Soil Biology & Biochemistry 64 (2013) 37–47

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Nutrient mineralisation and microbial functional diversity in a restored bog approach natural conditions 10 years post restoration

Roxane Andersen [a,c,d], Corey Wells [b,*], Merrin Macrae [b], Jonathan Price [b]

[a] The James Hutton Institute (Macaulay Land Use Research Institute), Craigiebuckler, Aberdeen AB15 8QH, UK
[b] Department of Geography and Environmental Management, University of Waterloo, Waterloo, ON N2L 3G1, Canada
[c] Peatland Ecology Research Group (PERG), Université Laval, Québec G1V 0A6, Canada
[d] Environmental Research Institute, University of the Highlands and Islands, Thurso, Caithness KW147JD, UK

ARTICLE INFO

Article history:
Received 27 August 2012
Received in revised form
27 March 2013
Accepted 4 April 2013
Available online 20 April 2013

Keywords:
Ombtrophic peatlands
Peatland restoration
Belowground processes
Microbial functional diversity
Nutrient dynamics
Cutover peatlands
Mineralization
Carbon utilization profiles

ABSTRACT

Peatland restoration has been implemented on sites exploited for horticultural peat for over a decade in Eastern Canada. However, little is known about nutrient dynamics and microbial processes in this region. Belowground nitrogen (N) and phosphorus (P) transformations and carbon utilisation by microorganisms were examined in a harvested peatland 10 years after restoration measures were implemented to assess whether restoration is returning the peatland to a state that falls within the natural range of variation found in a neighbouring bog. N mineralisation rates were almost 10-fold higher in the surface (0–10 cm) compared to the subsurface (10–20 cm) layers for all sites and were highly variable within sites. P pools were small (<0.02 μg g^{-1} dry peat) and mineralisation rates of P were low in all sections. In the surface layer, the net mineralisation and ammonification rates appeared to be highest in unrestored sites but lowest in restored sites. In contrast, the capacity of microorganisms in using different carbon (C) sources, also described as microbial functional diversity, was highest at restored sites but lowest at unrestored sites. The preferable C sources varied between sites and were significantly correlated with aboveground vegetation composition. Our study suggests that microbial activity and nutrient transformations differ between natural and unrestored harvested peatlands. Our results indicate that the presence of vegetation regrowth in the unrestored area of a peatland alters belowground processes by stimulating microbial activity and increasing the uptake of nutrients, leading to smaller pools of inorganic N available in the peat. When restoration has been carried out, microbial activity is even higher than in natural conditions, possibly leading to high immobilization of N, and net mineralisation rates are very low. This research indicates that while belowground processes have shifted from unrestored conditions following restoration, they do not appear to be fully re-established to a degree similar to natural conditions 10 years post-restoration.

1. Introduction

Peatlands cover approximately 12% of the total Canada's land area (Bridgham et al., 2006) and store an estimated 155 Gt C (Tarnocai et al., 1998), representing more than the combined carbon stock of both Canadian forests (biomass and soils) and agriculture (Roulet, 2000). Globally, the drainage and conversion of peatlands for fuel and other land uses have severely degraded peatland ecosystems (Joosten and Clarke, 2002; Holden et al., 2004). While representing a small proportion of the disturbances to peatlands in Canada, the harvesting of peat for horticultural purposes has a strong impact at the regional scale, affecting up to 70% of the peatlands in some regions of Quebec and New Brunswick (Strack et al., 2011). As a consequence of harvesting, the spontaneous regeneration of peatlands back into carbon accumulating ecosystems is difficult due to the modification of vegetative and hydrologic conditions unsuitable for *Sphagnum* recolonisation (Price, 1996; Quinty and Rochefort, 2003). Although plant colonisation of harvested peatlands does occur, the species pool is dominated by ruderal and forested species atypical of bogs (Poulin et al., 2012).

The drainage and harvesting of peatlands alter nutrient dynamics (Holden et al., 2004; Macrae et al., 2012) and affect microbial communities in peat (Andersen et al., 2013). The removal of vegetation cover and lowering of the water table exposes humified substrate and poor-quality organic matter to aerobic conditions,

* Corresponding author.
E-mail addresses: roxane.andersen@uhi.ac.uk (R. Andersen), corey.m.wells@gmail.com (C. Wells).

0038-0717/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.soilbio.2013.04.004

thus hindering microbial activity (C-limitation) because much of the C is refractory (Bayley et al., 2005; Andersen et al., 2006, 2010a). It is also in the acrotelm that most of the phosphorus is tightly retained, therefore its removal during harvesting leads to strong P limitation in the underlying exposed peat. Accelerated mineralisation in the former catotelm alters nitrogen cycling, where reduced uptake in the absence of active microbial and plant communities increases nitrogen pools in harvested systems (Wind-Mulder et al., 1996; Holden et al., 2004) which may affect the vegetation growth and carbon uptake (Bardgett et al., 2008) and potentially increase nutrient loading in runoff from these systems (Kljøve, 2001; Andersen et al., 2010b; Strack et al., 2011). The higher water table fluctuations that are often observed in harvested peatlands (Price, 1996; Holden et al., 2006; Price and Ketcheson, 2009) are also likely to interfere with nutrient mineralisation patterns and carbon cycling, both of which are strongly affected by redox potential (Artz, 2009).

Returning a peatland back into a carbon accumulating state requires the re-introduction of a hydrologic regime that promotes a raised and stable water table that can support *Sphagnum* mosses and other plants critical for peat accumulation. Methods aimed to restore harvested peatlands have been developed and tested for over a decade (Rochefort et al., 2003) and recent studies have shown that typical bog vegetation can quickly become dominant following restoration (Poulin et al., 2012). However, peat formation and carbon sequestration also depend on belowground processes that regulate organic matter turnover and affect the vegetation responses. Therefore, assessing the long-term success of peatland restoration requires evaluating if nutrient pools change over time and if microbial communities develop towards natural conditions under the growing vegetation. While vegetation assemblages typical of peatlands rapidly become dominant following restoration, other ecosystem attributes seem to lag behind in their recovery. For instance, hydrology (Price et al., 2003; McCarter and Price, 2013), water and peat chemistry (Andersen et al., 2010b), C balance (Waddington et al., 2003), methane dynamics (Waddington and Day, 2007) and microbial communities (Andersen et al., 2006, 2010a) were all found to differ between restored and natural sections of the Bois-des-Bel peatland in the first decade following its restoration. Modelling has estimated that it may take up to 20 years to establish a functional acrotelm and to reinitiate C accumulation in peatlands restored using the moss-transfer technique (Lucchese et al., 2010). However, this will depend on the time required for nutrient cycling and carbon turnover to fall within the range of variation found in natural peatlands.

Following on the previous monitoring done at the BDB site 3 and 6 years after restoration measures were applied, an intensive monitoring program was set up 10 years post-restoration that included the characterization of nutrient mineralisation dynamics and evaluation of microbial functional diversity. Unlike in the previous studies, this work compared harvested peat with and without spontaneous colonisation by plants as well as peat from restored and natural sites, with three specific objectives: 1) To determine if N and P pools and mineralisation rates differ between natural, restored (10-years post-restoration) and unrestored sites across a range of vegetation covers; 2) to assess how vegetation composition across the various sites affects the capacity of the peat microbial community to use various carbon sources; a proxy for functional diversity, and 3) to relate nutrient cycling and microbial communities in natural, restored and unrestored conditions. We hypothesized that the unrestored bare site (without spontaneous colonisation) would display higher net mineralisation rates but lower microbial activity and functional diversity and we anticipated that the opposite would be true for the natural site, as observed in previous studies. We also hypothesized that the nutrient transformations and microbial properties in the restored site would be more similar to natural conditions than unrestored ones, given the presence of a thick *Sphagnum* carpet.

2. Materials and methods

2.1. Study area and site description

The study took place at the Bois-des-Bel (BDB) bog (47°58′N, 69°26′W) (Fig. 1). Between 1972 and 1980, an 11.5 ha portion of the BDB peatland was drained, vacuum-harvested and subsequently abandoned for 20 years. In fall 1999, 8.4 ha of the harvested portion were restored using the *Sphagnum*-moss transfer technique (Rochefort et al., 2003). Straw mulch was also spread (4000 kg ha^{-1}) and a phosphorus fertilizer (15 g m^{-2}) was applied throughout the site (Rochefort et al., 2003). A 3.1 ha area remained unrestored, 2 ha being used for comparison with the restored zone and 1 ha for buffer area (not monitored) between the restored and unrestored zones. The unrestored section comprises an area of bare peat in the northeast end and an area where trees and shrubs have successfully established in the south but where the moss layer is still absent. A semi-forested natural ombrotrophic peatland surrounds the unrestored and restored areas, where *Picea mariana* (Mill.) Britt., E.E Sterns & Poggenburg and *Larix laricina* (Du Roi) K.Koch are the main tree species. Dense ericaceous shrubs, *viz. Kalmia* angustifolia L., *Ledum groenlandicum* (Oeder) Kron & Judd, *Chamaedaphne calyculata* (L.) Moench and *Vaccinium angustifolium* (Aiton) constitute the shrub layer, whilst *Sphagnum fuscum* (Schimp.) H. Klinggr , *Sphagnum magellanicum* (Brid), *Sphagnum rubellum* (Wilson), and *Sphagnum capillifolium* (Ehrh.) Hedw dominate the moss carpet (Lachance et al., 2005). In the Southeastern region of Canada, natural and anthropogenic changes have led to increased afforestation of many open bogs (Pellerin and Lavoie, 2003): therefore they are not pristine, but the BDB "natural" site remains a typical example of the least affected peatlands found in this highly disturbed region (Lachance et al., 2005), and a target for restoration.

2.2. Nutrient concentrations and net mineralisation rates

Sample locations were selected based on vegetation and microtopography to capture the range of variation in microhabitats across BDB (see Appendix 1 and Fig. 1). A total of 14 sub-sites were sampled monthly between May and August 2010 (inclusive, $n = 3$ periods), within the restored (RES, $n = 5$ sites), unrestored vegetated and bare (UNRv & UNRb, $n = 3$ sites each), and natural (NAT, $n = 3$ sites) sections of BDB. "Bare" refers to sampling subsites where bare peat was exposed, with little or no vegetation or litter and no *Sphagnum*.

In each sampling date, two adjacent 20 cm deep peat cores were extracted from each sub-site and cut into two equal 10 × 10 cm samples (0–10 cm and 10–20 cm). The first core was used to determine extractable total inorganic nitrogen (TIN), ammonium (NH_4^+), and nitrate (NO_3^-) concentrations in the peat. The second core, referred to as the 'incubation' core, was placed in a plastic bag to exclude vegetation roots and the effects of rainfall, and then repositioned back into its original pit (Eno, 1960). After one month, incubated samples were retrieved and returned to the lab where they were used to estimate the net mineralisation rates (Eno, 1960; Hart et al., 1994). Briefly, both cores were homogenized by hand and two 5 g subsamples were removed. One subsample was mixed with 50 mL of distilled water for determination of water-extractable P (WEP). The second subsample was extracted in 50 mL of 2 M KCl for determination of NH_4^+ and NO_3^-. Subsamples were shaken for one hour and the extractant was subsequently gravity filtered using 1 μm porosity filter paper (Whatman No. 42)

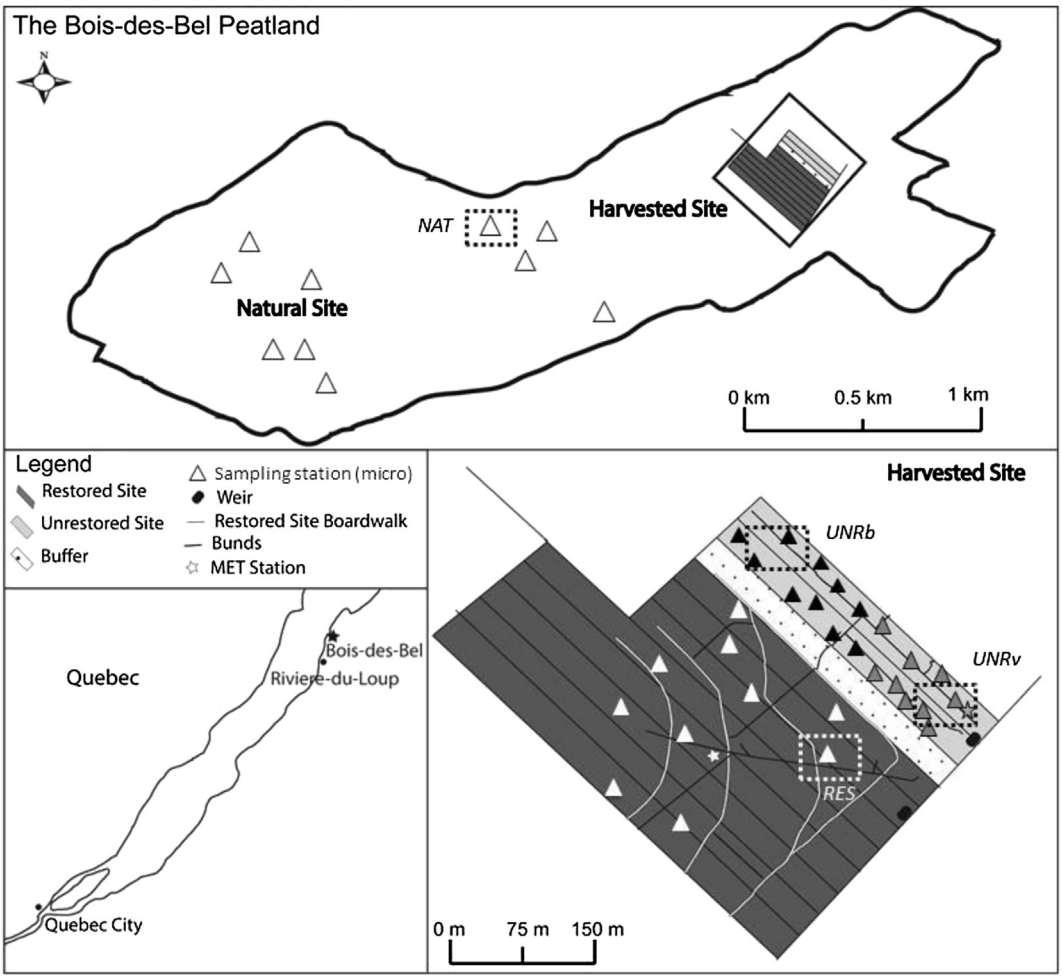

Fig. 1. Schematic representation of the study site (RES, UNRb, UNRv) with adjacent natural section (NAT); showing the area where cores have been taken for mineralisation rates and nutrient pools estimates (dotted rectangles) and where samples have been taken for carbon utilisation profiles characterization (triangles, see legend). Modified from McCarter and Price (2013).

and frozen until analysis. Filtered samples were analysed for NH_4^+–N, NO_3^-–N, and soluble reactive phosphorus (SRP) using standard colorimetric techniques (Bran Luebbe AA3 autoanalyzer, Seal Analytical, USA) at the University of Waterloo Biogeochemistry Lab.

Net ammonification and net nitrification rates (μg N g^{-1} dry peat day^{-1}) as well as net P mineralisation were calculated from the average difference between concentrations of NH_4^+, NO_3^-, or SRP in the incubated core at the end of the incubation period and concentrations of NH_4^+, NO_3^-, or SRP extracted from the initial (not incubated) cores. Net N mineralisation rates were calculated as the sum of the net nitrification rates and net ammonification rates determined in the incubated cores.

Peat physical and chemical properties are analysed at each depth for all sites and are shown in Table 1. Bulk density (g/cm^3) was determined as the mass of oven-dry soil divided by the total core volume. Organic matter content was calculated by loss on ignition (LOI) (Rowell, 1995). Soil moisture was determined gravimetrically and expressed in percentage. C/N ratios were determined using Mass Spectrometry (Environmental Isotope Lab, University of Waterloo).

2.3. Carbon utilisation by the microbial community

The microbial functional diversity was assessed using the MicroResp system (Campbell et al., 2003) from samples collected similarly in the beginning, the middle, and end of the 2010 growing season. However, in this case, on each sampling date, 10 randomly chosen replicate locations were sampled in one type of microhabitat from NAT, RES, UNRb and UNRv sub-sites of the BDB peatland (Appendix 1, Fig. 1) for a total of 40 samples per date. Aboveground vegetation (percent cover) was evaluated at each sampling location in 25 cm^2 quadrats. Samples were kept at 4 °C between the field and the laboratory and were analysed within one week. For each sample, one third (32 wells) of a 96-well plate was prepared with 0.30 g of peat individually weighed in each well (Artz et al., 2006) and incubated for 72 h at 25 °C. Then, 16 carbon sources were added

Table 1
Peat physical properties. Values averaged (NAT $n = 3$; RES $n = 5$; UNRv $n = 3$, UNRb $n = 3$) over all peatland sub-sites (± standard deviation). LOI refers to loss on ignition.

Site	Depth	Bulk density (g/cm^3)	LOI (%)	Moisture (% Grav.)
NAT	0–10	0.08	99 ± 1.3	92 ± 0.6
	10–20	0.08	97 ± 1.2	93 ± 1.0
RES	0–10	0.10	96 ± 4.2	84 ± 1.7
	10–20	0.13	92 ± 6.4	84 ± 1.4
UNRv	0–10	0.18	95 ± 5.3	68 ± 9.4
	10–20	0.18	95 ± 4.8	77 ± 2.1
UNRb	0–10	0.20	93 ± 7.0	78 ± 3.5
	10–20	0.17	91 ± 0.7	79 ± 1.2

to the peat (one carbon source per well, replicated two times for each sample) and included a selection of carboxylic acids, amino acids, and carbohydrates commonly found in root exudates: malic acid, citric acid, α-ketoglutaric acid, γ-amino butyric acid, oxalic acid, glucose, fructose, galactose, arabinose, trehalose, cysteine, alanine, arginine, lysine, as well as lignin (a complex compound) and water (a negative control).

Detection microplates, containing 150 μl purified agar (1%), cresol red indicator dye (12.5 μg ml^{-1}), potassium chloride (150 mM) and sodium bicarbonate (2.5 mM) were read in a spectrophotometer at absorbance wavelength 570 nm and then placed onto a MicroResp seal on top of each deep-well plate containing the peat and C sources. The deepwell + detection plates were incubated for 6 h at 25 °C, after which the detection plates were removed and read again in the spectrophotometer. The CO_2 production rates were then calculated from the difference between absorbance at times 6 h and 0 h for each well. Catabolic evenness, the variability of substrate use across the range of substrates tested, was estimated as $E = 1/\sum p_i^2$ where p_i is the respiration response to individual substrates as a proportion of total respiration activity induced by all substrates for a soil (Degens et al., 2001). Average microbial activity was estimated as the average well colour development (AWCD; $\Sigma p_i/n(p)$).

2.4. Statistical analyses

All the statistical analyses were performed in R (R Development Core Team, 2009). In all cases, normality of distribution and homogeneity of variance were verified prior to analyses and appropriate transformations were used when required.

For mineralisation rates, we analysed the two depths separately because they reflect different functional horizons (fresh litter versus older peat) as in Bayley et al. (2005). We used one-way permutational ANOVAs (function "lm", package "stats" (Chambers et al., 1992) to test the effects of time in the growing season (beginning, middle, end) on net ammonification, net nitrification, net N mineralisation and net P mineralisation. However, since there was no true replication of microhabitats, we compared the main site types (RES, NAT, UNRv, UNRb) without performing any statistical analysis.

Due to the large area covered by each site type, the distance between the sample locations and the scale at which microbial processes occur, we considered the 10 samples per site type to be independent and treated them as replicates. However, to account for spatial auto-correlation between samples, we tested the effect of geographical coordinates (latitude and longitude) using a redundancy analysis (RDA). The proportion of the variance explained by location was small but significant (4.47%, $p = 0.005$) so further analyses were conducted on the residuals, using coordinates as co-variables. We tested the effects of site type (RES, NAT, UNRv, UNRb) and time in the growing season (beginning, middle, end) on microbial catabolic evenness and AWCD using two-way ANOVAs (function "aov" package "stats"), and on carbon utilisation profiles using permutational multivariate analysis of variance (Anderson, 2001) using the function "adonis" from the "vegan" package (Oksanen et al., 2008).

The relationships between aboveground vegetation composition and carbon utilization were tested with Canonical correlation analysis (function "CCorA", "vegan" package). We then used forward selection ("fwd.sel" and "packfor" package in R) and redundancy analysis (RDA, function "rda" in "vegan" package) to assess the influence of vegetation composition on microbial C utilization potential.

3. Results

3.1. Nitrogen and phosphorus mineralisation rates

Monthly median net mineralisation and nitrification rates did not vary temporally throughout the study ($p > 0.05$) and consequently median daily net N mineralisation rates are provided (μg N g dry peat^{-1} day^{-1}). Ammonification and net N mineralisation rates were higher in the surface 0–10 cm and decreased with depth whereas net nitrification rates were comparable in magnitude among depths. Median net N mineralisation rates were dominated by ammonification processes, with the conversion of organic N to NH_4^+ exceeding nitrification in all sections except the RES (Fig. 2). In the UNRv and NAT, mean net N mineralisation rates were accounted for largely by ammonification, and net nitrification rates were low. For the 0–10 cm surface layer, the transformation processes appeared to be greatest in the UNR section, with larger rates at the bare (UNRb) than vegetated (UNRv) sites. Conversely, the NAT and RES appeared to have smaller net N mineralisation

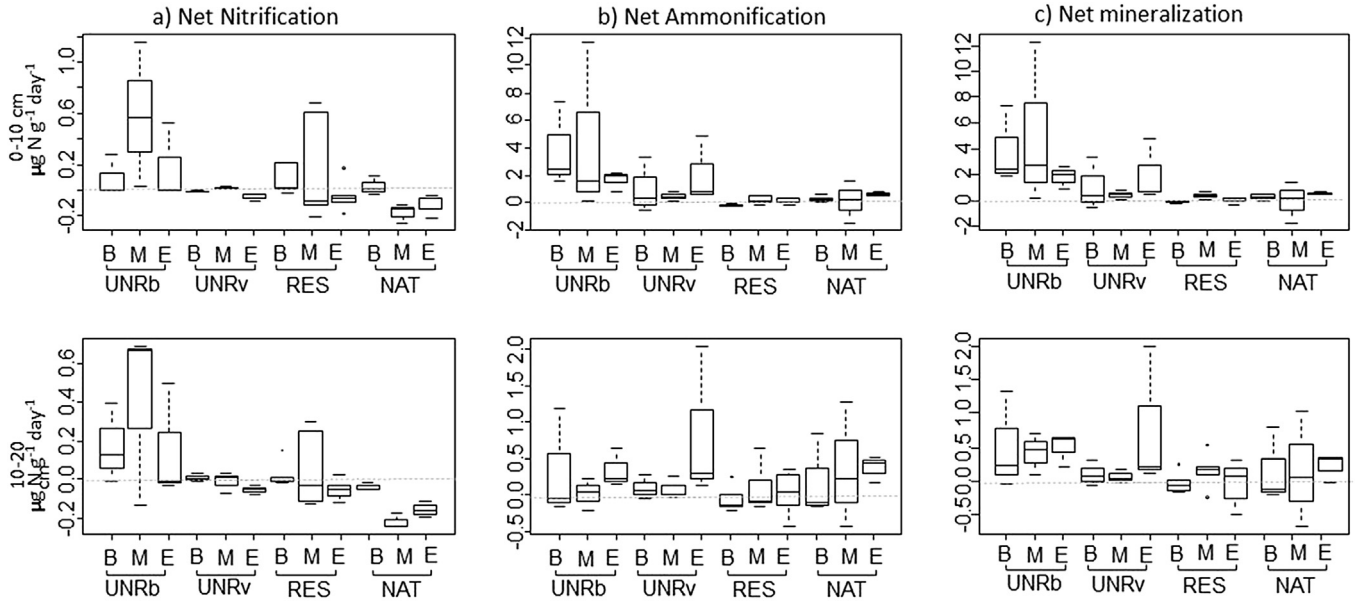

Fig. 2. Daily net N transformation rates in the 0–10 cm and 10–20 cm layers across Unrestored bare (UNRb), Unrestored vegetated (UNRv), Restored (RES) and Natural (NAT) sections of the BDB peatland in the Beginning (B), Middle (M), and End (E) of the 10th growing season following restoration. Note the differences in scales between graphs.

rates (Fig. 2). As was observed for NH_4^+, net nitrification was also high at the UNRb. Net nitrification was close to zero in the UNRv and RES, whereas net NO_3^- immobilization was observed in the NAT site (Fig. 2). Although patterns in net nitrification rates were consistent between both the 0–10 and 10–20 cm depths, neither mineralisation nor ammonification rates appeared to differ between sites within the 10–20 cm layer (Fig. 2). The mineralisation of SRP was negligible ($<1.0 \times 10^{-3}$ μg P g dry peat^{-1} day^{-1}) throughout the season (not shown). Both water-extractable SRP concentrations and P mineralisation rates were too low to detect differences among sections or dates with any degree of certainty.

3.2. N and P pools

Over the entire study period and for all sites, TIN (NH_4^+ and NO_3^-) pools in the peat within the upper 0–10 cm depth were comprised primarily NH_4^+ (>70% of TIN) (Table 2). A marginal decrease in NH_4^+ concentration relative to NO_3^- was observed at the 10–20 cm depth for the UNRb, RES, and NAT sites whereas a stronger decrease with depth was observed at the UNRv site (Table 2). Nitrate concentrations (site-wide median = 3.9 μg N g^{-1} dry peat) were lower than NH_4^+ at all sites (site-wide median = 12.2 μg N g^{-1} dry peat) and appeared to show no difference in concentration with depth (Table 2). NO_3^- concentrations were comparable across all sites although the NAT site displayed the greatest values for both depths. Ammonium (and thus TIN) concentrations appeared to be larger at the NAT and UNRb sites in comparison to the UNRv and RES sites. The higher mean N pools observed at the NAT site were primarily due to elevated N concentrations at the NAT site in first half of the growing season rather than in the second half (data not shown). Differences in N concentrations across sites were more apparent at the 0–10 cm depth than the 10–20 cm depth. Concentrations of SRP within the peat were consistently very low (<0.02 μg P g^{-1} dry peat) at all sites and at both depths over the study period (data not shown). C/N ratios (Appendix 1) in peat samples collected at the end of the season were high (>55) across all sites. The high C/N ratios are due to very low N contents (<1%) in peat rather than high carbon, which ranged from 39% to 55%. Analytical uncertainty increases at low N concentrations such as those reported here, and consequently the absolute values (C/N ratios) reported should be treated with some caution, and relative differences across sites should be emphasized instead. C/N ratios were generally lower and less variable at the UNR sites (mean 64, range 58–79) than at the RES (mean 82, range 57–119) and NAT sites (mean 98, range 67–134).

3.3. Microbial functional diversity and carbon utilisation profiles

Unlike N mineralisation rates, the catabolic evenness, which describes the uniformity of the utilisation of various carbon sources by the microbial community, changed over time, decreasing from the beginning to the end of the season in UNRv, increasing slightly over the summer in UNRb, and remaining stable and similar throughout the season in NAT and RES (Table 3, Fig. 3a). At all sites the microbial potential activity (AWCD) was the highest in the early season and lower on the two later sampling dates. On the other hand, the microbial communities were more active in RES than in any other sites throughout the growing season. The lowest rates of utilisation were found in UNRb, while UNRv and NAT had similar and intermediate average well colour development (AWCD) (Table 3 and Fig. 3b).

Fructose, malic acid, and oxalic acid were the preferred source in sites. The significant effect of site was mostly a result of higher CO_2 production for most carbon sources in the RES and lower in UNRb (Table 3, Figs. 4–8). Interestingly, UNRv and NAT had similar patterns for almost all carbon sources, with intermediate values of CO_2 production. A limited set of plant species retained by forward selection explained up to 33.1% of the variance in CO_2 utilization ($F = 10.83$, $p = 0.005$) and more distinct patterns emerged: 1) utilization of all carbon sources increased with increasing cover of vegetation, and in particular with the cover of *Sphagnum*, and 2) the amino acids arginine, lysine, cysteine and alanine seemed preferentially used where the cover of *Polytrichum strictum* and trees were greater (some RES but mostly UNRv, Fig. 4), while glucose, fructose, citric acid and lignin are preferred under *Sphagnum* (under RES and NAT) (Figs. 5–7).

4. Discussion

4.1. General trends in nutrient dynamics and microbial activity

Mean daily net N mineralisation rates measured in the upper 10 cm of our natural site (0.23 μg N g^{-1} dry peat day^{-1}) were comparable to those measured in other undisturbed bogs. Verhoeven et al. (1994) recorded net mineralisation rates of less than 0.5 μg N g^{-1} dry peat day^{-1} in their comparison of Dutch and American bogs. A mean net N mineralisation rate of 0.4 μg N g^{-1} dry peat day^{-1} was also observed in a bog near Juneau, Alaska (Fellman and D'Amore, 2007). The decreasing in mineralisation rates with depth in our findings was also in agreement with the study conducted by Verhoeven et al. (1990). This may be due to the changes in microbial metabolic activity, which were determined by factors like temperature, substrate quality and redox conditions within the deeper layers of the peat (Verhoeven et al., 1990). Nutrient mineralisation rates were not significantly different throughout the season ($p > 0.05$), although this could be a consequence of high within-site variability (Fig. 2). Microbial potential activity and carbon utilization rates, in contrast, varied significantly with sampling time: for all sites, values were higher in the beginning than in the middle or the end of the growing season. This corresponds to a previous study conducted by Andersen et al. (2010a). However, for both mineralisation rates and carbon utilisation rates, spatial variability

Table 2
TIN, NH_4^+, and NO_3^- concentrations (μg N g^{-1} dry peat, median, minimum value, maximum value and mean value) for each peatland site and for the two depths sampled.

Depth (cm)	Site	NH_4^+ (μg g^{-1} dry peat)				NO_3^- (μg g^{-1} dry peat)				TIN (μg g^{-1} dry peat)			
		Med.	Min	Max	Mean	Med.	Min	Max	Mean	Med.	Min	Max	Mean
0–10	UNRb	15.8	8.9	54.1	22.7	3.7	1.3	8.5	3.9	20.0	10.1	62.6	26.6
	UNRv	8.7	3.4	24.1	9.5	1.1	0.5	5.2	1.8	9.8	5.1	29.4	11.3
	RES	12.0	5.1	24.5	12.5	4.8	2.0	9.9	4.9	16.8	7.3	34.3	17.3
	NAT	15.9	8.8	80.6	26.3	6.8	2.9	13.0	7.4	26.5	16.0	92.3	33.8
10–20	UNRb	10.8	4.0	24.6	11.8	3.5	1.0	5.5	3.0	14.3	5.4	28.3	14.7
	UNRv	6.3	2.7	8.3	5.8	4.7	3.0	4.8	4.2	9.3	7.4	13.1	9.9
	RES	8.4	4.5	34.5	10.5	3.9	1.9	7.8	4.3	11.8	8.8	42.3	14.8
	NAT	19.8	14.0	55.3	24.9	10.0	4.0	13.4	9.1	33.1	18.7	67.4	34.0

Table 3
Effect of sampling season (beginning, middle, end) and site (NAT, RES, UNRv, UNRb) on carbon utilisation profiles, catabolic evenness and average well colour development (AWCD, proxy for activity). Significant effects (Pr (>*F*) < 0.05) are shown in bold.

Model	d.f	C utilization profiles		Catabolic evenness		AWCD	
		F value	Pr(>*F*)	F value	Pr(>*F*)	F value	Pr(>*F*)
TIME	2	16.22	**0.001**	4.78	**0.009**	21.19	<**0.001**
SITE	3	66.59	**0.001**	6.82	<**0.001**	106.41	<**0.001**
T x S	6	1.78	0.056	6.50	<**0.001**	2.10	0.054
Residuals	107	0.48		N.A.		N.A.	
Total	119						

across sites exceeded temporal variability observed within a site (Table 3, Figs. 2–4).

Similar to other studies, NH_4^+ comprised the majority of TIN in the peat, with NO_3^- making up less than 20% of the available TIN at all sites over the study period (Rosswall and Granhall, 1980; Hemond, 1983; Williams and Wheatley, 1992; Bayley et al., 2005). Our results are consistent with the typical behaviour of TIN in ombrotrophic bogs, where larger populations of ammonifying bacteria are observed and the nitrification of organic N is restricted as a result of acidic, waterlogged conditions that adversely affect nitrifying bacteria (Collins et al., 1978; Bowden, 1987; Stark and Firestone, 1995; Holden et al., 2004). In addition, under poorly aerated conditions, methanotrophs have been known to outcompete nitrifying bacteria, inhibiting nitrification (Megraw and Knowles, 1987). As a result, the conversion of NH_4^+ to NO_3^- is restricted, thereby limiting NH_4^+ loss and increasing its concentration in the peat profile relative to NO_3^-. This process was also observed by Andersen et al. (2006) and Croft et al. (2001) in the same peatland. Despite being lower than NH_4^+, NO_3^- pools were in the upper range for ombrotrophic peatlands (Andersen et al., 2011). The relatively elevated NO_3^- concentrations at the natural site are surprising; however, in the Bas-St-Laurent region where this study was carried out, high density farmland and fertiliser use in the vicinity of the BDB could have led to increased levels of the nutrients, as suggested by a recent review on water chemistry in peatlands of the province of Québec (Andersen et al., 2011). Atmospheric N deposition along with N fixation is the only source of N in ombrotrophic peatlands. The dry atmospheric deposition is unknown for eastern Canada while wet atmospheric deposition has been estimated to be as high as 0.8 g N m^2 yr^{-1} for the region and thus may be an important source of external N at Bois-des-Bel (Turunen et al., 2004).

4.2. Belowground processes in unrestored peat

The microbial communities from the BDB restored peatland have been studied previously in two other studies (Andersen et al., 2006, 2010). In the latter, Biolog™ EcoPlates were used to evaluate the catabolic diversity of the microbial communities in the same peatland 7 years after restoration. Unlike MicroResp which uses whole soil as a substrate, Biolog was biased towards the cultivable portion of the microbial community, and the authors did not distinguish between the vegetated and bare portion of the unrestored sites. Based on the findings from previous studies, we hypothesized that the unrestored site without vegetation (UNRb) would display higher mineralisation rates but lower microbial activity than in the natural or restored sites. We anticipated correctly that due to dewatering, a deeper aerobic layer would enhance mineralisation at the unrestored site (Holden et al., 2004). This also in agreement with Williams and Wheatley (1988), who observed an increase in ammonifying and nitrifying bacteria following water table drawdown in which mineralised N increased substantially in the 20 cm surface horizon, which led to the lower C/N ratios as observed in the unrestored sites. Similarly, Croft et al. (2001) investigated the change in nitrogen cycling between vacuum-harvested peatlands and natural analogues and they found that harvested peatlands consistently demonstrated higher mineralisation potentials of nitrogen to ammonium compared to natural systems. This was attributed to moisture deficiencies, greater temperature and water table fluctuations in harvested sites. Given the inverse relationship between higher moisture content and decreasing nitrification, we can explain the higher rates of nitrification observed at the UNRb, where water tables and moisture content in peat cores were low on average compared to the other sites (Table 1, Appendix 1). Under the drained condition in harvested peatlands, enhanced oxidation of organic matter reduces the amount of substrate available for methanogens, thereby lowering CH_4 production (Waddington and Day, 2007). With less CH_4 available, it reduced the competition between methanotrophs and nitrifiers, which resulted in higher nitrification process at the unrestored bare sit. Peat NO_3^- concentrations were also greater at the unrestored bare site than at the unrestored site with vegetation (UNRv) and restored sites, likely due to the buildup of NO_3^- from increased nitrification.

Moisture content and water level at the UNRv site were similar to UNRb site as shown in Table 1. Consequently, it was hypothesized that mineralisation rates and microbial activity would not vary between the vegetated and bare sections of the UNR. However, the concentration of NH_4^+ and NO_3^- at UNRv site is lower than the UNRb

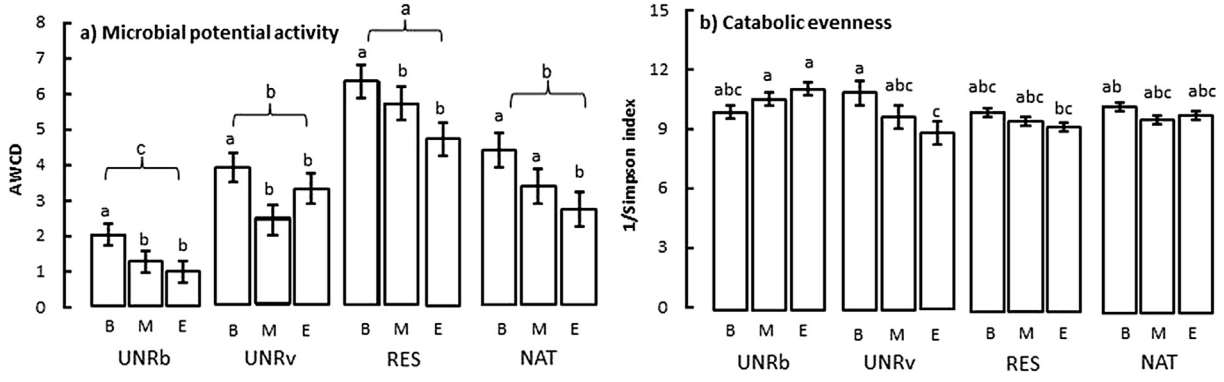

Fig. 3. a) Microbial activity (estimated as Average Well Colour Development, AWCD; mean ± std. err.) and b) Catabolic Evenness (mean ± std. err.) across Unrestored bare (UNRb), Unrestored vegetated (UNRv), Restored (RES) and Natural (NAT) sections of the BDB peatland in Beginning (B), Middle (M) and End (E) of the 10th growing season post-restoration. Significant differences (Tukey HSD test) are indicated by different letters according to results from Table 3.

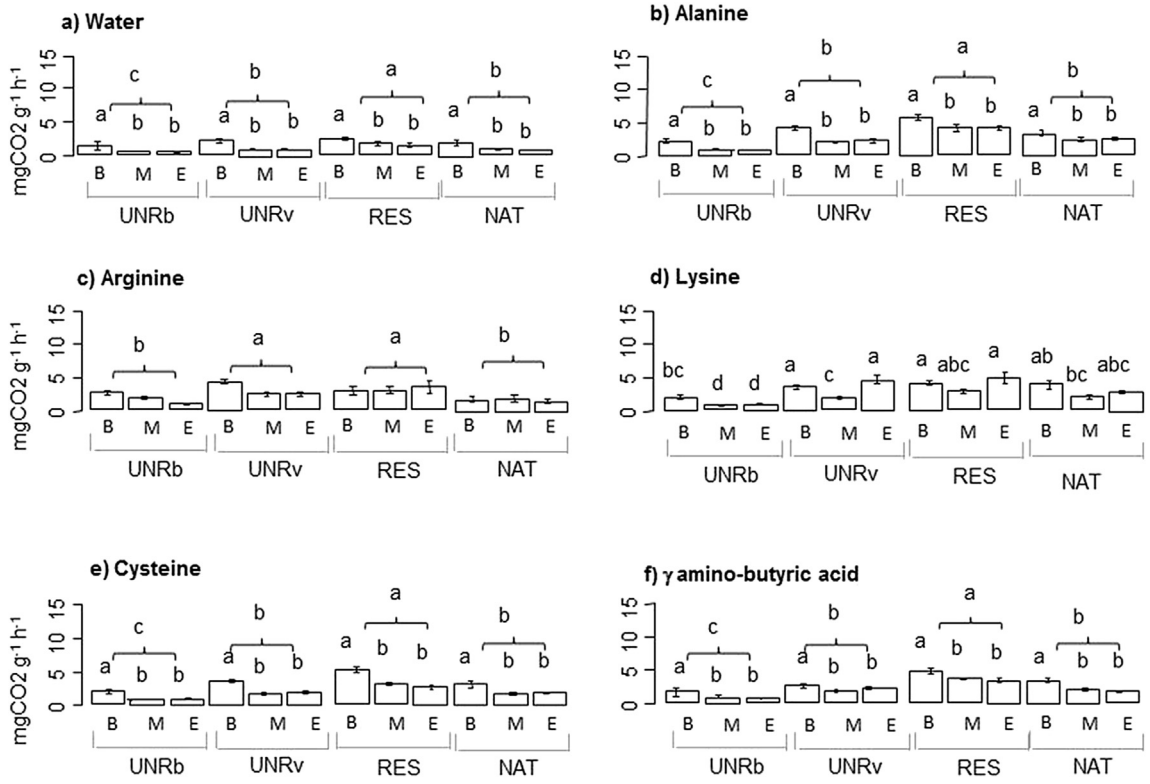

Fig. 4. Respiration rates (mean C–CO_2 $g^{-1}h^{-1}$ ± std. err.) across sections at the different sampling dates for a) water (the negative control) and the amino acids b) Alanine c) Arginine d) Lysine e) Cysteine and f)γ amino-butyric acid. Significant differences (Tukey HSD tests on individual compounds) are indicated by different letters.

site. This may be due to the influence of vegetative uptake, a mechanism lacking in the latter. Furthermore, rates of nitrification (both depths), ammonification (0–10 cm) and net mineralisation (0–10 cm) were lower at UNRv than UNRb (Fig. 2). This may indicate higher immobilization of N by active microbial community at the UNRv site (Figs. 3–7).

Indeed, under bare peat (UNRb), microbial communities exhibited a similar or greater catabolic evenness compared to other sites, showing that the microbial community could retain its capacity to degrade multiple substrates even following a profound disturbance that exposed deep peat. This is in accordance with recent studies, which reported that high potential diversity have been found through peat profiles (Tveit et al., 2012) and in eroded peat (Sen et al., 2012) using DNA-based approaches. On the other hand, lower average well colour development (AWCD) and generally low rates of respiration for individual carbon sources indicate less active microbial biomass in unrestored bare site, as observed by Andersen et al. (2006). With access to low quality organic matter (C-limitation and P-limitation) and in the presence of lower C/N ratios, the microbial community would be less efficient in breaking

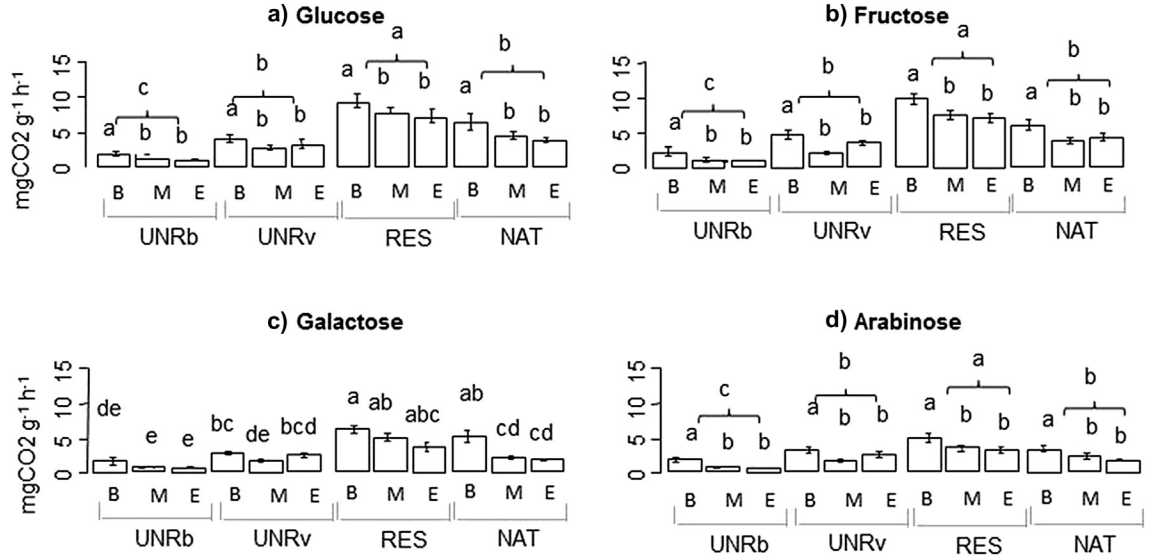

Fig. 5. Respiration rates (mean C–CO_2 $g^{-1}h^{-1}$ ± std. err.) across sections at the different sampling dates for the carbohydrates a) Glucose, b) Fructose, c) Galactose and d) Arabinose. Significant differences (Tukey HSD tests on individual compounds) are indicated by different letters.

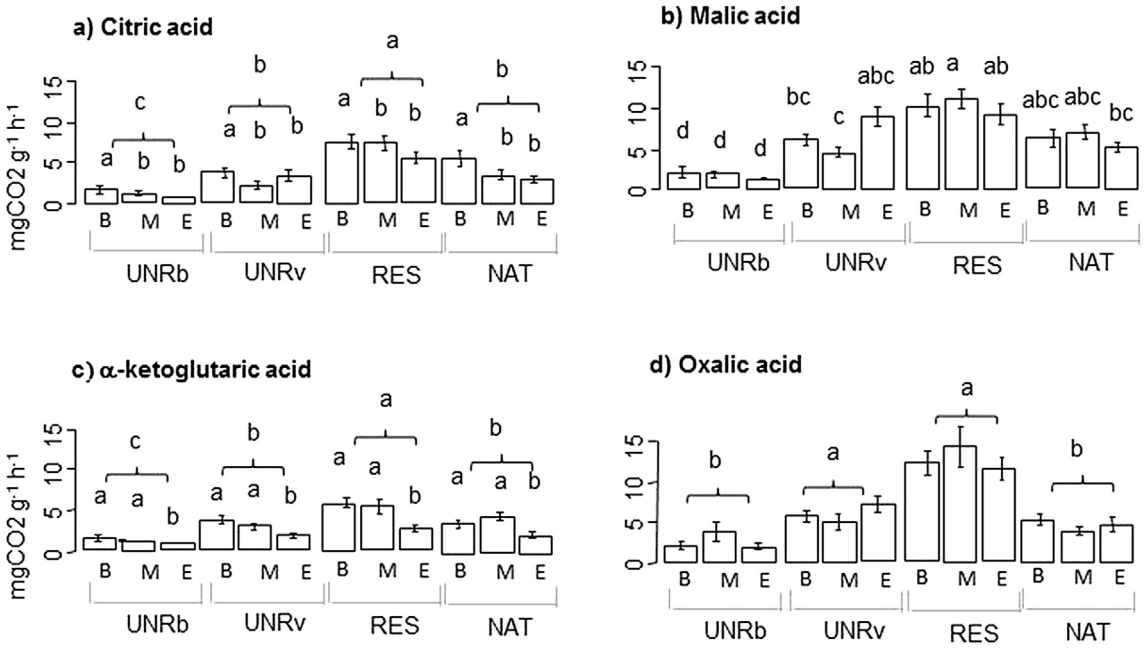

Fig. 6. Respiration rates (mean C–CO_2 $g^{-1}h^{-1}$ ± std. err.) across sections at the different sampling dates for the carboxylic acids a) Citric acid, b) Malic acid, c) α-ketoglutaric acid and d) Oxalic acid. Significant differences (Tukey HSD tests on individual compounds) are indicated by different letters.

down organic matter (Fisk et al., 2003) and less prone to immobilization. Andersen et al. (2006) also showed K deficiency in the unrestored bare site, leading to reduced carbon fixation in the microbial biomass. This explains the high mineralisation rates we observed at BDB and supports this idea of no build-up of biomass (low immobilization). On the contrary, the value of potential carbon utilization for samples from vegetated unrestored site was similar to natural site despite different substrates and vegetation covers (Table 1). While the old humified peat found at the vegetated unrestored site is likely C-limited and has a similar C/N ratios, the presence of a large network of roots from shrubs and trees might locally supply fresh organic carbon through rhizodeposition, attracting microorganisms and increasing the potential activity. Furthermore, in the harvested drained peat where plants have developed (UNRv), the low concentration of phosphorus that we observed may have increased the allocation of C by the plants to their mycorrhizal partners, therefore stimulating the growth of fungal biomass and influencing enzymatic activity and capacity to use various substrates to access nutrients (Potila et al., 2009). Following this and the fact that microbial respiration at the community level is significantly correlated with the composition of the aboveground vegetation, we suggest that the similar and intermediate values of microbial activity in natural and vegetated unrestored sections could be a consequence of high proportion of mycorrhiza within the microbial community, associated with the numerous host species (ericaceous shrubs such as *Vaccinium* sp., *Chamaedaphneae calyculata* or *Ledum groenlandicum*; trees such as *Larix laricina*, *Picea mariana* or *Betula* sp.) which are absent from UNRb.

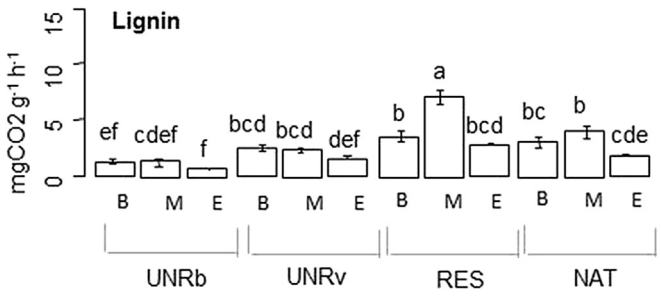

Fig. 7. Respiration rates (mean C–CO_2 $g^{-1}h^{-1}$ ± std. err.) across sections at the different sampling dates for lignin. Significant differences (Tukey HSD tests on individual compounds) are indicated by different letters.

4.3. Impact of restoration on belowground processes

Daily net N mineralisation rates measured in the restored site appeared to be similar to those in the natural sites. Nevertheless,

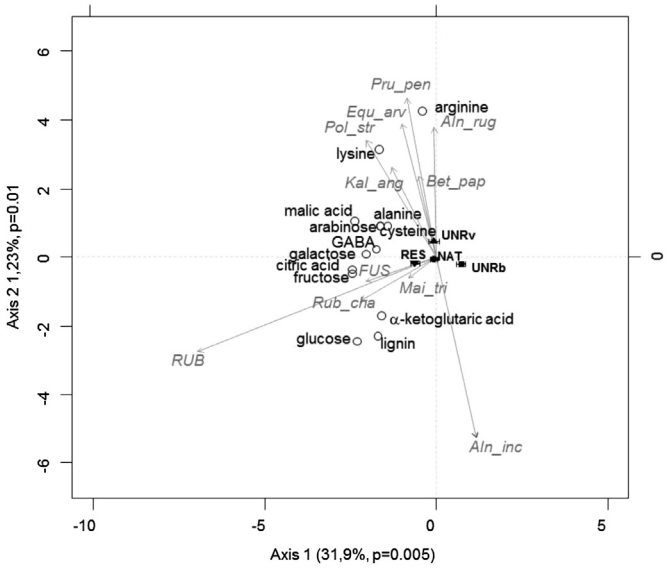

Fig. 8. First two axes of the Redundancy Analysis (RDA) showing the relationships between carbon utilisation profiles and Hellinger-transformed vegetation cover of species retained by a forward selection process. The centroids of the sites scores for each site types are shown with standard deviation.

since net mineralisation is defined as the difference between gross mineralisation and gross immobilization, similar net rates do not mean similar processes. In the restored site, the low net mineralisation rates could come from high gross mineralisation rates compensated by high immobilization rates. Interestingly, the highest C/N ratios and the highest microbial utilization rates for all carbon sources were also found in the restored peat throughout the season. The combination of fresh organic matter (low bulk density combined with the new *Sphagnum* and vascular plants and roots growth) and few ericaceous shrubs are thought to create favourable conditions for the development of an active microbial biomass (Andersen et al., 2010a). Our results further suggest that the microbial community in the restored site and in the unrestored site where spontaneous colonisation has occurred exhibit high potential to degrade the new organic matter coming from the litter of the plants (high mineralisation). The microbial community also could be efficiently recycling the nutrients in the presence of organic matter with high C/N ratios (Schimel and Weintraub, 2003); thus retaining them in the microbial loop to build biomass (high immobilization) and leading to low net mineralisation rates. This might be a consequence of lower peat nitrogen (TIN, NH_4^+, NO_3^-) concentrations in those sites compared to the natural sites (Table 2).

The restoration approach at BDB involved reintroducing *Sphagnum* diaspores followed by the application of a phosphorus fertilizer (15 g m^{-2}) to facilitate moss such as *Polytrichum strictum* and vascular plant establishment (Rochefort et al., 2003; Shantz and Price, 2006). We were therefore interested in investigating the dynamics and abundance of P in the restored peat substrate a decade since restoration. It is known that, in undisturbed bogs, P is tightly conserved in the vegetation, notably in the *Sphagnum* capitula (Damman, 1978), hence small pools of soluble phosphorus in the peat were expected at the NAT. Under drained and mined conditions, it has been observed that concentrations of P in peat are even lower compared to their natural counterparts, usually as a result of the removal of the upper peat horizons where most of the P is usually found (Wind-Mulder and Vitt, 2000; Andersen et al., 2006; Sottocornola et al., 2007), but also due to leaching of P in the upper layers of the harvested peat (Renou et al., 2000). Our study indicates that 10 years post restoration, concentrations of SRP within the peat are very low (<0.02 μg P g^{-1} dry peat) and rates of P mineralisation were negligible for all sites over the study period. Therefore, despite the initial addition of P to RES during restoration, the pools available in the peat are not different than in natural conditions 10 years post restoration, possibly because it is retained in the capitula of the newly established *Sphagnum* (Andersen et al., 2010a) that is now dominating the vegetation composition (Poulin et al., 2012).

The strongest pattern in our carbon utilisation profiles is the division of the sites with vegetation cover (RES, UNRv, NAT) from the bare sites (UNRb), visible as the separation of the sites along the first axis of the RDA in Fig. 8, which explained nearly a third of the variation in the data set. Therefore, it seems that even in peat under similar physical constraints (humified substrate, fluctuating water table, reduced water moisture); biological drivers, such as the presence of vegetation and associated roots and rhizosphere microorganisms, could alter belowground processes: as vegetative uptake and N immobilization by the microbial community in the peat increase, available pools of N in the peat diminish and net mineralisation rates decrease. Furthermore, not only did the presence of plants impact the potential activity of the microbial community and mineralisation rates, certain plants were associated with a preferential utilization of particular sources of carbon (Fig. 8). It was already suggested by Yan et al. (2008) that amino acids discriminate microbial populations at the plant species level and by Roberts et al. (2009), who described different vegetation types support a unique free amino acid soil signature. Other studies observed that microbial activity of vascular plant litters generally differed from that of mosses (Straková et al., 2011), and that for instance *Eriophorum vaginatum* stimulated the utilization of citric and malic acids by the microbial community. Our results further suggest that in peatlands, changes in moss communities could have an impact on belowground carbon utilisation, with a shift from amino acids to carbohydrates and organic acids as a preferred carbon source within the microbial community when the moss layer shifts from *Polytrichum strictum* to *Sphagnum* sp. This is in line with the idea that the *Sphagnum* bryosphere exerts a key control on C and N cycling in peatlands (Lindo and Gonzalez, 2010), and further investigation might unravel how this change in dominant moss species is reflected in the structure of the whole microbial community, in the suite of enzymes that are expressed within the community (Straková et al., 2012), and in the availability of nutrients to other plants. The higher rate of degradation of lignin in the restored site is particularly interesting and puzzling: it generally involves phenol oxidases, and occurs in the presence of oxygen. A recent study using metagenomic and metatranscriptomic approaches for the first time on peatland soil detected the genetic potential for these enzymes, in all peat layers of an arctic peatland (Tveit et al., 2012). The authors suggested that the degradation of lignin and other inhibitory compounds could therefore occur if the peat soils get oxygenated. An increased number of drought-rewetting cycles at higher temperatures has been suggested as a potential mechanism that provides such conditions in which the enzymes may be more active (Fenner and Freeman, 2011). In the restored site, there is an active layer of vegetation and a higher microbial biomass than in the other sites (Andersen et al., 2006, 2010a) and the water table is more variable than in the natural site. Therefore, there could be enough phenol-oxidases in the newly formed peat to increase the degradation of lignin in the Micro-Resp assays. If such a potential is translated *in situ*, it could have profound impact for the carbon turnover in restored peatlands, hence for the recovery of the carbon sink function. We suggest that approaches targeting enzymes (enzymatic assays) and active microbial communities (RNA-based) would be useful in monitoring the belowground compartments.

5. Conclusion: integrating belowground processes in long-term monitoring

After ten years of restoration, nutrient dynamics at the restored site appeared to be more similar to those occurring in a natural condition than in an unrestored condition. However, the potential carbon utilization was significantly higher in the restored site than in other sections of the BDB peatland. Nevertheless, the high carbon utilisation potential coupled with low mineralisation rates suggest an efficient microbial community that had the capacity to retain the nutrients, which, from the perspective of belowground process, indicates that restoration at BDB is following a suitable trajectory. On the other hand, higher rates of carbon utilization (hence CO_2 production under aerobic conditions), including potential degradation of complex carbon compounds such as lignin, might delay organic matter accumulation and peat formation. Despite a good *Sphagnum* cover and depth, the restored section in BDB is still not a carbon sink (Lucchese et al., 2010) and our study suggests that this may be the consequence of enhanced belowground carbon turnover in comparison with natural conditions.

Our study highlighted for the first time that from a microbial functional perspective, there are fewer differences between a natural peatland and a vegetated unrestored peatland compared to one that has been restored. These findings suggest that some vegetation types (trees and shrubs) may override peat properties (bulk density, moisture, degree of decomposition) in regulating belowground processes through their influence on microbial community structure, at least in the uppermost horizons where

this study was focused. We anticipate that as the ericaceous and tree cover increases in the RES over time, there could be a shift in microbial functional diversity and potential activity towards values observed under natural and unrestored vegetated conditions. We believe that it will be important to compare field data against the 17–20 year acrotelm development model suggested by Lucchese et al. (2010) to understand how well such model ties in complex processes like nutrient dynamics and carbon turnover.

Acknowledgements

The authors would like to thank F. Salvador, M. Gauthier, B. Vimard, C. Cameron, R.R.E Artz, J. Goetz and N. Ronholm for their field assistance and help in the lab. Thanks to anonymous reviewers for constructive comments and helpful suggestions on a previous version of the manuscript. This research was supported by a post-doctoral grant from FQRNT to R. Andersen, and NSERC Discovery Grants to J.S. Price and M.L. Macrae (C. Wells), as well as by the Industrial Research Chair in Peatland Management (L. Rochefort).

Appendix A

Appendix 1
Peatland sites with corresponding sub-sites categorized by dominant vegetation and specific site characteristics. For NAT, sub-site letters SHo, SL, and SH refer to *Sphagnum* hollow, *Sphagnum* lawn and *Sphagnum* hummock, respectively. For UNR and RES, sub-site letters V and B refer to vegetated and bare, respectively. Sub-sites followed by * were sampled for microbial functional diversity ($n = 10$). Average seasonal water levels were recorded from wells installed adjacent to each sub-site. Range in seasonal water table (maximum/minimum) is shown in parentheses.

Peatland site	Sub site	Description	Average (range) water table (cm below ground surface)	C/N ratio (10 cm, 20 cm)
NAT	SHo	Hollow dominated by *Sphagnum* and Herbaceous	26 (32, 20)	(134, 119)
NAT	SL	Lawn dominated by *Sphagnum*, Ericaceous and *Picea mariana* saplings present	24 (31, 16)	(69, 82)
NAT	SH*	Hummock dominated *Sphagnum* Ericaceous present	25 (31, 15)	(115, 67)
UNRv	V1	>70% ericaceous cover Dry, humified catotelmic peat with woody debris	65 (82, 55)	(60, 79)
UNRv	V2	60–80% vegetation cover Mixture of ericaceous and *Equisetum* arvense with *Larix Larcinia* saplings Dry, humified catotelmic peat with woody debris	52 (76, 42)	(58, 65)
UNRv	V3*	>80% vegetation cover Herbaceous and shrub cover Dry, humified catotelmic peat with woody debris	47 (75, 36)	
UNRb	B1*	<20% vegetation cover Sparse *E. arvense* growth Dry, humified catotelmic peat with woody debris	55 (71, 47)	(61, 64)
UNRb	B2	<10% vegetation cover Sparse ericaceous Dry, humified catotelmic peat with woody debris	60 (68, 54)	
UNRb	B3	No vegetation present Dry, humified catotelmic peat with woody debris	48 (58, 40)	
RES	V1	*Sphagnum* hummock Ericaceous and Herbaceous dominant (mostly *Eriophorum vaginatum*)	61 (79, 47)	(92, 75)
RES	V2	*Sphagnum* hummock 40–50% Herbaceous (mostly *E. vaginatum*) Some ericaceous present	38 (58, 20)	(91, 119)
RES	V3*	*Sphagnum* hummock/lawn 30–40% Herbaceous (*E. vaginatum*) Sparse ericaceous cover	24 (41, 7)	
RES	V4	Isolated *Sphagnum* patches 40% *E. vaginatum* tussocks 40% moist., dense peat with trace woody debris *P. mariana* saplings	28 (50, 5)	
RES	V5	No *Sphagnum* present >60% moist, dense peat Herbaceous and ericaceous present	30 (48, 8)	(58, 57)

References

Andersen, R., Francez, A., Rochefort, L., 2006. The physicochemical and microbiological status of a restored bog in Québec: identification of relevant criteria to monitor success. Soil Biology and Biochemistry 38, 1375–1387.
Andersen, R., Grasset, L., Thormann, M., Rochefort, L., Francez, A., 2010a. Changes in microbial community structure and function following Sphagnum peatland restoration. Soil Biology and Biochemistry 42, 291–301.
Andersen, R., Rochefort, L., Poulin, M., 2010b. Peat, water and plant tissue chemistry monitoring: a seven-year case-study in a restored peatland. Wetlands 30, 159–170.
Andersen, R., Rochefort, L., Landry, J., 2011. La chimie des tourbières au Québec: une synthèse de 30 années de données. Le Naturaliste Canadien 135, 5–14.
Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial diversity in natural and disturbed peatlands: a review. Soil Biology & Biochemistry 57, 979–994.
Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.
Artz, R.R.E., 2009. Microbial community structure and carbon substrate use in northern peatlands. In: Baird, A.J., Belyea, L.R., Comas, X., Reeve, A.S., Slater, L.D. (Eds.), Carbon Cycling in Northern Peatlands. American Geophysical Union, Washington, pp. 111–129.
Artz, R.E., Chapman, S.J., Campbell, C.D., 2006. Substrate utilization profiles of microbial communities in peat are depth dependent and correlate with whole soil FTIR profiles. Soil Biology & Biochemistry 38, 2958–2962.
Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change through carbon cycle feedbacks. The ISME Journal 2, 805–814.
Bayley, S., Thormann, M.N., Szumigalski, A.R., 2005. Nitrogen mineralisation and decomposition in western boreal bog and fen peat. Ecoscience 12, 455–465.
Bowden, W.B., 1987. The biogeochemistry of nitrogen in freshwater wetlands. Biogeochemistry 4, 313–348.
Bridgham, S.D., Megonigal, J.P., Keller, J.K., Bliss, N.B., Trettin, C., 2006. The carbon balance of North American wetlands. Wetlands 26 (4), 889–916.
Campbell, C.D., Chapman, S.J., Cameron, C.M., Davidson, M.S., Potts, J.M., 2003. A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Applied and Environmental Microbiology 69, 3593–3599.
Chambers, J.M., Freeny, A., Heiberger, R.M., 1992. Analysis of variance; designed experiments (Chapter 5). In: Chambers, J.M., Hastie, T.J. (Eds.), Statistical Models in S. Wadsworth & Brookes/Cole.
Collins, V.G., D'Sylva, B.T., Latter, P.M., 1978. Microbial populations in peat. In: Heal, O.W., Perkins, D.F. (Eds.), Production Ecology of British Moors and Montane Grasslands. Springer–Verlag KG, Berlin, p. 96.
Croft, M., Rochefort, L., Beauchamp, C.J., 2001. Vacuum-extraction of peatlands disturbs bacterial population and microbial biomass carbon. Applied Soil Ecology 18, 1–12.
Damman, A., 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30, 480–495.
Degens, B.P., Schipper, L.A., Sparling, G.P., Duncan, L.C., 2001. Is the microbial community in a soil with reduced catabolic diversity less resistant to stress or disturbance? Soil Biology & Biochemistry 33, 1143–1153.
Eno, C., 1960. Nitrate production in the field by incubating the soil in polyethylene bags. Soil Science Society of America 24, 277–279.
Fellman, J.B., D'Amore, D.V.D., 2007. Nitrogen and phosphorus mineralisation in three wetland types in Southeast Alaska, USA. Wetlands 27, 44–53.
Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nature Geoscience. http://dx.doi.org/10.1038/NGEO1323.

Fisk, M., Ruether, K., Yavitt, J., 2003. Microbial activity and functional composition among northern peatland ecosystems. Soil Biology and Biochemistry 35, 591–602.
Hart, S.C., Nason, G., Myrold, D.D., Perry, D.A., 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. Ecology 75, 880–891.
Hemond, H.F., 1983. The Nitrogen budget of Thoreau's bog. Ecology 64, 99–109.
Holden, J., Chapman, P., Labadz, J., 2004. Wetland restoration artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. Progress in Physical Geography 28, 95–123.
Holden, J., Evans, M.G., Burt, T.P., Horton, M., 2006. Impact of land drainage on peatland hydrology. Journal of Environmental Quality 35, 1764–1778.
Joosten, H., Clarke, D., 2002. Wise Use of Mires and Peatlands: Background and Principles Including a Framework for Decision-making. International Mire Conservation Group and International Peat Society.
Kljøve, B., 2001. Characteristics of nitrogen and phosphorus loads in peat mining wastewater. Water Research 35, 2353–2362.
Lachance, D., Lavoie, C., Desrochers, A., 2005. The impact of peatland afforestation on plant and bird diversity in southeastern Québec. Ecoscience 12, 161–171.
Lindo, Z., Gonzalez, A., 2010. The Bryosphere: an integral and influential component of the earth's biosphere. Ecosystem 13, 612–627.
Lucchese, M., Waddington, J.M., Poulin, M., Pouliot, R., Rochefort, L., Strack, M., 2010. Organic matter accumulation in a restored peatland: evaluating restoration success. Ecological Engineering 36, 482–488.
Macrae, M.L., Devito, K.J., Strack, M., Waddington, J.M., 2012. Effect of water table drawdown on peatland nutrient dynamics: implications for climate change. Biogeochemistry. http://dx.doi.org/10.1007/s10533-012-9730-3.
McCarter, C.P., Price, J., 2013. The hydrology of the bois-des-bel peatland restoration: 10 years post restoration. Ecological Engineering 55, 73–81.
Megraw, S., Knowles, R., 1987. Active methanotrophs suppress nitrification in a humisol. Biology and Fertility of Soils 4, 205–212.
Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2008. Vegan: Community Ecology Package. R Package Version 1.15-0. Available at: http://cran.r-project.org/.
Pellerin, S., Lavoie, C., 2003. Recent expansion of jack pine in peatlands of southeaster Québec: a paleoecological study. Ecoscience 10, 247–257.
Potila, H., Wallander, H., Sarjala, T., 2009. Growth of ectomycorrhizal fungi in drained peatland forests with variable P and K availability. Plant and Soil 316, 139–150.
Poulin, M., Andersen, R., Rochefort, L., 2012. A new approach for tracking vegetation change after restoration: a case study with peatlands. Restoration Ecology 21 (3), 363–371.
Price, J.S., 1996. Hydrology and microclimate of a partly restored cutover bog, Quebec. Hydrological Processes 10, 1263–1272.
Price, J.S., Ketcheson, S.J., 2009. Water relations in cutover peatlands. In: AGU (Ed.), Carbon Cycling in Northern Peatlands, pp. 277–287.
Price, J.S., Heathwaite, A.L., Baird, A.J., 2003. Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetland Ecology and Management 11, 65–83.
Quinty, F., Rochefort, L., 2003. Peatland Restoration Guide. Canadian Sphagnum Peat Moss Association and the New Brunswick Department of Natural Resources and Energy, Quebec.
R Development Core Team, 2009. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: http://www.R-project.org.
Renou, F., Jones, S., Farrell, E.P., 2000. Leaching of phosphorus fertiliser applied on cutaway peatland forests recently established in central Ireland. Pour une gestion harmonieuse des tourbières. In: Proceedings of the 11th International Peat Congress, vol. II. Québec.
Roberts, P., Newsham, K., Bardgett, R., Farrar, J., Jones, D., 2009. Vegetation cover regulates the quantity, quality and temporal dynamics of dissolved organic carbon and nitrogen in Antarctic soils. Polar Biology 32, 999–1008.
Rochefort, L., Quinty, F., Campeau, S., Johnson, K., Malterer, T., 2003. North American approach to the restoration of sphagnum dominated peatlands. Wetlands Ecology and Management 11, 3–20.
Rosswall, T., Granhall, U., 1980. Nitrogen cycling in a subarctic ombrotrophic mire. Ecological Bulletin 30, 209–234.
Roulet, N.T., 2000. Peatlands, carbon storage, greenhouse gases, and the kyoto protocol: prospects and significance for Canada. Wetlands 20 (4), 605–615.
Rowell, D.L., 1995. Soil Science: Methods and Applications. Wiley, New York.
Schimel, J.P., Weintraub, M.N., 2003. The implication of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. Soil Biology & Biochemistry 35, 549–563.
Sen, R., Elliot, D., Nwaishi, F., Smith, G., Caporn, S., 2012. Soil microbial diversity and spatiality across peatland vegetation mosaics undergoing restoration in the southern Pennines, UK. In: Proceedings of the 14th International Peat Congress, Stockholm, Sweden, 3rd–8th of June 2012.
Shantz, M.A., Price, J.S., 2006. Hydrological changes following restoration of the Bois-des-Bel Peatland, Quebec, 1999–2002. Journal of Hydrology 331, 543–553.
Sottocornola, M., Boudreau, S., Rochefort, L., 2007. Peat bog restoration: effect of phosphorus on plant re-establishment. Ecological Engineering 31, 29–40.
Stark, J.M., Firestone, M.K., 1995. Mechanisms for soil moisture effects on activity of nitrifying bacteria. Applied and Environmental Microbiology 61, 218–221.
Strack, M., Tóth, K., Bourbonniere, R., Waddington, J.M., 2011. Dissolved organic carbon production and runoff quality following peatland extraction and restoration. Ecological Engineering 37, 1998–2008.
Straková, P., Niemi, R.M., Freeman, C., Peltoniemia, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R., 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Biogeosciences 8, 2741–2755.
Straková, P., Penttilä, T., Laine, J., Laiho, R., 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. Global Change Biology 18, 322–335.
Tarnocai, C., Lal, R., Kimble, J., Follett, R., Stewart, B., 1998. The amount of organic carbon in various soil orders and ecological provinces in Canada. In: Lai, R., Kimble, J.M., Follett, R.L.F., Stewart, B.A. (Eds.), Soil Processes and the Carbon Cycle, pp. 81–92.
Turunen, J., Roulet, N.T., Moore, T.R., Richard, P.J.H., 2004. Nitrogen deposition and increased carbon accumulations in ombrotrophic peatlands in eastern Canada. Global Biogeochemical Cycles 18, 1–12.
Tveit, A., Schwacke, R., Svenning, M.M., Urich, T., 2012. Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. The ISME Journal, 1–13.
Verhoeven, J., Maltz, E., Schmitz, M.B., 1990. Nitrogen and phosphorus mineralisation in fens and bogs. Journal of Ecology 78 (3), 713–726.
Verhoeven, J., Whigham, D., van Kerkhovan, M., O'Neill, J., Maltby, E., 1994. A comparative study of nutrient-related processes in geographically separated wetlands: towards a science base for functional assessment procedures. In: Mitsch, W.J. (Ed.), Global Wetlands. Elsevier, Amsterdam, pp. 123–143.
Waddington, J.M., Day, S.M., 2007. Methane emissions from a peatland following restoration. Journal of Geophysical Research 112, 1–11.
Waddington, J.M., Greenwood, M., Price, J.S., 2003. Mulch decomposition impedes recovery of net carbon sink function in a restored peatland. Ecological Engineering 20, 199–210.
Williams, B., Wheatley, R., 1988. Nitrogen mineralisation and water-table height in oligotrophic deep peat. Biology and Fertility of Soils 6, 141–147.
Williams, B., Wheatley, R., 1992. Mineral nitrogen dynamics in poorly drained blanket peat. Biology and Fertility of Soils 13, 96–101.
Wind-Mulder, H., Vitt, D.H., 2000. Comparison of water and peat chemistries of a post-harvested and undisturbed peatland with relevance to restoration. Wetlands 20, 616–628.
Wind-Mulder, H., Rochefort, L., Vitt, D.H., 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. Ecological Engineering 7, 161–181.
Yan, W., Artz, R.R.E., Johnson, D., 2008. Species-specific effects of plants colonising cutover peatlands on patterns of carbon source utilisation by soil microorganisms. Soil Biology and Biochemistry 40, 544–549.