stursova, M., Takacs-Vesbach, C., Waldrop, M.P., Wallenstein,
738 M.D., Zak, D.R., Zeglin, L.H., 2008. Stoichiometry of soil enzyme activity at global scale.
739 *Ecology Letters* 11, 1252-1264.

740 Swanson, W., De Jager, N.R., Strauss, E., Thomsen, M., 2017. Effects of flood inundation and
741 invasion by *Phalaris arundinacea* on nitrogen cycling in an Upper Mississippi River
742 floodplain forest. *Ecohydrology* 10, e1877.

743 Wang, M., Moore, T.R., 2014. Carbon, Nitrogen, Phosphorus, and Potassium Stoichiometry in
744 an Ombrotrophic Peatland Reflects Plant Functional Type. *Ecosystems* 17, 673-684.

745 Wang, W.Q., Sardans, J., Wang, C., Zeng, C.S., Tong, C., Bartrons, M., Asensio, D., Penuelas,
746 J., 2018. Shifts in plant and soil C, N and P accumulation and C:N:P stoichiometry associated
747 with flooding intensity in subtropical estuarine wetlands in China. *Estuarine Coastal and*
748 *Shelf Science* 215, 172-184.

749 Wang, W.Q., Wang, C., Sardans, J., Tong, C., Jia, R.X., Zeng, C.S., Penuelas, J., 2015a. Flood
750 regime affects soil stoichiometry and the distribution of the invasive plants in subtropical
751 estuarine wetlands in China. *Catena* 128, 144-154.

752 Wang, W.Q., Wang, C., Sardans, J., Zeng, C.S., Tong, C., Peñuelas, J., 2015b. Plant invasive
753 success associated with higher N-use efficiency and stoichiometric shifts in the soil–plant
754 system in the Minjiang River tidal estuarine wetlands of China. *Wetlands ecology and*
755 *management* 23, 865-880.

756 Wang, X.L., Xu, L.G., Wan, R.G., Chen, Y.W., 2016. Seasonal variations of soil microbial
757 biomass within two typical wetland areas along the vegetation gradient of Poyang Lake,
758 China. *Catena* 137, 483-493.

759 Wilson, J.S., Baldwin, D.S., Rees, G.N., Wilson, B.P., 2011. The Effects of Short-Term
760 Inundation on Carbon Dynamics, Microbial Community Structure and Microbial Activity in
761 Floodplain Soil. *River Research and Applications* 27, 213-225.

762 Wolf, K.L., Noe, G.B., Ahn, C., 2013. Hydrologic Connectivity to Streams Increases Nitrogen
763 and Phosphorus Inputs and Cycling in Soils of Created and Natural Floodplain Wetlands.
764 *Journal of Environmental Quality* 42, 1245-1255.

765 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-
766 Bares, J., Chapin, T., Cornelissen, J.H., Diemer, M., 2004. The worldwide leaf economics
767 spectrum. *Nature* 428, 821-827.

768 Xu, S.Q., Liu, X., Li, X.J., Tian, C.J., 2019. Soil organic carbon changes following wetland
769 cultivation: A global meta-analysis. *Geoderma* 347, 49-58.

770 Zechmeister-Boltenstern, S., Keiblinger, K.M., Mooshammer, M., Peñuelas, J., Richter, A.,
771 Sardans, J., Wanek, W., 2015. The application of ecological stoichiometry to plant–
772 microbial–soil organic matter transformations. *Ecological Monographs* 85, 133-155.

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Tables

Table 1 Effects of vegetation type, growing season, and their interaction on plant and moss parameters. *F*-values and associated *P*-values (* for $P < 0.05$, ** for $P < 0.01$ and *** for $P < 0.001$) are indicated (see values of variables in [Supplementary Table S2](#)).

	Vegetation type		Growing season		VT × GS	
Aboveground biomass (AGB)	3.5		189.0	***	13.4	**
C content of AGB	3.5		2.4		0.0	
N content of AGB	17.1	**	0.7		4.5	*
P content of AGB	111.7	***	119.9	***	27.4	***
Litter (L)	14.6	**	7.4	*	1.9	
C content of L	10.0	*	18.0	**	0.4	
N content of L	1.2		9.5	*	0.2	
P content of L	4.5		4.9		2.0	
Moss biomass (MB)	3.2		2.9		7.8	*
C content of MB	3.0		0.6		0.6	
N content of MB	6.5	*	0.8		1.1	
P content of MB	13.2	**	4.7		2.1	
Belowground biomass (BGB)	10.8	**	4.4		0.7	
C content of BGB	7.9	*	4.9		0.1	
N content of BGB	1.9		12.1	**	3.0	
P content of BGB	0.4		32.9	***	1.3	

Table 2 Synthesis of the effects of vegetation gradient and growing season on plant and moss parameters. Vegetation gradient is considered from lakeshore to upland (*i.e.* from *C. elata* to *S. nigricans* community) while growing season is considered from beginning to peak of growing season. ↘ indicates a significant decrease of the value (↘→ indicates a significant decrease only between two vegetation types), ↗ indicates a significant increase of the value and the absence of arrow indicates the absence of a significant effect (see [Table 1](#)).

	Vegetation gradient	Growing season
Aboveground biomass (AGB)		↗
C content of AGB		
N content of AGB	↘	
P content of AGB	↘	↘
Litter (L)	↘→	↘
C content of L	↘	↗
N content of L		↘
P content of L		
Moss biomass (MB)		
C content of MB		
N content of MB	↘	
P content of MB	↘	
Belowground biomass (BGB)	↘	
C content of BGB	↘	
N content of BGB		↘
P content of BGB		↘

791 **Table 3** Effects of soil layer, vegetation type, growing season, and their interaction on soil physico-chemical, microbial and enzymatic parameters.
792 *F*-values and associated *P*-values (* for *P* < 0.05, ** for *P* < 0.01 and *** for *P* < 0.001) are indicated (see values of variables in [Supplementary](#)
793 [Table S3](#)).

794

	Soil layer		Vegetation type		Growing season		SL × VT		SL × GS		VT × GS		SL × VT × GS	
Bulk density (BD)	243.2	***	21.5	**	1.9		6.2	***	0.3		1.7		0.6	***
Soil water content (SWC)	171.2	***	15.4	**	3.7		2.6	*	0.9		3.1		0.1	
Soil pH	139.8	***	18.4	**	145.3	***	1.0		0.5		2.8		1.3	
Soil organic matter (LOI)	423.1	***	23.4	**	0.6		16.1	***	0.2		1.7		0.2	
Soil organic C (TOC)	160.8	***	15.7	**	0.9		7.0	***	0.3		1.2		0.4	
Soil N (TN)	422.8	***	30.0	***	0.3		11.2	***	0.7		1.9		0.6	
Soil P (TP)	240.3	***	13.5	**	1.3		18.4	***	0.2		0.3		0.6	
Soil available C (DOC)	402.0	***	10.7	**	0.0		10.6	***	1.8		4.8	*	0.5	
Soil available N (DN)	139.8	***	2.7		138.3	***	5.2	**	3.9	*	3.1		1.8	
Soil available P (DP)	372.6	***	19.2	**	2.0		6.5	***	0.2		2.9		1.1	
Ammonium (N-NH ₄)	193.5	***	7.2	*	0.6		4.6	**	6.0	**	0.0		0.5	
Nitrate (N-NO ₃)	41.4	***	17.7	**	40.3	***	2.6		2.1		3.2	*	0.5	
Microbial biomass C (MBC)	467.0	***	6.0	*	4.1		14.6	***	0.9		2.9		1.9	
Microbial biomass N (MBN)	804.2	***	11.1	**	4.1		11.5	***	0.5		1.0		0.6	
Microbial biomass P (MBP)	525.9	***	47.4	***	0.3		22.2	***	0.1		0.7		0.6	
β-glucosidase (BG))	206.9	***	67.5	***	13.6	**	4.4	**	2.7		8.1	**	4.1	**
Leucine aminopeptidase (LAP)	642.1	***	16.0	***	20.5	***	0.6		19.2	***	18.2	***	0.7	
β -1, 4-N-acetylglucosaminidase (NAG)	156.0	***	54.3	***	29.4	***	12.0	***	2.0		0.7		10.0	***
Phosphatase (PHO)	169.7	***	29.9	***	21.8	***	7.2	***	21.6	***	6.9	**	4.5	**

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796

Table 4 Synthesis of the effects of soil depth increase, vegetation gradient and growing season, on soil physico-chemical, microbial and enzymatic parameters. Soil depth increase is considered from surface organic to lower mineral layer, vegetation gradient from lakeshore to upland (*i.e.* from *C. elata* to *S. nigricans* community), while growing season is considered from beginning to peak of growing season. ↘ indicates a significant decrease of the value (↘→ indicates a significant decrease only between two vegetation types), ↗ indicates a significant increase of the value and the absence of arrow indicates the absence of a significant effect (see Table 3).

	Increasing soil depth	Vegetation gradient	Growing season
<i>Soil physico-chemical parameters</i>			
Bulk density (BD)	↗	↗	
Soil water content (SWC)	↘	↘	
Soil pH	↗	↗	↗
Soil organic matter (LOI)	↘	↘	
Soil organic C (TOC)	↘	↘	
Soil N (TN)	↘	↘	
Soil P (TP)	↘	↘	
Soil available C (DOC)	↘	↘→	
Soil available N (DN)	↘		↗
Soil available P (DP)	↘	↘	
Ammonium (N-NH ₄)	↘	↘→	
Nitrate (N-NO ₃)	↘	↘	↘
<i>Microbial parameters</i>			
Microbial biomass C (MBC)	↘	↘	
Microbial biomass N (MBN)	↘	↘	
Microbial biomass P (MBP)	↘	↘	
<i>Enzymatic parameters</i>			
β-glucosidase (BG)	↘	↘	↗
Leucine aminopeptidase (LAP)	↘	↘	↗
β -1, 4-N-acetylglucosaminidase (NAG)	↘	↘	↗
Phosphatase (PHO)	↘	↘	↗

Figure legend

Fig. 1 Aboveground plant biomass (a), moss biomass (b), N content in aboveground plant biomass (c) and P content in aboveground plant biomass (d) according to the vegetation type $\times$ growing season interaction (Table 1). Each bar represents the mean value $\pm$ SE; $n = 4$. For (a), (b) and (c), different letters denote significant differences among plant communities according to the selected growing season period with $a > b > c$. For (d), stars indicate significant differences between the beginning and the peak of growing season according to the selected plant community with * for $P < 0.05$, ** for $P < 0.01$ and *ns* for $P > 0.05$. CE = *C. elata*, CP = *C. panicea*, SN = *S. nigricans*, GS = growing season.

Fig. 2 Soil total P content (a), available P content (b), microbial biomass C (c) and leucine aminopeptidase activity (d) according to the soil layer $\times$ vegetation type interaction (Table 3). Each bar represents the mean value $\pm$ SE; $n = 8$. Different letters denote significant differences among plant communities according to the selected soil layer with $a > b > c$. CE = *C. elata*, CP = *C. panicea*, SN = *S. nigricans*. LAP = leucine aminopeptidase.

Fig. 3 Soil available C (a) and nitrate (b) contents according to the vegetation type $\times$ growing season interaction (Table 3). Each bar represents the mean value $\pm$ SE; $n = 12$. Different letters denote significant differences among vegetation types according to the selected growing season period with $a > b$. CE = *C. elata*, CP = *C. panicea*, SN = *S. nigricans*.

827

828 **Fig. 4** Soil available N (a) and ammonium (b) content according to the soil layer × growing
829 season interaction ([Table 3](#)). Each bar represents the mean value ± SE; n= 12. Stars indicate
830 significant differences between the beginning and the peak of growing season according to the
831 selected soil layer with * for $P < 0.05$, ** for $P < 0.01$, *** for $P < 0.001$ and *ns* for $P > 0.05$.
832 GS = growing season.

833

834 **Fig. 5** Principal component analysis (PCA) illustrating the relationship between stoichiometry
835 of C, N and P in the plant material (above and belowground biomass, moss and litter), in the
836 bulk soil and in its dissolved fraction, and in the microbial biomass in the organic layer at the
837 two sampling periods, April and July. Samples are labelled with sampling period (A: April, J:
838 July) and vegetation type (CE: *Carex elata*, CP: *Carex panicea*, SN: *Schoenus nigricans*).
839 Variables are labelled as in [Tables 1-4](#).

840

Fig. 1

845 **Fig. 2**

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Fig. 3

Fig. 4

857 **Fig. 5**

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