Carbon stability in a Scottish lowland raised bog: Legacy effects of historical land use and implications for global change

Authors: Heike Schimmel[1*], Melanie Braun[1], Jens-Arne Subke[2], Wulf Amelung[1,3], Roland Bol[3]

[1] Institute of Crop Science and Resource Conservation (INRES), Soil Science and Soil Ecology, University of Bonn, Nussallee 13, 53115 Bonn, Germany

[2] Department of Biological and Environmental Sciences, University of Stirling, FK9 4LA Stirling, UK

[3] Institute of Bio- and Geosciences (IBG-3) Agrosphere, Forschungszentrum Jülich, Wilhelm-Johnen-Straße, 52425 Jülich, Germany

*Corresponding author
heike.schimmel@uni-bonn.de

Accepted refereed manuscript of: Schimmel H, Braun M, Subke J, Amelung W & Bol R (2021) Carbon stability in a Scottish lowland raised bog: potential legacy effects of historical land use and implications for global change. *Soil Biology and Biochemistry*, 154, Art. No.: 108124. https://doi.org/10.1016/j.soilbio.2020.108124

Abstract

Peatlands comprise major global stocks of soil organic carbon (SOC). Many degraded peatlands are currently being restored, but little is known to which degree former disturbances leave a ‘legacy’ in such restored peatlands, and subsequently how this impacts their response to global change. Our aims were to investigate if after 20 years of restoration (i) carbon stability may still be affected by the former land use and if (ii) restored peatlands are less susceptible to nutrient input but (iii) more sensitive to temperature. We sampled the top- and subsoil of a formerly drained, a previously drained and afforested part and an unmanaged control site of a Scottish bog. We incubated peat from each part for determination of basal respiration, nutrient limitation and temperature sensitivity (Q_{10}) of aerobic peat degradation. Lowest respiration rates were identified at the afforested site while nutrient addition had no significant effect on topsoil organic matter decomposition at all sites. Q_{10} values were significantly higher in the topsoil (2.6 ± 0.3 to 2.8 ± 0.2) than in the subsoil. For the subsoil, the drained site (2.0 ± 0.0) showed significantly lower Q_{10} values than the afforested one (2.6 ± 0.6), while the control site had a Q_{10} of 2.1 ± 0.0, indicating contrasting temperature sensitivities of potential SOC losses following specific forms of disturbance. Overall, our data indicate that afforestation left a legacy on potential subsoil SOC losses with global warming. Such effects must be considered when integrating restored bogs into global data bases on peatlands’ responses to global change.

Key words: peatlands, carbon dioxide, restoration, Q_{10}, incubation, nutrient limitation

1. Introduction

The anthropogenic use of peatlands enhances the emissions of carbon dioxide (CO_2) through drainage and aeration of the peat. The aeration of naturally water saturated conditions leads to increased decomposition of soil organic matter (SOM) and greenhouse gas emissions, mainly in form of CO_2. The conversion of pristine peatlands to arable and forested land accounts for 80% of the loss of peatlands worldwide (Joosten and Couwenberg, 2008). In Scotland, the majority of disturbed peat soils are affected by drainage and agricultural purposes, 17% of the deep peat soils (defined as > 40-50 cm depth; Vanguelova et al., 2018) are afforested while less than 10% of the lowland raised bogs are in a near-natural state (Artz et al., 2012; Vanguelova et al., 2018). Changes in soil chemical properties through aeration and litter input impact the soil carbon (C) cycle. Aerobic conditions favour microbial activity and enhance decay and thus, drive C emissions.

Pristine peatlands act as C sinks and store large amounts of C through the incomplete decomposition of organic matter. Generally, the C balance of peatlands is slightly positive with methane as the main C source. Drainage and usage shift the main emissions towards CO_2, resulting in a net negative C balance (Parish et al., 2008). In the past 30 years, the rising awareness of the negative effects of peatland use has led to more frequent restoration efforts in order to regenerate peatlands as long-term C stores. However, the long-term success of this restoration work is still uncertain, especially if different land uses have left legacies in carbon stability, nutrient limitations and temperature sensitivity.

Peatland restoration efforts may alter the quality, i.e. stability of soil organic carbon (SOC) in peat. Rewetting leads to a major deceleration of decomposition but former aeration can have reduced substrate quality by enhanced decomposition of SOM (Clymo, 1984; Drollinger et al., 2020). Nevertheless, Heller and Zeitz (2012) found that aerated and degraded peat contains less stable SOM than pristine peat. Restoration can return peat properties close to the natural state (Hermans et al., 2019), but how long it takes and how it affects the carbon stability is largely unknown so far.

Even though restoration work attempts to restore the original functions of peatlands, former land use might have changed nutrient statuses in these ecosystems. As bogs are one major type of peatlands, they are in contrast to minerotrophic fens only rain-fed and thus, poor in nutrients. Changes in nutrient availability through land use are likely to have a particular influence here, as decomposition in pristine bogs is primarily limited by water saturation, a low pH and low nutrient concentrations (Chapin et al., 2003; Lafleur et al., 2005; Moore et al., 2008; Updegraff et al., 1995). However, aerated conditions and litter input through drainage and afforestation favour nitrogen (N) and phosphorus (P) mineralisation and hence, higher nutrient concentrations (Sundström et al., 2000; Wells and Williams, 1996). Especially under afforestation additional fertilization increases N and P availability (Anderson, 2001) which can remain high even several years after restoration (Gaffney et al., 2018; Konings et al., 2019). An increase in nutrient concentrations might result in intensified microbial activity (Vitousek et al., 2010) and thus, in higher decomposition rates (Silvola et al., 1985). How far management has offset potential nutrient limitations and whether there is a legacy despite of restoration is still uncertain. Due to the high atmospheric N deposition in Central Scotland, it is of particular importance to examine potential shifts in nutrient limitations and their impact on decomposition in restored and intact bogs.

Besides nutrient input, restored bogs have to cope with climate change and rising temperatures. A warmer climate might promote C loss from bogs as microbial activity increases with temperature, resulting in an intensified decomposition of SOM (Gregorich et al., 2017; Zimmermann et al., 2009). As one third of the global soil carbon pool is stored in peat, (Gorham, 1991), their sensitivity to temperature rise is of particular importance (Davidson and Janssens, 2006). Sensitivity of soil respiration to temperature rise is often indicated by the Q_{10} value, which gives the increase in soil respiration at a temperature rise of 10°C (Kirschbaum, 1995). Previous studies showed that more recalcitrant SOM is more sensitive to temperature than labile SOM (Bol et al., 2003; Hardie et al., 2011). Anthropogenic use of bogs through drainage promotes decomposition and peat degradation, resulting in an enrichment of stable and recalcitrant SOM moieties (Drollinger et al., 2020;

Tfaily et al., 2014). Waddington et al. (2001) showed that strongly decomposed SOM in a cutover bog had higher Q_{10} values than intact bogs. Yet, how restoration affects the temperature sensitivity of formerly used bogs remains largely unknown.

Understanding how restored bogs react to increasing loads of nutrients and to temperature rise is important in predicting its response to global change. To elucidate the resilience of restored bogs to such processes, the potential decomposition of SOM can be estimated via the measurement of CO_2 emissions (Smirnova et al., 2014). The aim of this study was to elucidate how anthropogenic disturbances and afterward restoration impact on the carbon stability of the peat, especially regarding their response to nutrient inputs and temperature rise. In detail, we hypothesize that after 20 years of restoration, carbon stability in restored bogs remain altered compared to undisturbed bogs and that restored bogs are still less sensitive to nutrient input but more sensitive to temperature rise. To test these hypotheses, we analysed peat from a near-natural and restored lowland raised bog which was partly drained or drained and afforested before restoration as well as undisturbed parts of the bog and incubated the samples under different nutrient supplies and temperatures under controlled conditions in the lab.

2. Materials and Methods

2.1. Site description

Peat cores were collected at the Flanders Moss National Nature Reserve in the Central Belt of Scotland. It is located 15 km west of Stirling (56.159°N, 4.200°W) in a temperate oceanic climate with an average annual precipitation of 1131 mm a^{-1} (1961-1990) and a mean annual temperature of 9.3°C. Flanders Moss is a lowland raised ombrotrophic bog with a current size of 860 ha of which 550 ha are in a near-natural condition. In the mid-1970s, a part of the bog was drained and planted with conifers. Another 100 ha of the bog were drained in the early 1980s. Restoration work at Flanders Moss started 1997 by removing planted conifers and by damming the ditches. The stumps at the afforested site were mulched to level the surface. The restoration measures of afforested sites depend on site conditions (Payne et al., 2018) and mulching is one possibility to deal with stumps during restoration work. Other possibilities are stump flipping and leaving stumps completely in the peat (Artz et al., 2018; Forest Research, 2009). Since then management intends to restore the original structure mainly by controlling the water table.

2.2. Sampling

Samples were taken in the southeast of the bog and in two different historical land use systems in November 2018. Historical land uses were *Drainage* (only drained without any further usage) and *Forestry* (drained and afforested). Additionally, one *Control* site without management was sampled (Figure 1). At each system we sampled three independent replicates, which were around 20 m apart from each other and not affected by surrounding management. At the formerly drained site, samples were taken between ditches and more than 3 m apart from a ditch. The different land uses were around 300 m apart from each other. The formerly afforested site borders the woody edge of the bog; to exclude boundary effects we sampled around 100 m away from the edge. Water table height at the date of sampling was very close to the surface at all three sites (< 5 cm). We used a Russian Peat Corer and sampled a depth of 1 m. The Russian Peat Corer is a half-cylindrical sampler for soft sediments and water saturated samples, which gives semi-disturbed samples without sediment loss during sampling (Pitkänen et al., 2011).

[Figure 1]

Cores were divided into six sections (0-10, 10-20, 20-40, 40-60, 60-80 and 80-100 cm) for basic soil biochemical analysis. The topsoil of all 9 sites was additionally sampled using a border spate. Peat samples from 0 – 10 cm ("topsoil") and 40 – 60 cm ("subsoil") were used for the incubation experiment. These depths were chosen to compare two depths which were both affected by drainage (drainage depth 70-80 cm) but have a different degree of decomposition. Samples were kept cool until their transport to the laboratory at the University of Bonn. Samples for incubation were stored at 4°C for one month while all other samples for C, N and P contents were frozen for four months to maintain the status quo.

2.3. Soil analyses

The C and N content was determined for all sampled depths. To do so, the frozen samples were defrosted at 4°C. For determination of the water content, 10 g of wet peat was oven-dried at 105°C; remaining samples were oven-dried at 40°C and milled. The C and N contents were determined on milled samples using a CN analyser (Elementar Vario Micro Tube, Germany). Based on sample weight, water content and C content of the samples, the C stock for the first meter depth was calculated. We are aware that this procedure might be biased as the soil core extraction can compact the peat and that a loss of water from the samples makes a sample volume measurement difficult. The calculated C stock is therefore only an estimation which is used to indicate differences between sites.

The following soil analyses were only carried out with the samples chosen for incubation (0-10 cm and 40-60 cm). The determination of the maximum water holding capacity (WHC_{max}) and the actual peat moisture was performed mainly after Alef and Nannipieri (1995), modified by using 10 g wet peat instead of 20 g due to the low bulk density. The pH value was measured by adding 1M KCl to 10 g wet peat until 25 ml suspension was obtained. The degree of humification was determined using von Post humification index. Values range from 1 to 10 with 1 indicating no humification and 10 indicating completely humified peat (Ad-hoc-AG Boden, 2005). Total P content was determined via aqua regia extraction. Extracts were measured using inductively coupled plasma optical emission spectrometry (ICP-OES Ultima 2, Horiba Scientific, Japan). All described soil analyses were carried out in duplicates.

2.4. Soil Respiration Measurements

All incubation studies were carried out using a respirometer (Respicond VIII, Nordgren Innovations AB, Sweden). Respicond VIII continuously measures every 60 min the CO_2 released from up to 94 samples. The plastic vessels are cylindrically shaped and have a volume of 250 ml. Closed vessels are placed in a water bath with a constant temperature which is covered by lid, enabling an incubation in the dark. Through decreases of electrical conductivity in the potassium hydroxide solution (KOH), which traps released CO_2, the respirometer measures the CO_2 release per hour in each vessel (Nordgren, 1988), based on the following equation:

$$(1)\ CO_2 = A * \frac{C_{t0} - C_{t1}}{C_{t0}}$$

where A is a conductivity constant that depends on the molarity of the KOH solution, C_{t0} is the conductance of the fresh KOH measured at the beginning of the incubation time, and C_{t1} is the conductance at time t. Every incubation run was carried out with at least four blanks of empty vessels.

2.4.1. Nutrient addition

To assess the impact of nutrient input on SOM stability, we added N and P to topsoil samples (0-10 cm) in an incubation experiment. We here chose topsoil as nutrient input will enter the bog from the surface. An equivalent of 4 g dry peat was brought to 60 % of its WHC_{max} as this is reported to be an optimal soil moisture for incubation studies of peat (Wang et al., 2010) and recommended by ISO 17155 (2012), avoiding completely anaerobic conditions. We decided on 4 g dry peat as some samples had very low bulk densities and high WHC_{max}, so that the maximum filling height to avoid O_2 limiting conditions was reached with 4 g dry peat. Living plants and living organic material like large roots were removed from the peat in order to avoid autotrophic respiration (Glatzel et al., 2004) and samples were put into plastic vessels. The peat was incubated at 20°C to provide optimal conditions for degradation. The respective ISO 16072 (2002) guideline recommends an incubation temperature of 20-25°C. Also, Creamer et al. (2014) reported that, independent of the geographical origin, samples incubated at 20°C showed a constant response while samples incubated at lower temperatures showed large variations. The samples had three days to equilibrate before nutrients were added. There were four different treatments with each three replicates per sample:

1. Control without nutrient addition (blank treatment),
2. Nitrogen addition (N treatment),
3. Phosphorus addition (P treatment),
4. Nitrogen and phosphorus addition (NP treatment).

NH_4NO_3 was chosen as N source and KH_2PO_4 as P source. The amount of added N was based on the annual atmospheric N deposition in Flanders Moss, which is 11.67 kg N a^{-1} ha^{-1} (average 2012-2014; Centre for Ecology and Hydrology, 2019). We took the fivefold amount and added 0.5002 mg N g dry $peat^{-1}$ to ensure non-limited conditions. For an estimation of P addition, an N:P ratio of 15:1 in the topsoil was assumed (Güsewell, 2004; Olde Venterink et al., 2003; Wang and Moore, 2014). Based on the added N and to achieve a N:P ratio of 15:1, 0.0333 mg P g dry $peat^{-1}$ were added. Nutrients were dissolved in deionized water and added with 0.5 ml solution each. For the blank treatment without nutrient addition the samples received 0.5 ml of deionized water. Nutrients were added twice. The first addition was after 3 days equilibrium time, the second addition was after 26 days. Peat was homogenized with a spoon after adding nutrients to distribute the nutrients evenly in the peat. In total, peat was incubated for 45 days. During the experiment, the KOH was changed when the half of the capacity of the KOH to trap CO_2 was reached. One sample (*Forestry*, P treatment) had to be excluded from the experiment after 10 days because KOH solution got into the sample when changing the lye.

2.4.2. Temperature Rise

For determination of Q_{10} values we incubated peat from 0-10 cm and 40-60 cm depth. Again, an equivalent of 4 g of dry peat was rewetted to 60 % of its WHC_{max} with deionized water and homogenized with a spoon. All samples were incubated with four replicates each. Samples were preincubated at 5°C for three days to stabilize respiration and to level the effects of water addition (Blagodatsky et al., 2000; Meyer et al., 2018). Temperature steps were 5, 10, 15, 20 and 25°C. The temperature was held for 24 h each and KOH was changed every 24 h. The first 12 h after heating and changing KOH solution were equilibration time for the microorganisms to adapt to new circumstances. The subsequent 12 h were used as a medium respiration and used for the calculation as the average CO_2 release per hour (Meyer et al., 2018).

2.5. Data Analysis

The calculation of Q_{10} values was performed in R (version 4.0.3). The average soil respiration per hour from the four vessels was used as the medium respiration rates for further calculations. To calculate the relationship between soil respiration and temperature, an exponential function was used. The equation (2) fits the soil respiration over the whole temperature range, where SR_T is the soil respiration at a certain temperature, *a* and *b* are fitted parameters and *T* is temperature:

(2) $SR_T = a \times \exp^{b \times T}$

By inserting b into the equation (3), the Q_{10} value is calculated as:

(3) $Q_{10} = \exp^{10 \times b}$ (Meyer et al., 2018)

Statistical analyses were performed in SigmaPlot (version 13.0). Normal distribution of the data was tested using Shapiro-Wilk test, P value to reject normality was 0.05. Equal variance was tested using Brown-Forsythe-Test, with a P value to reject of 0.05. When data did not meet assumptions for normal distribution, data were log-transformed. Normally distributed data with three groups were tested for significance with a one-way ANOVA. Samples which were spatially dependent of each other were tested for significant differences with a Repeated Measures ANOVA. To determine the influence of former land use and nutrients on respiration rates, a two-way ANOVA was performed with normally distributed data. ANOVA was followed by Holm-Sidak's post-hoc test. When comparing Q_{10} values of top- and subsoil for significant differences, a paired t-test was conducted for normally distributed data. Differences were considered significant for $p < 0.05$.

3. Results

3.1. Peat characteristics

Contents of total organic carbon (C_{org}) varied between 452.2 and 514.0 g kg^{-1} soil and did not differ significantly between sites (Appendix Table A.1). The control and the drained site showed significantly higher C_{org} contents in subsoil layers than in the topsoil ($p < 0.05$) while there were no significant differences between depths at the afforested site ($p > 0.05$). Total N (N_{tot}) contents at the drained and afforested site were significantly higher in the topsoil than in the subsoil ($p < 0.05$) while there were no significant differences between depths at the control site. In 60-80 cm and 80-100 cm depth, the N_{tot} contents of both restored sites were significantly lower than at the control site ($p < 0.05$). The C:N ratios ranged from 33.2 to 75.2 and increased with depth at the two restored sites ($p < 0.05$). Bulk densities varied between 0.04 g cm^{-3} and 0.21 g cm^{-3} and significantly decreased with depth at all three sites ($p < 0.05$) but were not significantly different between sites. The upper 0-10 cm of the formerly afforested site tended to have the highest values for the bulk density and for the C stock (Appendix Table A.1).

3.2. Basal respiration

The cumulative basal respiration (blank treatment) over the incubation period of 45 days ranged from 18.6 ± 5.5 mg CO_2 g dry peat^{-1} at the afforested site to 34.3 ± 9.1 mg CO_2 g dry peat^{-1} and 40.0 ± 28.3 mg CO_2 g dry peat^{-1} at the drained and the control site, respectively (Table 1). Samples of the control and drained site respired in total 2.4% and 2.0% of its total C content (C_{tot}), respectively, while the afforested site respired 1.1% of its C_{tot} ($p > 0.05$). Interestingly, in 0-10 cm depth, respiration and C stock showed a reversed trend as the site with the highest C stock had the lowest respiration rates (Appendix Table A.1; Figure 2).

[Figure 2]

3.3. Nutritional dependence of carbon mineralization

After nutrient addition, the samples showed weak responses compared to the blank treatment. There was no significant effect of added nutrients on respiration rates at all three sites. Adding N led to decreased respiration rates, reducing the cumulative CO_2 release at all three sites compared to the treatment without added nutrients, however, differences were not significant ($p > 0.05$; Table 1). Under the P treatment the control site respired similar amounts of CO_2 than under the blank treatment. Respiration at the drained and the afforested site increased compared to the blank treatment but the difference was not significant ($p > 0.05$; Table 1). Also, adding together N and P had no significant effect on the samples compared to the blank treatment at all three sites ($p > 0.05$; Table 1). Generally, respiration rates did not differ significantly under nutrient treatments but the afforested site had overall significantly lower respiration rates than the other two sites ($p < 0.05$, Table 1).

Table 1: Mean accumulated mg CO_2 g dry peat^{-1} after nutrient addition with standard deviation [n=3]. Nutrient treatments are coded as followed: Blank = no nutrient addition, N = Nitrogen addition, P = Phosphorus addition, NP = Nitrogen and phosphorus addition. Significant differences (p < 0.05) between sites are indicated by lower case letter (^{a}, ^{b}).

Treatment	*Control*	*Drainage*	*Forestry*
Blank	39.95 ± 28.3^a	34.32 ± 9.1^a	18.60 ± 5.5^b
N	33.78 ± 17.3^a	32.72 ± 15.4^a	12.20 ± 5.6^b
P	39.06 ± 24.3^a	40.85 ± 14.5^a	21.28 ± 7.2^b
NP	45.64 ± 33.9^a	32.92 ± 14.3^a	13.83 ± 4.2^b

3.4. Temperature dependence of carbon mineralization

In the topsoil, the aerobic CO_2 production was highest at the control site, increasing from 11.9 ± 7.7 µg CO_2 g^{-1} h^{-1} at 5°C to 93.7 ± 45.7 µg CO_2 g^{-1} h^{-1} at 25°C, while the drained and the afforested site had lower respiration rates. The afforested site showed a higher temperature sensitivity with a Q_{10} value of 2.8, however with no significant difference in Q_{10} with the other two sites ($p > 0.05$; Figure 3).

[Figure 3]

In the subsoil, respiration rates were significantly lower than in the topsoil ($p < 0.05$) by a factor of 3 to 10. Again, the control site had the highest CO_2 production, ranging from 3.6 ± 0.6 µg CO_2 g^{-1} h^{-1} at 5°C to 21.8 ± 3.4 µg CO_2 g^{-1} h^{-1} at 25°C (Figure 3). Q_{10} values of the control site showed no significant differences to both restored sites ($p < 0.05$), but the drained site had significant lower values than the afforested site ($p < 0.05$). Generally, Q_{10} values in the subsoil were significantly lower than in the topsoil ($p < 0.05$).

4. Discussion

4.1. Restoration effects on SOM decomposition

Anthropogenic use alters bog systems by aeration of the peat, resulting in an enhancement of decomposition (Leifeld et al., 2012). Therefore, we assumed that drainage and afforestation have changed SOM chemical properties and thus decomposition rates in restored bogs compared to intact bogs. In both incubation experiments the afforested site had the lowest respiration rates across all treatments, contrasting with higher CO_2 efflux at the intact and the drained sites (Figure 2 and Table 1). Scanlon and Moore (2000) showed that the degree of decomposition is the most important factor controlling CO_2 production. Thus, the lower respiration rates at the afforested site might be caused by enhanced decomposition under forest management in the past, leaving behind lower substrate quality and elevated SOM recalcitrance (Bader et al., 2018; Wüst-Galley et al., 2016). Particularly, young and labile SOM have presumably been lost in the course of management, thus exposing more decomposed and recalcitrant peat at the surface (Leifeld et al., 2012). The assumption of more decomposed topsoil peat at the restored sites is supported by the relative enrichment of N and lower C:N ratio in the topsoil of the drained and the afforested site, as generally a narrower C:N ratio indicates increased microbial activity and mineralization (Krüger et al., 2015). Therefore, it can be assumed that the SOM of the restored sites was more decomposed, presumably through aeration during management (Bader et al., 2018). Also, the von Post humification index supports the theory that especially afforestation has enhanced decomposition as the afforested site had the highest humification values (Appendix Table A.2). In summary, past anthropogenic disturbance has likely increased peat mineralisation and caused a lowered substrate quality, which renders the current SOM more stable to decomposition than the fresh, undisturbed peat of the control plots. This increased carbon stability may have also applied for the drained site, which was not the case. There, differences in C stability could not be detected after 20 years of restoration. Hence, we have to at least partly refute our initial hypothesis that usage of peat still affects decomposition of restored bogs and thus assume additional effects from, e.g., altered litter quality and restoration practices.

There are several kinds of anthropogenic use of bog, which will presumably also influence the effects and success of restoration. At Flanders Moss, sections of the bog were drained, and some drained sections further afforested. Here, we observed a significant difference in the respiration rates of both restored sites (Table 1). Under afforestation, there is additional litter input from highly resistant wood-derived and lignin-rich material (Hermans et al., 2019; Minkkinen et al., 2008). Additionally, for restoration, roots and stumps were mulched and mixed with surrounding peat and left in the peat body. These residues are more resistant to decomposers and need higher activation energy for decomposition than labile organic compounds (Kleber, 2010). In contrast to our results, Hermans et al. (2019) found no differences in CO_2 production between shallow cores from restored forest-to-bog plots and pristine bog plots, but higher a CO_2 efflux from an afforested bog. It indicates that restoration has levelled the influence of former forest plantation regarding decomposition and CO_2 production. There, trees were felled and left in furrows but the peat was not mixed with the stumps. Thus, at Flanders Moss we suspect that the impacts of the forest litter, and particularly of the mulched stumps in the peat, contribute to the lower respiration rates of the formerly afforested bog relative to intact or drained peat soils. Consequently, for the afforested site we can confirm our hypothesis, i.e. that here the former usage changed decomposition and even more than 20 years of restoration could not yet diminish these effects. We conclude, that the legacy effect on SOM decomposition in bogs is mainly dependent on the type of former usage.

4.2. Stability of SOM against increasing nutrient inputs in restored bogs

Bogs are naturally nutrient-poor ecosystems (Finlayson and Milton, 2016; Updegraff et al., 1995) but anthropogenic disturbance and enhanced mineralization can increase nutrient concentrations (Devito and Dillon, 1993; Gaffney et al., 2018). Therefore, it was suggested that nutrient limitations might have been offset by past anthropogenic use and that consequently, the intact site might show a higher susceptibility to nutrients than the restored sites. In this study, however, the nutrient additions did not lead to significant changes in respiration rates in either intact or restored sites. We observed that the mean values of all three sites indicated slightly decreased respiration after N addition, which cannot be statistically proven. Yet, this finding is consistent with literature evidences as a decrease in respiration after N addition was also observed for forest litter and soils as well as for peat soils (Aerts and Toet, 1997; Bowden et al., 2004; Mo et al., 2006), while also the opposite, an increase in peat decomposition under higher N supply, has been reported (Bragazza et al., 2006). According to the “microbial nitrogen mining” theory, decomposition might decline when N is sufficiently available (Craine et al., 2007), because microorganisms do not need to decompose recalcitrant material to access additional N sources. In this regard, the observed but statistically not significant decreased respiration after N addition supports the microbial N mining theory in that former N loads now provide a legacy in a way that increased atmospheric N deposition reduces the need for N mining and therewith “stabilizes” OM against rapid microbial mineralization.

High atmospheric N deposition in bogs dilutes P concentrations so that potentially shifts to P-limitation can occur (Larmola et al., 2013). A shift from N- and P-co-limitation to P-limitation was already observed in Central Europe and Eastern Canada, where atmospheric N deposition negates N-limitation in bogs (Wang and Moore, 2014). Generally, our samples showed large C:N:P ratios, which are based on data being affected by a high heterogeneity in nutrient contents between samples (Appendix Table A.1 and Table A.2). This variation might be caused by different predominant vegetation types during peat formation (Zhang et al., 2017). Nevertheless, all samples show low P contents and large C:P ratios, thus, a P-deficiency can be expected (Wang et al., 2014). The high N:P ratios of the incubated samples confirm P-limited conditions, which occur at N:P ratios >20:1 (Güsewell, 2004; Wang and Moore, 2014). Thus, we had expected an increase in respiration after P addition (Wright and Reddy, 2007). However, the P addition had no significant effect on neither the respiration rates of the intact nor of the restored sites compared to the blank treatment. Consequently, these potential P-limited conditions are more reflected in P contents and C:N:P ratios than in respiration rates upon P addition. We assume that all three sites are P-limited regardless of their former land use, but that other factors like water saturation and resulting anaerobic conditions influence decomposition more than this P-limitation.

The key factor that controls decomposition in peatlands is water saturation (Moore and Knowles, 1989; Scanlon and Moore, 2000). Generally, O_2 availability is the main factor determining CO_2 production (Fenner and Freeman, 2011; Philben et al., 2015). This assumption is confirmed by the fact that several samples showed peaks in respiration after venting the vessels, which indicate primarily O_2 limitation on decomposition in bog peat (Appendix Figure B.1; values directly after venting the vessels are excluded from calculation of respiration rates). Yet, these observations indicate that the height of the water table in the analysed bog is more important for decomposition and CO_2 evolution than nutrient limitation. This primary limitation in oxygen is likely to outweigh the secondary limitation in nutrients, as the observed weak response to the added nutrients implies that decomposition is not primarily nutrient-limited, because the microbial community of bogs might already be adapted to nutrient-limited conditions (Hoyos-Santillan et al., 2018). As this seems to apply for the intact as well as for the restored sites, we have to refute our stated hypothesis, that the intact site shows a higher susceptibility to nutrient input. Future lab studies in this regard should thus be performed under variable water levels.

4.3. Stability of SOM against temperature rise of restored bogs

To estimate potential feedback effects to climate change on the C balance of the restored bogs we determined the temperature sensitivity of SOM decomposition. The carbon quality temperature (CQT) hypothesis states that older and recalcitrant SOM is more sensitive to temperature than younger SOM moieties (Bosatta and Ågren, 1999; Davidson and Janssens, 2006). However, beside age, SOM quality also depends on land use (Kögel-Knabner and Amelung, 2014). Particularly drainage and afforestation can change SOM chemical properties and enhance decomposition (Wüst-Galley et al., 2016), making the remaining OM potentially more sensitive to temperature (Conant et al., 2008). This is in concordance with our findings, as the formerly afforested site had Q_{10} values similar to values found in cutover bogs (Waddington et al., 2001), which were in the subsoil significantly higher than those found at the formerly drained site. The higher temperature sensitivity can be attributed to the input and preservation of chemically recalcitrant litter in course of afforestation, resulting in low substrate quality and highest C stability. Hence, drainage alone has left no legacy in temperature sensitivity, while afforestation has stabilized both top- and subsoil against rapid decomposition but in agreement with the CQT hypotheses it has also made the site more sensitive to temperature rise, a legacy effect of former land use that remains detectable 20 years after restoration.

As temperature sensitivity is affected by SOM quality, it is also a function of soil depth. In peatlands, SOM quality decreases with depth (Byrne and Farrell, 1997) and according to the CQT theory, Q_{10} values and hence temperature sensitivity should increase with depth (Hardie et al., 2011; Hilasvuori et al., 2013; Waddington et al., 2001). However, this was not confirmed in our study: the Q_{10} values of Flanders Moss were larger for the topsoil than for the subsoil, both for the intact part of the bog and the restored sites. Boone et al. (1998) found that soil Q_{10} was higher when roots were included in the measurement. The topsoil peat in this study was slightly decomposed; yet, fine roots likely remained in the peat and could thus have contributed to the higher Q_{10} values of topsoil.

There are other studies that did not find a depth and age dependency in temperature sensitivity of SOM (Conen et al., 2006; Wang et al., 2010), and some studies even found a higher temperature sensitivity of younger SOM (Bader et al., 2018; Christensen et al., 1999). Bader et al. (2018) assigned higher Q_{10} values to intensive land use and remaining highly decomposed topsoil peat after management. As discussed above, especially the afforested site was disturbed intensively for afforestation and restoration but nevertheless, according to the von Post humification index, the subsoil was more decomposed in all three sites than the topsoil peat (Appendix Table A.2). Likely, the temperature sensitivity did not solely depend on depth and quality of SOM but also on further factors like O_2 availability and nutrient status (Davidson et al., 2006; Sihi et al., 2016; Szafranek-Nakonieczna and Stêpniewska, 2014).

5. Conclusion

Anthropogenically modified peatlands are widely rewetted to restore their carbon sink function and their natural resilience to environmental changes. The aim of this study was to assess the effects of restoration in a Scottish bog that had been drained and partly further afforested. We have to refute our initial hypothesis that both restored bogs showed a legacy of former land use in carbon stability, nutrient limitations and temperature sensitivity compared to intact bogs. Instead, the type of former land use and presumably the type of restoration mainly determined the success of restoration. Whereby, SOM of the formerly drained and afforested site was likely of lower quality and more stable against decomposition but it was also more sensitive to temperature rise than in the intact and formerly drained bog. More research is still needed to see how different restoration measures affect the restoration of bogs and also to scale the findings for different levels of oxygen availability.

Acknowledgement

This project was funded by Geoverbund ABC/J. We also thank Scottish Natural Heritage for enabling the sampling at Flanders Moss National Nature Reserve.

References

Ad-hoc-AG Boden, 2005. Bodenkundliche Kartieranleitung: mit 103 Tabellen und 31 Listen, 5., verbesserte und erweiterte Auflage. ed. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele und Obermiller), Stuttgart.

Aerts, R., Toet, S., 1997. Nutritional controls on carbon dioxide and methane emission from Carex-dominated peat soils. Soil Biology and Biochemistry 29, 1683–1690. doi:10.1016/S0038-0717(97)00073-4

Alef, K., Nannipieri, P. (Eds.), 1995. Methods in applied soil microbiology and biochemistry, 2. print. ed. Academic Press, London.

Allison, S.D., Czimczik, C.I., Treseder, K.K., 2008. Microbial activity and soil respiration under nitrogen addition in Alaskan boreal forest. Global Change Biology 14, 1156–1168. doi:10.1111/j.1365-2486.2008.01549.x

Anderson, R., 2001. Deforesting and restoring peat bogs: a review, Forestry Commission technical paper. Forestry Commission, Edinburgh.

Artz, R.R.E., Donnelly, D., Cuthbert, A., Evans, C., Reed, M., Kenter, J., Clark, J., 2012. Restoration of lowland raised bogs in Scotland: Emissions savings and the implications of a changing climate on lowland raised bog condition - Final Report.

Artz, R.R.E., Faccioli, M., Roberts, M., Anderson, R., 2018. Peatland restoration – a comparative analysis of the costs and merits of different restoration methods.

Bader, C., Müller, M., Schulin, R., Leifeld, J., 2018. Peat decomposability in managed organic soils in relation to land use, organic matter composition and temperature. Biogeosciences 15, 703–719. doi:10.5194/bg-15-703-2018

Blagodatsky, S.A., Heinemeyer, O., Richter, J., 2000. Estimating the active and total soil microbial biomass by kinetic respiration analysis. Biology and Fertility of Soils 32, 73–81. doi:10.1007/s003740000219

Bol, R., Bolger, T., Cully, R., Little, D., 2003. Recalcitrant soil organic materials mineralize more efficiently at higher temperatures. Journal Plant Nutrition and Soil Science 300–307.

Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396, 570–572.

Bosatta, E., Ågren, G.I., 1999. Soil organic matter quality interpreted thermodynamically. Soil Biology and Biochemistry 31, 1889–1891. doi:10.1016/S0038-0717(99)00105-4

Bowden, R.D., Davidson, E., Savage, K., Arabia, C., Steudler, P., 2004. Chronic nitrogen additions reduce total soil respiration and microbial respiration in temperate forest soils at the Harvard Forest. Forest Ecology and Management 196, 43–56. doi:10.1016/j.foreco.2004.03.011

Bragazza, L., Freeman, C., Jones, T., Rydin, H., Limpens, J., Fenner, N., Ellis, T., Gerdol, R., Hájek, T., Iacumin, P., Kutnar, L., Tahvanainen, T., Toberman, H., 2006. Atmospheric nitrogen deposition promotes carbon loss from peat bogs. Proceedings of the National Academy of Sciences of the United States of America 103, 19386–19389.

Byrne, K.A., Farrell, E.P., 1997. The Influence of Forestry on Blanket Peatland, in: Humic Substances, Peats and Sludges. Elsevier, pp. 262–277. doi:10.1016/B978-1-85573-805-8.50029-X

Centre for Ecology and Hydrology, 2019. UK Deposition Data | UK Pollutant Depostion [WWW Document]. URL http://www.pollutantdeposition.ceh.ac.uk/data (accessed 6.4.19).

Chapin, C.T., Bridgham, S.D., Pastor, J., Updegraff, K., 2003. Nitrogen, phosphorus and carbon mineralization in response to nutrient and lime addition in peatlands. Soil Science 168, 409–420. doi:10.1097/01.ss.0000075286.87447.5d

Christensen, T.R., Jonasson, S., Callaghan, T.V., Havström, M., 1999. On the potential CO2 release from tundra soils in a changing climate. Applied Soil Ecology 11, 127–134. doi:10.1016/S0929-1393(98)00146-2

Clymo, R.S., 1984. The Limits to Peat Bog Growth. Philosophical Transactions of the Royal Society B: Biological Sciences 303, 605–654. doi:10.1098/rstb.1984.0002

Conant, R.T., Drijber, R.A., Haddix, M.L., Parton, W.J., Paul, E.A., Plante, A.F., Six, J., Steinweg, J.M., 2008. Sensitivity of organic matter decomposition to warming varies with its quality: Temperature sensitivity of organic matter decomposition. Global Change Biology 14, 868–877. doi:10.1111/j.1365-2486.2008.01541.x

Conen, F., Leifeld, B., Seth, B., Alewell, C., 2006. Warming mobilises young and old soil carbon equally. Biogeosciences Discussions, European Geosciences Union 3, 1355–1366.

Craine, J.M., Morrow, C., Fierer, N., 2007. Microbial nitrogen limitation increases decomposition. Ecology 88, 2105–2113. doi:10.1890/06-1847.1

Creamer, R.E., Schulte, R.P.O., Stone, D., Gal, A., Krogh, P.H., Lo Papa, G., Murray, P.J., Pérès, G., Foerster, B., Rutgers, M., Sousa, J.P., Winding, A., 2014. Measuring basal soil respiration across Europe: Do incubation temperature and incubation period matter? Ecological Indicators 36, 409–418. doi:10.1016/j.ecolind.2013.08.015

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. doi:10.1038/nature04514

Davidson, E.A., Janssens, I.A., Luo, Y., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. Global Change Biology 12, 154–164. doi:10.1111/j.1365-2486.2005.01065.x

Devito, K.J., Dillon, P.J., 1993. The influence of hydrologic conditions and peat oxia on the phosphorus and nitrogen dynamics of a conifer swamp. Water Resources Research 29, 2675–2685. doi:10.1029/93WR00622

Drollinger, S., Knorr, K.-H., Knierzinger, W., Glatzel, S., 2020. Peat decomposition proxies of Alpine bogs along a degradation gradient. Geoderma 369, 114331. doi:10.1016/j.geoderma.2020.114331

Fenner, N., Freeman, C., 2011. Drought-induced carbon loss in peatlands. Nature Geoscience 4, 895–900. doi:10.1038/ngeo1323

Finlayson, C.M., Milton, G.R., 2016. Peatlands, in: Finlayson, C. Max, Milton, G. Randy, Prentice, R.C., Davidson, N.C. (Eds.), The Wetland Book. Springer Netherlands, Dordrecht, pp. 1–18. doi:10.1007/978-94-007-6173-5_202-1

Forest Research, 2009. Stump Harvesting: Interim Guidance on Site Selection and Good Practice.

Gaffney, P.P.J., Hancock, M.H., Taggart, M.A., Andersen, R., 2018. Measuring restoration progress using pore- and surface-water chemistry across a chronosequence of formerly afforested blanket bogs. Journal of Environmental Management 219, 239–251. doi:10.1016/j.jenvman.2018.04.106

Glatzel, S., Basiliko, N., Moore, T., 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Québec, Canada. Wetlands 24, 261–267. doi:10.1672/0277-5212(2004)024[0261:CDAMPP]2.0.CO;2

Gorham, E., 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecological Applications 1, 182–195.

Gregorich, E.G., Janzen, H., Ellert, B.H., Helgason, B.L., Qian, B., Zebarth, B.J., Angers, D.A., Beyaert, R.P., Drury, C.F., Duguid, S.D., May, W.E., McConkey, B.G., Dyck, M.F., 2017. Litter decay controlled by temperature, not soil properties, affecting future soil carbon. Global Change Biology 23, 1725–1734. doi:10.1111/gcb.13502

Güsewell, S., 2004. N : P ratios in terrestrial plants: variation and functional significance: Tansley review. New Phytologist 164, 243–266. doi:10.1111/j.1469-8137.2004.01192.x

Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Rowland, A.P., Ostle, N.J., Flowers, T.H., 2011. Abiotic drivers and their interactive effect on the flux and carbon isotope (14C and δ13C) composition of peat-respired CO2. Soil Biology and Biochemistry 43, 2432–2440. doi:10.1016/j.soilbio.2011.08.010

Heller, C., Zeitz, J., 2012. Stability of soil organic matter in two northeastern German fen soils: the influence of site and soil development. Journal of Soils and Sediments 12, 1231–1240. doi:10.1007/s11368-012-0500-6

Hermans, R., Zahn, N., Andersen, R., Teh, Y.A., Cowie, N., Subke, J.-A., 2019. An incubation study of GHG flux responses to a changing water table linked to biochemical parameters across a peatland restoration chronosequence. Mires and Peat 1–18. doi:10.19189/MaP.2018.DW.354

Hilasvuori, E., Akujärvi, A., Fritze, H., Karhu, K., Laiho, R., Mäkiranta, P., Oinonen, M., Palonen, V., Vanhala, P., Liski, J., 2013. Temperature sensitivity of decomposition in a peat profile. Soil Biology and Biochemistry 67, 47–54. doi:10.1016/j.soilbio.2013.08.009

Hoyos-Santillan, J., Lomax, B.H., Turner, B.L., Sjögersten, S., 2018. Nutrient limitation or home field advantage: Does microbial community adaptation overcome nutrient limitation of litter decomposition in a tropical peatland? Journal of Ecology 106, 1558–1569. doi:10.1111/1365-2745.12923

ISO 16072, 2002. Soil quality- laboratory methods for determination of microbial soil respiration.

ISO 17155, 2012. Soil quality - Determination of abundance and activity of soil microflora using respiration curves.

Joosten, H., Couwenberg, J., 2008. Peatlands and carbon, in: Assessment on Peatlands, Biodiversity and Climate Change: Main Report., Global Environment Centre, Kuala Lumpur and Wetlands International. Wageningen, pp. 99–117.

Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. Soil Biology and Biochemistry 27, 753–760. doi:10.1016/0038-0717(94)00242-S

Kleber, M., 2010. What is recalcitrant soil organic matter? Environmental Chemistry 7, 320. doi:10.1071/EN10006

Kögel-Knabner, I., Amelung, W., 2014. Dynamics, Chemistry, and Preservation of Organic Matter in Soils, in: Treatise on Geochemistry. Elsevier, pp. 157–215. doi:10.1016/B978-0-08-095975-7.01012-3

Konings, W., Boyd, K.G., Andersen, R., 2019. Comparison of plant traits of sedges, shrubs and Sphagnum mosses between sites undergoing forest-to-bog restoration and near-natural open blanket bog: a pilot study. Mires and Peat 1–10. doi:10.19189/MaP.2017.OMB.307

Krüger, J.P., Leifeld, J., Glatzel, S., Szidat, S., Alewell, C., 2015. Biogeochemical indicators of peatland degradation – a case study of a temperate bog in northern Germany. Biogeosciences 12, 2861–2871. doi:10.5194/bg-12-2861-2015

Lafleur, P.M., Moore, T.R., Roulet, N.T., Frolking, S., 2005. Ecosystem Respiration in a Cool Temperate Bog Depends on Peat Temperature But Not Water Table. Ecosystems 8, 619–629. doi:10.1007/s10021-003-0131-2

Larmola, T., Bubier, J.L., Kobyljanec, C., Basiliko, N., Juutinen, S., Humphreys, E., Preston, M., Moore, T.R., 2013. Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. Global Change Biology 19, 3729–3739. doi:10.1111/gcb.12328

Leifeld, J., Steffens, M., Galego-Sala, A., 2012. Sensitivity of peatland carbon loss to organic matter quality: Peat quality and carbon loss. Geophysical Research Letters 39. doi:10.1029/2012GL051856

Meyer, N., Welp, G., Amelung, W., 2018. The Temperature Sensitivity (Q10) of Soil Respiration: Controlling Factors and Spatial Prediction at Regional Scale Based on Environmental Soil Classes. Global Biogeochemical Cycles 32, 306–323. doi:10.1002/2017GB005644

Minkkinen, K., Byrne, K.A., Trettin, C., 2008. Climate Impacts of Peatland Forestry, in: Strack, M. (Ed.), Peatlands and Climate Change. pp. 98–122.

Mo, J., Brown, S., Xue, J., Fang, Y., Li, Z., 2006. Response of Litter Decomposition to Simulated N Deposition in Disturbed, Rehabilitated and Mature Forests in Subtropical China. Plant and Soil 282, 135–151. doi:10.1007/s11104-005-5446-7

Moore, T.R., Dalva, M., 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anerobic laboratory incubations. Soil Biology and Biochemistry Vol. 29, 1157–1164.

Moore, T.R., Knowles, R., 1989. The influence of water table levels on methane and carbon dioxide emissions from peatlands soils. Canadian Journal of Soil Science 69, 33–38. doi:10.4141/cjss89-004

Moore, T.R., Trofymow, J.A., Siltanen, M., Kozak, L.M., 2008. Litter decomposition and nitrogen and phosphorus dynamics in peatlands and uplands over 12 years in central Canada. Oecologia 157, 317–325. doi:10.1007/s00442-008-1076-0

Nordgren, A., 1988. Apparatus for the continuous, long-term monitoring of soil respiration rate in large numbers of samples. Soil Biology and Biochemistry 20, 955–957. doi:10.1016/0038-0717(88)90110-1

Olde Venterink, H., Wassen, M.J., Verkroost, A.W.M., De Ruiter, P.C., 2003. Species richness-productivity patterns differ between N-, P-, and K-limited wetlands. Ecology 84, 2191–2199. doi:10.1890/01-0639

Parish, F., Sirin, A., Charman, D., Joosten, H., Minayeva, T., Silvius, M., Stringer, L., 2008. Assessment on peatlands, biodiversity, and climate change. Global Environment Centre & Wetlands International, Kuala Lumpur, Wageningen.

Payne, R.J., Anderson, A.R., Sloan, T., Gilbert, P., Newton, A., Ratcliffe, J., Mauquoy, D., Jessop, W., Andersen, R., 2018. The future of peatland forestry in Scotland : balancing economics, carbon and biodiversity Scottish Forestry, 34–40.

Philben, M., Holmquist, J., MacDonald, G., Duan, D., Kaiser, K., Benner, R., 2015. Temperature, oxygen, and vegetation controls on decomposition in a James Bay peatland: CONTROLS ON PEAT DECOMPOSITION. Global Biogeochemical Cycles 29, 729–743. doi:10.1002/2014GB004989

Pitkänen, A., Turunen, J., Simola, H., 2011. Comparison of different types of peat corers in volumetric sampling. Suoseura - Finnish Peatland Society 62, 51–57.

Scanlon, D., Moore, T., 2000. Carbon dioxide production from peatland soil profiles: The influence of temperature, oxic/anoxic conditions and subtrate. Soil Science 165, 153–160. doi:10.1097/00010694-200002000-00006

Sihi, D., Inglett, P.W., Inglett, K.S., 2016. Carbon quality and nutrient status drive the temperature sensitivity of organic matter decomposition in subtropical peat soils. Biogeochemistry 131, 103–119. doi:10.1007/s10533-016-0267-8

Silvola, J., Välijoki, J., Aaltonen, H., 1985. Effect of draining and fertilization on soil respiration at three ameliorated peatland sites. Acta Forestalia Fennica 0. doi:10.14214/aff.7637

Smirnova, N., Demyan, M.S., Rasche, F., Cadisch, G., Müller, T., 2014. Calibration of CO2 Trapping in Alkaline Solutions during Soil Incubation at Varying Temperatures Using a Respicond VI. Open Journal of Soil Science 04, 161–167. doi:10.4236/ojss.2014.45019

Sundström, E., Magnusson, T., Hånell, B., 2000. Nutrient conditions in drained peatlands along a north-south climatic gradient in Sweden. Forest Ecology and Management 126, 149–161. doi:10.1016/S0378-1127(99)00098-5

Szafranek-Nakonieczna, A., Stêpniewska, Z., 2014. Aerobic and Anaerobic Respiration in Profiles of Polesie Lubelskie Peatlands. International Agrophysics 28, 219–229. doi:10.2478/intag-2014-0011

Tfaily, M.M., Cooper, W.T., Kostka, J.E., Chanton, P.R., Schadt, C.W., Hanson, P.J., Iversen, C.M., Chanton, J.P., 2014. Organic matter transformation in the peat column at Marcell Experimental Forest: Humification and vertical stratification: Organic matter dynamics. Journal of Geophysical Research: Biogeosciences 119, 661–675. doi:10.1002/2013JG002492

Updegraff, K., Pastor, J., Bridgham, S.D., Johnston, C.A., 1995. Environmental and Substrate Controls over Carbon and Nitrogen Mineralization in Northern Wetlands. Ecological Applications 5, 151–163. doi:10.2307/1942060

Vanguelova, E., Chapman, S., Perks, M., Yamulki, S., Randle, T., Ashwood, F., Morison, J., 2018. Afforestation and restocking on peaty soils – new evidence assessment.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecological Applications 20, 5–15. doi:10.1890/08-0127.1

Waddington, J.M., Rotenberg, P.A., Warren, F.J., 2001. Peat CO2 production in a natural and cutover peatland: Implications for restoration. Biogeochemistry 54, 115–130.

Wang, M., Moore, T.R., 2014a. Carbon, Nitrogen, Phosphorus, and Potassium Stoichiometry in an Ombrotrophic Peatland Reflects Plant Functional Type. Ecosystems 17, 673–684. doi:10.1007/s10021-014-9752-x

Wang, M., Moore, T.R., Talbot, J., Richard, P.J.H., 2014. The cascade of C:N:P stoichiometry in an ombrotrophic peatland: from plants to peat. Environmental Research Letters 9, 024003. doi:10.1088/1748-9326/9/2/024003

Wang, X., Li, X., Hu, Y., Lv, J., Sun, J., Li, Z., Wu, Z., 2010. Effect of temperature and moisture on soil organic carbon mineralization of predominantly permafrost peatland in the Great Hing'an Mountains, Northeastern China. Journal of Environmental Sciences 22, 1057–1066.

Wells, E.D., Williams, B.L., 1996. Effects of drainage, tilling and PK-fertilization on bulk density, total N, P, K, Ca and Fe and net N-mineralization in two peatland forestry sites in Newfoundland, Canada. Forest Ecology and Management 84, 97–108. doi:10.1016/0378-1127(96)03741-3

Wright, A.L., Reddy, K.R., 2007. Substrate-Induced Respiration for Phosphorus-Enriched and Oligotrophic Peat Soils in an Everglades Wetland. Soil Science Society of America Journal 71, 1579–1583. doi:10.2136/sssaj2007.0095

Wüst-Galley, C., Mössinger, E., Leifeld, J., 2016. Loss of the soil carbon storage function of drained forested peatlands. Mires and Peat 1–22. doi:10.19189/MaP.2015.OMB.189

Zhang, Z., Xue, Z., Lyu, X., Tong, S., Jiang, M., 2017. Scaling of soil carbon, nitrogen, phosphorus and C:N:P ratio patterns in peatlands of China. Chinese Geographical Science 27, 507–515. doi:10.1007/s11769-017-0884-8

Zimmermann, M., Meir, P., Bird, M.I., Malhi, Y., Ccahuana, A.J.Q., 2009. Climate dependence of heterotrophic soil respiration from a soil-translocation experiment along a 3000 m tropical forest altitudinal gradient. European Journal of Soil Science 60, 895–906. doi:10.1111/j.1365-2389.2009.01175.x

Figure

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 1: Aerial photo of Flanders Moss National Nature Reserve with the three different sampling sites marked with different colours, indicating the former land uses (blue = control site; red = drained site; green = drained and afforested site) (Esri ArcMap 10.3.1).

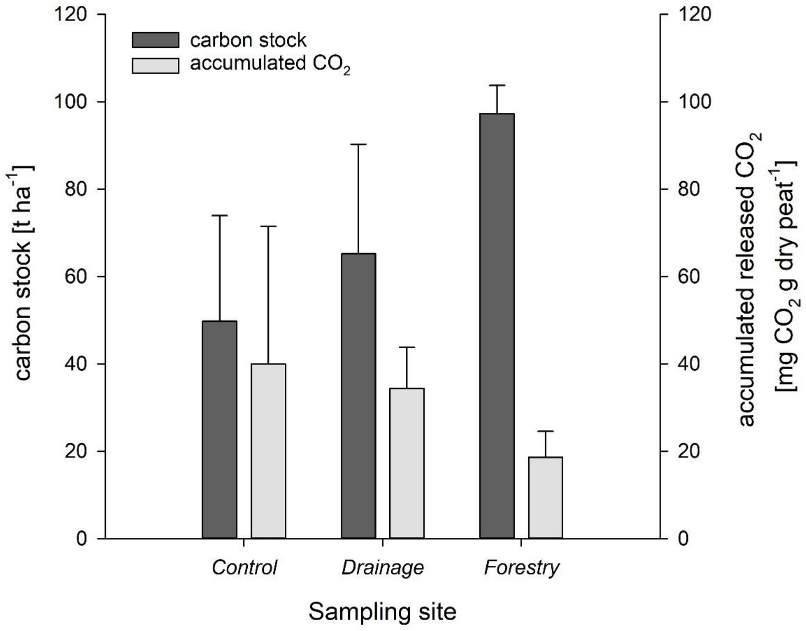

Figure 2: Comparison of the mean carbon stock [n=3] and mean accumulated basal respiration of the topsoil (0-10 cm) [n=3] with standard deviation.

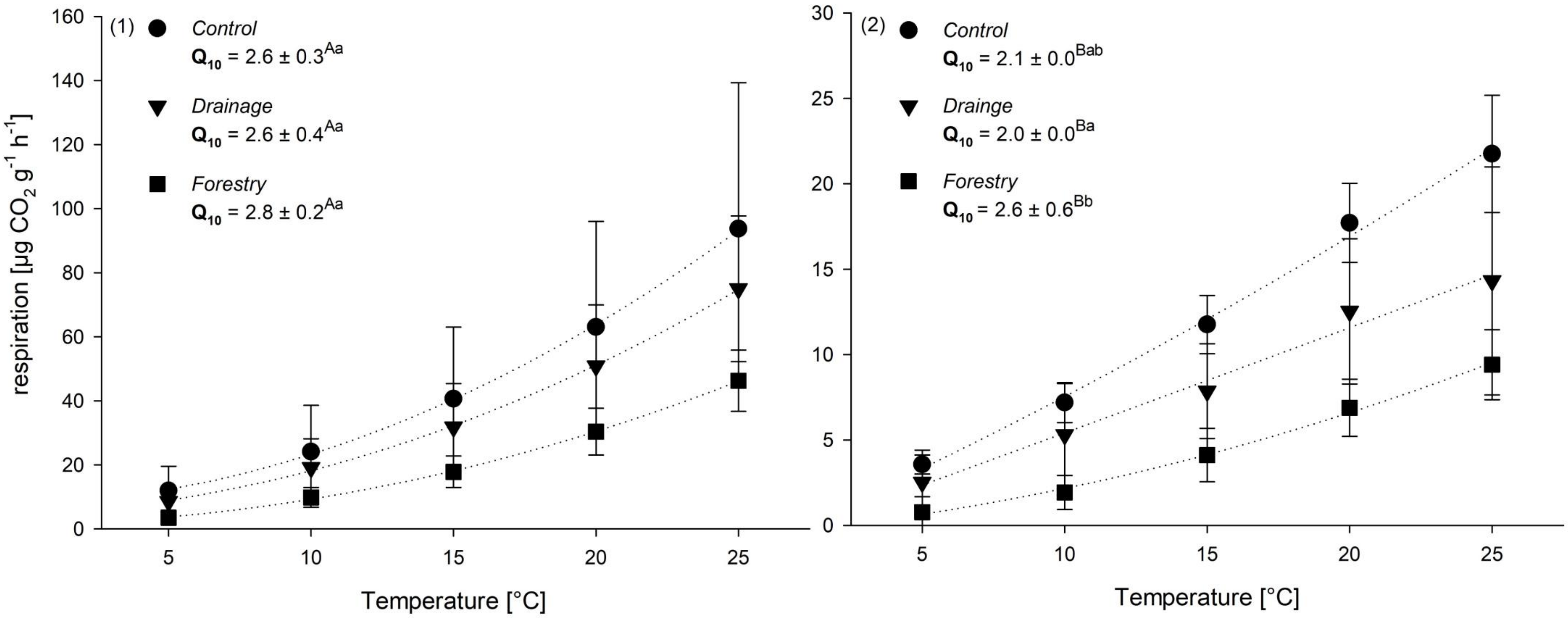

Figure 3: Mean hourly respiration per gram dry peat with increasing temperature of (1) the topsoil (0-10 cm) and (2) the subsoil (40-60 cm) with standard deviation and Q_{10} values (note the differences in y-axis scale). Significant differences ($p < 0.05$) in Q_{10} values between top- and subsoil are indicated by capital letter (^{A}, ^{B}) and between sites within one depth are indicated by lower case letters (^{a}, ^{b}).