Effects of short-term ecosystem experimental warming on water-extractable organic matter in an ombrotrophic Sphagnum peatland (Le Forbonnet, France)

Frédéric Delarue a, Fatima Laggoun-Défarg e a,*, Alexandre Buttler b, c, d, Sébastien Gogo a, e, Vincent E.J. Jassey b, Jean-Robert Disnar a

a Université d’Orléans, CNRS/INSU – Institut des Sciences de la Terre d’Orléans, UMR 6113, Campus Géosciences – 1 A, rue de la Férollerie, 45071 Orléans cedex 2, France
b Laboratoire de Chrono-Environnement, UMR CNRS 6249, UFR des Sciences et Techniques, 16 route de Gray, Université de Franche-Comté, F-25030 Besançon, France
c École Polytechnique Fédérale de Lausanne EPFL, Ecological Systems Laboratory ECOS, Station 2, 1015 Lausanne, Switzerland
d Swiss Federal Research Institute WSL, Station 2, 1015 Lausanne, Switzerland
e INRA, Science du Sol UR272, Centre de recherches d’Orléans, 2163 avenue de la Pomme de Pin, CS 40001 Ardon, 45075 Orléans cedex 2, France

A R T I C L E   I N F O
Article history:
Received 12 January 2011
Received in revised form 5 July 2011
Accepted 14 July 2011
Available online 23 July 2011

A B S T R A C T
In a future warmer world, peatlands may change from a carbon sink function to a carbon source function. This study tracks changes in water-extractable organic matter (WEOM) after 1 year of in situ experimental warming using open top chambers (OTCs). WEOM was studied in the upper peat layers (0–10 cm) through analysis of water-extractable organic carbon (WEOC), stable C isotopic composition (δ13C), specific UV absorbance at 280 nm and sugar composition of cores taken from an open bog (DRY sites) and a transitional poor fen (WET sites). At the DRY sites, the impact of OTCs was weak with respect to WEOM parameters, whereas at the WET sites, the air warming treatment led to a decrease in peat water content, suggesting that the supply of heat by OTCs was used mainly for evapotranspiration. OTCs at the WET sites also induced a relative enrichment at the surface (0–5 cm depth) of aliphatic and/or aromatic compounds with concomitant decrease in WEOC, as a result of decomposition. On the contrary, WEOM and sugar content increased in the deeper peat layer (7.5–10 cm depth) probably as a result of increased leaching of phenolic compounds by roots, which then inhibits microbial activity. The different response to experimental warming at DRY and WET sites suggests that the spatial variability of moisture is critical for understanding the impact of global warming on the fate of OM and the carbon cycle in peatlands.

© 2011 Elsevier Ltd. All rights reserved.
Water-extractable OM (WEOM) reflects OM decomposition (Said-Pullicino et al., 2007) and can therefore be a suitable indicator of the consequences of experimental warming. WEOM consists of a heterogeneous mixture of more or less labile organic compounds soluble in water (Balesdent, 1996; Zsolnay, 2003) and is provided by both freshly decomposed litter and products of microbial metabolic activity (Charman, 2002; Zaccone et al., 2009). Within such pools, the most labile OM has been studied mainly through the analysis of sugars, which are considered readily degradable constituents used preferentially by microorganisms (Haider, 1992; Volk et al., 1997). In investigating sugar composition and its link to microbial activity, Medeiros et al. (2006) showed that some sugars such as mannitol, a polyol or reduced sugar, can also be seen as an indicator of osmotic stress. On the other hand, the less labile OM of the WEOM is often investigated by way of specific ultraviolet absorbance at 280 nm (SUVA280), which provides an estimate of aromaticity of the WEOM (Traina et al., 1990; Kalbitz et al., 2003; Weishaar et al., 2003).

The aim of the present work was to investigate the impact of in situ experimental warming on WEOM properties in the upper 10 cm of peat, where most of the labile OM is decomposed. We hypothesized that peatland warming has detectable consequences on WEOM properties and that some biogeochemical parameters can be used as early indicators of change. We considered the impact of OTCs on the peat temperature recorded at 7 cm depth. First, we used the dry mass/wet mass (DM/WM) ratio and the mannitol content for assessing environmental conditions related to water table depth and/or soil humidity, and second we inferred the fate of labile and recalcitrant OM in relation to changes in decomposition processes, using water-extractable organic carbon (WEOC), isotopic composition ($\delta^{13}$C), SUVA280 and sugar composition (neutral monosaccharides, neutral disaccharides and polyols). The study was performed at the undisturbed Sphagnum-dominated “Le Forbonnet” peatland, using a transitional poor fen site (“WET”) and an open bog site (“DRY”).

2. Materials and methods

2.1. Study site

The study site is an undisturbed, ombrotrophic Sphagnum-dominated mire situated in the Jura Mountains (Le Forbonnet peatland, France, 46°49'35"N, 6°10'20"E) at an altitude of 840 m above sea level. It is characterized by cold winters (avg. −1.4 °C) and mild summers (avg. 14.6 °C). The annual mean temperature at the site over a 1-year period from 5th November 2008 to 30th November 2009 was 6.5 °C, and the annual precipitation 1200 mm (see also Delarue et al., in press).

Two sites were selected with respect to plant groups and hence hydrology. The first site (“WET”) was a transitional Sphagnum-dominated poor fen, relatively flat and homogeneous, characterized by a moss cover dominated by Sphagnum fallax and a lack of S. magellanicum. Vascular plants such as Eriophorum vaginatum, Vaccinium oxyccocus and Andromeda polifolia were recorded in very low abundance. Scheuchzeria palustris and Carex limosa occurred outside the studied plots. The second site (“DRY”) was a Sphagnum bog directly adjacent to the fen area. Patterns of hummocks with S. magellanicum, V. oxyccocus, E. vaginatum and Calluna vulgaris, and hollows with lawns of S. fallax, Carex rostrata and A. polifolia characterized the sampling area. The terms “WET” and “DRY” are used to denote the existence of a wetness and trophic gradient inferred from the vegetation. The vegetation is known to be determined largely by water level (Wheeler and Proctor, 2000; Okland et al., 2001) and the presence and dominance of S. fallax, S. magellanicum and E. vaginatum is a good indicator of environmental conditions along the gradient poor-fen with hollows and lawns, and bog with hummocks (Pedersen, 1975; Gerold, 1995).

2.2. Experimental design, sampling and WEOM extraction

OTCs are passive warming chambers (Aronson and McNulty, 2009). They were designed following the International Tundra Experiment (ITEX) to obtain quasi-natural transmittance of visible wavelengths and to minimize the transmittance of re-radiated infrared wavelengths (Marion et al., 1997). The hexagonal chambers are made of transparent polycarbonate and are 50 cm high, 1.7 m wide at the top and 2.4 m wide at the base. They were raised 10 cm above the soil surface to allow air to circulate. Six OTCs were installed in May 2008 at the DRY and the WET sites. At each site, six plots were selected in representative surfaces and then randomly allocated to treatment. Three plots were equipped with OTCs, while three others were taken as controls. The plots were named as follows: at the DRY site, plots equipped with OTCs as DRY-OTC, and control plots as DRY-CTL; the corresponding plots at the WET site were WET-OTC and WET-CTL. Among the 12 sampling plots, the maximal distance between the two most distant plots was ca. 30 m. The monitoring of peatland temperature was performed in November 2008 and of air temperature in July 2009. These two parameters were measured every 30 min at 7 cm depth and 10 cm above the soil surface, respectively, using thermocouple probes and a data logger (CR-1000 Campbell).

Peat cores were extracted from each plot in June 2009, after 13 months of experiment. The twelve cores (13 cm diameter, 25 cm long) were cut into 2.5 cm slices that were sub-sampled for various analyses. One subsample was dried at 50 °C for 1 week to measure the dry mass and the wet mass (DM/WM ratio). Another was directly frozen at −18 °C for WEOM extraction and associated analyses. It was later split into two parts. For each subsample, ca. 3 g milled frozen peat were placed in 10 ml ultrapure water and manually homogenized for WEOM extraction. After 10 min incubation at ambient temperature (20 °C) to defrost the peat, the water extract (ultrapure water + peat water extract) was filtered through a glass fibre filter (GF6, Schleicher & Schuell, 1 µm pore size). Filtration was performed under vacuum to optimize water extraction. Ultrapure water was then added to obtain an aliquot volume of 25 ml. The first water extract was divided into two sub-aliquots: one for WEOC and $\delta^{13}$C analyses, and one for the SUVA280, while the second water extract was used for carbohydrate and polyol analyses (Fig. 1).

2.3. Methods

2.3.1. Water-extractable organic carbon (WEOC) and stable carbon isotopic composition ($\delta^{13}$C)

WEOC content and isotopic composition were determined using liquid-chromatography-isotope ratio monitoring-mass spectrometry (LC-irMS; Thermo Isolink), in bulk mode. Prior to analysis, samples were acidified to pH 1 (Fig. 1) with H3PO4 (85%). The inorganic C was eliminated by bubbling He through the mixture (ca. 5 min). Standardisation involved a benzoic standard for WEOC analysis, and pure CO2, IAEA and USGS simple molecule standards for $\delta^{13}$C (Albéric et al., 2010).

2.3.2. SUVA280

Solutions were acidified to pH 6–7 (Fig. 1) following the recommendation of Weishaar et al. (2003). UV absorbance was measured at 280 nm using a UV spectrophotometer (Gibson®). SUVA280 was calculated as absorbance divided by WEOC concentration (Hansson et al., 2010) and is expressed as mg C·m−2·l−1.
2.3.3. Neutral and reduced sugars analysis
After water extraction (Fig. 1), deoxy-6-glucose (0.4 mg ml\(^{-1}\) in water) was added as internal standard (Wicks et al., 1991). The sample was evaporated to dryness under vacuum. The sugars were then dissolved in pyridine containing 1 wt% LiClO\(_4\) and left 16 h at 60 °C for anomer equilibration (Bethge et al., 1996), after which they were silylated (Sylon BFT, Supelco) and analysed using a Perkin–Elmer gas chromatograph fitted with a 25 m × 0.25 mm i.d. CPSil5CB column (0.25 μm film thickness) and flame ionization detector. The oven temperature was raised from 60 to 120 °C (held 1 min) at 30 °C min\(^{-1}\), to 240 °C at 3 °C min\(^{-1}\) and finally to 310 °C (held 10 min) at 20 °C min\(^{-1}\). The injector split was off before injection and was turned on after 2 min. The injector was at 240 °C and the detector at 300 °C. A mixture of nine neutral monosaccharides, neutral disaccharides and polyols (fructose, glucose, mannose, sucrose, trehalose, arabinol, glycerol, inositol and mannitol) was used as external standard for compound identification through peak retention times and for individual response coefficient determination. Concentration is expressed in mg g\(^{-1}\) or μg g\(^{-1}\) dry mass. Replicate analyses gave an analytical precision of 5%.

2.3.4. Statistical analysis
The differences induced from OTC treatment at DRY and WET plots, in terms of air temperature, peat temperature and biogeochemical parameters were analyzed using the \(t\)-test (Statistica98®). Statistical significance was determined at \(p < 0.05\) level; \(p\)-values between 0.05 and 0.10 were considered as indicating a trend (Sullivan et al., 2008).

3. Results

3.1. OTC warming effect on air and soil temperature
By comparison with control plots, at both DRY and WET sites the daily mean air temperature showed a significant increase in OTCs in July, August and September (Table 1). At the DRY site the increase reached 0.8 °C through the period considered, whereas at the WET site it ranged from 0.7 °C to 1.0 °C. The maximum air temperature reached higher values in OTCs, up to 3.0 °C at the DRY site and up to 4.5 °C at the WET site (Table 1). OTCs had no significant effect on the minimum temperature (Table 1). The rise in mean temperature can therefore be considered to be a result of the increase in maximum air temperature.

The mean peat temperature at 7 cm depth did not show any significant OTC effect at the DRY site (Table 1), whereas at the WET site it showed a significant effect in March, with an increase of 0.2 °C, which appears to be the result of a significant rise in minimum peat temperature. No significant difference in minimum peat temperature was observed at the DRY site, whereas at the WET site, the minimum peat temperature was significantly higher in November, March and April under the effect of the OTCs (Table 1). The maximum peat temperature showed no significant OTC effect at either DRY or WET sites. Daily thermal amplitude in the soil (Fig. 2) was higher in OTCs in April, May and June for DRY (but differences are not significant), whereas the opposite trend appeared for WET (differences significant at many periods of the year). These findings were confirmed by measurements carried out during 2010.

3.2. Water-extractable OM properties

3.2.1. Dry matter vs. wet matter (DM/WM)
DM/WM ratio varied from 8.9% to 6.6% at the DRY-CTL plots, and from 9.4% to 6.8% at the DRY OTC ones (Fig. 3A). Given the large standard errors, it was not possible to detect OTC effect on DM/WM at the DRY situation. In contrast to the DRY site, at the WET site the DM/WM content fell from 15.83 to 1.27 mg g\(^{-1}\) for WET-CTL and from 9.28 to 1.60 mg g\(^{-1}\) for WET-OTC (Fig. 3B). At the surface (0–2.5 cm), the
3.2.3. Isotopic composition ($\delta^{13}$C)

The $\delta^{13}$C values, between $-27.05\%$ and $-27.88\%$ for DRY-CTL and $-27.05\%$ and $-27.83\%$ for DRY-OTC, with rather large standard errors, did not evidence any significant difference vs. with OTCs and controls at the DRY site (Fig. 3A). At the WET site, the $\delta^{13}$C values, ranging from $-26.47\%$ to $-27.83\%$ for WET-CTL and from $-27.23\%$ to $-27.73\%$ for WET-OTC, also did not differ significantly (Fig. 3B), although some trends were detectable. At the surface peat (0–2.5 cm) and at depth 2.5–5 cm, the trends (p-values 0.08 and 0.05 respectively) indicated lower isotopic signatures for OTCs vs. control plots, whereas the trend was reversed at depth 7.5–10 cm (p-value 0.09).

3.2.4. SUVA$_{280}$

The SUVA$_{280}$ index tended to increase with depth, with no significant difference between OTCs and control plots at either DRY or WET sites (Fig. 3). Values ranged from 2.32 to 1.21 mg C l$^{-1}$ m$^{-1}$ for DRY-CTL and from 2.48 to 1.47 mg C l$^{-1}$ m$^{-1}$ for DRY-OTC. At the WET site, SUVA$_{280}$ varied from 3.46 to 0.73 mg C l$^{-1}$ m$^{-1}$ for WET-CTL and from 3.52 to 1.06 mg C l$^{-1}$ m$^{-1}$ for WET-OTC. It showed a trend between OTCs and control plots only at 2.5–5 cm (p-value 0.07), with higher values for OTC treatment.

Table 1

| Effect of OTCs on temperature of air (10 cm above soil surface) and peat (–7 cm depth) during a 3 month period (July–September 2009) for air temperature and during a 8 month period (November 2008–June 2009) for soil temperature at DRY and WET sites.† |

<table>
<thead>
<tr>
<th>Δ Air temperature (°C)†</th>
<th>10 cm above Sphagnum capillitum</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>July (n = 11)</td>
</tr>
<tr>
<td></td>
<td>August (n = 31)</td>
</tr>
<tr>
<td></td>
<td>September (n = 22)</td>
</tr>
<tr>
<td>Dry 1 cm</td>
<td>$T_{\text{mean}}$ $0.8^{**}$</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{max}}$ $3.4^*$</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{min}}$ 0.2</td>
</tr>
<tr>
<td>Wet 1 cm</td>
<td>$T_{\text{mean}}$ $0.9^{**}$</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{max}}$ $4.0^{**}$</td>
</tr>
<tr>
<td></td>
<td>$T_{\text{min}}$ 0.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Δ Peat temperature (°C)†</th>
</tr>
</thead>
<tbody>
<tr>
<td>7 cm depth</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Dry 1 cm</td>
</tr>
<tr>
<td>$T_{\text{mean}}$ -0.6</td>
</tr>
<tr>
<td>$T_{\text{max}}$ 0.0</td>
</tr>
<tr>
<td>$T_{\text{min}}$ -1.0</td>
</tr>
<tr>
<td>Wet 1 cm</td>
</tr>
<tr>
<td>$T_{\text{mean}}$ 0.6</td>
</tr>
<tr>
<td>$T_{\text{max}}$ -0.2</td>
</tr>
<tr>
<td>$T_{\text{min}}$ 1.2</td>
</tr>
</tbody>
</table>

† Values correspond to difference in temperature between OTC plots and control plots. Significant values are in bold: *p < 0.05; **p < 0.01; ***p < 0.001 (n = 3); $T_{\text{mean}}$, daily mean temperature; $T_{\text{max}}$, daily maximum temperature; $T_{\text{min}}$, daily minimum temperature.

WEOC content was significantly lower in OTCs than control plots. With depth, WEOC decreased and the difference between OTCs and controls was still significant at 2.5–5 cm and again at 7.5–10 cm (Fig. 3B).

3.2.5. Neutral monosaccharides, disaccharides and polyols

Three types of sugars were in the WEOM: neutral monosaccharides, neutral disaccharides and polyols (also termed reduced sugars; Table 2). The mannitol content was 221 and 344 mg g$^{-1}$, respectively at 2.5–5 cm and 5–7.5 cm depth for DRY-CTL, and only 88 and 81 mg g$^{-1}$ for DRY-OTC at the same depths. Thus, at the DRY site, the OTCs induced a significant decrease in mannitol content at these two depths. At the WET site, the mannitol content tended to increase in the OTCs at 7.5–10 cm (51 mg g$^{-1}$ for WET-CTL vs. 198 mg g$^{-1}$ for WET-OTC), whereas it tended to decrease in OTCs for fructose at 5–7.5 cm. At the WET site, glucose, mannose, glycerol and inositol contents also exhibited significant differences induced by the OTCs but only at specific depths (Table 2). At 0–2.5 cm, the glycerol content was significantly lower in OTCs (169 mg g$^{-1}$ for WET-CTL and 105 mg g$^{-1}$ for WET-OTC). Inositol showed a significantly lower yield in OTCs at 5–7.5 cm (139 mg g$^{-1}$ for WET-CTL and 12 mg g$^{-1}$ for WET-OTC). At 7.5–10 cm, the glucose content was significantly higher in OTCs (0.42 mg g$^{-1}$ for WET-CTL and 0.97 mg g$^{-1}$ for WET-OTC). Mannose content showed the same significant pattern as glucose (3 mg g$^{-1}$ for WET-CTL and 20 mg g$^{-1}$ for WET-OTC). Fructose, glucose, mannose and glycerol all showed a clear decrease with depth.

4. Discussion

4.1. Impact of OTCs is different for DRY and WET sites

From July to September 2009, the mean air temperature increased by 0.7–1 °C in the OTC plots vs. control plots (Table 1). Subsequent
measures showed that this warming also happened in 2010. Based on this significant effect \((p < 0.001)\) and considering results from many other studies on the impact of OTCs on mean air temperature (e.g. Marion et al., 1997; Hollister and Webber, 2000; Dorrepaal et al., 2003; Sullivan et al., 2008), it seems reasonable to assume that OTCs are likely to have also increased the air temperature at the OTC sites before core sampling, despite the lack of full data coverage for air temperature between the start of the experiment (May 2008) and the soil sampling date (June 2009).

In general, the effect of OTCs on the peat temperature amplitude, relative to controls, was more often significant during winter, with identical patterns at DRY and WET sites. In both cases, the mean amplitude was significantly lower in OTCs than in control plots, suggesting a loss of sensitivity to environmental temperature variation. As heat diffuses faster in water than in air (Rosenberg et al., 1983; Hollister, 1998), the lower temperature amplitude in peat under OTC treatment can be interpreted as a consequence of a decrease in thermal conductivity in relation to soil humidity at both DRY and WET sites, at least in winter. For Dabros and Fyles (2010), the decrease in thermal conductivity resulted from an increase in evapotranspiration and led to a decrease in average temperature. Our data do not allow us to draw such conclusions on

Fig. 3. Effect of OTCs on DM/WM ratio, WEOC content \((\text{mg} \, \text{g}^{-1})\), \(\delta^{13}\text{C} \, (\%)\) and \(\text{SUVA}_{280} \, (\text{l} \, \text{mg} \, \text{C}^{-1} \, \text{m}^{-1})\) in surface peat (0–10 cm) of OTC (black symbols) and control (empty symbols) plots from DRY (A) and WET (B) sites (mean values and standard errors are given; significant differences between OTCs and controls are indicated, \(^*p < 0.05; ^{**}p < 0.01; n = 3\).
The study highlights certain difficulties using OTCs or at least points under the OTCs. Moreover, the DM/WM ratio is likely to provide straightforward information on changes in humidity and/or water table level, and is not possible to directly assign the consumption of heat to evapotranspiration. Overall, significant differences appeared mainly during winter, probably as a result of the low temperature range, which entailed a decrease in variance and thus facilitated the appearance of significant differences. During early summer, the daily thermal amplitude (Fig. 2) indicated that at DRY sites, the temperature reached higher and lower extremes, with a tendency for OTC sites to have a higher temperature concomitantly. Furthermore, in contrast to various other studies (Dorreaal et al., 2003; Sullivan et al., 2008) in which soil temperature was determined at 5 cm depth, we carried out the measurements at 7 cm, which perhaps makes it more difficult to detect induced warming. In general, soil temperature is typically measured at one depth and does not take into account the phenomenon of thermal diffusion and its interaction with the “architecture” of the peat, i.e. density, which controls heat exchange and evapotranspiration (Tsueyoba et al., 2001; Admiral and Lafleur, 2007). It thus appears that understanding the response of peatlands to higher air temperatures requires a thermodynamic approach combined with a better characterization of the vertical variability in physical parameters affecting thermal diffusion. Such an approach may also facilitate understanding of the high environmental spatial variability in peatlands, as suggested by the weaker responses and the greater standard errors at the DRY site vs. the WET site.

4.2. OTC-induced warming affects the dynamics of water-extractable organic matter

Since WEOM is an organic fraction extracted from wet peat using mild conditions and consists of available OM pools (Zaccione et al., 2009), it can be a suitable substrate for inferring in situ OM dynamics, particularly under the short term effects of climate change as simulated by OTCs (13 months in our study).

Moreover, the DM/WM ratio is likely to provide straightforward information on changes in humidity and/or water table level, and is also linked to the type of bulk OM in relation to the vegetation. At the DRY site, the ratio did not reveal a specific effect of the OTCs (13 months in our study).

For the DRY sites, there was no evidence to support such a pattern and data tended to indicate, on the contrary, colder soils. This differs from the studies of Tsueyoba et al. (2009), it was not possible to directly assign the consumption of heat to evapotranspiration. Overall, significant differences appeared mainly during winter, probably as a result of the low temperature range, which entailed a decrease in variance and thus facilitated the appearance of significant differences. During early summer, the daily thermal amplitude (Fig. 2) indicated that at DRY sites, the temperature reached higher and lower extremes, with a tendency for OTC sites to have a higher temperature concomitantly. Furthermore, in contrast to various other studies (Dorreaal et al., 2003; Sullivan et al., 2008) in which soil temperature was determined at 5 cm depth, we carried out the measurements at 7 cm, which perhaps makes it more difficult to detect induced warming. In general, soil temperature is typically measured at one depth and does not take into account the phenomenon of thermal diffusion and its interaction with the “architecture” of the peat, i.e. density, which controls heat exchange and evapotranspiration (Tsueyoba et al., 2001; Admiral and Lafleur, 2007). It thus appears that understanding the response of peatlands to higher air temperatures requires a thermodynamic approach combined with a better characterization of the vertical variability in physical parameters affecting thermal diffusion. Such an approach may also facilitate understanding of the high environmental spatial variability in peatlands, as suggested by the weaker responses and the greater standard errors at the DRY site vs. the WET site.

4.2. OTC-induced warming affects the dynamics of water-extractable organic matter

Since WEOM is an organic fraction extracted from wet peat using mild conditions and consists of available OM pools (Zaccione et al., 2009), it can be a suitable substrate for inferring in situ OM dynamics, particularly under the short term effects of climate change as simulated by OTCs (13 months in our study).

Moreover, the DM/WM ratio is likely to provide straightforward information on changes in humidity and/or water table level, and is also linked to the type of bulk OM in relation to the vegetation. At the DRY site, the ratio did not reveal a specific effect of the OTCs (Fig. 3), but did at the WET site, resulting in higher dry matter content under the OTCs. Therefore, although in situ continuous measurements of peat humidity were missing, we can assume that...
higher air temperature created by the OTC treatment at the WET sites resulted in greater extent of evapotranspiration and thus drier soil in the OTCs than for control sites. Similarly, mannitol, as well as the non-reducing disaccharide trehalose are considered as osmolytes that can accumulate in microbial and plant cells in response to osmotic stress such as reduction in moisture or increase in temperature (Bohnert et al., 1995; Chaturvedi et al., 1997; Wales, 2004; Medeiros et al., 2006). Under OTCs at the DRY site, mannitol had a lower concentration in the rooting zone (2.5–7.5 cm depth), which could indicate a decrease in osmotic stress. This decrease did not correspond to a significant change in the peat water content at the DRY site (Table 2; Fig. 3). Conversely, mannitol at the WET site, particularly at 7.5–10 cm, had a greater content under the OTCs. Combined with the higher DM/WM value, this underlines a possible greater osmotic stress and indicates a likely decrease in groundwater level or more probably in soil moisture under the effect of the OTCs (Table 2; Fig. 3).

Unlike at the WET site, at the DRY site, except for mannitol content, no significant changes in the WEOM parameters were recorded between OTCs and control sites, indicating that 13 months’ incubation with OTCs did not affect the WEOM dynamics. Therefore, the following discussion focusses only on the WET site.

At 0–5 cm at the WET site, the effect of OTCs resulted in a significant decrease in WEOC and glycerol (Table 2; Fig. 3), which could correspond to changes in the early decomposition of the peat, i.e. senescence (Thormann et al., 2007) or a change in plant composition and thus the quality of new OM input. Vegetation surveys, including vascular plants and mosses, using quantitative frequency measurements (Buttler, 1992) and their analysis with redundancy analysis (RDA), showed that the site effect (DRY vs. WET) was highly significant (p < 0.001) on vegetation communities in the two consecutive years 2008 and 2009, but that the OTC effect did not induce significant changes at the community level (p 0.97 and 0.77 for respectively 2008 and 2009). Consequently, the changes in WEOM properties cannot be assigned to a shift in vegetation composition and to consecutive changes in fresh OM input, but would rather be attributable to changes in senescence processes affecting OM features. Furthermore, at the same 0–5 cm depth, there was a decrease in δ13C values of the WEOM as a result of 13C depletion under the OTCs treatment (Fig. 3). Several authors had studied factors that might influence δ13C values, such as species-specific vegetation pattern and photosynthetic fractionation (Smith and Epstein, 1971; Brader et al., 2010), as well as peat water content and temperature (Ménot and Burns, 2001), the nature of the microbial community (Andrews et al., 2000) and the metabolic OM transformation (Blair et al., 1985). No OTC effect on plant communities being observed, no impact of plant species and/or photosynthetic fractionation was to be expected. On the other hand, it was demonstrated in this study, that the presence of OTC entailed a lowering of the upper peat water content. Ménot and Burns (2001) admitted that carbon isotopic fractionation during photosynthesis was only weakly influenced by a moisture change from 72% to 78%. Accordingly, the change in the DM/WM ratio values here might not be considered as a factor controlling δ13C values. Even if the peat moisture was affected by OTC treatment, there was no evidence of a temperature change in the upper peat layers (ca. 0–5 cm). It is therefore difficult to consider temperature as a δ13C value controlling factor especially as mosses and vascular plants exhibit the same photosynthetic pathways (Ménot and Burns, 2001). The δ13C changes might therefore be attributed here mainly to microbial community changes and consequently to OM status changes. For Zacccone et al. (2011), decay and humification might involve selective degradation of OM which, in turn, might affect δ13C value. It is also well known that (i) a relative enrichment in aromatic compounds (lignin-derived compounds and humic substances) induces a depletion in 13C and more precisely that (ii) these lignin-derived compounds are generally depleted in 13C by 3–6% relative to sugars (Benner et al., 1987; Kracht and Gleixner, 2000; Kalbitz et al., 2003). A preferential consumption of carbohydrates might therefore lead to a relative enrichment in aromatic compounds with a lowering of δ13C values. SUVA280, which provides an estimate of the aromaticity of the WEOM (Traina et al., 1990; Weisshaar et al., 2003), effectively tended to indicate a relative enrichment in aromatic compounds in the 2.5–5 cm depth interval. Although WEOC content (strongly correlated with total sugars; p < 0.001) tended to confirm this pattern, individual sugars did not confirm such a conclusion for the 0–5 cm peat layer (Table 2; Fig. 3). Even if our preferred hypothesis is a stimulated WEOM decomposition in the upper peat layers under the effect of the OTCs, we cannot exclude an associated increase in humic substances. At 5–7.5 cm, sugars such as fructose and inositol showed significantly lower contents under OTCs than control plots, while WEOC, SUVA280 and δ13C were not affected by the OTC treatment (Fig. 3). In contrast to the soil surface, at 7.5–10 cm, the effect of OTCs resulted in an enrichment in δ13C, a slight but significant increase in WEOC and an increase in sugar content (Table 2; Fig. 3). Albeit the composition of the surface vegetation did not change, we cannot exclude below ground changes such as an increase in root exudate (e.g. phenolic compounds) by vascular plants, i.e. E. vaginatum. Such changes would be congruent with changes in δ13C; WEOC and sugars, and this would highlight a relatively good preservation of labile dissolved OM and carbohydrates at this depth. Such preservation could be enhanced by a release of phenolic compounds, which can block enzymatic activity, allowing the most labile OM, i.e. fructose, glucose, mannose and inositol, to be accumulated. It has been shown that phenolics produced by Sphagnum have a potential inhibitory effect on fungal and bacterial breakdown activity and/or on enzymes implied in OM decomposition (Wetzel, 1992; Fenner et al., 2005; Opelt et al., 2007; Mellegard et al., 2009).

5. Conclusions

This study highlights some difficulties in predicting peatland OM response to a rise in air temperature induced by OTCs:

(i) It appears that peat temperature alone is not sufficient for characterizing the impact of OTCs on environmental conditions. There is a need for continuous measurement of humidity at the soil surface and in peat for understanding thermal diffusion at the air–soil interface and with depth.

(ii) The differences in warming responses between DRY and WET sites indicate that spatial variability is a key component for understanding the fate of peatland C in the perspective of global warming.

(iii) Our results, which cover a 1 year simulated warming and so only reflect a single season, must be extrapolated with caution. Even if the plant assemblage did not show significant changes during such a short duration, below ground changes such as a shift in root biomass and/or exudate cannot be excluded.

Despite the short duration of the OTC manipulative warming, WEOM shows, at the WET site, (i) a relative enrichment in aliphatic and/or aromatic compounds as a result of the increased consumption of WEOC in the upper peat layers and (ii) an accumulation of WEOC and sugars in the deeper layers, probably via the effect of increased phenolic compounds leached by roots. Beyond these patterns our work shows that WEOM, in some moisture conditions,
is an efficient indicator for understanding early decay processes and the fate of OM.

Acknowledgments

The work was funded as part of the PEATWARM initiative through an ANR (French National Agency for Research) Grant (ANR-07-VUL-010). We are indebted to the Regional Scientific Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., 2006. Plant performance in a warmer temperature monitoring. N. Lottier for analytical assistance and Council of Natural Heritage of the Franche-Comté Region for access to Le Forbonnet site. We would like to thank M.-L. Toussaint for temperature monitoring, N. Lottier for analytical assistance and E. Rowley-Jolivet and B. Corboz for revision of the English version. We also are grateful to two anonymous reviewers for constructive comments.

Associate Editor—J.R. Maxwell

References


