Multilocus patterns of nucleotide diversity, population structure and linkage disequilibrium in Boechera stricta, a wild relative of Arabidopsis

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Characteristics of dissolved organic matter following 20 years of peatland restoration

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A B S T R A C T

The changes in the amounts and composition of dissolved organic matter (DOM) following long-term peat restoration are unknown, although this fraction of soil organic matter affects many processes in such ecosystems. We addressed this lack of knowledge by investigating a peatland in south-west Germany that was partly rewetted 20 years ago. A successfully restored site and a moderately drained site were compared, where the mean groundwater levels were close to the soil surface and around 30 cm below surface, respectively. The concentrations of dissolved organic carbon (DOC) at 4 depths were measured over one year. The specific absorbance was measured at 280 nm and the fluorescence spectra were used to describe the aromaticity and complexity of DOM.

The investigations showed that 20 years of peatland restoration was able to create typical peatland conditions. The rewetted site had significantly lower DOC concentrations at different depths compared to the drained site. The specific UV absorbance showed that the rewetted site had a lower level of aromatic DOM structures. The decreasing specific UV absorbance might indicate an increasing contribution of small organic molecules to DOM. It was hypothesized that the decreasing DOC concentrations and the relative enrichment of small, readily degradable organic molecules, reflect the slower decomposition of organic matter after the re-establishment of the water table. Seasonal trends provided substantial evidence for our hypothesis that reduced DOC concentrations were caused by reduced peat decomposition. During summer, the elevated DOC values were accompanied by an increase in DOM aromaticity and complexity. Our results demonstrated a close link between C mineralization and DOC production. We concluded that long-term peatland restoration in the form of the successful re-establishment of the water table might result in reduced peat decomposition and lower DOC concentrations. The restoration of peatlands seems to have a positive impact on C sequestration.

1. Introduction

During the last few decades, land use has changed dramatically across the globe (Lambin and Geist, 2006). These changes disturb the ecosystems and are generally accompanied by the quick loss of carbon (C) (Körner, 2003). Usually, the carbon reaches the atmosphere either directly as carbon dioxide (CO_2) or indirectly as dissolved organic matter (DOM). In the light of climate change, care should be taken to avoid such C losses. Nevertheless, land use change remains the second most important source of anthropogenic CO_2 (IPCC, 2007).

Soils are the largest terrestrial C pools (IPCC, 2007) and recover extremely slowly after disturbances have occurred. Therefore, soil C cycling is the key to developing efficient mitigation strategies of land use-induced C losses (Dawson and Smith, 2007).

In this context, peatlands are key ecosystems; they represent the largest pool of the terrestrial organic C (Gorham, 1991). Pristine peatlands are sinks for atmospheric C because decomposition is slowed down as a result of the prolonged absence of oxygen (Freeman et al., 2001). However, human activities have led to profound effects on peatland biogeochemistry, vegetation and C losses (van Seters and Prince, 2002; Strack et al., 2008; Limpens et al., 2008; Waldron et al., 2008). However, it has been demonstrated that the restoration of peatlands, which is presently typically motivated by nature conservation concerns (Pfadenhauer and Klötzli, 1996; Cooper and MacDonald, 2000), can also be beneficial (with respect to the economic aspects of

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the Kyoto Protocol) in terms of C sequestration and greenhouse gas (GHG) dynamics (Wilson et al., 2007, 2008).

The effect that rewetting of peatlands has on DOM has received little attention so far, despite the fact that peatlands are generally recognized as a substantial source of DOM to surface water (Mladenow et al., 2007; Clark et al., 2008; Thacker et al., 2008). Following the principle of "slow in and rapid out" (Körner, 2003), any potential restoration effects on the C cycles may only be observed following long-term studies (over several decades at least). Therefore, neither short-term nor medium-term data are able to show potential effects from changes to the biogeochemistry of peatland areas that have undergone long-term restoration.

Wallage et al. (2006) found that three years after fen blocking, the DOC concentrations were not only significantly lower than those of the adjacent drained fen, but also significantly lower than the DOC of an undrained fen. Worrall et al. (2007) found that the elevated concentrations of dissolved organic carbon (DOC) following peat drain-blocking only existed in the short-term (in the year after the blocking). Kalbitz et al. (2002) and Waddington et al. (2008) also found elevated DOC concentrations in peatlands that have been undergoing restoration for a few years. The long-term changes in DOC following successful peatland restoration, which includes the re-introduction of appropriate peatland vegetation and maintaining the water table close to the surface throughout the whole year, remain virtually unknown. In addition, the changes in dissolved organic matter (DOM) composition to peat restoration are poorly understood. Dissolved organic matter is a heterogeneous mixture of decomposition products reflecting its precursor material and environmental conditions (Kalbitz et al., 2000).

Ponnamperuma (1972) stated that under anoxic conditions fermentative metabolisms are dominant, promoting the production of DOC rather than the immediate production of CO_2. As a consequence, the enrichment of water-soluble intermediate metabolites can be assumed (Mulholland et al., 1990; Fiedler and Kalbitz, 2003; Sahrawat, 2004). Decomposition is generally prevented under anaerobic conditions (Moore and Dalva, 2001; Jungkunst et al., 2008), and metabolites such as acetate, formate, propionate, and lactate may accumulate. This might lead to higher DOC concentrations than those generated under aerobic conditions.

In degraded peatlands, greater peat decomposition resulted in low DOC concentrations in soil solution and groundwater (Kalbitz et al., 2002). In addition, the dissolved organic matter contained a larger portion of aromatic compounds than the DOM of more intact peatlands (Kalbitz et al., 2003). It is assumed that C mineralization is mainly fuelled by DOM, leaving behind the more refractory DOM components, i.e. aromatic and complex compounds (Kalbitz et al, 2003). The majority of these compounds are derived from lignin. Specific UV absorbance (e.g. 280 nm) and fluorescence spectroscopy can be used for the initial assessment of the contribution of aromatic and complex compounds to DOM (Kalbitz and Geyer, 2001; Kalbitz et al., 2003).

The present study focused on assessing the changes in the amount and composition of DOM to long-term peat restoration. A rewetted site and an adjacent drained site in the same peatland area were investigated. At the rewetted fen, the water table was re-established in 1984, i.e. 20 years before the present measurements were undertaken. We assumed the following:(1) the presence of higher DOC concentrations at the rewetted site was a result of anaerobic conditions; (2) a considerable depletion of aromatic and complex compounds at the rewetted site; and (3) a seasonality of DOC concentrations and DOM properties, i.e. higher DOC concentrations of DOC during summer than in winter as a result of higher microbial activity in the warmer months of the year. It was further hypothesized that the higher microbial activity during summer would result in an accumulation of DOM components that degrade only with difficulty, i.e. lignin-derived moieties with many aromatic and complex structures.

2. Materials and methods

2.1. Study sites

The study site 'Donauried' was previously presented in another study (Fiedler et al., 2008). The area is located at an altitude between 440 and 450 m a.s.l., with a mean annual temperature of 7.4 °C and a mean annual precipitation of 670 mm. The south western part of the Donauried (total area 47,150 ha) area comprises the largest coherent fen area (2987 ha) in southern Germany (LFU, 1999). Since the 19th century, the area has been intensively drained in order to be used for a broad range of purposes (as arable land, grassland, the excavation of peat and gravels, and as a drinking water reservoir). The historical peat layer (= 7 m) has gradually declined over the years. The average loss amounted to 7.2 mm a^{-1} between 1951 and 1990 (Flinsbach et al., 1997), which is equivalent to 5.67 t C ha^{-1} a^{-1}. The first nature conservation areas established for the protection of peat areas were created in 1966 and cover now 17% of the region's total fen area. The first attempts to regulate the water flow in drain ditches by weirs were made in 1972. Currently, an area of about 50 ha is being rewetted by way of leading the water flow into the drain ditches. In addition, water has been diverted from the nearby river since 1984 for rewetting purposes.

In the present study, a permanently drained site was compared with a site that was rewetted in 1984. Both sites were formerly used for peat extraction.

2.2. Measurements, sampling and analyses

For monitoring the ground water level (GWL) three PVC wells per site (1 m, diameter of 6 cm, Stockmann, Warendorf, Germany) were installed. The reduction–oxidation potential (Eh) was measured using platinum electrodes (5 replicates per depth) and an Ag/AgCl reference electrode (Fiedler et al., 2003). The soil temperatures were measured with thermocouples once per minute and automatically logged at hourly intervals (SITEC, Meeder, Germany). The hourly values were summarized as mean daily value.

In order to quantify the carbon content of DOM, i.e. DOC (dissolved organic carbon), freely drained pore water was collected using slit PVC pipes (length 10 cm, diameter 2.5 cm, 3 replicates per depth) coated with filter gauze (polypropylene, Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands) and attached to a stainless-steel capillary (diameter 2 mm). The end of the capillary was closed using a three-way stop-cock (Fleischhacker GmbH & Co. KG, Schwerte, Germany). Pore waters were sampled using a syringe. Approximately 50 mL of water was sampled, transferred to a bottle and transported to the laboratory in a cool box, where the samples were filtered (0.45-µm, Macherey-Nagel GmbH & Co. KG, Düren, Germany). Prior to analysis, the samples were acidified (85% H_3PO_4). DOC was determined using a total C/N water analyser (DimaTOC 100, Dimatec Analysentechnik GmbH, Essen, Germany). All water probes were measured three times (error of measurement ± 1.7%).

The entire equipment was installed at depths of 5 (only Eh electrodes), 10, 20, 40 and 60 cm. GWL, Eh, temperature and DOC were monitored over one year (1st of April 2004 to 31th of March 2005).

The composition of DOM was analyzed in May, June, July, August and December 2004, and in January, February, and March 2005, representing a summer (soil temperature > 10 °C) and a winter situation (soil temperature < 5 °C) (Table 1). Specific UV absorbance values (280 nm, $SUVA_{280}$; UVIKON 930, BIO-TEK Instruments, Bad Friedrichshall, Germany) were corrected to 1 mg C L^{-1}. Additionally, synchronous fluorescence spectra (SFM 25, BIO-TEK Instruments, Bad Friedrichshall, Germany) were recorded and a humification index (HIX_{syn}) was calculated by dividing the intensity of the fluorescence bands or shoulders of a longer by a shorter wavelength (460 nm/ 345 nm; analytical error < 2%). To prevent overestimation of these

Table 1
Descriptive statistics of parameters determined at rewetted and moderately drained sites means and standard deviations (SD) of all values (italicised numbers in brackets refer to the number of samples investigated); statistically significant differences between sites and depth for each carbon component are indicated by different letters.

Parameters	Rewetted fen				Moderately drained fen			
Soil classification:	Calcari-Sapric Histosol[a]				Calcari-Fibric Histosol[a]			
Location:	48°28′59.15″N, 10°11′51.92″E				48°28′59.63″N, 10°12′19.50″E			
Natural protection area:	Since 1966				Since 1992			
Dominant vegetation:	*Typha spp.*, *Carex spp.*, *Equisetum spp.*				*Festuca ovina*, *Thymus pulegiodes*, *Arabis hirsute*, *Bromus erectus*, *Campanula rotundifolia*, *Deschampsia ceaspitosa*			
Soil depth [cm]	0–18	−34	−49	−67	0–22	−32	−64	−100
BD [g cm^{-3}]	0.17	0.20	0.21	0.16	0.25	0.17	0.14	0.14
C_{org} [g kg^{-1}]	398	399	403	401	185	159	115	128
Sampling period: 01.04.2004–31.03.2005								
Soil depth [cm]	10	20	40	60	10	20	40	60
GWL [cm below surface]	9 ± 14				29 ± 17			
Eh [mV]	−116 ± 97	−165 ± 51	−165 ± 97	−121 ± 99	469 ± 183	548 ± 172	−34 ± 215	−96 ± 72
Soil temperature [°C]	9.1 ± 5.8	8.7 ± 4.8	8.7 ± 4.4	8.7 ± 2.8	10.4 ± 7.4	10.2 ± 6.5	10.2 ± 5.1	8.9 ± 3.6
DOC [mg C L^{-1}]	52^{A} ± 27 *(17)*	52^{A} ± 29 *(63)*	60^{A} ± 45 *(58)*	64^{A} ± 54 *(68)*	82^{B} ± 35 *(17)*	92^{B} ± 34 *(32)*	88^{B} ± 35 *(43)*	81^{B} ± 34 *(64)*
Sampling season: summer (May–August 2004)								
GWL [cm below surface]	7 ± 8				39 ± 14			
Soil temperature [°C]	15.1 ± 2.5	13.8 ± 1.8	13.8 ± 1.8	11.6 ± 1.0	18.0 ± 3.1	16.9 ± 2.6	15.1 ± 1.7	12.4 ± 1.4
DOC [mg C L^{-1}]	n.d.	44 ± 15 *(17)*	49 ± 20 *(13)*	56 ± 31 *(21)*	n.d.	71 ± 32 *(6)*	67 ± 22 *(11)*	76 ± 30 *(16)*
HIX_{syn}	n.d.	0.54 ± 0.03	0.52 ± 0.04	0.49 ± 0.04	n.d.	0.53 ± 0.09	0.51 ± 0.08	0.42 ± 0.02
UV-A [L mg^{-1} C cm^{-1}]	n.d	0.032 ± 0.01	0.024 ± 0.006	0.019 ± 0.007	n.d.	0.033 ± 0.032	0.032 ± 0.016	0.024 ± 0.008
Sampling season: winter (December 2004–March 2005)								
GWL [cm below surface]	2 ± 4				12 ± 8			
Soil temperature [°C]	2.4 ± 1.4	3.4 ± 1.5	3.6 ± 1.0	5.4 ± 0.7	1.8 ± 1.6	2.7 ± 1.4	4.0 ± 1.8	4.9 ± 1.2
DOC [mg C L^{-1}]	33 ± 35 *(13)*	33 ± 36 *(14)*	62 ± 90 *(9)*	46 ± 58 *(12)*	21 ± 24 *(11)*	47 ± 38 *(13)*	51 ± 49 *(15)*	49 ± 54 *(18)*
HIX_{syn}	0.58 ± 0.04	0.53 ± 0.04	0.46 ± 0.02	0.47 ± 0.02	0.64 ± 0.4	0.55 ± 0.05	0.47 ± 0.02	0.40 ± 0.02
UV-A [L mg^{-1} C cm^{-1}]	0.016 ± 0.008	0.017 ± 0.007	0.019 ± 0.014	0.029 ± 0.017	0.024 ± 0.004	0.022 ± 0.007	0.025 ± 0.007	0.025 ± 0.014

($P<0.01$), n.d. = not defined; BD = bulk density; C_{org} = content of organic carbon, GWL = groundwater level, HIX_{syn} = humification index (ε 460 nm/345 nm), UV-A = UV absorbance at ε 280 nm.

[a] FAO-WRB (1998).

indices, the DOC concentrations were adjusted to 10 mg C L^{-1} by the addition of ultra-pure water (Kalbitz and Geyer, 2001).

2.3. Statistical analyses

The data sets were tested for normality using the Kolmogorov–Smirnov test. Since the data were not normally distributed, the Mann–Whitney *U*-test was used to test the annual mean of DOC for significant differences ($P<0.01$). Since the discriminant function analysis is based on a linear combination of interval variables, data sets of seasonal data (DOC concentration, HIX_{syn}, UV absorbance) were transformed to obtain normal distribution.

Discriminant function analysis was used to identify whether peatland sites can be identified by their DOM characteristics (DOC concentration, HIX_{syn}, UV absorbance). Groups were classified according to seasons and peatland site (SMD = summer drained, SW = summer rewetted, WMD = winter drained, WW = winter rewetted). Wilks' lambda distribution was used for the stepwise selection of variables.

3. Results

3.1. Environmental parameters

Evidence for different land use management, i.e. drainage control, was given by significant differences ($P<0.01$) in annual groundwater levels (GWLs). The rewetted fen exhibited GWLs of 9 ± 14 cm below surface and the drained fen GWLs of 29 ± 17 cm below surface (Table 1). These hydrological differences are representative of the last few decades and lead to substantial differences in the plant community. At the rewetted site, hydrophytes such as *Typha* and *Carex spp.* were dominant, while the drained area was populated by dry meadow species (Table 1). Similarly, the water content also had a great influence on the redox and temperature regime. Strict anoxic conditions (annual averages at different depths: −165 ± 97 to −116 ± 97 mV) were found in the permanently water saturated zone of the rewetted fen (Table 1). Moderately anoxic conditions (annual average 124 ± 282 mV) were found only in the upper 5 cm. In the drained fen under examination, the zone above the GWL was characterized by oxic conditions (469 ± 183 and 548 ± 172 mV in 10 and 20 cm; 539 ± 198 in 5 cm); moderately anoxic to anoxic conditions were observed below the GWL (−34 ± 215 to −96 ± 72 mV). The annual average soil temperatures were one to two degrees higher in moderately drained areas compared to rewetted ones (e.g. 10.4 ± 7.4 °C compared to 9.1 ± 5.8 °C in 10 cm).

3.2. DOC concentrations

From April to March, the mean DOC concentrations of the rewetted fen ranged between 52 and 64 mg C L^{-1} over the entire profile, and were hence significantly ($P<0.01$) lower than those of the moderately drained fen (mean from 82 to 92 mg C L^{-1}; Table 1, Fig. 1). The DOC concentrations at the rewetted site were lower than those at the moderately drained site, despite higher C contents and stocks that were present at the rewetted site (Table 1). At the rewetted site, average annual DOC concentrations increased with depth from 52 mg C L^{-1} at a depth of 10 cm to 64 mg C L^{-1} at a depth of 60 cm. At moderately drained sites, maximum mean DOC concentrations were found at a depth of 20 cm (92 mg C L^{-1}), i.e. at the zone just above the site-specific mean groundwater table.

The DOC concentrations varied considerably and there was no obvious correlation between the DOC concentrations and temperature. Discriminant analysis confirmed that the DOC concentrations were significantly lower and more variable during winter at either of the two fens investigated (Fig. 2, Table 2). All samples taken during summer had DOC concentrations of more than 20 mg C L^{-1}, while only 9% of samples taken during the winter months had DOC concentrations of below

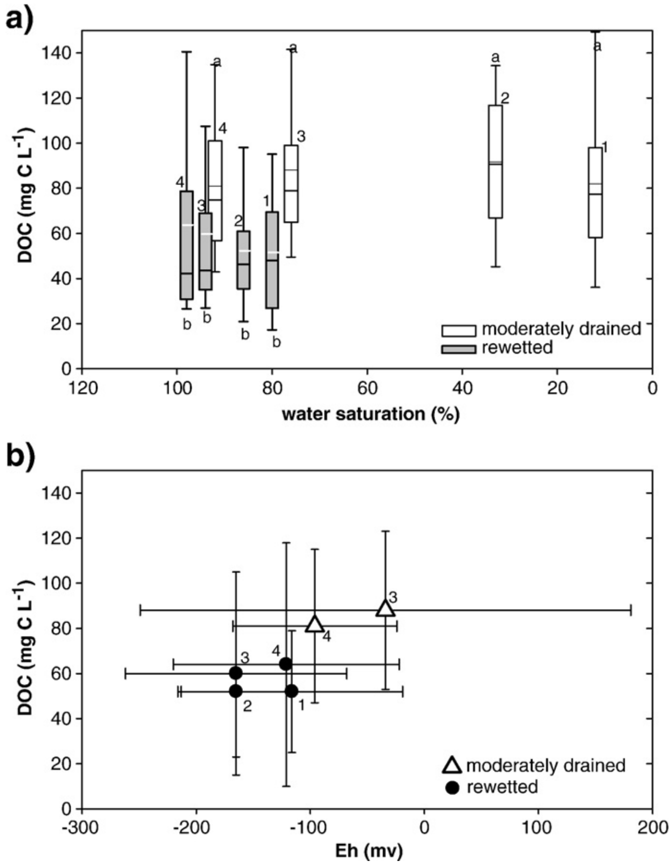

Fig. 1. Relationship between the DOC concentrations (mean = thin line) of rewetted and moderately drained sites. a) Water saturation: 1 at a soil depth of 10 cm, 2 at 20 cm, 3 at 40 cm, and 4 at 60 cm, and b) redox potentials of 1 at a soil depth of 10 cm, 2 at 20 cm, 3 at 40 cm, and 4 at 60 cm depths. Different letters indicate statistically significant differences between the sites and depths investigated ($P<0.001$).

20 mg C L^{-1}. In addition, the DOC concentrations peaked episodically during the winter months to values greater than 200 and 150 mg C L^{-1} in rewetted and moderately drained fen, respectively.

3.3. Composition of DOM

The specific UV absorbance ($SUVA_{280}$) revealed clear differences in the chemical composition of the DOM of the two sites and seasons. Average $SUVA_{280}$ values ranged from 0.016 to 0.032 mg C cm^{-1} (Table 1). The $SUVA_{280}$ values of the rewetted fen were significantly

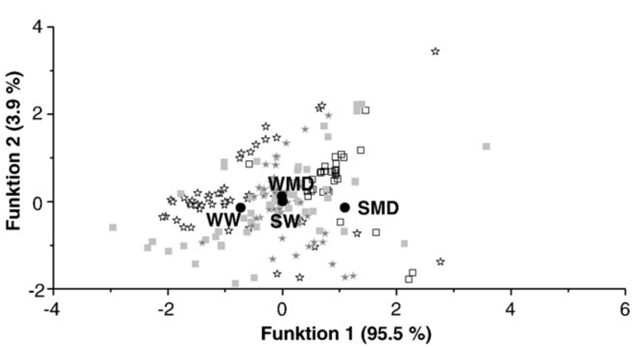

Fig. 2. Scatter plot of a discriminant analysis including DOC concentrations, HIX_{syn} and UV absorbance. Groups were defined according to season (winter or summer) and site ■ = SMD (summer-moderately drained), □ = WMD (winter-moderately drained), ★ = SW (summer-rewetted), or ☆ = WW (winter-rewetted). Group centroids are shown as black dots.

Table 2
Results of discriminant analyses of the variables (UV absorption, DOC concentrations and humification indices) obtained from pore water sampled during the winter and summer seasons.

	Discriminant function	
	DF1	DF2
Wilks' lambda	0.724	0.938
Eigenvalue	0.359	0.15
Degree of freedom	59	3
Cumulative variance [%]	96	99
Canonical correlation coefficient	0.514	0.121
Correlation coefficient[a]		
UV absorption	0.554	0.829
DOC	0.409	−0.764
HIX_{syn}	−0.242	0.616

[a] Pooled within-group correlation between the discriminating variables and the canonical discriminant function.

lower than those of the moderately drained fen (Fig. 2, Table 2). A maximum was observed at the moderately drained site in summer (0.097 L mg^{-1} C cm^{-1}), and minimum at the rewetted fen in winter (0.0016 L mg^{-1} C cm^{-1}).

The average $SUVA_{280}$ values in both fens were highest at a depth of 20 cm and lowest at a depth of 60 cm during summer. A regular spatial pattern could only be observed at the rewetted fen (lowest values at a depth of 10 cm, highest at a depth of 60 cm) during winter.

The $SUVA_{280}$ values were high for both fens during summer, and decreased during the winter to 0.016 mg C cm^{-1} (at a depth of 10 cm at the rewetted site, Table 1). Concentrations of DOC and $SUVA_{280}$ values showed a significant ($P<0.001$) and inverse non-linear correlation during summer (Fig. 3); during winter, this correlation was linear but less pronounced ($P<0.05$, $P<0.001$).

The average values of the humification indices deduced from fluorescence spectra (HIX_{syn}) ranged from 0.40 to 0.64 in all samples.

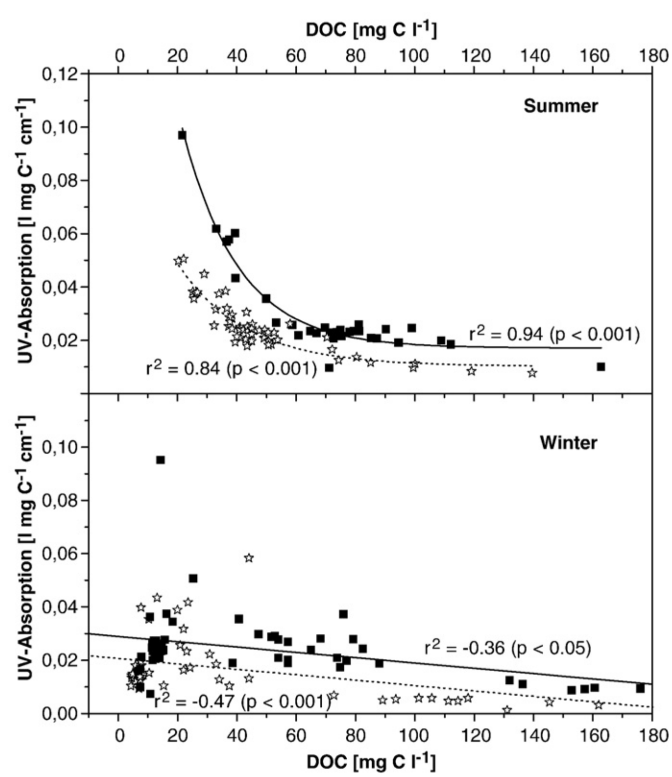

Fig. 3. UV absorbance at 280 nm ($SUVA_{280}$) in relation to DOC concentrations at the rewetted (☆) and moderately drained sites (■) during winter and summer. The data sets represent all soil depths.

HIX_{syn} values of the moderately drained fen were significantly higher than those of the rewetted fen. Maximum HIX_{syn} values were observed at the rewetted fen during winter (0.78), and minimum values at the moderately drained site during summer (0.29). However, the average HIX_{syn} tended to be higher in summer than in winter. At both sites investigated, HIX_{syn} varied with the soil depth. For example, HIX_{syn} of the rewetted fen tended to decrease at a depth between 0.58 (10 cm) and 0.47 (60 cm) (Table 1).

The $SUVA_{280}$ and HIX_{syn} values of the samples of the two fens investigated displayed a significant ($P<0.001$) and positive (0.75 and 0.72) correlation during the summer, whereas no clear pattern was found for the values obtained during the winter.

$HIX_{syn,}$ $SUVA_{280}$ values and DOC concentrations revealed significant group memberships to the given combinations of seasons and sites (winter-rewetted site to winter-moderately drained site, summer-rewetted site to summer-moderately drained site). Fig. 2 and Table 2 show that function 1 discriminated mainly between the given groups and UV absorbance seemed to be the best predictor for the observed differences.

4. Discussion

Twenty years following peatland restoration was sufficient to create typical peatland conditions. The groundwater levels were kept close to the surface throughout the year and strong reducing conditions were measured over the entire peat profile. The redox potentials of the different horizons of the rewetted site were even lower than those of deeper horizons of the drained site, despite the fact that all these horizons were exposed to similar water saturation conditions (Fig. 1a). However, the present study was unable to verify our hypothesis that rewetting would lead to elevated DOC concentrations as a consequence of reduced peat decomposition and an enrichment of water-soluble metabolites. On the other hand, rewetting led to a decreased specific UV absorbance, which suggests that lower concentrations of aromatic compounds are barely biodegraded (Kalbitz et al., 2003). In turn, an increasing contribution of small organic molecules, which are readily biodegradable, can be assumed (Kalbitz et al., 2003). Therefore, the changes in the composition of DOM suggested decelerated decomposition. At a first glance, the low DOC concentrations and the depletion in aromatic compounds seem to be contradictory findings.

Our hypotheses were proposed on the basis that the reduced efficiency of anaerobic organic matter decomposition would lead to accumulation of water-soluble intermediate metabolites at the cost of the final product, CO_2. Therefore, higher DOM concentrations and lower aromaticity (i.e. elevated biodegradability) than under aerobic conditions were expected. However, it may also be assumed that particularly poor conditions for decomposition will not only lead to curtailed CO_2 production but also to reduced production of DOM. Such an effect may be associated with continuous rewetting, although no supporting evidence can be found in the literature. We are only aware of one study that also found reduced DOC concentrations following rewetting (Wallage et al., 2006). Interestingly, this study is the only one that deals with long-term effects, i.e. 3 and 4 years after rewetting due to drain-blocking. Based on these findings, it can safely be assumed that short-term responses of the peatland DOM dynamics to rewetting are different from long-term responses.

According to Wilson et al. (2008), a high input of more labile substrates can be assumed to occur immediately after restoration. It is therefore possible that the increased DOC concentrations observed at shorter time scales represent such flushes. Kalbitz et al. (2002) also found elevated DOC concentrations in restored peatlands and suggested that this was mainly the result of oxic conditions during summer, since the water table could not be maintained at a certain level throughout the entire year.

The water table oscillations mentioned in the literature are often typical for moderately drained or imperfectly restored peatlands, but untypical for successfully rewetted peatland areas. Increased DOC concentrations occurring after the drop of the water table have been explained by the oxidation of peat material (Blodau et al., 2004) or by what is known as the enzymatic 'latch' mechanism (Freeman et al., 2001). We do not think that our findings can be explained by this hypothesis, which suggests that phenols and phenol oxidase have a central role in controlling C dynamics in peatlands. This hypothesis explains increasing DOC concentrations after drawdown of the water table as a result of the increasing activity of phenol oxidase, which leads to decreasing phenol concentration, and hence to slower rate of peat decomposition. Finally, the increased availability of oxygen results in an increased peat decomposition, including DOC production. The raising of the water table led to increased peat decomposition and it is assumed that DOC production continued for an unknown period of time. This would mean that the reductive conditions resulted in low DOC concentrations and high proportions of phenols. However, our study only detected small DOC concentrations and a low UV absorbance, which indicates low phenol levels. Kalbitz et al. (2002) suggested that the adsorbed pool of carbon that accumulated during dry periods and was mobilized upon rewetting was responsible for increased DOC concentrations observed upon rising water tables. This proposed mechanism can explain why the maximum individual DOC concentrations at the moderately drained site were found at a zone just around the site-specific mean groundwater table.

The relationship between water saturation, prevailing redox conditions and DOC concentrations also suggests that the long-term recovery of the water table creates biogeochemical conditions that are different from the short-term elevation of the water table: There is no clear correlation between water saturation and DOC concentrations. Both parameters only showed a significant correlation ($P<0.05$; $r^2=0.95$) for the mean annual values at the rewetted site. At all depths both fens exhibited significantly different DOC concentrations even at soil depths of 40 and 60 cm where water saturation was rather similar (Fig. 1a). But these horizons differed significantly in the redox conditions, which underlines the fact that water saturation does not always represent the actual redox conditions. Apparently, redox potentials below −100 mV are associated with low DOC concentrations (Fig. 1b). Such redox conditions indicate the change from sulfate to carbon dioxide as the dominant electron acceptor (Fiedler et al., 2007). Our results therefore suggest that, in comparison with moderately reduced conditions, strongly reduced conditions lead to decreasing DOC concentrations. At the same time, this redox step is highly important with respect to further reduction in energy efficiency during mineralization. Recent findings imply a close correlation between DOC production and C mineralization (Moore et al., 2008). However, the strength and the slope of this positive correlation depend strongly on the composition of soil organic matter (Moore et al., 2008). Nevertheless, significantly reduced mineralization due to anaerobic conditions (Moore and Dalva, 1997; Jungkunst et al. 2008) is expected to be accompanied by a clear decrease in DOC.

The proposed decrease in DOC as a result of reduced C mineralization is supported by the seasonality of DOC concentrations and the measured spectroscopic properties. The seasonal variations in the DOC concentrations measured in the present study are consistent with findings by other authors (Christ and David 1996; Bonnett et al., 2006; Bossio et al., 2006) who reported lower DOC concentrations in winter than in summer. In turn, increased microbial activity at higher temperatures led to an increase in DOC production, which is followed by an enhanced C mineralization (Kalbitz et al., 2004). Elevated DOC concentrations during the summer were accompanied by the accumulation of aromatic compounds that do not easily degrade. Kaiser et al. (2001) also found a relative increase in more recalcitrant aromatic DOC compounds during summer, while the concentrations of easily degradable organic compounds were higher during winter when biological activity and C mineralization were low.

5. Conclusion

In the past, peat restoration was mainly motivated by nature conservation issues. However, restoration programmes can also have a positive effect on C sequestration. The reduction of the export of DOC from peatlands should be given greater priority because these fluxes are an important component in the C cycle of such catchments (Worrall et al., 2003). The present study demonstrated that in contrast to water tables around 30 cm below soil surface, water tables that were consistently close to the surface led to lower DOC levels. It turned out that peat restoration was not successful if the water tables were not kept close to surface during summer, since this led to even higher DOC concentrations compared to non-rewetted sites. Therefore, it is important to maintain shallow water tables, especially during times of high biological activity. Furthermore, the short-term and long-term effects of rewetting might be very different. Therefore, it is important to take into account the usually small time scales of the relevant studies when intending to up-scale and generalize the respective results. It seems that a period of one to five years is far too short in order to predict the response of DOC to peat restoration effectively.

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