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Invasion of a *Sphagnum*-peatland by *Betula* spp and *Molinia caerulea* impacts organic matter biochemistry. Implications for carbon and nutrient cycling

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Abstract Peatlands act as a sink of carbon (C) through the accumulation of dead remains of plants. Under global changes triggered by human activities, it is not only the sink capacity of peatland that is in danger, but also the C already stored. Invasion of *Sphagnum* peatlands, mainly by *Molinia caerulea* and *Betula* spp, is a growing preoccupation. This study aims to assess the extent of the influence of this invasion on the biochemical characteristics of the peat. Elemental analysis, sugar and Rock–Eval pyrolysis parameters were measured in 50 cm profiles collected in invaded and intact plots. The results show that oxygen index ratios ($OICO_2$/OICO) can be used to detect new C substrate injection as invading plants have a lower ratio than *Sphagnum* spp and *Sphagnum* peat. Total hemicellulosic sugar contents and organic matter (OM) degradation indices (R400, PPI) suggest that the invading plants promote a faster OM decomposition probably through a faster degradability and a relatively higher nutrient content of their litter. Differences in terms of nutrient status between areas of the peatland are suggested to be of great importance in determining the extent of OM transformation likely due to stoichiometric constraints.

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Introduction

Plants considered as engineer species are able to create and sustain conditions that are suitable for their own growth and expansion by modulating the availability of resources to other species (Jones et al. 1994). *Sphagnum* species, by regulating the availability of Nitrogen (N), producing a recalcitrant litter and by creating conditions unfavorable to other organisms (decreasing pH and micronutrient availability) are one such engineer species (van Breemen 1995). Under increased N deposition (Tomassen et al. 2003; Tomassen et al. 2004), *Sphagnum* may lose its engineering capabilities, making *Sphagnum* peatlands susceptible to invasion by vascular plants, mainly *Molinia caerulea* and *Betula* spp. Vascular plants act on the soil Organic Matter (OM) quantity and quality through their litter and their roots. For nutrients such as N and Phosphorus (P), litterfall is the dominant pathway to return to the soil (Schlesinger 1997). Roots through the death of their tissues and their exudates are major contributors to C and nutrient cycling (Fontaine et al. 2007).

During the development of ecosystems, soil pH decreases and C content increases (Ford 1990; Charman 2002). Allogenic changes, such as soil exploitation for agriculture, leads to a decrease in soil C content (Schlesinger 1997). Nowadays, human activities trigger vegetation changes in ecosystems. Knowing how such changes will affect the soil C quantity and quality is of uttermost importance in the context of climate change: depending on the direction of the C flux induced, the vegetation changes may increase or buffer greenhouse gas concentrations in the atmosphere (Cornelissen et al. 2007). Peatlands, which contain a third of the world soil C (Gorham 1991), are among the ecosystems that undergo vegetation change because of human activity. N supply to peatlands has been demonstrated to stimulate the growth of invading species such as *Betula pubescens* and *Molinia caerulea* (Tomassen et al. 2004). It has also been shown that the presence of *Molinia caerulea* decreases the growth of *Sphagnum* species (Hogg et al. 1995), which are the main peat-forming species. Considering that *Molinia caerulea* is N limited and that N deposition is high in Europe, invading species may expand in peatlands at the expense of *Sphagnum* species, which would imply a decrease in the C sink capacity of such systems. In addition, the vascular plants, because of their higher nutrient content may produce a litter that decomposes more rapidly than that of *Sphagnum* species (Coulson and Butterfield 1978; Clymo and Hayward 1982; Comont 2006), potentially leading to an increased rate of C and nutrient mineralization, which may sustain the development of the invading species. Furthermore, in the form of root exudates, vascular plants can inject labile C in deep peat layers. In peatlands, the lack of labile C is a factor limiting microbial activity (Bergman et al. 1998).

The aim of this study is to assess how the recent invasion of a *Sphagnum* peatland by *Betula* spp. and *Molinia caerulea* affects the soil OM dynamics. Rather than the separate effects of the different colonizing species, it is the global effect of vascular plant colonisation of the peatland that is tested here. Bulk organic geochemical analyses (elemental and carbohydrate composition, Rock–Eval pyrolysis) were used to compare peat from intact and colonised plots. As nutrient availability may be an important factor controlling soil processes, analyses of surface peat water and of an incoming drain were performed. Bulk organic geochemical analyses have proved to be efficient in revealing both the botanical origin of the OM and the degradation processes that these precursors undergo in lake sediments (Jacob et al. 2004), marine sediments (Knies 2005), mineral soils (Disnar et al. 2003) and peat profiles (Bourdon et al. 2000; Comont et al. 2006; Laggoun-Défarge et al. 2008). Thus, in the present report, some of these techniques were used to compare the biochemical composition of OM from areas colonised by the invading vascular plants versus intact areas of a peatland.

Material, sampling and methods

Study site

The site studied is La Guette peatland (154 m, 47°19′ North and 2°14′ East) located in the south-eastern part of the French Centre Region (Neuvy-sur-Barangeon, Cher). The mean annual precipitation and temperature is 883 mm and 11°C, respectively (for the period 1989–2001). It is a transitional fen (pH about 4, [Ca] > [Mg], Table 1) that has been invaded by *Molina caerulea* and *Betula* spp (*Betula verrucosa* and *Betula pubescens*) for 30 years with an acceleration of the invasion in the last decade. The dominant *moss* species are *Sphagnum cuspidatum* and *Sphagnum rubellum*. A drain connected to the eastern part of the peatland intermittently discharges water directly into the peatland (Fig. 1). The chemical composition of water collected on May 2008 from this drain is given in Table 2. Surface water from the studied plots (see below) was collected seasonally (May 2008, September 2008, December 2008 and March 2009). Their characteristics are presented in Table 1.

Experimental design and core sampling

The peatland was divided into two areas. It can be assumed that the two sub-areas of the peatland (West area and East area) were colonised relatively independently. The East area differs from the West area by a lower water table. The water table varied between −5.5 cm and −26 cm below the vegetation in the West area, and between −5.5 cm and −40 cm in the East area (period from September 2008 to December 2009). Differences in the water table

Table 1 Annual mean (4 sampling dates, May 2008–March 2009) characteristics of surface water sampled in the four studied plots from La Guette peatland (annual mean ± standard error, $n = 4$ other than Al, $n = 1$, not detected in the three other samplings)

	West open	West closed	East open	East closed
pH	3.98 ± 0.21	3.73 ± 0.22	4.03 ± 0.34	3.93 ± 0.23
Conductivity (μS cm^{-1})	49.0 ± 6.47	65.0 ± 9.36	51.9 ± 8.25	63.9 ± 12.6
DOC (mg l^{-1})	16.2 ± 0.72	26.5 ± 1.59	13.9 ± 1.73	20.9 ± 1.87
K (mg l^{-1})	0.16 ± 0.03	0.20 ± 0.04	0.22 ± 0.02	0.59 ± 0.14
Na (mg l^{-1})	2.82 ± 0.11	2.39 ± 0.10	2.95 ± 0.03	3.37 ± 0.29
Mg (mg l^{-1})	0.28 ± 0.06	0.29 ± 0.03	0.21 ± 0.01	0.27 ± 0.03
Ca (mg l^{-1})	0.71 ± 0.16	0.76 ± 0.12	0.45 ± 0.02	0.73 ± 0.17
Si (mg l^{-1})	1.99 ± 0.24	1.94 ± 0.33	2.93 ± 0.32	3.11 ± 0.55
Fe (mg l^{-1})	0.42 ± 0.11	0.88 ± 0.10	0.52 ± 0.06	0.66 ± 0.004
Al (mg l^{-1})	0.17	0.27	0.36	0.76

Data from seasonal monitoring are not shown

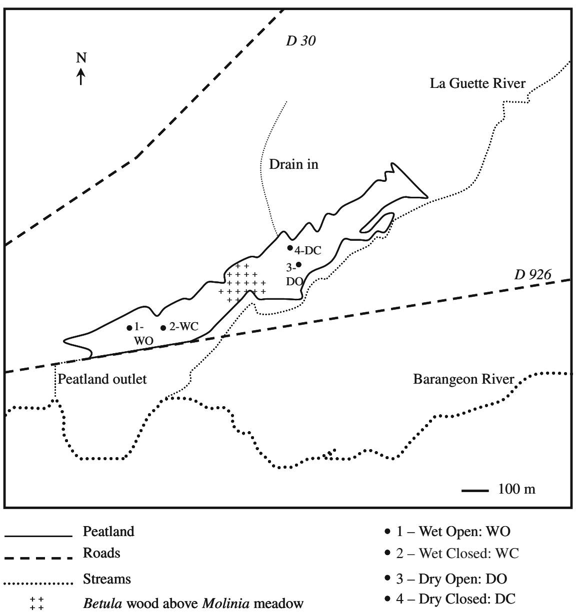

Fig. 1 Map of La Guette peatland (Neuvy-sur-Barangeon, France) showing the location of the studied plots with different vegetation (open versus closed) and from the two hydrological areas (wet versus dry)

occurred mainly during the summer. These differences may be caused by higher altitude and/or water works near the peatland. To distinguish the two areas in relation to their hydrology, the West area is referred to as wet and the East area as dry.

To test differences (1) between plots with different vegetation, (2) between areas from different hydrological areas, and (3) in vegetation-area interaction,

Table 2 Chemical composition of the water sampled in the inlet drain on May 2008

	Concentration in mg l^{-1}
$N\text{-}NO_3^-$	0.31
$N\text{-}NH_4^+$	0.08
N total	1.14
S total	0.95
Ca	3.19
Fe	1.40
K	1.89
Mg	0.53
Mn	0.04
Na	4.46
Si	4.26

two areas were considered: the wet area (named W) and the dry area (named D), and within each area, an intact plot (named O for open vegetation) and a colonised plot (with both *Betula* spp and *Molinia caerulea*, named C for closed vegetation) were chosen. The location of each sampling plot, WO, WC, DO and DC, the characteristics of their surface water and their vegetation are reported in Fig. 1 and Tables 1 and 3, respectively.

On June 2008, four cores (50 cm long) were collected with a Russian corer in each vegetation situation (open and closed), in each area of the peatland (wet and dry), within plots of a 4 m^2 surface area (total of 16 cores). This surface was chosen to

Table 3 Plant cover percentages of the main plant species in the four studied plots from La Guette peatland

Strata	Species	Wet open	Wet closed	Dry open	Dry closed
Moss	*Sphagnum cuspidatum*	35	25	20	50
	Sphagnum rubellum	25	0	5	0
	Other	5	40	15	0
Herbaceous	*Molinia caerulea*	20	35	40[a]	90[a]
	Scheuzeria palustre	5	0	0	0
	Eriophorum vaginatum	75	55	40	5
Shrub	*Calluna vulgaris*	70	25	45	0
	Erica tetralix	5	40	45	45
Tree	*Betula* spp	0	25	0	15

[a] In the dry open, *M. caerulea* is sparse but present everywhere on the plot, whereas in the dry closed, it was present as well-developed tussocks

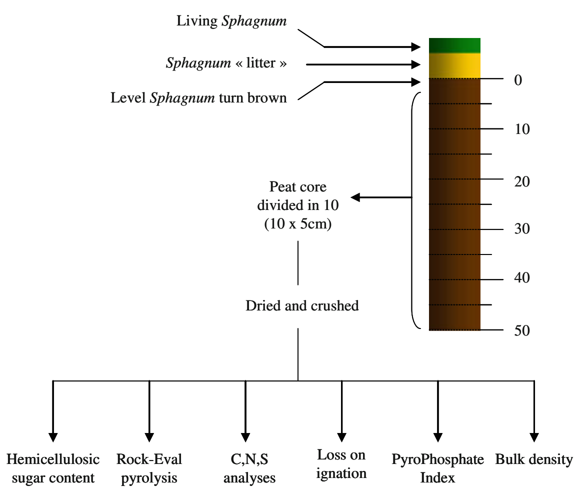

Fig. 2 Diagram of a peat core sampled and analyses performed

limit spatial heterogeneity and because totally intact areas were small. Most cores were collected in *Sphagnum* habitats in both open and closed vegetation. The litter of vascular plants was not included in the cores. *Sphagnum* species have no litter in the sense used for vascular plants. As assumed by most litter bag studies, the litter compartment of *Sphagnum* refers to the segment below the photosynthetic part and above the dark brown part (Bragazza et al. 2007). The top of the cores corresponded to the level where *Sphagnum* litter becomes brown (Fig. 2). The trees (*Betula* spp) in the wet area were cut down by the manager in 2002, but they remained alive and tillers are now growing up to 3 m. In the dry area, intact tall stands (15 m) of *Betula* spp are present. In the laboratory, the cores were frozen until processing. After defreezing, they were cut into 10 sections each 5 cm long (Fig. 2). Roots which were present at all depths of the cores were removed. The samples were dried at 50°C and crushed with an annular grinder. Dry weight was measured after drying to assess the bulk density. The different analyses were then conducted.

Organic matter (OM) content

The crushed peat (100 mg) was weighed in a crucible, placed in an oven and burnt at 550°C during 4 h. As peat contains mostly OM and as La Guette peatland is acidic (no carbonates present), the mass loss on ignition was considered to be only OM (expressed in % of dry weight).

Carbon (C), nitrogen (N) and sulfur (S) content analysis

C, N and S content was determined by combustion of dried and crushed samples at 1100°C, using a CNS-2000 LECO apparatus.

Rock–Eval pyrolysis

The Rock–Eval technique was primarily developed to diagnose oil-producing hydrocarbon (HC) source rocks by measuring the ratio of the amount of hydrogen and oxygen cracked during the pyrolysis cycle to the total organic carbon (hydrogen index = HI, and oxygen index = OI, respectively) and by determining the temperature of maximum hydrocarbon cracking (Espitalié et al. 1985a, b; Lafargue et al. 1998). The technique was further adapted to assess the biochemical quality of soil OM. Disnar et al. (2003) showed that Rock–Eval parameters can reveal the chemical evolution of the OM during the process of humification. Rock–Eval parameters were used here to assess OM quality between plots with different vegetation and from the two hydrological areas.

The analyses were carried out on 30 mg of powdered dry peat with a ''Turbo'' Rock–Eval 6® pyrolyser manufactured by Vinci® Technologies (Espitalié et al. 1985a, b; Lafargue et al. 1998). Briefly, the samples were first pyrolysed under inert atmosphere (N_2), and the residual C was subsequently burnt in an oxidation oven. The amount of HC released during pyrolysis was detected by a flame ionisation detector, while online infrared detectors continuously measured the released CO and CO_2. The standard pyrolysis program started with an isothermal stage of 2 min at 200°C. The pyrolysis oven temperature was then raised to 650°C at 30°C min^{-1}, and held for 3 min at this temperature. The oxidation phase started at an isothermal stage at 400°C, followed by an increase to 850°C at 30°C min^{-1} and held at this final temperature for 5 min. Rock–Eval parameters were calculated by integration of the amounts of HC, CO and CO_2 produced during the thermal cracking of the OM, between well-defined temperature limits. Our work focused on the following parameters derived from signals recorded during the pyrolysis and oxidation phases:

– HI = hydrogen index (mg HC g^{-1} TOC) corresponds to the quantity of HC released during pyrolysis relative to TOC.
– $OICO_2$ = CO_2 oxygen index = (mg CO_2 g^{-1} TOC) corresponds to the quantity of CO_2 released during pyrolysis, relative to TOC.
– OICO = CO oxygen index (mg CO g^{-1} TOC) corresponds to the quantity of CO released during pyrolysis, relative to TOC.
– OIRe6 = Rock–Eval 6 oxygen index (mg O_2 g^{-1} TOC) corresponds to the quantity of oxygen released as CO and CO_2 during pyrolysis, relative to TOC.
– $OICO_2$/OICO parameter is the ratio of the amount of pyrolysed CO_2 to the amount of pyrolysed CO.
– R400 parameter is the ratio of the part of the HC signal produced below 400°C to the total HC signal. It corresponds to an index of OM transformation as it results from the thermal decomposition of biological compounds such as cellulose and lignin before 400°C, and humic substances after 400°C (Disnar et al. 2003; Sebag et al. 2006; Disnar et al. 2008).

Pyrophosphate index (PPI)

The pyrophosphate index (Kaila 1956) was calculated following Gobat et al. (1986). The humic compounds of peat (0.5 g) were extracted with a sodium pyrophosphate at 0.025 M overnight. The mixtures were filtered (Whatman 2V) and the filtrates were completed with deionised water to 250 ml. The optical density of the solution was measured at 550 nm with a spectrophotometer (Hitachi U1100). The pyrophosphate index was obtained by multiplying the optical density measured by 100.

Neutral monosaccharide analyses

Hemicellulosic content measurement has been described elsewhere (Comont et al. 2006; Disnar et al. 2008). Briefly, a dry peat sample was hydrolysed with diluted H_2SO_4 at 100°C overnight. The extract was neutralized, centrifuged and evaporated. Monosaccharides were (1) extracted with methanol, which was then evaporated, (2) diluted in pyridine, (3) derivated with N,O-bis-(trimethylsilyl)trifluoroacetamide (BFTSA) before the injection into a GC (Perkin-Elmer, FID). Deoxyglucose was used as an internal standard.

Statistical analyses

Two-way factorial ANOVAs were conducted for each variable at each depth to test for differences between plots with different vegetation, areas with different hydrology and for interaction between vegetation and hydrology. Normality of residues and variances homogeneity were tested (Kolmogorov and Smirnov test and Levene test, respectively). Data were transformed to improve the ANOVA assumptions fulfillment (log, square root or inverse). The Pearson product moment correlation was used to test for correlation. The level of significance of all tests was set to $P < 0.05$. Statistica (Statsoft Inc 2008) was used to conduct the tests.

Results

Results of whole cores showed that the depth of peat differed between the sampling plots (Tables 4, 5). In the lower part of the cores (35–50 cm), the degree of humification (PPI) varied within a given area, whereas in the middle part (15–35 cm) the differences between areas were more marked (Table 4). This shows that peat from the lower and the middle part of the cores had different ages and experienced dramatic differences in terms of source materials (depending on the stage of development, a peatland exhibits different types of vegetation) and degradation conditions. However, PPI, C, N and S peat contents tended to converge toward the top of the core (Table 4), suggesting that source materials and degradation conditions in all plots became more similar. Analyses and discussion were carried out only on peat from the first three depths so as to compare peat with ages that were as similar as possible.

Statistical analyses on the first three depths showed that there was only one significant vegetation and area interaction, on the bulk density (Table 6). This interaction was much less significant than the two main effects (at least one order of magnitude, Table 6). Thus, for bulk density as well as for all the other factors, only the main effects were considered.

From the statistical results (Table 6), the response variables could be separated into four groups. The first group was composed of variables exhibiting differences between plots with different vegetation and from different areas of the peatland, at the same depth or at different depths: bulk density, PPI, HI, total hemicellulose (Table 6; Fig. 3). The second group showed differences only between plots with different vegetation: OIRe6 and $OICO_2$/OICO (Table 6; Fig. 4). The third group showed differences between peatland areas: R400, C/S ratio (Table 6; Fig. 5) and S content (Table 6). The fourth group was composed of variables showing no or isolated differences: C/N ratio, OM content, C and N content (Table 6).

Variables affected by the vegetation and the areas of the peatland

At all depths, the colonizing vegetation significantly increased the peat bulk density compared to the intact vegetation (Fig. 3a–c). Also, other than at the surface, the peat was denser in the wet area than in the dry area.

At the surface, the peat was more decomposed (higher PPI) in closed vegetation plots than in open ones and no differences were observed between hydrological areas (Fig. 3d). However, at the depth of 10–15 cm, the opposite was observed: the peat was more decomposed in the wet area than in the dry area and no differences were revealed with vegetation (Fig. 3f). In between (5–10 cm), the peat showed the same degree of decomposition in all plots (Fig. 3e).

At all depths, total hemicellulose was measured in significantly higher concentrations in the dry area than in the wet area (Fig. 3g–i). Peat hemicellulosic content was higher in the open vegetation plots only at the surface (Fig. 3g).

Variables affected by the vegetation

At all depths, both OIRe6 and $OICO_2$/OICO ratios were higher in the plots with open vegetation than in those with closed vegetation (Fig. 4). OIRe6 tended to decrease with depth in both plots, whereas $OICO_2$/OICO remained constant (Fig. 4).

Variables affected by the hydrology of the peatland

The R400 (Fig. 5a–c) and the S content were lower in the wet area of the peatland than in the dry area. The differences in S contents explain the differences observed in the C/S ratio (Fig. 5d–f) as the C content showed no significant differences (Table 6).

Variables showing no significant differences

Other than the C/N ratio at 10–15 cm, C/N ratio, C, N and OM contents did not differ between plots (Table 6). OM contents at depths 5–10 cm and 10–15 cm were highly similar between plots with different vegetation (both $P > 0.88$), but at the surface, the level of significance decreased by an order of magnitude ($P = 0.08$), without being significant at the level set previously.

Table 4 Depth-related evolution of biochemical properties of peat from the four studied plots in La Guette peatland

Plot	Depth (cm)	Bulk density (g cm^{-3})	C (mg g^{-1})	S (mg g^{-1})	N (mg g^{-1})	MO (%)	PPI
Wet open	0–5	0.05 ± 0.02	423 ± 15.2	2.19 ± 0.61	9.8 ± 2.74	89 ± 2.9	14 ± 4.3
	5–10	0.10 ± 0.02	413 ± 19.6	3.50 ± 0.22	13.1 ± 3.08	83 ± 2.6	27 ± 3.4
	10–15	0.16 ± 0.01	403 ± 21.5	3.01 ± 0.37	13.5 ± 1.54	81 ± 1.9	41 ± 7.8
	15–20	0.18 ± 0.03	453 ± 10.5	2.53 ± 0.28	15.0 ± 0.90	88 ± 1.5	50 ± 19.0
	20–25	0.20 ± 0.02	462 ± 9.6	1.78 ± 0.06	13.0 ± 2.13	86 ± 1.5	88 ± 13.0
	25–30	0.32 ± 0.03	441 ± 15.7	1.22 ± 0.14	10.9 ± 1.97	78 ± 2.4	104 ± 11.3
	30–35	0.24 ± 0.03	510 ± 27.9	1.52 ± 0.09	8.9 ± 1.43	87 ± 3.3	121 ± 11.5
	35–40	0.17 ± 0.03	520 ± 20.1	1.51 ± 0.18	10.1 ± 1.94	90 ± 4.7	137 ± 23.1
	40–45	0.13 ± 0.01	499 ± 10.1	2.34 ± 0.27	9.3 ± 2.42	92 ± 2.0	109 ± 11.6
	45–50	0.12 ± 0.03	403 ± 54.8	2.05 ± 0.44	6.7 ± 0.58	74 ± 10.0	73 ± 7.2
Wet closed	0–5	0.08 ± 0.01	409 ± 9.5	3.48 ± 0.17	13.1 ± 1.22	81 ± 0.5	23 ± 2.3
	5–10	0.12 ± 0.01	436 ± 15.8	3.21 ± 0.15	15.5 ± 0.91	86 ± 2.0	24 ± 2.4
	10–15	0.19 ± 0.01	417 ± 9.2	2.52 ± 0.12	13.9 ± 1.19	80 ± 1.6	43 ± 9.2
	15–20	0.27 ± 0.02	350 ± 7.7	1.72 ± 0.05	9.7 ± 0.73	64 ± 1.9	67 ± 6.6
	20–25	0.35 ± 0.02	317 ± 30.4	1.28 ± 0.16	8.1 ± 0.71	56 ± 4.1	85 ± 6.9
	25–30	0.37 ± 0.07	345 ± 56.6	1.23 ± 0.41	6.7 ± 1.42	57 ± 9.4	107 ± 9.5
	30–35	0.21 ± 0.01	423 ± 69.1	1.53 ± 0.22	6.6 ± 1.51	70 ± 10.9	104 ± 15.8
	35–40	0.33 ± 0.05	176 ± 38.9	1.00 ± 0.28	2.0 ± 1.07	32 ± 7.1	50 ± 11.2
	40–45	0.85 ± 0.11	45 ± 7.7	0.16 ± 0.07	0.0 ± 0.00	9 ± 1.4	13 ± 1.7
	45–50	0.84 ± 0.14	40 ± 7.1	0.19 ± 0.05	0.0 ± 0.00	8 ± 1.3	14 ± 1.2
Dry open	0–5	0.03 ± 0.01	410 ± 16.6	3.83 ± 0.39	13.9 ± 1.09	86 ± 3.6	17 ± 1.0
	5–10	0.04 ± 0.00	399 ± 17.7	4.04 ± 0.11	15.1 ± 0.61	84 ± 2.5	17 ± 1.4
	10–15	0.10 ± 0.01	361 ± 30.7	3.60 ± 0.15	15.7 ± 0.69	75 ± 5.4	19 ± 2.9
	15–20	0.17 ± 0.03	373 ± 24.2	3.06 ± 0.21	18.9 ± 1.08	73 ± 5.2	31 ± 6.3
	20–25	0.21 ± 0.02	358 ± 21.3	2.49 ± 0.13	18.1 ± 0.75	70 ± 5.0	42 ± 5.5
	25–30	0.26 ± 0.01	339 ± 15.6	2.17 ± 0.08	16.5 ± 0.99	64 ± 2.9	63 ± 2.5
	30–35	0.26 ± 0.01	318 ± 21.4	1.96 ± 0.13	14.8 ± 0.85	60 ± 4.4	69 ± 2.1
	35–40	0.31 ± 0.03	273 ± 32.7	1.55 ± 0.20	12.5 ± 1.59	50 ± 5.1	76 ± 5.8
	40–45	0.38 ± 0.05	195 ± 50.6	1.12 ± 0.24	9.1 ± 2.03	37 ± 8.0	61 ± 7.3
	45–50	0.51 ± 0.14	66 ± 25.3	0.39 ± 0.15	3.0 ± 1.33	21 ± 2.6	35 ± 3.2
Dry closed	0–5	0.07 ± 0.01	412 ± 6.1	4.33 ± 0.38	15.4 ± 0.71	85 ± 0.6	24 ± 1.6
	5–10	0.09 ± 0.01	389 ± 7.9	4.61 ± 0.28	17.5 ± 0.77	81 ± 1.7	25 ± 3.0
	10–15	0.17 ± 0.01	379 ± 7.7	3.47 ± 0.39	17.5 ± 1.11	75 ± 1.8	31 ± 5.7
	15–20	0.21 ± 0.01	397 ± 8.3	2.81 ± 0.19	18.1 ± 0.57	77 ± 0.7	40 ± 7.3
	20–25	0.20 ± 0.00	402 ± 13.3	2.83 ± 0.18	18.0 ± 0.62	77 ± 2.2	45 ± 4.4
	25–30	0.19 ± 0.02	426 ± 16.5	2.71 ± 0.10	18.2 ± 1.58	79 ± 2.6	51 ± 7.8
	30–35	0.18 ± 0.01	417 ± 16.3	2.65 ± 0.20	16.3 ± 1.49	77 ± 2.8	60 ± 8.6
	35–40	0.18 ± 0.01	399 ± 9.9	2.35 ± 0.13	14.6 ± 1.07	72 ± 1.9	90 ± 7.7
	40–45	0.17 ± 0.01	424 ± 8.8	2.30 ± 0.20	14.5 ± 0.89	75 ± 0.7	93 ± 2.8
	45–50	0.18 ± 0.01	388 ± 41.5	2.17 ± 0.29	12.1 ± 1.66	69 ± 6.6	96 ± 7.4

Mean (±1 S.E., $n = 4$) bulk density, carbon, sulfur and nitrogen contents, organic matter amount and pyrophosphate index (arbitrary units)

Table 5 Depth-related evolution of biochemical properties of peat from the four studied plots in La Guette peatland

Plot	Depth (cm)	HI (mg HC g^{-1} TOC)	$OICO_2$ (mg CO_2 g^{-1} TOC)	OI CO (mg CO g^{-1} TOC)	OI Re6 (mg O_2 g^{-1} TOC)	R400	$OICO_2$/OICO
Wet open	0–5	383 ± 22.8	217 ± 17.1	63 ± 3.9	194 ± 14.0	0.54 ± 0.01	3.42 ± 0.21
	5–10	395 ± 15.3	185 ± 14.4	48 ± 1.1	162 ± 11.0	0.50 ± 0.01	3.86 ± 0.25
	10–15	423 ± 17.5	173 ± 13.5	45 ± 1.1	152 ± 9.8	0.48 ± 0.01	3.90 ± 0.32
	15–20	400 ± 13.2	180 ± 16.6	44 ± 3.3	156 ± 13.3	0.46 ± 0.02	4.05 ± 0.30
	20–25	418 ± 19.8	158 ± 14.7	45 ± 2.2	141 ± 11.9	0.40 ± 0.02	3.46 ± 0.18
	25–30	393 ± 46.5	139 ± 16.2	45 ± 4.2	127 ± 13.6	0.34 ± 0.02	3.11 ± 0.22
	30–35	437 ± 38.2	147 ± 22.7	49 ± 7.4	135 ± 20.4	0.34 ± 0.02	3.03 ± 0.19
	35–40	393 ± 40.2	148 ± 19.0	50 ± 5.6	136 ± 17.0	0.35 ± 0.01	2.98 ± 0.07
	40–45	325 ± 17.7	179 ± 17.3	66 ± 6.8	168 ± 16.3	0.38 ± 0.01	2.70 ± 0.09
	45–50	323 ± 17.8	146 ± 9.1	55 ± 1.3	137 ± 7.3	0.38 ± 0.01	2.65 ± 0.11
Wet closed	0–5	338 ± 13.1	146 ± 3.2	65 ± 6.2	143 ± 3.7	0.51 ± 0.01	2.32 ± 0.24
	5–10	446 ± 6.0	146 ± 2.7	51 ± 5.6	135 ± 1.9	0.52 ± 0.01	2.98 ± 0.37
	10–15	465 ± 5.2	125 ± 5.6	57 ± 7.6	124 ± 6.2	0.44 ± 0.02	2.30 ± 0.32
	15–20	454 ± 6.9	116 ± 5.9	54 ± 4.7	115 ± 3.6	0.38 ± 0.01	2.23 ± 0.28
	20–25	452 ± 7.1	97 ± 2.8	54 ± 3.4	101 ± 2.0	0.34 ± 0.01	1.82 ± 0.17
	25–30	456 ± 8.2	76 ± 9.4	46 ± 7.8	81 ± 11.2	0.34 ± 0.01	1.69 ± 0.11
	30–35	485 ± 25.5	86 ± 3.4	53 ± 9.3	93 ± 7.4	0.33 ± 0.01	1.75 ± 0.25
	35–40	408 ± 16.9	91 ± 1.5	63 ± 7.9	102 ± 5.4	0.35 ± 0.01	1.50 ± 0.17
	40–45	371 ± 11.6	82 ± 2.3	67 ± 5.2	97 ± 1.9	0.40 ± 0.00	1.26 ± 0.13
	45–50	341 ± 19.2	78 ± 2.2	65 ± 4.1	94 ± 2.2	0.40 ± 0.01	1.20 ± 0.10
Dry Open	0–5	385 ± 5.0	185 ± 8.1	54 ± 3.1	165 ± 5.7	0.56 ± 0.01	3.45 ± 0.28
	5–10	377 ± 7.9	186 ± 4.4	53 ± 2.5	166 ± 2.0	0.56 ± 0.01	3.54 ± 0.24
	10–15	428 ± 11.9	164 ± 3.0	43 ± 3.1	144 ± 2.6	0.52 ± 0.03	3.83 ± 0.29
	15–20	449 ± 19.8	155 ± 5.8	41 ± 1.9	136 ± 5.0	0.50 ± 0.01	3.82 ± 0.15
	20–25	457 ± 11.2	147 ± 5.5	40 ± 1.8	129 ± 4.3	0.46 ± 0.01	3.72 ± 0.19
	25–30	463 ± 2.7	133 ± 4.2	39 ± 2.2	119 ± 3.7	0.42 ± 0.01	3.45 ± 0.19
	30–35	438 ± 8.6	112 ± 13.6	36 ± 1.5	102 ± 10.0	0.38 ± 0.01	3.14 ± 0.40
	35–40	398 ± 26.4	108 ± 2.7	39 ± 2.1	101 ± 2.1	0.35 ± 0.00	2.82 ± 0.19
	40–45	332 ± 45.8	103 ± 3.9	42 ± 3.2	99 ± 4.3	0.31 ± 0.02	2.48 ± 0.16
	45–50	286 ± 7.3	96 ± 1.7	47 ± 2.4	97 ± 1.4	0.28 ± 0.02	2.08 ± 0.12
Dry closed	0–5	349 ± 20.7	154 ± 12.3	69 ± 0.9	152 ± 8.4	0.56 ± 0.02	2.22 ± 0.20
	5–10	388 ± 4.5	147 ± 12.6	64 ± 2.9	143 ± 10.7	0.53 ± 0.01	2.30 ± 0.12
	10–15	421 ± 1.6	134 ± 11.5	55 ± 1.2	129 ± 9.0	0.49 ± 0.01	2.41 ± 0.17
	15–20	435 ± 1.8	128 ± 13.2	50 ± 3.4	122 ± 10.7	0.46 ± 0.01	2.57 ± 0.25
	20–25	428 ± 14.3	108 ± 14.9	50 ± 3.6	107 ± 12.4	0.45 ± 0.01	2.16 ± 0.21
	25–30	404 ± 14.8	105 ± 16.0	47 ± 3.6	103 ± 13.1	0.43 ± 0.01	2.22 ± 0.25
	30–35	399 ± 11.0	96 ± 15.1	46 ± 4.0	97 ± 12.4	0.42 ± 0.01	2.08 ± 0.25
	35–40	406 ± 9.0	85 ± 13.1	44 ± 2.6	87 ± 10.9	0.39 ± 0.01	1.90 ± 0.20
	40–45	447 ± 5.7	77 ± 12.3	43 ± 3.0	81 ± 10.6	0.35 ± 0.01	1.78 ± 0.17
	45–50	400 ± 17.7	76 ± 9.9	46 ± 1.4	81 ± 7.4	0.36 ± 0.02	1.67 ± 0.21

Rock–Eval parameters: Hydrogen index, $OICO_2$ (CO_2 released during pyrolysis, relative to TOC), OICO (CO released during pyrolysis, relative to TOC), OIRe6 (O_2 released as CO and CO_2 during pyrolysis, relative to TOC), R400 ratio (the part of the HC signal produced below 400°C compared to the total HC signal) and $OICO_2$/OICO ratio

Table 6 Statistical results of the two-way ANOVAs for each response variable

		0–5 cm		5–10 cm		10–15 cm	
		F	*P*	*F*	*P*	*F*	*P*
Bulk density	Area	2.51	0.14	9.65	***0.01***	12.6	***0.004***
	Vegetation	12.1	***0.005***	8.01	***0.02***	25.1	***0.0003***
	Area × vegetation	0.46	0.51	1.44	0.25	5.35	***0.04***
PPI	Area	0.59	0.46	1.98	0.18	5.84	***0.03***
	Vegetation	8.76	***0.01***	0.81	0.39	1.06	0.32
	Area × vegetation	0.22	0.64	4.24	0.06	0.54	0.47
HI	Area	0.15	0.71	13.6	***0.003***	2.35	0.15
	Vegetation	5.71	***0.03***	9.78	***0.01***	2.53	0.14
	Area × vegetation	0.07	0.79	3.14	0.10	4.29	0.06
Total hemicellulose	Area	18.4	***0.001***	20.3	***0.001***	6.81	***0.02***
	Vegetation	11.8	***0.005***	2.02	0.18	0.15	0.70
	Area × vegetation	2.21	0.16	0.84	0.38	0.52	0.49
OIRe6	Area	0.61	0.45	0.48	0.50	0.04	0.84
	Vegetation	15.1	***0.002***	8.19	***0.01***	8.20	***0.01***
	Area × vegetation	3.72	0.08	0.01	0.93	0.70	0.42
$OICO_2$/OICO	Area	0.03	0.88	3.69	0.08	0.003	0.96
	Vegetation	24.3	***0.0003***	16.3	***0.002***	28.2	***0.0002***
	Area × vegetation	0.08	0.79	0.48	0.50	0.09	0.77
R400	Area	9.12	***0.01***	12.1	***0.005***	6.20	***0.03***
	Vegetation	1.75	0.21	0.05	0.83	4.24	0.06
	Area × vegetation	1.81	0.20	4.01	0.07	0.01	0.94
S	Area	8.94	***0.01***	23.0	***0.0004***	6.41	***0.03***
	Vegetation	4.64	0.05	0.51	0.49	1.08	0.32
	Area × vegetation	0.90	0.36	4.59	0.05	0.16	0.70
C/S	Area	8.00	***0.02***	19.1	***0.001***	7.10	***0.02***
	Vegetation	3.93	0.07	0.01	0.91	0.98	0.34
	Area × vegetation	1.06	0.32	3.39	0.09	0.07	0.80
C/N	Area	2.47	0.14	4.26	0.06	7.20	***0.02***
	Vegetation	1.17	0.30	1.96	0.19	0.12	0.73
	Area × vegetation	0.48	0.50	0.00	0.97	0.09	0.78
OM content	Area	0.09	0.77	0.70	0.42	3.14	0.10
	vegetation	3.57	0.08	0.01	0.92	0.02	0.89
	Area × vegetation	1.82	0.20	1.76	0.21	0.11	0.75
C	Area	0.14	0.72	3.64	0.08	4.21	0.06
	Vegetation	0.26	0.62	0.14	0.72	0.66	0.43
	Area × vegetation	0.40	0.54	1.11	0.31	0.01	0.93
N	Area	3.09	0.10	1.03	0.33	2.36	0.15
	Vegetation	1.68	0.22	1.63	0.23	0.08	0.79
	Area × vegetation	0.53	0.48	0.20	0.66	0.002	0.96

All bold *P* values are inferior to 0.05

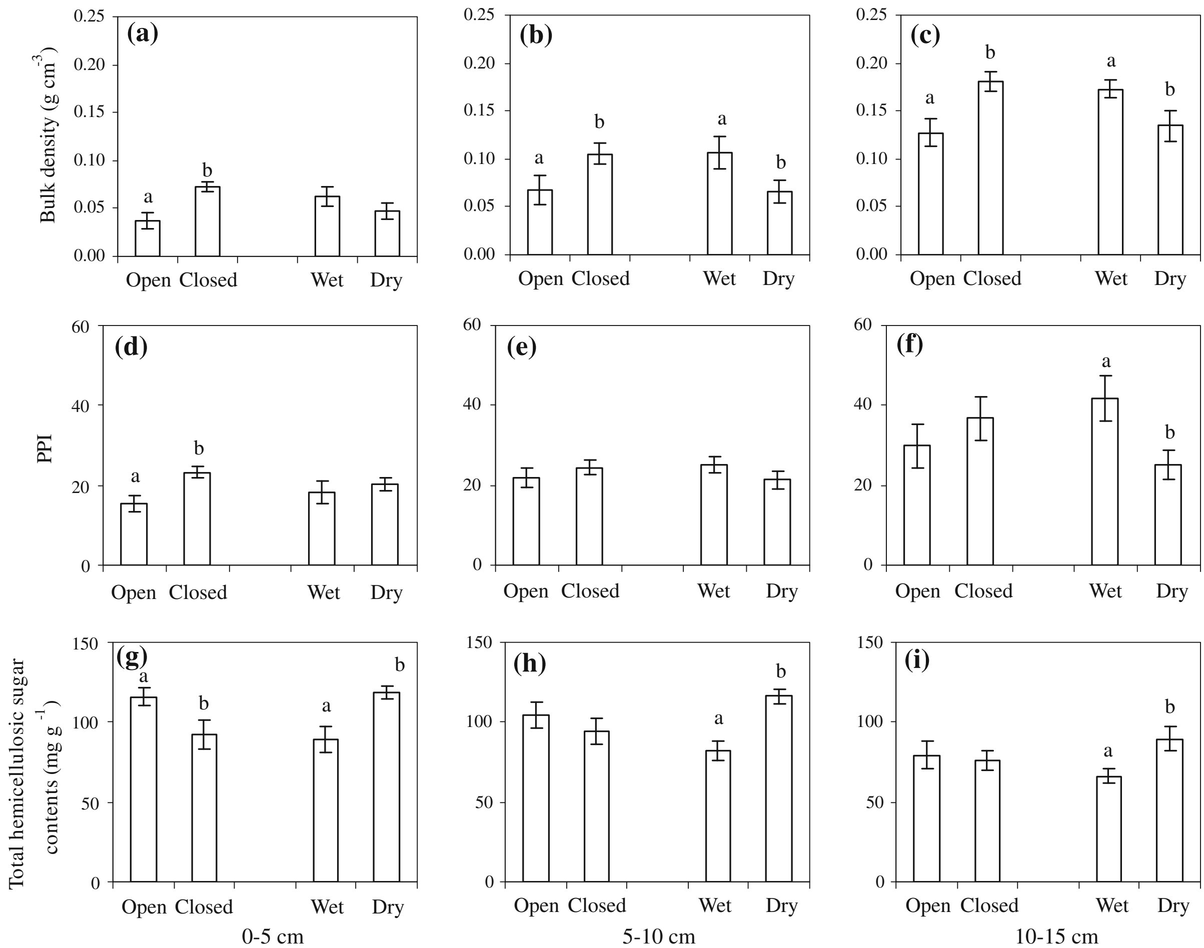

Fig. 3 Bulk density (**a**, **b**, **c**), pyrophosphate index, PPI (**d**, **e**, **f**), and total hemicellulosic sugar content (**g**, **h**, **i**) of the uppermost peat (0–15 cm) from different vegetation plots (open and closed) and from the two hydrological areas of the peatland (wet and dry). The *error bars* represent one standard error ($n = 8$)

Rock–Eval indices: R400 and $OICO_2$/OICO

Rock–Eval indices are more widely used for oil-producing rocks and petroleum reservoir studies. However, these indices, especially R400, have also proved to be valuable in characterizing a wide range of soils and in studying processes such as humification (Disnar et al. 2003). Hemicellulose is a part of fresh unmodified OM. Our results on peat from 0 to 15 cm depth show that the R400 index was positively correlated with the amount of hemicellulose ($R = 0.76$, $P < 0.001$, $n = 48$, Fig. 6).

In order to highlight the influence of botanical sources on the resulting peat biochemistry, litter from the dominant precursors of the undisturbed peatland (*Sphagnum cuspidatum* and *Sphagnum rubellum*) and those from the two dominant species invading the peatland (*Molinia caerulea* and *Betula verrucosa*) were analysed (Table 7). By comparing the precursors' biochemical characteristics to the peat composition, markers of sources were expected to be found. All oxygen indices (OI) measured by Rock–Eval pyrolysis varied greatly between plants (Table 7). Figure 7 shows that OICO did not discriminate the different source materials. In contrast, $OICO_2$ was a good parameter to separate *Sphagnum* spp. and vascular plant litters. However, the roots of *Molinia caerulea* presented $OICO_2$ values closer to that of

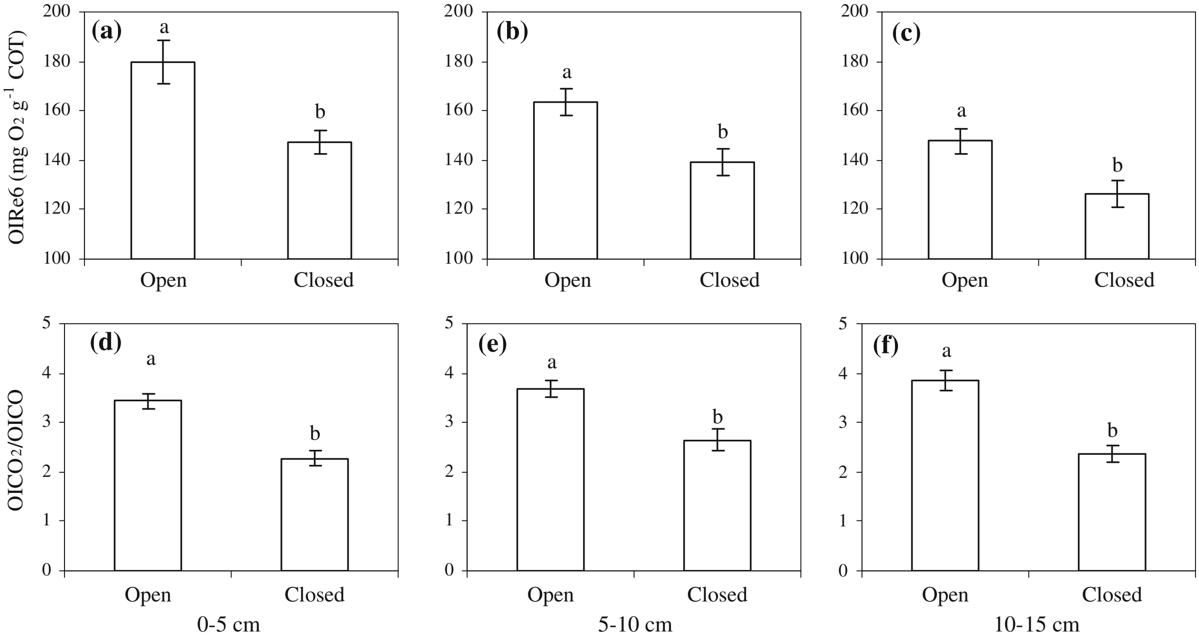

Fig. 4 Rock-Eval 6 oxygen index (OIRe6) and the ratio of the amount of pyrolysed CO_2 to the amount of pyrolysed CO ($OICO_2$/OICO) of the uppermost peat (0–15 cm depth) from different vegetation plots (open and closed). The *error bars* represent one standard error ($n = 8$)

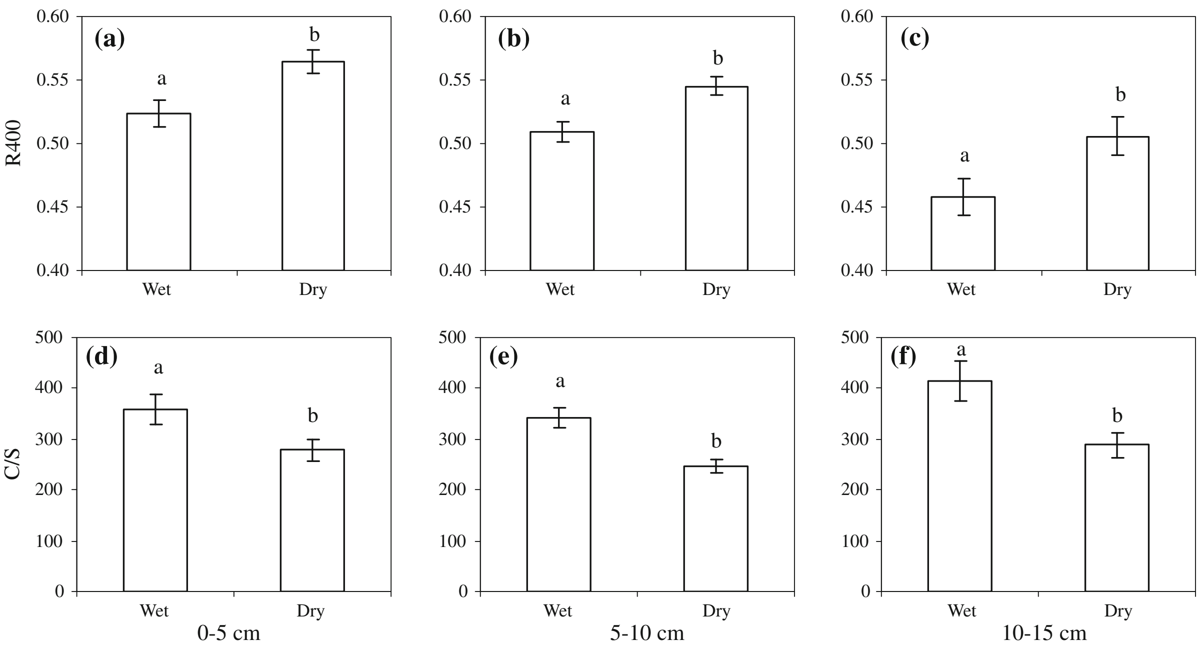

Fig. 5 R400 index and C/S ratio of the uppermost peat (0–15 cm depth) from the two hydrological areas of the peatland (wet and dry). The *error bars* represent one standard error ($n = 8$)

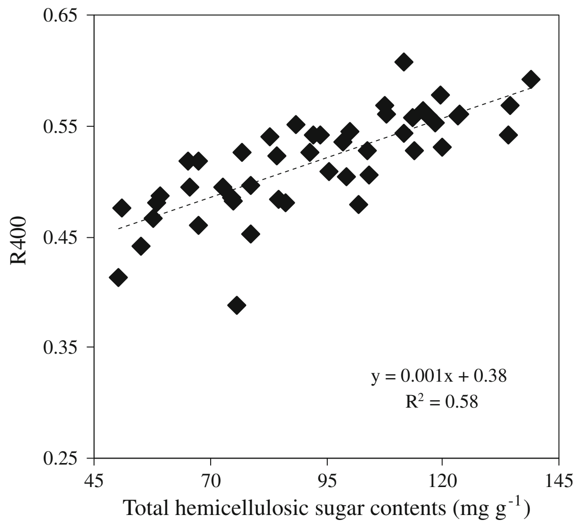

Fig. 6 Correlation between R400 and hemicellulosic sugar content of the uppermost peat (0–15 cm depth) ($n = 48$)

Sphagnum spp. than their aboveground counterparts. The $OICO_2$/OICO ratio was found to discriminate vascular plants (litter and roots) well from *Sphagnum* species (Table 7). Above- and belowground parts of vascular plants exhibited similar ratios (between 1 and 2), lower than the *Sphagnum* ratio (above 3).

Discussion

Relevance of indices from Rock–Eval pyrolysis in assessing peat biochemistry

R400

Hydrocarbons from living vegetation and litter, mainly composed of lignocellulosic compounds, are cracked early during the temperature rise of the Rock–Eval pyrolysis cycle (mostly before 400°C). In contrast, transformed OM such as humic substances resulting from the biological and chemical degradation of fresh litter is cracked later (mostly after 400°C). Thus, the R400 index reflects the relative abundance of fresh unmodified OM (Disnar et al. 2003) and can be considered as an indicator of OM transformation. While R400 has been used successfully to reveal humification processes in forest soils (Disnar et al. 2003), this has not so far been undertaken with peat soils. In the process of OM degradation, fresh organic

Table 7 Litter biochemical indicators of the dominant mosses (*Sphagnum* spp.) and vascular plants (*Betula verrucosa*. and *Molinia caerulea*) in La Guette peatland

	OM (%)	C (mg g^{-1})	N (mg g^{-1})	S (mg g^{-1})	HI (mg HC g^{-1} TOC)	OI (mg CO_2 g^{-1} TOC)	OICO (mg CO g^{-1} TOC)	OIRe6 (mg O_2 g^{-1} TOC)	R400	$OICO_2$/OICO
Sphagnum cuspidatum litter	98.5	428.2	2.2	0.61	404	252	79	228	0.76	3.20
Sphagnum rubellum litter	98.1	431.7	2.2	0.53	460	301	86	268	0.73	3.52
Senescent leaves of *Betula verrucosa*	96.8	501.3	6.2	0.59	544	135	105	158	0.63	1.29
Branches of *Betula verrucosa*	nm	nm	nm	nm	506	133	130	171	0.63	1.02
Roots of *Betula verrucosa*	nm	nm	nm	nm	459	143	71	145	0.66	2.01
Molinia caerulea litter	92.9	446.7	1.0	0.45	635	150	139	188	0.78	1.08
Shoots of *Molina caerulea*	nm	469.2	nd	0.48	576	126	61	126	0.83	2.07
Roots of *Molinia caerulea*	nm	nm	nm	nm	534	214	157	245	0.83	1.36

Sphagnum litter corresponds to the white-yellow part below the green or red photosynthetic part

nm Not measured, *nd* not detected

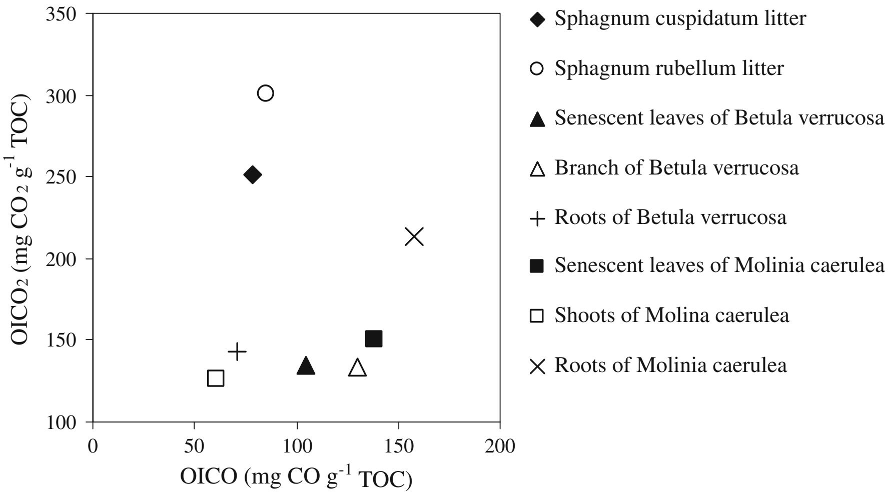

Fig. 7 Correlation between CO_2 oxygen index ($OICO_2$) and CO oxygen index (OICO) of significant source material litter from La Guette peatland

compounds such as hemicellulose are decomposed and transformed by the soil biota. This results in a loss in the polysaccharide content of peat, which would be revealed by a decrease in R400. In our case, this was confirmed by the significant positive correlation between R400 and the peat hemicellulose content (Fig. 6). This result suggests that the R400 index could be used in peat material in the same way as it has been used in mineral soil.

$OICO_2$/OICO

In the case of this study, the $OICO_2$/OICO ratio was found to be the most appropriate index to separate *Sphagnum* material from both above- and below-ground vascular plant material. Jacob (2003) suggested that in lacustrine sediments a high $OICO_2$/OICO ratio may reflect input of well preserved initially oxygen-rich material. Such conditions were fulfilled in the present study. First, *Sphagnum* mosses were richer in oxygen than vascular plant organs (*see* values of oxygen indices in Table 7). Second, *Sphagnum* mosses create conditions favorable for the preservation of OM through the combined action of their soluble and bound polysaccharides (sphagnan) that bind nutrients and release H^+ (Clymo 1967, Painter 1991) and their polyphenolic networks and lipid coating that protect cell walls (van Breemen 1995). These conditions of high oxygen content and good preservation conditions were suitable for using the $OICO_2$/OICO ratio as a possible index of source materials.

Impact of vascular plant invasion on OM biochemical quality

Injection of labile OM in the peat profile

The $OICO_2$/OICO ratio of *Sphagnum* litters was similar to those found in the surface peat of open plots ($\sim$3.4), probably reflecting the deposition and preservation of *Sphagnum* litter. However, the ratios of surface peat from closed plots were intermediate between those of vascular plants and *Sphagnum* species. As roots were removed from peat samples these results suggest that root materials (dead roots and root exudates) contributed to the formation of the peat in closed plots. Thus, differences in $OICO_2$/OICO ratios may reflect the injection of labile OM into peat. *Molinia caerulea* produces a very extensive root system that can reach 80 cm in depth (Taylor et al. 2001). This injection of fresh OM not only occurred at the surface but may also occur in deeper layers of the peat profile as suggested by differences observed between open and closed vegetation plots in both dry and wet areas of the peatland (Tables 4, 5). Fontaine et al. (2007) showed that in mineral soils this injection of root materials can lead to an increase in the mineralization of deep recalcitrant C through a priming effect. They pointed out that such an effect may not occur in wetlands as anaerobic conditions may overrule it. These authors, however, did not take into account the fact that water level fluctuates and peat as deep as 15 cm can be temporarily exposed to aerobic conditions. Furthermore, in cases of vascular plant invasion, oxygen can be directed to deep layers at the root-soil interface (Conrad 1996). None of the parameters measured in this study can assess for the occurrence of a priming effect, but the results obtained encourage further studies in this direction.

New litterfall quality and OM decomposition

Surface peat from closed plots (wet and dry pooled together) contained less hemicellulosic sugars than open plots (wet and dry pooled together) (Fig. 3g), reflecting higher OM degradation (Comont et al. 2006). Deeper in the profile, such differences between plots with different vegetation were not observed (Fig. 3h, i). Moreover, PPI showed that the surface peat from the closed plots was more decomposed than the peat from the open plots, irrespective of the hydrological status of the peatland. The increased decomposition in closed vegetation plots was supported by water analyses (Table 1). Dissolved organic carbon (DOC) concentration and conductivity were higher in closed than in open vegetation. These results suggest that the vascular plant invasion of the *Sphagnum* peatland increased OM decomposition. Furthermore, compared to *Sphagnum* species, *Molinia caerulea* and *Betula* spp have higher litter decomposability (Chamie and Richardson 1978; Bartsch and Moore 1985; Berendse 1998). This would explain the results obtained.

Increased OM decomposition in closed plots as suggested would result in a decrease of OM content, but the results showed that there were no significant differences between plots at the level of significance set ($P < 0.05$). However, there was a trend of lower OM content in peat from closed plots toward the surface ($P < 0.1$), which supports higher decomposition in closed plots than in open plots.

Bulk density showed almost significant differences in all cases (Fig. 3a–c), suggesting that this variable integrates the physico-chemical effect of both vascular plants and hydrologic differences between areas. The bulk density was significantly higher in the closed plots than in the open ones. Minkkinen and Laine (1998a) showed in pine mires that drainage first increases the peat bulk density, then increases OM decomposition, and finally, the pressure of the growing trees further compacts the peat. Thus, the high bulk density in La Guette closed plots could be attributed to the development of the root system of trees. Simultaneously, despite a lower water table in the dry area than in the wet area, the peat from 5 to 10 cm deep was denser in the wet area than in the dry area. Thus the drainage effect may not be sufficient to impact peat physico-chemistry in the way suggested by Minkkinen and Laine (1998a).

Increased OM decomposition can also produce denser peat, without necessarily decreasing the C content (Minkkinen and Laine 1998b). The hemicellulosic sugar content and R400 results actually suggest a higher OM degradation in the wet area of the peatland. Moreover, no significant differences in C content were observed between plots. It is thus argued that the difference in terms of OM degradation between wet and dry areas would lead to denser peat in the wet area.

Impact of the incoming drain on OM decomposition

The differences in peat hemicellulosic sugar contents and R400 index between peatland areas (higher in the dry area) suggest that OM was better preserved in the dry area. As the water table was lower in the latter area, resulting in longer aerobic periods that would promote OM decomposition, these results are puzzling. A possible explanation may come from the fact that this area of the peatland intermittently receives nutrients from a drain flowing directly into the peatland at this location (Fig. 1; Table 2), which is not the case throughout the peatland. Soluble elements such as K and S had concentrations in surface water that decreased with distance from the drain (Fig. 8). This could not be demonstrated with N as concentrations were below the detection limits in the samples measured. It was shown that the water within the peatland actually flows from the east to the west (Binet et al. personal communication). The dry area was thus richer in soluble nutrients than the wet area and this could be the result of nutrient inputs from the drain.

Depending on the availability in mineral nutrients in the media, the microbial biomass may balance demand for mineral nutrients with consumption of supplementary C that would result in C overflow due to stoichiometric constraints (Manzoni and Porporato 2009). From an experiment of wheat decomposition under nutrient-limiting conditions (in this case, N), Hadas et al. (1998) hypothesized that the C that could

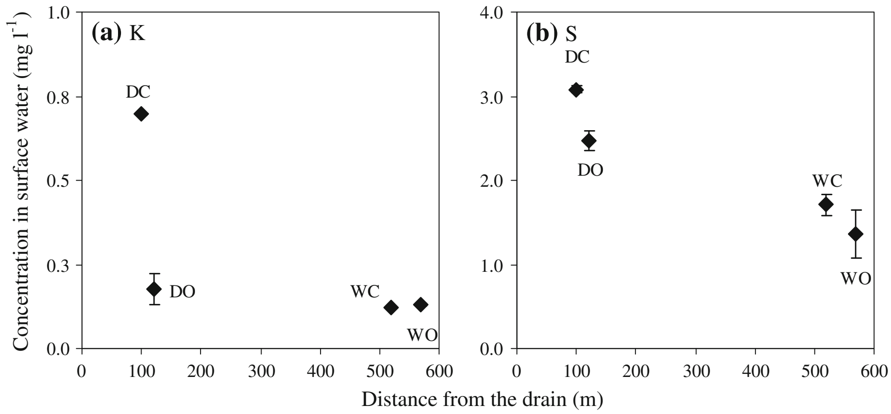

Fig. 8 Concentrations of total soluble K (**a**) and S (**b**) in surface water sampled on May 2008 from the four studied plots in relation to the distance between these plots and the incoming drain of La Guette peatland ($n = 3$). *WO* wet open, *WC* wet closed, *DO* dry open, *DC* dry closed

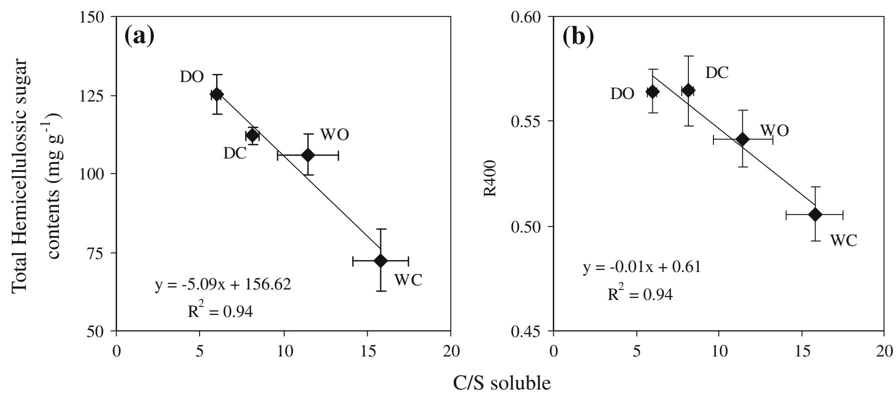

Fig. 9 Hemicellulosic sugar contents (**a**) and R400 (**b**) ($n = 4$) of surface peat (0–5 cm depth) in relation to C/S ($n = 3$) of surface water sampled on May 2008 from the four studied plots in La Guette peatland. *WO* wet open, *WC* wet closed, *DO* dry open, *DC* dry closed

not be mineralized to CO_2 because of the lack of nutrients would flow into a "polysaccharide-like" pool. In the same way, in the wet area, which was poorer in mineral nutrients, such a process could occur, with polysaccharide consumption. The incomplete degradation of such material would result in the excretion of a transformed OM. In the dry area, where mineral nutrients were found in higher concentrations, less C would need to be incorporated and less hemicellulose would flow into the "polysaccharide-like" pool, resulting in a better preservation of OM in this dry area than in wet nutrient-poor plots. The negative correlations between C/S ratio in free water and the surface peat hemicellulose content (Fig. 9a) and R400 (Fig. 9b) support this hypothesis: for an equivalent amount of soluble C, more hemicellulose was degraded and more transformed OM was produced as the availability of S (less S for the same amount of C) decreased (Fig. 9).

In the wet area, where soluble S may be limiting, the microbial community may have found in the solid OM, i.e. peat, the amount of S required for its growth and thus rejected the excess C (C overflow) in the form of transformed OM. Manzoni and Porporato (2009) and Hadas et al. (1998) based their argument of C overflow on models developed for mineral soils. From the results presented in Fig. 9, although obtained with only 4 points, the hypothesis of C overflow under nutrient limiting conditions deserves to be tested on peat soils and La Guette peatland offers a good case of study.

Conclusion

Rock–Eval analysis on peat samples from La Guette peatland showed that R400 and the $OICO_2$/OICO ratios were valuable indices to assess OM degradation and to discriminate litters of *Sphagnum* species from those of vascular plants, respectively. These indices were used to highlight differences between areas with different water levels and vegetation types in the peatland. The $OICO_2$/OICO profiles showed that invading species through their roots may inject labile OM into deep peat. The R400, coupled to hemicellulosic sugar analyses, showed that OM was more decomposed in plots invaded by vascular plants. These results suggest that invasion of a peatland by vascular plants such as *Betula* spp and *Molinia caerulea* affected both surface and deep peat processes.

This study also highlights the important impact of the incoming drain on soil processes. It is suspected that the drain may have enriched the dry area of the peatland in nutrients that modified decomposition conditions in this area compared to the wet one. The microbial community in the dry nutrient-rich area may not have needed to decompose peat to cover its nutrient requirements. In contrast, in the wet nutrient poor area, microbes may have needed to consume more C substrates with the production of a polysaccharide-like pool, i.e. more transformed OM.

All these conclusions obtained with bulk peat analyses could be supported by (1) applying molecular analyses (i.e. lipids) to better discriminate the source materials, (2) surveying the site in the long term, with the present study as the "time zero", to monitor indices of vascular plant colonization.

Finally, these results highlight issues that need to be addressed to fully assess the impact of *Sphagnum* peatland invasion by vascular plants: (1) test for the priming effect induced by labile C injection in deep peat, (2) test the C overflow hypothesis in nutrient-limiting conditions.

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