Decomposition rate, and carbon and nitrogen dynamics of *Sphagnum* litter: lessons from a peat bog

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ABSTRACT

Decomposition rates and changes of carbon and nitrogen contents of *Sphagnum* litter in mire vegetation can help to explore the ecological effects of climate change and the role of environmental factors from a local to an ecosystem scale. The objective of the study was to determine the relationship between mentioned parameters in small and isolated *Sphagnum* dominated mires. Measurements had been conducted throughout a year by placing litterbags filled with *Sphagnum* biomass in three vegetation types (open peat bog, poor fen, alder carr*)* of a mire ecosystem in Hungary. Peat decomposition rates differed to a great extent; the slowest decomposition rate (39.1±9.52%) was in the alder carr, indicating that slower decomposition could be characteristic for this kind of vegetation type of mire. Between *Sphagnum* dominated microhabitats, open peat bog showed medium (65.57±4.05) while poor fen the fastest (68.61±5.5) rates in decomposition. The C/N ratio of the *Sphagnum* litter showed significant decrease (*P* <0.005) in all studied micro-environments. Slower N release was observed from litter of *Alnus* dominated association (31.3±6.9%) compared to *Sphagnum* dominated ones (56.5±8.3%). Our findings showed that the decomposition rates were more dependent on vegetation type than C/N ratio and this relationship was also revealed at a small spatial scale.

INTRODUCTION

Decomposition is one of the most important processes in the biogeochemical cycling of ecosystems especially in the carbon cycle (Berg and McClaugherty 2008). The amount of available nutrients depends on the rate of decomposition and determines productivity, especially in mire ecosystems (Haraguchi *et al.* 2002). Decomposition rates are usually low in these ecosystems due to low temperature, water-logging, anoxic and acidic conditions and the low nutrient concentration of the litter (Aerts *et al.* 2006). These ecosystems can accumulate a large amount of organic matter, thus they are considered as the largest terrestrial carbon storage of the earth (Charman *et al.* 2013). As the main litter producers are *Sphagnum* mosses, the growth biomass accumulation and decomposition rates in these habitats mainly depend on local environmental conditions in them (*i.e.* in habitats), therefore understanding decomposition processes of this ecosystem can be an emphasized question of mire ecology. Decomposition rates mainly depend on the activity of microorganisms (Kulichevskaya *et al.* 2007) which are influenced to a great extent by specific substrates (Haraguchi *et al.* 2003) just as the amount of carbon available for dominant vegetation of a peatland (Limpens *et al.* 2008). Studies revealed that the nutrient conditions of the study site have stronger effect on the degree of decomposition rates than the quality of litter (Rejmánková and Houdková 2006). Changes

of environmental factors also influence decomposition, thus raised nitrogen influx and temperature (Malmer and Wallén 1999) or fertilization (Bubier *et al.* 2007) would increase the rate of the decay processes.

Studies showed that different type of mires had significantly different decomposition rates which were higher in mineral poor fens than bogs (Moore *et al.* 2007). The rate of decomposition is strongly dependent on litter position within the peat profile, which decreased with depth (Moore *et al.* 2007). However, there were also differences between different types of fens as mineral-rich fens had higher decomposition rates than the base-poor fens (Verrhoeven and Toth 1995).

Some works reported a higher decomposition rate for *Carex* sp. litter than for peat mosses, which they attributed to the presence of sphagnols (phenolic compounds) in mosses (Verrhoeven and Toth 1995, Certini *et al.* 2014). *Sphagnum* species also showed interspecific differences in resistance to decomposition (Rochefort *et al.* 1990, Belyea 1996). Peat accumulation is higher in hummock formation than in hollow ones due to the lower decomposition rates, or to higher productivity, which means that the decay of hollow-species (like *Sphagnum cuspidatum*, *Sphagnum fallax*) is faster (Rochefort *et al.* 1990). Otherwise, plant associations dominated by different plant species reflect variable production rates (Péli *et al.* 2015) and, consequently, can influence the decomposition rates.

Changes in C/N ratio of *Sphagnum* litter are also a good trait to indicate the environmental changes by controlling decay processes. Although the nitrogen content of peat mosses is low while it can be significant in case of bog's herbaceous plants (Aerts *et al.* 1999). The local microclimate (sunny and shady sites) basically determines the carbon cycle of the vegetation (Péli *et al.* 2015) which affects the C/N ratio. A positive correlation showed between shady habitat and decreased C/N ratio in case of hummock species, *Sphagnum capillifolium* (Manninen *et al.* 2011). Increased C/N ratio was reported in hummock *Sphagnum* species responded to drought (Bu *et al.* 2013), as well.

In this study we report an *in situ* investigation of the relationship between decomposition rates and C, N contents of *Sphagnum* litter in three plant associations of two *Sphagnum* dominated mires. This study was designed to compare decomposition rates and carbon, nitrogen contents estimated by *Sphagnum* litterbag incubation and investigate their relation to different habitats represented by different plant associations. The relative ecological importance of these variables at the local scale is essential for understanding responses of ecosystem processes to environmental changes. We hypothesised that the investigated parameters would correlate with different vegetation types and they can identify with characteristic features. Specifically, we assumed that (i) mass loss would be positively related to C, N releases of litter bags; (ii) litter will decay a slower in *Alnus* carr than in *Sphagnum* dominated ones; (iii) carbon release would be significantly faster than nitrogen release; (iv) nutrient releases would differ between habitats, *i.e.* depend on plant association/composition.

MATERIALS AND METHODS

Site description

The vegetation at the study sites of Nyírestó and Báb-tava (48°11′3″N, 22°30′6″E and 48°11′16″N, 22°29′0″E) is a mire ecosystem dominated by *Sphagnum angustifolium* and *Sphagnum palustre, Eriophorum vaginatum, Eriophorum angustifolium, Juncus effusus*, *Carex lasiocarpa* and *Vaccinium oxycoccos* (Szurdoki and Nagy 2002). Mires located in the Bereg Plain (NE Hungary), which are silted backwaters of Tisza River. The presence of raised bog associations on the Bereg-plain is southernmost occurrences in the plains of Europe. The mean annual precipitation is 630–660 mm and the mean annual temperature range is 9.4–9.5°C and the climate is moderately warm with cold winter. Average sizes of these ox-bows were less than 5 hectares. The study sites belong to Hortobágy National Park (Fig. 1.) and have been under protection for 60 years.

Investigations were carried out in three different associations of mires: open peat bog (*Eriophoro vaginati–Sphagnetum)*, poor fen (*Eriophoro angustifoliae–Sphagnetum)* and al-
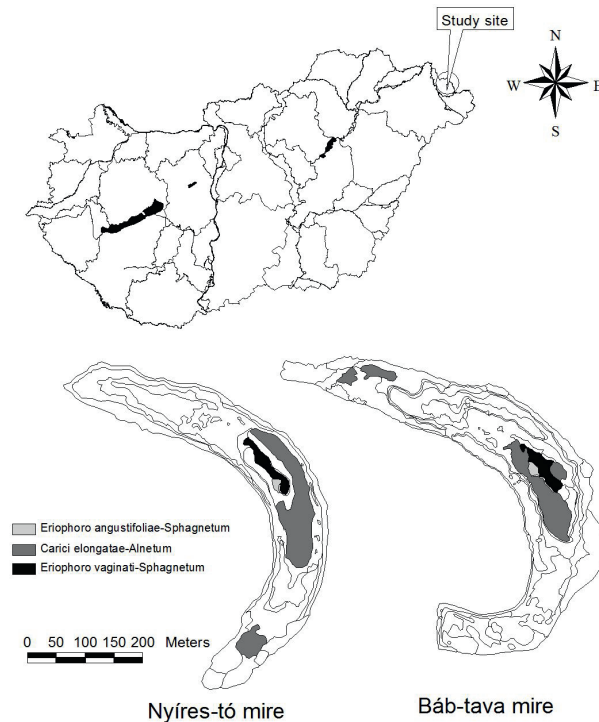
Fig. 1. Locations of the investigated mires in Hungary showing three different plant associations (*Carici elongatae–Alnetum* – alder carr, *Eriophoro vaginati–Sphagnetum* – open peat bog, *Eriophoro angustifoliae–Sphagnetum* – poor fen) in Nyíres-tó and Báb-tava mires, respectively.

der carr (*Carici elongatae–Alnetum*) (Fig. 1.). Open peat bog and alder carr were dominant in the middle of the bed. The dominant peat mosses were *Sphagnum angustifolium* and *Sphagnum palustre*. In the early 1960-ties, Báb-tava was burnt which caused the degradation of vegetation (Simon 1992). Due to arid years and human effects, the cover of tree–dominated associations increased and the habitats of protected rare species decreased. After the artificial flooding of the mires, degradation processes slowed down and quick regeneration started. The average pH value changed between 3.5 and 6.0. In the open peat bog and poor fen habitats, *Sphagnum* covered the entire surface besides vascular plants dominated by *Eriophorum vaginatum, Eriophorum angustifolium, Juncus effusus, Carex lasiocarpa* and *Vaccinium oxycoccos*. At the poor fen habitat the cover of *Eriophorum angustifolium* was higher while trees and shrubs were negligible. Alder carr dominated by mainly *Alnus glutinosa* mixing with *Frangula alnus* or *Betula pubescens*, *Sphagnum* coverage was low (Péli *et al.*

2015). Dominant herbs were *Carex elongata*, *Lysimachia vulgaris* and different mosses like *Sphagnum angustifolium* and *Sphagnum fimbriatum* were also present.

Litter decomposition and carbon and nitrogen analysis

Decomposition rates were determined *in situ* by litterbag technique in three associations of two peat bog areas. To eliminate the possible differences among the locations samples were collected from each association then mixed to get a well homogenous sample. At each location, *Sphagnum angustifolium* was used for decomposition samples as it was the most common and frequent peat moss in both investigated mires. Litterbags were used containing only one type of litter (*Sphagnum angustifolium*), based on the dominant and common peat moss in all experiment fields. On the other hand, the peat moss cover of the alder carr association was dominant while could not be found in large numbers. However, *S. an-*

gustifolium was also used for the experiment in this habitat with the aim of comparing the rates of decomposition. Decomposition rates of alder trees (which were dominant in this association) are not relevant as they refer to other two sites and not during the one year of incubation. We sampled only capitula and the 10 upper centimetre parts (living biomass) of the mosses to make sure that these parts did not start to decay yet and all brownish parts were eliminated. The samples were collected at the end of the growing season in October. Materials were dried for 24 hours at 40°C and used for filling 10×10 cm mosquito netting bags (mesh size = 0.3 mm in which water can flow through) with 1.0 g *Sphagnum*. Applied mesh size was provided for the natural decomposition processes allowing free movement of organic and inorganic matters in natural field condition. All bags were labelled with unique identification numbers and also their weight was measured. Samples were placed horizontally and buried at approximately 15 cm from the surface, at a distance of 1–2 meters from each other in all three associations in October. Six litterbags were sampled from each site after 12 months of decomposition. After one year of incubation, the litterbags were removed and cleaned of extraneous litters, soil particles, foreign materials and roots, then the contents were dried for 24 hours at 40°C and weighed. The relative mass loss was calculated from the initial mass and the mass after removal from the field. Removed *Sphagnum* litter was also analysed for carbon and nitrogen content as described below.

Decomposition rates were expressed as percentage of mass loss after 12 month of field burial as follows:

Decomposition rates (%) = $((w_0 - w_1)/w_0)$ $\times 100$ (1)

where w_0 is the weight of sample in the bag before burial and w_1 is the weight of the same content after 12 months.

Constant decomposition (k–values) was calculated by O l s o n's (1963) model:

Xt = X0 e^{-kt}   (2)

where *X0* and *Xt* are litter dry weight at the beginning of incubation and at time re-

spectively, *t* is time in days (365), and *k* is the constant of decomposition. We performed the calculation of *k* linear regressions of *ln* (X0/Xt) *vs* time. The *k* constant was calculated for the complete incubation (365 days) in the field.

Sphagnum decomposed samples were oven-dried (40°C) to constant weight and finely ground to be analysed for C and N by flash combustion method using a Carlo-Erba (Fisons) NA 1500 elemental analyser. Pure data of carbon and nitrogen content refer to mg kg^{-1} from which C:N ratio of *Sphagnum* litter was calculated. Control samples, which were used to estimate the initial C and N contents of the litter, were analysed after autumn collection prior to putting samples to litter bags and placing them for one year in all the three habitats of peat bogs.

For each litter bag the release of C, N was calculated as percentage (%) of initial total content:

Carbon, nitrogen release (%) = $((x_0 w_0 - x_1 w_1)/(w_0 w_0)) \times 100$ (3)

where x_0 is the mean nutrient concentration of plant litter before burial and x_1 is the nutrient concentration in the litter bag after one year of burial.

Statistical analyses

Differences among mass loss, C/N ratio, C and N release of *Sphagnum* litters at different plant associations were analysed by the Student's *t*-test and analyses of variance (ANOVA) using Statistica 5.1 software. One- and two-way ANOVA was applied to examine significant differences between decomposition rates, and C and N releases; *Tukey's HSD* test was used to test for significant differences in variability among plant associations and between habitats.

RESULTS

Analysis of the litterbag samples revealed differences in decomposition rates between association types (Table 1) as well as between mires. The decomposition rates of biomass

Table 1. *Sphagnum* litter decomposition in three plant: mass loss, the constant of decomposition rates (k-values). Different letters indicate statistically significant differences of the same association between different habitats ($P < 0.005$). Statistically significant differences ($P < 0.01$) between different associations in the same habitat are indicated by an asterisk. Differences were compared using Student's *t*-test. Control samples were analyzed in autumn before the litter bag experiment was started. Results are shown as ± SE of mean (n = 6).

Site	Plant association	Field incubation		
		Mean mass loss (%)	*k*-values (year^{-1})	C:N ratio
Nyíres-tó	*Carici elongatae–Alnetum*	39.10±9.52a*	0.0014±0.0004a*	26.38±1.57
Mire	*Eriophoro vaginati–Sphagnetum*	65.57±4.05	0.0029±0.0003	27.80±1.47
	Eriophoro angustifoliae–Sphagnetum	65.93±9.34	0.003±0.0008	29.86±4.63
Báb-tava	*Carici elongatae–Alnetum*	62.78±5.64b	0.0027±0.00004b	30.18±3.41
Mire	*Eriophoro vaginati–Sphagnetum*	64.26±8.57	0.0029±0.00006	29.48±3.60
	Eriophoro angustifoliae–Sphagnetum	68.61±5.50	0.003±0.0005	25.07±2.65
	Control	37.04±2.44		

increased in the order alder carr < open peat bog < poor fen (Table 1) (significant differences by Tukey's test between alder carr and *Sphagnum* dominated ones) similarly as C/N ratio in case of Nyíres-tó mire (Fig. 2a). The largest mass loss was detected in case of poor fen which reflects increased decomposition in both mires. To examine the variance of Nyíres-tó mire results showed significant differences between two *Sphagnum* dominated associations and alder carr ($P < 0.01$) considering decomposition rates (Table 1). Comparing two habitats (Nyíres-tó and Báb-tava mires) significant differences in decomposition rates were observed only at alder carr site ($P < 0.005$). *In situ* decomposition litterbags study showed that the litter mass loss after one year of decomposition varied between 63% and 69% in the case of Báb-tava mire and 39% and 66% for Nyíres-tó mire, respectively. Poor fen showed the largest mass loss (69%) due to increased decomposition processes (Table 1).

Measured nitrogen content of litters varied more than the carbon ones which implied a progressive decrease in C/N ratio compared to control (Fig. 2a). Carbon/Nitrogen contents showed significant decrease ($P < 0.005$) in all investigated associations compared to control (Fig. 2a). Otherwise, there was a small variability in C/N ratios after one year of decomposition between associations, which did not show significant differences. The most significant effects in terms of C/N ratio were observed in the poor fen site, with the smallest value (68%) (Fig. 2a). However, there were no significant differences between the habitats or the associations. Following one year incubation, the highest value (30.18 ± 3.4) in C/N ratio was observed at the alder carr habitat of Báb-tava which was less with about 20% than control (37.04 ± 2.44) (Table 1).

The release of C was significantly ($P < 0.005$) different by Tukey's test between plant associations as well as between of habitats (Nyíres-tó and Báb tava) (Fig. 2b, Table 2). Particularly lower C release was found in alder carr association than in Nyíres-tó mire. N release in alder carr site was slower than *Sphagnum* dominated associations (Fig. 2c). Nitrogen release differed between habitats and plant associations (Table 2). The release of both nutrients significantly differed between plant associations with interaction be-
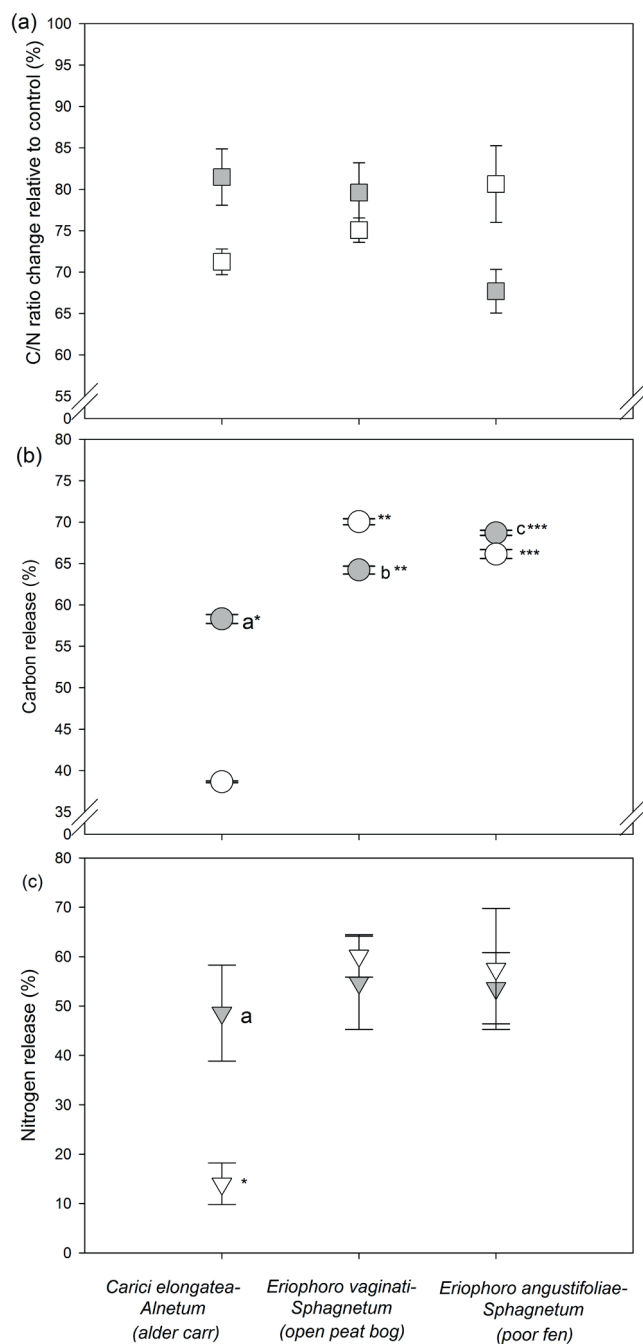
Fig. 2. C/N ratio of *Sphagnum* litter in control % (a) and mean percentage release of carbon (b), nitrogen (c) from the *Sphagnum* litter of three different associations studied of Nyíres-tó (C/N ratio – □; C release – ○; N release – ▽) and Báb-tava (C/N ratio – ■; C release – ●; N release – ▼) mires after one year of burial. In Fig. (a) all data are significantly different from control values (*P* <0.0001). In Figs (b) and (c) different letters indicate statistically significant differences of the same association between different habitats *(P* <0.005). Statistically significant differences (*P* <0.01) between different associations in the same habitat are indicated by an asterisk. Control samples were analyzed after autumn collection before the experiment. Error bars presented standard deviation (n = 6).

Table 2. Two-way ANOVA results for N and C release from *Sphagnum* litter after one year of burial. The two independent variables are habitat (Nyíres-tó and Báb-tava mires) and plant association types (*Eriophoro vaginati–Sphagnetum* – open peat bog, *Eriophoro angustifoliae–Sphagnetum* – poor fen, *Carici elongatae–Alnetum* – alder carr). F – value of ANOVA; df – degree of freedom; *P* value – probability value of significance

Nutrient	Source	F	df	*P* value
N	Habitat	2.27	1	0.157
	Plant association	9.62	2	<0.005
	Habitat x plant association	9.95	2	<0.005
C	Habitat	735.2	1	<0.005
	Plant association	4113.7	2	<0.005
	Habitat x plant association	1644.6	2	<0.005

tween investigated variables. There was significant differences only in N release of alder carr habitats (Fig. 2c).

Significant positive correlation ($P < 0.0001$) was found between in decomposition rates, carbon and nitrogen release respectively, all indicating a net loss of nutrients (Fig. 3). The mean annual release of C ($61 \pm 11\%$) was significantly higher ($P < 0.0001$) than N ($37 \pm 15\%$) nutrient loss.

DISCUSSION

Our data, sampled at three plant associations of two mires indicate significant differences in *Sphagnum* litter decomposition associated with dynamics of C, N content of *Sphagnum* litters in a relatively small separated area. A tight correlation between decomposition and nutrient release was revealed even in the case of different plant associations.

The difference between decomposition rates was mostly determined by the quality of leaf-litter inside each ecosystem (Aerts 1997) which changed with spatial and temporal diversity of environmental factors (Bragazza *et al.* 2008). The smallest mass loss was detected in *Carici elongatae–Alnetum* association (alder carr) ($39.1 \pm 9.5\%$) which is more than double of that reported in Dutch peatlands (Hoorens *et al.* 2003). *Sphagnum* dominated associations showed higher decomposition rates than alder carr. Similarly, CO_2 flux measurements of the open peat bog habitat of Nyíres-tó mire (Péli *et al.* 2015) showed also higher CO_2 uptake (increased activity) in any season than alder carr ones. Results can suggest that the decreased nitrogen availability limited the activity of microbial communities
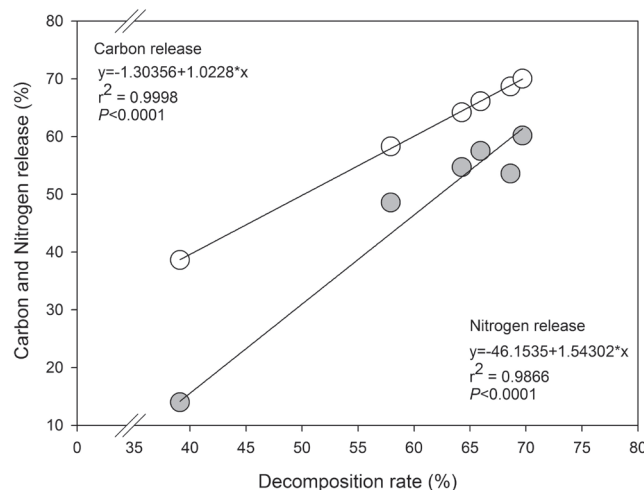

Fig. 3. Relationship between decomposition rates and the carbon, nitrogen release, respectively (○ indicated the carbon and ● nitrogen release). Data represent three different associations of Nyíres-tó and Báb-tava mires; mean values were calculated based on six litter bags retrieved after 1 year of incubation.

in *Sphagnum* dominated associations (poor fen and open peat bog) in contrast with carbon, which is easily accessible (B r a g a z z a *et al.* 2007). The investigated Hungarian sites showed significantly higher decomposition than the northern peat bogs, *e.g.* mass loss of Canadian peat bogs were 13–17% (W a d d i n g - t o n *et al.* 2003). It is not only due to the different climatic zones since decomposition rates showed differences in certain *Sphagnum* species (J o h n s o n and D a m m a n 1991): hollow former species (*e.g. Sphagnum cuspidatum*) showed half as high decomposition rates than hummock former *Sphagnum fuscum*. Namely, based on the microtopography of mires, differences were found in decomposition rates between hummock and hollow formations (N u n g e s s e r 2003, Wu *et al.* 2011). The decay rate of hummock forming *Sphagnum* species is smaller than that of hollow species as they retain their physiological structures for a longer time under peat layer (R o c h e f o r t *et al.* 1990, J o h n s o n *et al.* 1990, J o h n s o n and D a m m a n, 1991). Therefore, peat accumulation is faster in the case of hummock than hollow (O h l o s o n and D a h l b e r g 1991), the latter's decomposition rates are higher than ridge (J o h n s o n and D a m m a n 1993, L i m - p e n s and B e r e n d s e 2003). In our investigated mires, the dominant hollow former peat moss *Sphagnum angustifolium* showed faster decomposition rates than both of hummocks' and hollow former peat mosses' which were reported from northern areas (W a d d i n g t o n *et al.* 2003, M o o r e *et al.* 2007). Results also showed differences in decomposition rates inside a relatively small association due to presumably litter quality, different bacterial composition and anaerobic properties. It should be noted that the Canadian peat mosses are typically raised bog species which are not found on the present area of Hungary.

Consequently, decomposition (also mineral and carbon cycles) is considerably determined by characteristic features and compositions of litter from dominant plant species of a certain ecosystem. Otherwise, *Actinomyces* species which live on the roots of *Alnus glutinosa* insure continuous high nitrogen supply of alder trees contribute to delaying decomposition of dead plant material. It can partly explain the smallest mass loss in alder carr habitat.

Increased decomposition of *Eriophoro angustifoliae–Sphagnetum* association (poor fen) in the case of Báb-tava could be attributed to substantial disturbance of the area, as the mire was highly damaged in the 1960's (S i m o n 1992), while the nutrient content should have increased. The reason is that considerable part of the mire was burnt in the early 1960-ties on the other hand Báb-tava is surrounded by maize fields which caused pollution by fertilizers.

Sphagnum dominated associations were characterised by a higher N mineralisation compared to alder carr, which resulted faster litter decomposition. Carbon release was more significantly correlated with decomposition (mass loss) than the release of nitrogen related to litter quality.

Nitrogen immobilization depending on the plant association type could also show differences between *Sphagnum* dominated vegetation (B r a g a z z a *et al.* 2008). Otherwise the ratio of element contents and losses is significantly higher in the case of our mires following one year decomposition compared to northern boreal bogs (T h o r m a n n *et al.* 1999, C e r t i n i *et al.* 2014). Lower N content and higher C/N ratio can be observed in *Sphagnum* dominated associations than in *Alnus* ones of Nyíres-tó similarly to Glenn's with co-authors (G l e n n *et al.* 2006) comparable study. In this study, at the poor fen site they measured less than half of total N content and two times greater C/N ratio of *Sphagnum spp*. than that of *Carex* species. On the other hand, *Sphagnum* did not show great differences in carbon, nitrogen contents for a lack of senescence and the seasonal variations hardly appeared in C/N ratios (C e r t i n i *et al.* 2014). Some works reported a negative correlation between decomposition rates and C/N ratios and a positive correlation between the former and total N content (U p d e g r a f f *et al.* 1995, S z u m i g a l s k i and B a y l e y 1996).

CONCLUSIONS

Significant differences in terms of litter decomposition rates between the *Sphagnum* dominated areas and *Alnus*-covered (alder carr) area were found in the mires of Bereg plain. A higher mass loss was associated with

Sphagnum dominated areas and lower decomposition rates with *Alnus* dominated association. Differences in C/N ratio might be linked to the characteristic features of habitat vegetation. Different plant functional types living under different physical and biotic conditions were expressed in the litter quantity and quality of certain microhabitats. Decomposition rates were highly variable among plant associations. The rate of nutrient release and that of decomposition were significantly correlated. These results help to reveal the role of certain plant associations of mire ecosystem in the carbon cycle since they have basic role in controlling the carbon balance. Based on decomposition and the carbon and nitrogen content of the investigated type of ecosystem acts consequently as C sinks. The climatic effects on peatland vegetation basically influence their plant composition and their metabolisms which reflected a shift in decomposition and nutrient contents.

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