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**Changes in litter decomposition across succession in a post-mined
peatland, northern Japan**

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Abstract

Litter decomposition along successional sere after peat mining was monitored for 3 years on post-mined peatland in Sarobetsu Mire, northern Japan. The litter of two dominant species (*Rhynchospira alba* and *Moliniopsis japonica*) was examined in 3 different successional habitats. We used the litterbag method to measure litter decomposition. We also measured changes in litter decomposition properties (carbon, nitrogen, and phospholipid fatty acids) with the environments (solar radiation and peat moisture). Bareground without litter showed the highest fluctuation of solar radiation and temperature, but the litter decomposition was slowest. Therefore, photodegradation and physical abrasion had affected weakly on litter decomposition. The concentrations of carbon, nitrogen, and phosphorus were not different between the two litter species showing that the litter decomposition pathways of these two species were specific in each habitat because of stable isotopes. Phospholipid fatty acids indicated that fungi contributed more to litter decomposition than bacteria in vegetated habitats with time. These results suggested that biodegradation, particularly by fungi, was the determinant in litter decomposition. The fungal activity was determined by vegetation cover suggesting that restoration to the original vegetation was desirable soon after peat mining to return the *in-situ* litter decomposition.

Keywords: litterbag experiment, litter decomposition, stable isotope, phospholipid fatty acids (PLFAs), post-mined peatland

Introduction

Litter decomposition processes determine the accumulation of litter and the subsequent organic matter and function as a carbon sink in boreal wetlands (Parton et al. 2007). Global climate change alters the functions of wetlands via changing litter decomposition processes (Loisel and Gallego-Sala 2022). In addition, numerous boreal wetlands in Japan have been mined for commercial use and land use change (Tsuyuzaki and Zhang 2020). The restoration of post-mined peatlands is desired to return the original ecosystem function although passive restoration promotes the revegetation slowly or stagnant (Chimner et al. 2017).

Litter decomposition is advanced by 3 mechanisms, microbial degradation (biodegradation), physical fragmentation (abrasion), and photodegradation (Henry et al. 2008). These decomposition mechanisms are operated by temperature, light quantity, soil moisture, nutrient availability, etc. Because fungi and bacteria have a dominant role in biodegradation, the activities of fungi and bacteria are measured by fungal and bacterial phospholipid fatty acids (PLFAs) (Otaki et al. 2016). Photodegradation in arid ecosystems such as deserts contributes to litter decomposition because high solar radiation dissolves litter (Cybulski et al. 2000). Ground-surface movements promote the physical fragmentation of litter (Austin and Vivanco 2006).

Litter decomposition is slower on post-mined peatlands than on natural, un-mined ones (Fennessy et al. 2008), suggesting that the mechanisms of litter decomposition on peat-mined wetlands should be clarified to obtain a key factor for ecological restoration. In addition, a thick litter layer promotes the development of diverse seedbanks across succession on Sarobetsu Mire (Egawa et al. 2009). Vegetation controls litter decomposition via direct and indirect pathways. Species composition and abundance in the standing vegetation directly determine the litter composition, supply, and decomposition (Rejmánková and Houdková 2006; Porre et al. 2020). Of the direct effects, home-field advantage (HFA), faster litter decomposition on vegetation dominated by the litter species, has been hypothesized (Hunt et al. 1988, Ayres et al. 2009). HFA is detected in deciduous temperate forests in Hokkaido, Japan, along a xeric succession (Otaki and Tsuyuzaki 2019), while the effects of HFA have been

unclear in wetlands. Furthermore, vegetation indirectly influences litter decomposition by manipulating the environments, represented by light, temperatures, and water (van der Krift et al. 2002, Egawa and Tsuyuzaki 2015). Therefore, the mutual effects determine litter decomposition rates across succession. However, litter decomposition process has not been examined well across succession in post-mined peatlands.

Peat on Sarobetsu Mire in northern Japan was mined after 1970 or 33 years (Nishimura et al. 2009). The environments for litter decomposition are changed across the succession from baregrounds to grasslands, e.g., an increase in the shade (Egawa and Tsuyuzaki 2015), a decrease in temperature and solar radiation (Koyama and Tsuyuzaki 2010) and a change in peat nutrient (Nishimura and Tsuyuzaki 2014). Using this successional sere, we examined the effects of vegetation and its related factors on litter decomposition. Litter quality is evaluated by carbon, nitrogen, and phosphorus (Manzoni et al. 2010; Tsuyuzaki et al. 2022). Since species richness and evenness change across succession, the patterns of litter decomposition should be different among vegetation types (Asif et al. 2021).

The objectives of this study were: to clarify successional and seasonal changes in litter decomposition rates with changes in carbon, nitrogen, and phosphorus and to detect determinants of litter decomposition. We developed 3 hypotheses: (1) the contribution of 3 litter decomposition mechanisms will change across succession because of the alteration of environments, and particularly biodegradation will contribute more to vegetated habitats. (2) HFA will not appear clearly because the litter quality of examined species is comparable. (3) the biodegradation will perform by fungi more than by bacteria because the litter quality of monocotyledons will be favored by fungi rather than by bacteria in mesic habitats (Zhan et al. 2021).

Methods

Study Sites

The study site was a post-mined peatland in Sarobetsu Mire (45°06'N, 141°42'E, 8 m elevation). The mean annual temperature was 6.3 °C, 6.2 °C, and 6.8 °C in 2008, 2009 and

2010 with the daily minimum at -8.0 °C in January, -5.7 °C in February and -6.0 °C in February and with the daily maximum at 18.4 °C in July and August, 18.7 °C in August and 21.9 °C in August at Toyotomi Town, 6 km east from the study site (Japan Meteorological Agency 2021). The annual precipitation recorded 640.5 mm in 2008, 907.5 mm in 2009, and 1167.5 mm in 2010. Differences in summer rainfall during June and September were the causes of the interannual variations. Snow cover usually remains from November to April, including in 2008 and 2009, and frost occurs even in mid-June, due to radiation cooling (Yamada and Takahashi 2004).

In Sarobetsu Mire, *Sphagnum* peat was mined every year between 1970 and 2003 at 3-22 ha and 3-6 m deep. After extracting high-quality peat for commercial use, the residues returned to their original locations. The post-mined area was covered with open-water soon, and the residues floated and accumulated. The accumulation of floated residues formed a stable ground surface, and then plant colonization was processed. The successional sere after peat mining is bareground to *Rhynchospora alba* sedgeland and then *R. alba* sedgeland to *Moliniopsis japonica* grassland (Nishimura et al., 2009). We selected these two species for examining litter decomposition. We selected 3 habitats based on the vegetation types: bareground (hereafter, i.e., BG) mined in 1982, *R. alba* grassland (RA) mined in 1982, and *M. japonica* grassland (MJ) mined in 1977. We established a total of 20 m² experimental plots.

Litter Sampling and Quantification

We conducted vegetation surveys and biomass harvests to evaluate habitat structure and litter supply. The cover percentage and height were measured on each species within 20 1 m × 1 m plots in each habitat in mid-summer 2008. Litter thickness was measured at 20 points in each habitat by a ruler. Senescent litter produced in the current year was harvested at 40 15 cm × 15 cm plots on 28 to 29 October, 5 November, 2008, and 30 to 31 October, 2009 to estimate the litter production. The harvested samples were kept in paper bags and dried at 80°C in an incubator for 6-8 days. Then, the litter was separated into *R. alba* and others in RA and *M. japonica* and the others in MJ.

The litter of two examined species were harvested adjacent to RA and MJ on April 17 and October 22, 2008. Litter produced in the current and last years were selected in October and April, respectively. The harvested litter was brought to our lab and dried at 45 °C for 4-6 days. Morphological differences between these two species are (Kitamura et al. 1984; Koyama and Tsuyuzaki 2010): *R. alba* (Cyperaceae) develops filate leaves with 0.5-1.5 mm in width and does not develop rhizomes well while *M. japonica* (Poaceae) forms linear leaves with 5-10 mm wide.

We investigated the seasonal changes of litter chemistry during snow-accumulated periods by the litter sampled in April and October. We collected 5 litter samples randomly selected for each of the two species, *R. alba* and *M. japonica*. The recovered litter was dried at 80 °C for 5-7 days immediately after returning to the lab. The litter samples were homogenized by an electric grinder. The contents of nitrogen (%N) and carbon (%C) were measured by an isotope mass spectrometer (MAT252, Finningan Mat Ltd., Bremen). Carbon-to-nitrogen ratio (C/N) in litter was calculated on each sample based on %C and %N. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were also measured concurrently with %C and %N. Phosphorus (P, $\mu\text{g/g}$) was measured by a spectrophotometer (UV-1200, Shimadzu Corporation, Kyoto) at 880 nm after digestion by 7-ml acid solution ($\text{HNO}_3\text{:H}_2\text{SO}_4\text{:HClO}_4 = 5\text{:}1\text{:}1$, volume) with 300-mg litter.

The litterbags were made of a polyethylene net with 1-mm mesh, and were filled with 5 g of either *R. alba* or *M. japonica* litter. The litterbags were deployed on May 8, 2008 for litter collected in April and on November 12, 2008 for litter collected in October. The litterbags were placed on peat surfaces in BG because of no litter and on peat and litter surfaces in RA and MJ. In total, 3 litterbags were recovered 8 times from each layer in each habitat during snow-free periods for the 3 years, except BG in 2010 because of no bags. The recovered samples were kept in a cool box with refrigerant until drying. For measuring PLFAs, the samples were freeze-dried over 7 days immediately after returning to lab and were weighed (Otaki and Tsuyuzaki 2019). When PLFAs were not measured, the litterbags were dried at 80°C for 5-7 days.

PLFAs in each litter were identified and quantified by phospholipids extracted from the

litter under a gas chromatography (G-3000 Gas Chromatograph, Hitachi, Tokyo) and a gas chromatograph-mass spectrometer (Varian Saturn 2200, Agilent Technologies, Santa Clara) to estimate the bacterial and fungal biomass. The phospholipids were separated from the total lipids by thin-layer chromatography with a silica gel under a developer (91:30:8 = acetone: benzene: water). The phospholipids were subjected to mild alkaline methanolysis. Then, the fatty acid methyl esters were detected with the gas chromatography with a flame ionization detector using a 30-m 5% phenyl silicone capillary column (HP-5) exposed to helium as a carrier gas. The temperatures of the injector and detector were adjusted to 270 °C. The temperature in the oven was kept at 160 °C for 5 min and then rose at 1 °C/min up to 180 °C and at 10 °C/min up to 240 °C. PLFAs were identified and quantified in each sample by comparison with the internal standard, nonadecanoate fatty acid (19:0). Fatty acid methyl esters were identified by the standards and previous literature with a gas chromatograph-mass spectrometer (JMS-DX303HF, JEOL, Tokyo). In this study, the PLFAs of 16:1, 17:0, 18:1 and 18:2 were focused because the 16:1 and 17:0 were produced only by bacteria and 18:1 and 18:2 were by fungi (Šnajdr et al. 2011).

Measurements of Environmental Factors

The temperature (°C) and light intensity (lux) were measured at the center of each site by automatic loggers (HOBO UA-002-XX, Onset Computer Corporation, Pocasset) at 1-hour intervals from 8 May, 2008 to 8 November, 2009. The logger was established on litter, when available, or peat surfaces. Ultraviolet radiation (UV, 280-400 nm) was measured by a UV meter (ST-513, Sentry, Taipei). We measured photosynthetic active radiation (PAR) and UV at the ground surface and 1 m above as control in each plot at every census. At each plot, PAR or UV were measured 4 times at the same moment. We calculated daily mean, maximum and minimum temperatures in each day, and the moving average for 5 days on the mean, maximum, and minimum temperatures. The relative intensities of PAR and UV were calculated by (ground surface/above surface × 100) and averaged.

We measured peat moisture (% v/v) by time domain reflectometry (TDR) (EC-5,

Decagon Devices Inc., Pullman), of which probe length was 5 cm, at 1 and 5 cm in depths from June to November in 2009 and from May to October in 2010. The loggers recorded the data at 1-hour intervals by data loggers (Em5b, Decagon Devices Inc., Pullman). Volumetric water content (% v/v) was measured at every census by TDR (HydroSense, Campbell Scientific Australia Pty. Ltd., Wien) with a 12-cm probe inserted vertically into the ground 20 times in each habitat during 2008 and 2009.

Statistical Analysis

The amount of litter supply was compared between RA and MJ and between the years by generalized linear models (GLMs) under the assumption of gaussian distribution with the link function of identity. Interaction between the year and vegetation type (RA and MJ) was considered in the models.

GLMs detected the determinants of litter decomposition with the assumption of gaussian distribution. We developed 2 models: model I used chemical properties, and model II did not use them because we did not always measure the chemical properties. The response variable of models I and II was litter mass remaining. The explanatory variables of model I were habitat, litter species, layer, and date. Model II additionally used %C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C/N, and P with the explanatory variables of model I. Akaike's information criterion (AIC) selected the meaningful explanatory variables in the best models. The differences in 6 chemical properties in the initial litter were compared between the 2 litter species and 2 seasons (April and October) by GLMs with the same assumptions with the litter decomposition. We investigated the chemical properties of decomposed litter in the same way. These analyses did not consider interactions between the explanatory variables. GLMs examined the temporal changes in PLFAs with the explanatory variables of date, habitat, litter species, and layer.

GLMs compared the relative PAR and UV between the seasons and between the habitats with their interactions as well as the litter supply. The daily mean, maximum and minimum temperatures were compared between litter species, among habitats, and among date by GLMs. Peat moisture was compared between habitat, layer, and date. All statistical analyses were

performed by R (ver. 4.1.1) (R Development Core Team 2021).

Results

Habitat and Litter Supply

In total, 21 vascular plant species were recorded from the 40 plots of 1 m × 1 m. The total cover averaged 5% in BG, 74% in RA to 99% in MJ. As well as the cover, plant height increased from BG to MJ. These results showed that shade became stronger with progress the succession. On non-vascular plant species, a few *Sphagnum* mosses, most of which were *S. papillosum*, were recorded from MJ. Only 3 species grew on BG (Table 1). *Rhynchospora alba* showed the highest frequency (8) on BG, although the cover averaged 3% only. *R. alba*, of which cover averaged 69%, was predominant on RA. The other species showed less than 8% in cover on RA. *Moliniopsis japonica* (76% in cover) and *Carex middendorffii* (52%) were dominant in MJ.

BG produced the least litter for the 2 years, i.e., litter thickness was nearly zero. The mean of litter thickness was 3 times higher in MJ than in RA, 2.4 ± 1.3 cm (mean $\pm$ standard deviation) in RA and 8.7 ± 1.6 cm in MJ. *R. alba* on RA produced 191 ± 90 g/m² of litter in 2008 and 147 ± 67 g/m² in 2009. The other species on RA did not produce less litter in 2008 and did less than 67 g/m² and averaged 3 ± 11 g/m² in 2009. The litter supply on RA was 192 ± 91 g/m² and 150 ± 67 g/m² in 2008 and 2009, respectively. Therefore, litter on RA was supplied mostly by *R. alba*. *M. japonica* on JM produced 546 ± 412 g/m² in 2008 and 523 ± 366 g/m² in 2009. The other species supplied 213 ± 175 g/m² and 161 ± 122 g/m² on the grassland in 2008 and 2009, respectively. The total amount of litter was 759 ± 450 g/m² in 2008 and 685 ± 343 g/m² in 2009. The litter production of *M. japonica* on MJ was 4 to 5 times more than that of *R. alba* on RA. The total amount of litter supply was significantly different between RA and MJ (GLM, $p < 0.01$) and was not different between the years ($P = 0.252$).

Litter Decomposition

The initial litter of *R. alba* contained $46.6\% \pm 0.8$ of %C, $0.93\% \pm 0.96$ of %N and 104.2 µg/g

± 5.4 of P in October, while it did 46.3% ± 0.7 of %C, 0.90 ± 0.06 of %N and 115.0 µg/g ± 7.1 of P in April. The C/N of *R. alba* averaged 50.2 ± 3.6 in October and 51.6 ± 2.3 in April. *M. japonica* litter contained 49.3% ± 0.9 of %C, 0.81% ± 0.98 of %N, 48.8 µg/g ± 5.8 of P, and 61.1 ± 5.7 of C/N in October. These in *M. japonica* litter changed to 46.1% ± 0.5, 0.79% ± 0.05, 121.4 µg/g ± 5.7 and 61.1 ± 3.5 in April. These 4 chemical properties did not differ between the seasons (GLMs, $P > 0.01$), and between the 2 species (GLM, $P > 0.01$), showing that the litter did not change the chemical composition greatly during the snowfall period for both *R. alba* and *M. japonica*.

$\delta^{13}\text{C}$ in the initial litter of *R. alba* was -29.2‰ ± 0.9 in October and -27.3‰ ± 0.3 in April, while $\delta^{13}\text{C}$ in *M. japonica* was -27.1‰ ± 0.1 in October and -26.2‰ ± 0.3 in April. $\delta^{13}\text{C}$ was higher in April than in October (GLM, $p < 0.001$) and was higher in *M. japonica* litter than in *R. alba* litter ($p < 0.01$). The interaction between the litter species and season was not significant on $\delta^{13}\text{C}$. $\delta^{15}\text{N}$ in *R. alba* litter was 1.69‰ ± 0.20 in October and 0.20 ‰ ± 0.63 in April. $\delta^{15}\text{N}$ in *M. japonica* litter changed from -2.72‰ ± 0.29 in October to -3.15‰ ± 0.18 in April. $\delta^{15}\text{N}$ was higher in *M. japonica* litter than in *R. alba* litter ($p < 0.001$) with the interaction between litter species and season ($p < 0.01$). Although the chemical composition, %C, %N, and P, did not differ between the litter species, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were different between the litter species. These suggested that the transportation of carbon and nitrogen differed between the 2 litter species and occurred even in winter.

Litter mass remaining decreased with time, particularly in vegetated habitats, independent of the litter species (Fig. 1). Model I, which did not use chemical properties, discarded litter species (Table 2) and used habitat. The slopes of GLMs were steeper in RA and MJ. These results meant that the litter decomposition was faster in vegetated habitats, RA and MJ. Model II, including chemical properties, discarded %N and $\delta^{15}\text{N}$ in the final model, showing that N was not a strong determinant of litter decomposition for these 2 species. The litter decomposition did not correlate to the other examined variables, except $\delta^{13}\text{C}$, which remained in the model but was insignificant. When chemical properties were not considered (Model I), litter species did not remain in the model. However, the species remained in the model when

chemical properties were considered (Model II). In total, excluding N parameters, all the parameters remained in Model II.

%C, %N, C/N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and P were different among the dates and litter species (GLMs, $p < 0.01$) (Fig. 2). On the litter species, $\delta^{13}\text{C}$ was higher in *M. japonica* litter than in *R. alba* litter, while $\delta^{15}\text{N}$ was higher in *R. alba* litter than in *M. japonica* litter. %C and $\delta^{13}\text{C}$ did not differ between the habitats. %N was highest in MJ and $\delta^{15}\text{N}$ was also highest in MJ. C/N was higher in BG and RA. %C did not differ among the habitats, so the difference came from %N. P was highest in MJ, as well as %N and $\delta^{15}\text{N}$.

PLFAs indicated that bacteria and fungi were less abundant in the first year (Fig. 3). The amounts of PLFAs produced by bacteria did not change for the 3 years in any habitats, while those by fungi increased with time. In addition, fungal PLFAs were more in MJ with high vegetation cover. Litter species affected 18:1 PLFA concentration but did not do the 18:2 PLFA. The amount of PLFAs did not differ between the burial layers, i.e., on peat and litter.

Solar Radiation and Temperature

Light intensity was highest on BG (Fig. 4). With increasing vegetation cover across the succession, the light intensity decreased throughout the surveyed period. The light intensity was lower on the peat than on the litter because of shade. As well as the light intensity, relative PAR and UV decreased with increasing vegetation cover. The PAR and UV were higher in early spring because of no shade by shoots, although the date was not significant for determining PAR and UV.

The temperatures, expressed by mean, maximum, and minimum, differed among the habitats with above and below litter in 2008 and 2009 (Fig. 5). With increasing vegetation cover, the temperatures decreased. The temperature fluctuations, expressed by standard deviation, were higher above than below the litter, showing that the litter accumulation reduced the effects of heat derived from direct sunshine.

Peat moisture was lower at 1 cm in depth than 5 cm in all habitats for the 2 years from 2009 to 2010 (Fig. 6). The moisture was highest in RA and lowest in BG. The peat moisture

fluctuated in response to precipitation, particularly above the litter in BG. The peat moisture on the shallow peat layer was affected directly by precipitation. In contrast, peat moisture at 5 cm deep in RA was stable, probably because the water table was constantly higher than 5 cm deep in RA. The water content measured by a 12 cm probe inserted from the litter surface showed that MJ was driest. The content was higher in RA than in BG, although the difference was small. Since the locations for measuring water content in MJ contained the litter layer, the thick litter decreased the water content.

Discussion

Litter Decomposition and Litter Supply

The litter decomposition was fast in the vegetated habitat, MJ, independent of the litter species, showing that the characteristics of habitats determined the litter decomposition more than litter species. The 2 litter species showed equivalent %C, %N, and P suggesting that the litter quality did not differ greatly between them. $\delta^{13}\text{C}$ ranging from -34‰ to -24‰ in the initial litter for the 2 examined species indicated that these species are C_3 plants (Coplen et al. 2002). Therefore, HFA on litter decomposition was weak because of the non-significant difference in litter quality between the 2 species. There is little evidence of HFA on litter decomposition in an Italian mountain forest because the chemical composition in litter affects decomposition more in the early stages (Pastorelli et al. 2021). The litter species was not adopted in model I not including litter chemistry and was adopted in model II including litter chemistry. These also implied that the habitat differences were more important than the litter chemistry for the litter decomposition.

PAR, UV and temperature fluctuation decreased with increasing vegetation cover. Biodegradation does not favor high PAR and UV because microbial activities are inhibited by strong solar radiation, particularly by UV (Wei et al. 2022). The orders of water content and peat moisture were not synchronized with the successional sere, i.e., water content lowered as $\text{RA} < \text{BG} < \text{MJ}$. These results suggested that the litter decomposition rates were determined by temperature and solar radiation more than by water in peat. The inundation regime does not

affect the decomposition of refractory stem litter, while prolonged and stable inundation stimulates the degradation of labile leaf litter (Xie et al. 2019a). However, the litter was not inundated on the peat surface, as shown by seasonal changes in peat moisture at 1 cm and 5 cm in depths except during melting snow. Furthermore, the peat moisture was unstable in BG. Therefore, fast litter decomposition was not expected in BG because of less inundation and strong UV.

Although the litter decomposition rate on MJ was faster, litter accumulation was 2.5 times higher on MJ than on RA. Therefore, litter accumulation on MJ was due mostly to the litter input. *Rhynchospora alba* is an early colonizer on BG and *Moliniopsis japonica* is a late colonizer (Nishimura and Tsuyuzaki 2014), and PLFAs showed that fungal activities were higher in MJ. The quality and quantity of litter input affect litter decomposition processes more than the temperature on permafrost in northern Greenland because the litter input determines the composition and abundance of microbiome (Adamczyk et al. 2020). These results suggest that the carbon sink enlarges with the succession from *R. alba* to *M. japonica*.

Biological Decomposition

Biological decomposition processes had a dominant role in litter decomposition and differed between *R. alba* and *M. japonica* litter. However, the resultant litter decomposition rates did not differ between the 2 species. BG showed the least PLFAs produced by bacteria and fungi, suggesting that biodegradation in BG was less throughout the surveyed period.

Fungi showed a faster increase in PLFAs in MJ, while bacteria did not increase the PLFAs in most samples. Peat moisture was highest in RA, but the litter decomposition did not differ between RA and MJ. Higher water levels facilitate litter decomposition and organic carbon release from *Carex brevicuspis* leaf litter into the soil via water leaching and microbial activity (Zhu et al. 2021). However, this pattern was not observed in the litter of *R. alba* and *M. japonica*, probably because the temperature effects precluded the moisture effects on fungi. The activities of litter-decomposed fungi are often determined more by temperature than by moisture because moisture was higher than the threshold for litter decomposition in wetlands

(Xie et al. 2019b).

Photodegradation and Physical Abrasion

BG receiving high UV and PAR showed the slowest litter decomposition. The litter decomposition did not differ between the 2 burial layers, not adopted in the models I and II. These results indicated that photodegradation did not act strongly. Photodegradation is a determinant of litter decomposition in (semi-)arid ecosystems that receive high direct sunlight, although bacterial decomposition is weak due to dryness (Cybulski et al. 2000; Pancotto et al. 2005; Austin and Vivanco 2006). The photodegradation did not work highly in mesic habitats, i.e., post-mined peatlands in Sarobetsu Mire, with low temperatures. These suggest that peat moisture is related to the intensity of photodegradation.

As well as photodegradation, physical abrasion in the litterbags was weak in the post-mined peatland, as shown on BG. Leaves are more fragile than stems because of less recalcitrant components, such as cellulose and lignin (Fonseca et al. 2013). Although the 2 litter species did not produce their stems except the flowering stalks, physical abrasion was less. These also suggested the leaf morphology, i.e., filate and linear leaves, affected less the litter decomposition. In conclusion, the 3 proposed hypotheses were supported by the present results as: (1) the litter decomposition was performed weakly by photodegradation and physical abrasion even on bareground and was done mostly by biodegradation on the vegetated habitats. Therefore, the litter decomposition patterns and mechanisms changed across the succession. (2) HFA was not detected clearly in the 2 litter species. (3) Of the biodegradation, the activities of fungi, of which establishment was determined by vegetation cover, were critical for the litter decomposition. Ecosystem restoration should be conducted promptly after peat mining to return the original litter decomposition patterns before starting the distortion of ecosystems (Nishimura and Tsuyuzaki 2015).

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Author Contribution FT, MO and ST developed the research; FT and ST performed the field work, FT and MO performed the lab work, FT and ST wrote the manuscript.

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Data Availability The datasets are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Consent for Publication Everybody entitled so gave their consent for this research being published.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Conflicts of Interest The authors have not known competing financial interests or personal relationships that appear to influence the work reported in this paper.

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Table 1. Habitat characteristics evaluated by averaged cover (%) $\times$ averaged shoot height (cm) with frequency (n) in the summer of 2008. Species with $F > 20\%$ ($n > 12$) are shown. -: not observed. Species richness and total cover are shown by mean with standard deviation.

Species*	Habitat		
	Bareground	<i>R. alba</i> grassland	<i>M. japonica</i> grassland
<i>Moliniopsis japonica</i> (Hack.) Hayata	0.8×2 (1)	7.9×19 (18)	75.8×61 (20)
<i>Lobelia sessilifolia</i> Lamb.	-	1.6×10 (16)	7.8×37 (18)
<i>Rhynchospora alba</i> (L.) Vahl.	3.2×5 (8)	62.0×19 (20)	-
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	-	2.0×21 (8)	11.3×72 (17)
<i>Carex middendorffii</i> Fr. Schmidt	1.3×1 (1)	0.5×1 (1)	52.0×49 (18)
<i>Drosera rotundifolia</i> L.	-	0.8×2 (17)	-
<i>Iris laevigata</i> Fisch.	-	0.1×2 (3)	4.3×18 (11)
Total species richness	3	15	13
Plot species richness	0.5 ± 0.6	5.8 ± 2.2	6.0 ± 1.5
Total cover (%) with maximum height	5.2 ± 9.7 (38)	73.5 ± 23.2 (65)	98.8 ± 3.2 (115)

* The other species include: *Sanguisorba tenuifolia* Fisch. ex Link var. *alba* Trautv. et Mey. (10), *Andromeda polifolia* L. (7), *Hosta rectifolia* Nakai (7), *Vaccinium oxycoccos* L. (7), *Rubus chamaemorus* L. (6), *Lycopus uniflorus* Michx. (5), *Calamagrostis epigeios* (L.) Roth (4), *Gentiana triflora* Pall. (4), *Sphagnum* spp, mostly *S. papillosum* Lindb. (4), *Myrica gale* L. var. *tomentosa* C. DC. (3), *Sasa senanensis* (Franch. et Sav.) Rehder (3), *Solidago virgaurea* L. ssp. *leiocarpa* (Benth.) Hultén (3), *Thelypteris palustris* (Salisb.) Schott (2), *Ilex crenata* Thunb. var. *radicans* (Nakai ex H. Hara) Murai (1), and *Platanthera tipuloides* (L. f.) Lindl. ssp. *nipponica* (Makino) Murata (1).

Table 2. Litter mass remaining predicted by GLM with the assumption of a Gaussian distribution and identity link. The values show the intercepts and estimates of the models. AICs are used to select the parameters that led to the best GLMs by a backward method. Differences between models I and II are: explanatory variables in model I are habitat and litter species only and those in model II are habitat, litter species and litter chemistry. **: significant at $p < 0.001$, *: $p < 0.01$, NS: not significant. -: removed by AIC procedure. Blank: not inserted in the model at the first step. See also, Fig. 1.

	Model I (without chemical properties)	Model II (with chemical properties)
Number of samples	587	339
Intercept	-0.048**	-1.109**
Habitat (from bareground)		
<i>Rhynchospira alba</i> grassland	-0.111**	-0.115**
<i>Moliniopsis japonica</i> grassland	-0.145**	-0.079**
Litter (from <i>Rhynchospira alba</i>)		
<i>Moliniopsis japonica</i>	-	+0.034*
Carbon content (%)		+0.008*
Nitrogen content (%)		-
C/N		+0.004**
$\delta^{13}\text{C}$ (‰)		-0.020 ^{NS}
$\delta^{15}\text{N}$ (‰)		-
Phosphorus ($\mu\text{g/g}$)		-0.001**
AIC	-1115.2	-945.19

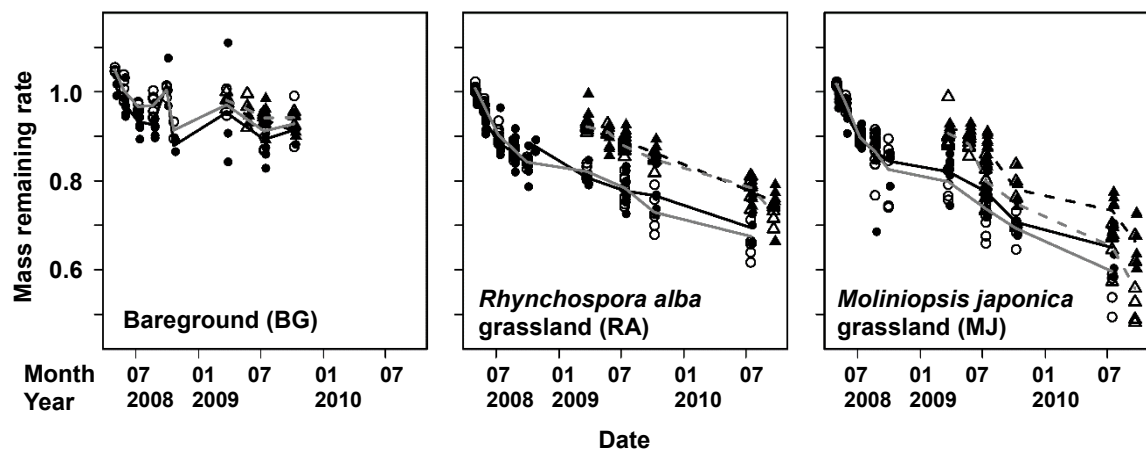


Fig. 1. Litter mass remaining in the 3 habitats for the 3 surveyed years from 2008 to 2010. Closed and open symbols show mass remaining of *Rhynchospora alba* litter and *Moliniopsis japonica* litter, respectively. Circles and triangles show mass remaining of litter established in the fall of 2007 and the spring of 2008, respectively. Solid and interrupted lines show averaged mass remaining of litter established in the fall of 2007 and the spring of 2008, respectively. O the statistical results, see Table 2.

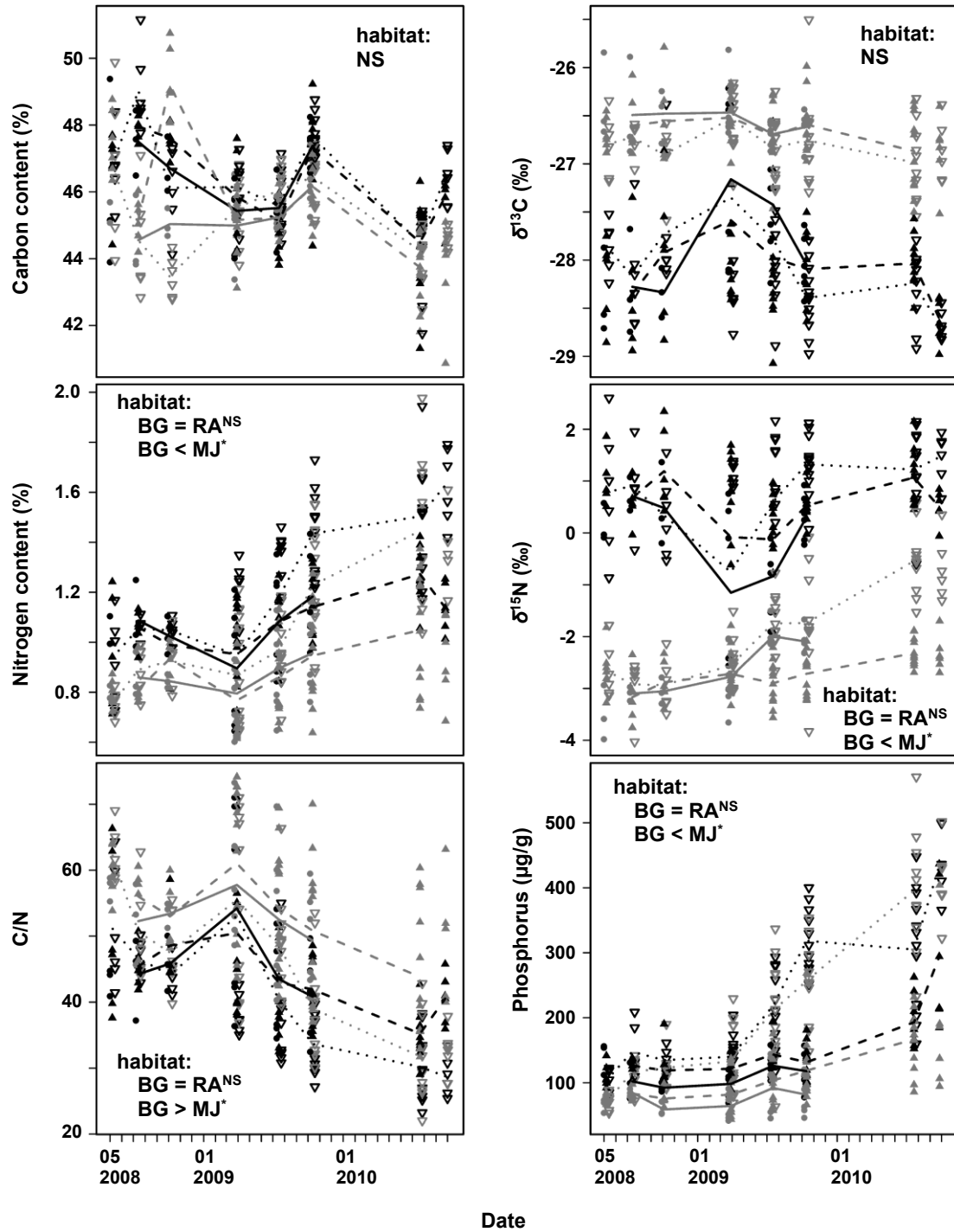


Fig. 2. Temporal changes in litter chemistry from 2008 to 2010. Solid circles, solid triangles and open reverse triangles indicate BG, RA and MJ. Solid, interrupted and dotted lines indicate mean values in BG, RA and MJ. Black and gray colors indicate litter of *R. alba* and *M. japonica*, respectively. The significant differences are indicated in each panel. All the intercepts, dates and litter species in the GLMs are significant at $p < 0.01$. *: significant at $p < 0.01$. NS: not significant. Inequality signs indicate the magnitude relations.

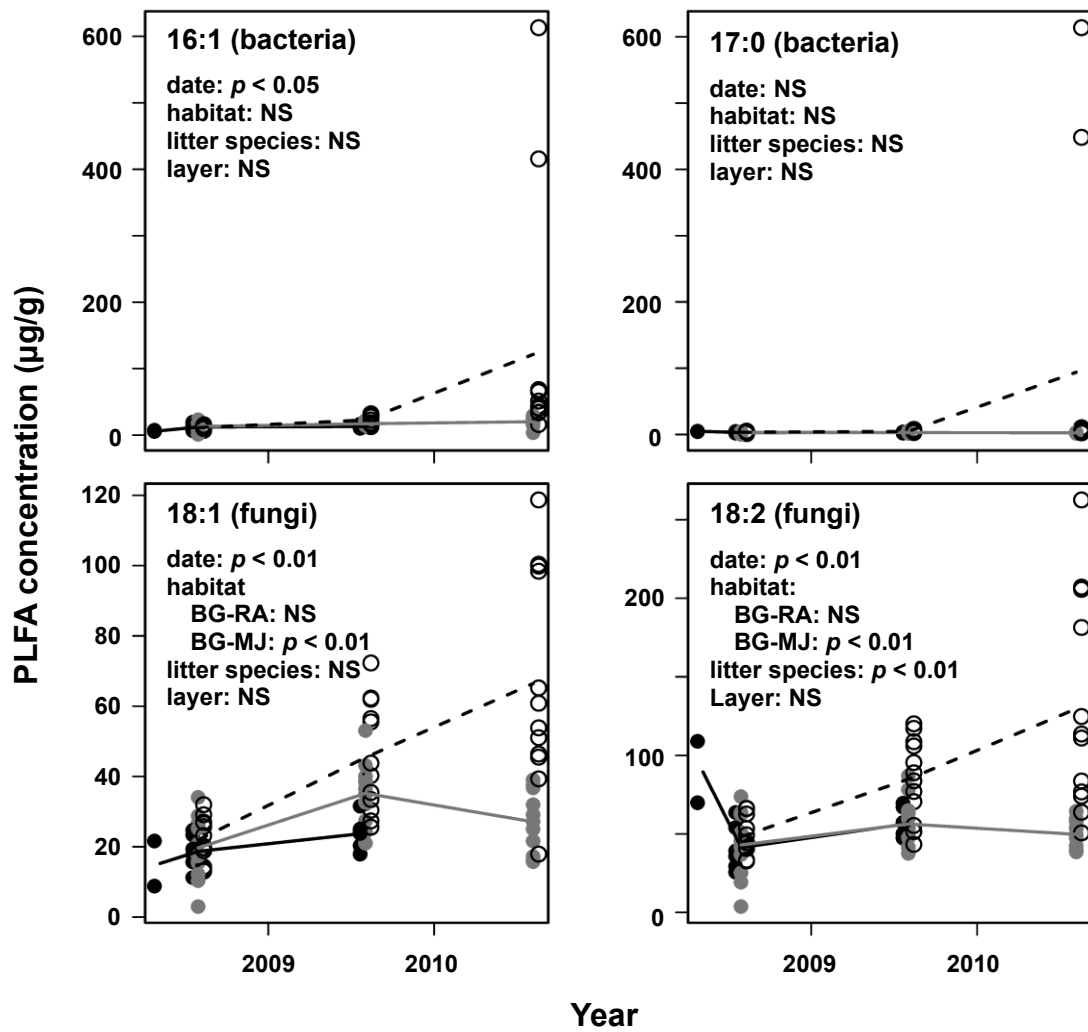


Fig. 3. Yearly fluctuations of 4 taxon-specific PLFAs (16:1 and 17:0 produced by bacteria and 18:1 and 18:2 by fungi) in the 3 habitats, bareground (BG, closed circles), *Rhynchospora alba* grassland (RA, grayed circles) and *Moliniopsis japonica* grassland (MJ, open circles). Solid, grayed and interrupted lines show the averages of PLFAs in bareground, *Rhynchospora alba* grassland and *Moliniopsis japonica* grassland. The significant differences among the habitats are shown under the taxon-specific PLFA.

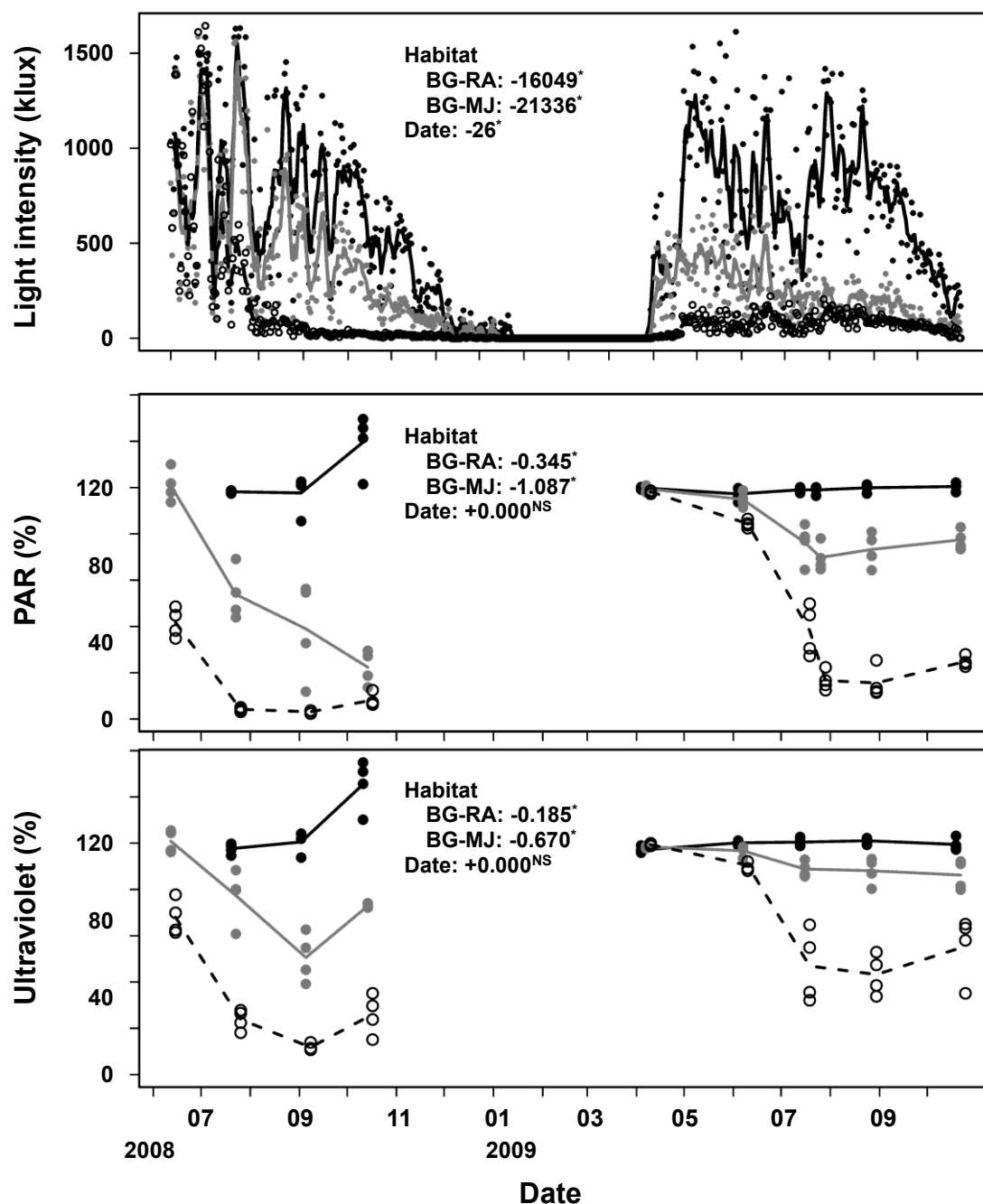


Fig. 4. Fluctuation of daily cumulative light intensity (klux), relative PAR and relative UV from June 2008 to October 2009. Solid, gray and open circles indicate BG, RA and MJ, respectively. Averaged relative intensities of PAR and UV are shown by solid, gray and interrupted lines for BG, RA and MJ, respectively. Solid, gray and open circles indicate bareground, *Rhynchospora alba* grassland and *Moliniopsis japonica* grassland. The light intensity is expressed by a cumulative value in a day. The moving average for 5 days is also shown by broken lines, as solid, gray and interrupted lines for bareground, *R. alba* grassland and *M. japonica* grassland. The results of GLMs are shown in each panel. *: significantly different at $p < 0.001$. NS: not significant at $p > 0.05$.

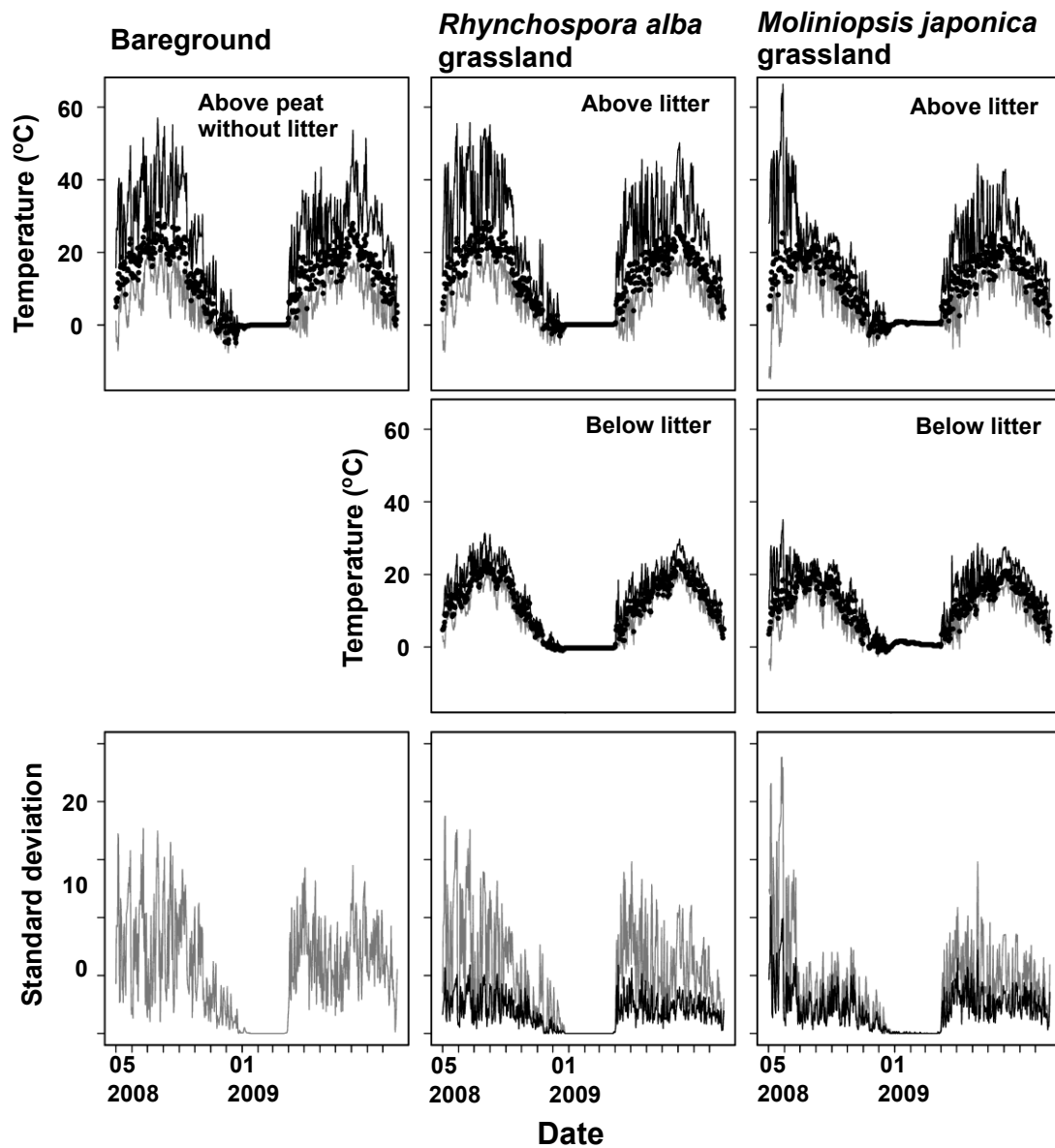


Fig. 5. Temperature fluctuations (mean, maximum, minimum and standard deviation in a day) in 3 habitats, bareground, *Rhynchospora alba* grassland and *Moliniopsis japonica* grassland. Mean (closed circles) is shown with the maximum (black lines) and minimum (gray lines) daily temperature. All the 4 parameters (mean, maximum, minimum and standard deviation) are significantly different among the 3 habitats and between the layers (GLMM, $p < 0.001$).

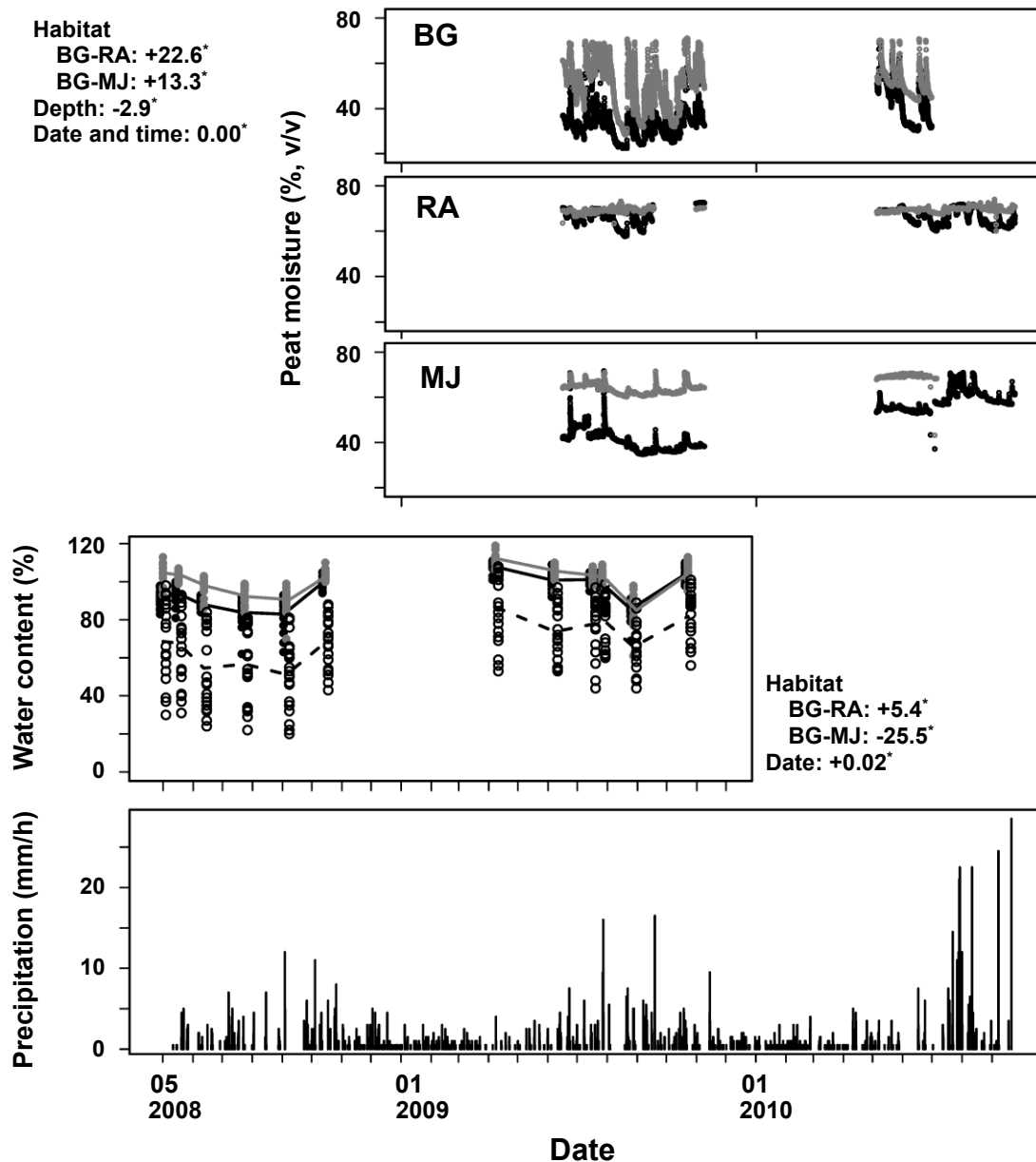


Fig. 6. Seasonal fluctuations of peat moisture (% v/v) during snow-free periods from early spring in 2009 to late fall in 2010 in 3 habitats, bareground (BG), *Rhynchospora alba* grassland (RA) and *Moliniopsis japonica* grassland (MJ) at 1 cm and 5 cm in depths and water content from 2008 to 2009 with daily precipitation (Toyotomi Town, 6 km east from the site). On water content, black, gray and open circles indicate BG, RA and MJ. The averaged peat moisture is shown by solid and black lines for bareground, solid and gray lines for RA and interrupted and black lines for MJ. The results of GLMs are shown in the sides of panels and are significantly different at $p < 0.001$.