Impact of forest-to-bog restoration on greenhouse gas fluxes

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Statement of originality

I hereby confirm that this PhD thesis is an original piece of work conducted independently by the undersigned and all work contained herein has not been submitted for any other degree.

All research material has been duly acknowledged and cited.

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Date:

Acknowledgements

General abstract

Large areas of northern peatlands have been drained and afforested in the second half of the 20th century with significant impacts on important ecosystem services, including loss of biodiversity and potential changes in C storage. A considerable effort is currently invested into restoring original peatland function and ecosystem services, with an increasing area of newly restored peatland areas over recent years. However, the effect of restoration on the greenhouse gas (GHG) budget is unknown. This study is the first quantification of CO_2, CH_4 and N_2O fluxes from forest-to-bog restoration sites spanning 0 to 17 years in age. Further, the impact of afforestation on peat decomposition is measured *in situ*, and the impact of afforestation on the biochemical composition of the peat in relation to CO_2 and CH_4 fluxes is investigated.

Results show that forest-to-bog restoration is successful from a GHG perspective, since all three major GHG fluxes of the restoration sites are changing along the chronosequence towards the fluxes from near pristine bog sites. The peat decomposition rate under the forest plantations is a big part of the total soil respiration at 126.8 ± 14.7 g C m^{-2} y^{-1} (44% of total soil CO_2 efflux) and our results indicate a slowing down of peat decomposition towards the near pristine bog. CH_4 fluxes increase with restoration age, whilst all sites remain a small sink for N_2O.

I observed changes in peat quality and nutrient availability in the pore water under forests. Different CO_2 fluxes between vegetation-free peat cores from different sites for the same temperature and water level show that these differences in peat quality and nutrient availability shape the biogeochemical processes in the peatlands. However only small differences in CH_4 fluxes between sites were evident, suggesting that on its own (and in absence of biotic interactions under field conditions), forestry effects on CH_4 flux are limited.

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1   Introduction

1.1   Importance of peatlands

Peat is defined as organic material that is accumulated under more or less waterlogged conditions and is made up of incompletely decomposed plant material (Rydin and Jeglum, 2006). The term "peatland", however, is not as uniformly defined. To be classified as a peatland, a peat-covered terrain has to generally show a minimum peat depth. In Canada the limit is 40 cm (National Wetlands Working Group, 1997), but in many countries it is 30 cm (Joosten and Clarke, 2002). In official UK mapping terms, this limit is 50 cm and the organic matter content in the upper 80 cm of the profile has to be over 50% (Avery, 1980). Although peatlands only cover about 3% of the Earth's surface (Joosten et al., 2012), they store about one third of the global soil carbon (C) (Joosten et al., 2012; Stocker et al., 2013), making them an important C store. As well as climate regulation through C sequestration, peatlands fulfil a number of other ecosystem services, including supporting unique biodiversity, regulating nutrients and water, preserving ecological and archaeological records and providing recreational spaces (De Groot et al., 2002).

Peatlands are commonly divided into ombrotrophic ("rain-fed") and minerotrophic ("mineral-fed") peatlands. Fens are minerotrophic; they are in contact with mineral-rich ground water. All ombrotrophic peatlands are bogs; they are isolated from mineral-soil-influenced ground water and are only fed by rain water, and are thus nutrient-poor (Rydin and Jeglum, 2006). Main vegetation groups on peatlands are bryophytes, graminoids and shrubs, but also trees may occur naturally in a range of peatland types. Bogs are diplotelmic, meaning that they can be divided in two layers: the catotelm and the acrotelm (Lindsay et al., 1988). The catotelm is the lower body of the compressed peat, which slows the water flow to such an extent that the peat remains saturated through precipitation alone. On top of the catotelm sits the acrotelm, which is a layer of about 10-50 cm (Figure 1.1). This layer protects the catotelm from external influences. The most active water movement is in this layer, and the vegetation and root mat are in here (Lindsay et al., 1988). However, in reality peatlands are structured in a more

complex way than this two-layer model. For example, the boundary between catotelm and acrotelm is not fixed over time, and the term 'mesotelm' has been used to describe the biogeochemical layer in which the water table fluctuates (Clymo and Bryant, 2008). The changing water table conditions in this zone have important implications for physical structure as well as biochemical conditions such as redox potential, which in turn strongly determines biological activity.
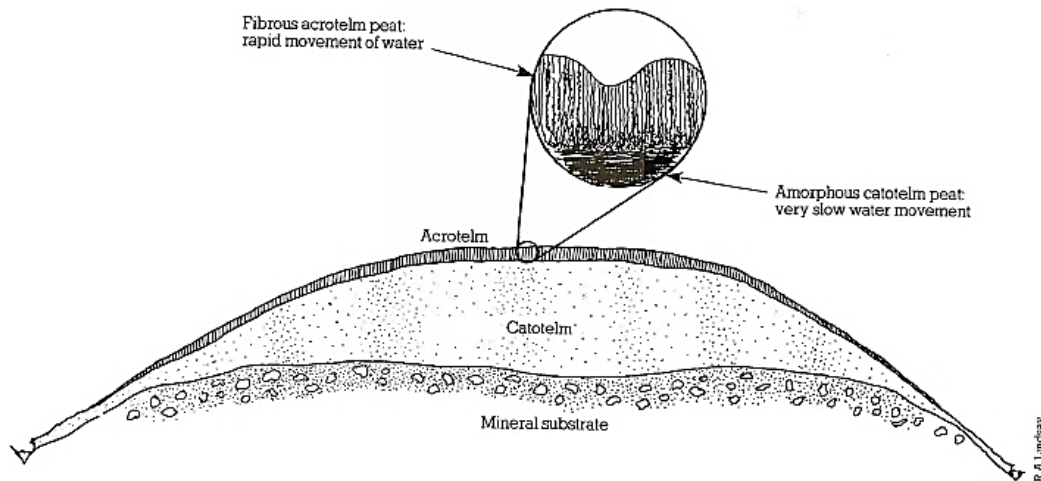
Figure 1.1 The 'diplotelmic' profile of a blanket bog, illustrating the change in detailed structure from the surface layer (acrotelm) to the underlying peat (catotelm). The vertical scale, particularly of the acrotelm, has been greatly exaggerated (diagram adapted from Lindsay et al. 1988).

1.2 Peatlands in the UK

In the UK the total area of peatland was estimated to cover 21,120 km^2, of which 82% was in Scotland (Cannell et al., 1993). This 17,270 km^2 in Scotland is 22% of the total land area (Figure 1.2; Chapman et al. 2009).

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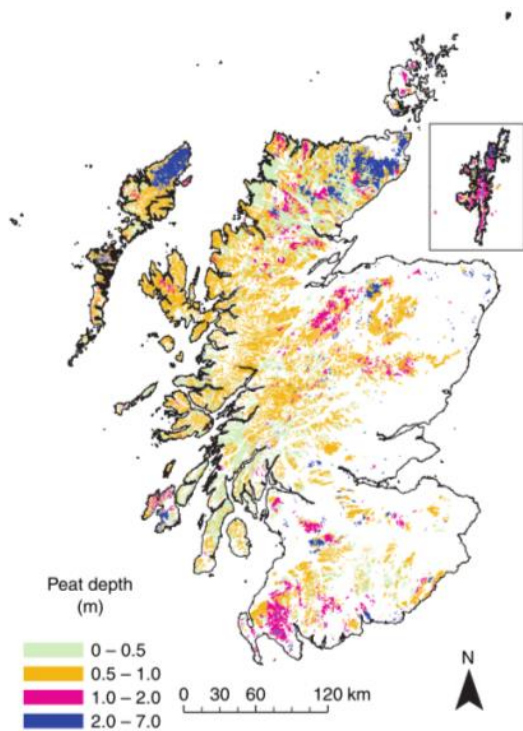
Figure 1.2 Average peat depth of peatlands in Scotland (adapted from Chapman et al., 2009).

The main type of peatland found in the UK is open bog. The dominant vegetation found are bryophytes, small-sedge species and dwarf shrubs, for which it is unusual to find any species that have a height of more than 50 cm. Bogs have distinctive micro topography, which can be split into five groups: hummocks, high ridges, low ridges, hollows and pools (Figure 1.3). Hummocks are mounds consisting of *Sphagnum* mosses, often with vascular plants. They can be up to 1 m high and 1-2 m in diameter. High ridges are characterised by a dominance of dwarf shrubs, mainly *Calluna vulgaris* in the UK. Low ridges are dominated by *Sphagnum* species, commonly *Sphagnum tenellum, Sphagnum magellanicum* and *Sphagnum papillosum.* A 'carpet' of *Sphagnum* is present in the hollows, particularly with *Sphagnum cuspidatum* in the UK (Lindsay et al., 1988). An abundant occurrence of sedges, herbs and trees in the bogs can be attributed to some kind of disturbance (Lindsay, 1995).
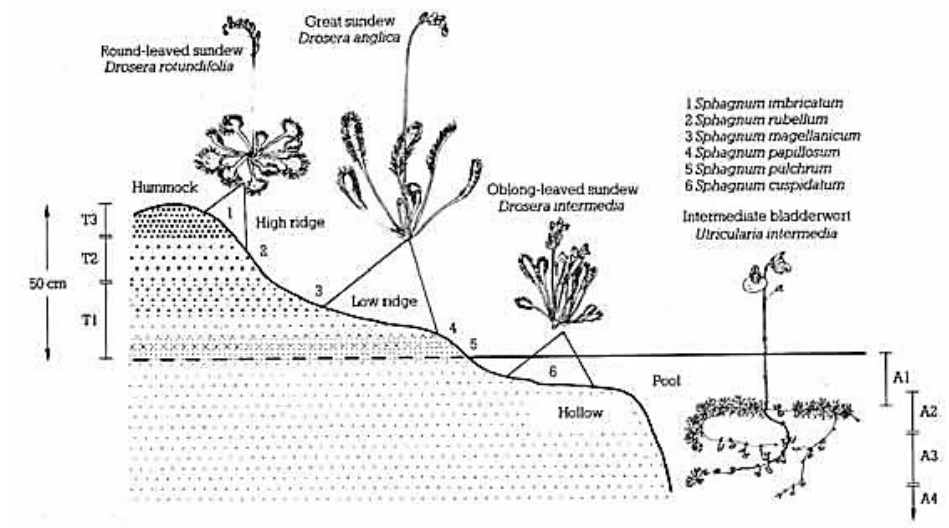
Figure 1.3 The zonation of vegetation types within the micro topography of a bog with illustration of some species of *Drosera* and *Sphagnum* (adapted from Lindsay et al. 1988).

Bogs in the UK can be split in two sub-categories: raised bogs and blanket bogs (Lindsay et al., 1988), which are both formed under cool, wet conditions. Raised bogs are usually isolated, dome shaped peat bodies (Lindsay, 1995), while blanket bogs can cover an entire landscape (Figure 1.4; Lindsay et al. 1988).

Figure 1.4 Near pristine blanket bog in the Flow Country, Scotland.

1.3 Peatland carbon cycle and greenhouse gas fluxes

Peatland vegetation takes up atmospheric CO_2 via photosynthesis, a part of which is fixed into biomass (Clymo and Reddaway, 1971; Loisel et al., 2012). When plants die, dead organic matter is deposited under both aerobic and anaerobic conditions. Aerobic decomposition of this organic matter by microorganisms produces CO_2. Under anaerobic conditions, the decomposition rate is extremely low, so that despite an also relatively low primary production, peatlands are a net C sink, evidenced by the presence of the accumulated peat layer. Under anaerobic conditions methane (CH_4) is produced by a specialized group of archaea in a process called methanogenesis (Zinder, 1993). CH_4 is a much stronger greenhouse gas (GHG) than CO_2; over a time span of 100 years, a mole of CH_4 has a potential to warm the atmosphere 28 - 34 times more than a mole of CO_2 (depending on the inclusion of climate-carbon feedbacks; (Stocker et al., 2013). CH_4 is produced from formate (HCO_2^-, hydrogenotrophy) or acetate ($CH_2CO_2^-$, acetoclasty) (Zinder, 1993), and is often correlated with plant productivity (Whiting and Chanton, 1993). Dorodnikov et al. (2011) showed with ^{14}C labelling strong evidence to suggest that CH_4 production is powered by recent plant photosynthate via root exudate in the rhizosphere. This is in line with earlier findings that CH_4 is only produced when there is plenty of labile carbon available (Couwenberg, 2009) and old (recalcitrant) carbon plays a minor role (Clymo and Bryant, 2008).

In an aerobic environment CH_4 can be oxidized and released to the atmosphere as CO_2, when this is done by microbes this process is called methanotrophy (Bridgham et al., 2012). Also anaerobic methane oxidation (AMO) can take place in peatlands. There is evidence to suggest AMO could potentially have an important role in peatland ecosystems (Blazewicz et al., 2012; Gauthier et al., 2015; Gupta et al., 2013; Smemo and Yavitt, 2007), but much about the process is still unknown (Smemo and Yavitt, 2011). In marine sediments AMO is linked to microbial sulphate reduction, denitrification, and Iron/Manganese reduction (Reeburgh and Heggie, 1977; Valentine, 2001). AMO seems to be influenced by the availability of CH_4 and the frequency of anaerobic conditions (Blazewicz et al., 2012). Whether methane is oxidised aerobically or anaerobically, the CH_4 flux

measured from a peatland surface is the balance between total CH_4 production and CH_4 oxidation within the peat profile.

There are various ways by which CH_4 can leave a peatland: 1) via diffusion from water surfaces or within air filled pores in peat, 2) via the formation and movement of CH_4 containing bubbles (ebullition), and 3) via plant mediated transport through the aerenchyma of vascular plants (Bridgham et al., 2012). Diffusion through soil pores could lead to oxidation of CH_4 in the aerobic peat layer by methanotrophic bacteria, but CH_4 transported by plants bypasses the aerobic layer and thus prevents oxidation. Similarly, ebullition bubbles rise quickly to the surface, which also leads to little oxidation (Schuldt et al., 2013). The presence of certain vascular plants (e.g. *Eriophorum vaginatum*) can therefore have a big impact on net CH_4 fluxes. Furthermore, exudations of labile compounds from vascular plant roots act as substrate for methanogens and thus stimulate CH_4 production (Ström et al., 2003).

Aquatic C plays an important role in the C cycle of peatlands and the main component is dissolved organic carbon (DOC). This is the soluble product of organic matter decomposition (Moore, 1997) and accumulates in the pore water in the peat, it is then transported by water movement into streams (Billett et al., 2006; Fraser et al., 2001). Furthermore, runoff water can also take up DOC by interacting with the vegetation and surface peat (Proctor, 2006). Part of the DOC is broken up by microbial and photochemical pathways (by absorption of solar radiation) and released to the atmosphere as CO_2 (Cory et al., 2014; Pickard et al., 2017; Tranvik et al., 2009).

Another GHG that can be emitted from peatlands is nitrous oxide (N_2O). It is not directly linked to the C cycle, but it can be an important component in peatland fluxes. Mole per mole, N_2O is an even stronger GHG than CH_4 with a warming potential of between 265 and 298 times that of CO_2 over a 100 year time span (Stocker et al., 2013). N_2O is produced by microbial processes, under both aerobic (nitrification) and anaerobic (denitrification) conditions (Davidson and Schimel, 1994). However, in highly anaerobic conditions, denitrification can take up N_2O from the atmosphere (Huttunen et al., 2003). Denitrification in peatlands is often

limited by the lack of nitrate (Verhoeven, 1986), whilst nitrification is limited by low oxygen content (Goreau et al., 1980) and low pH (Rosswall and Granhall, 1980). However nitrifying bacteria that are adapted to low pH have been found in a drained peatland (Lang et al., 1993). All described GHG and DOC pathways are visualised in Figure 1.5.
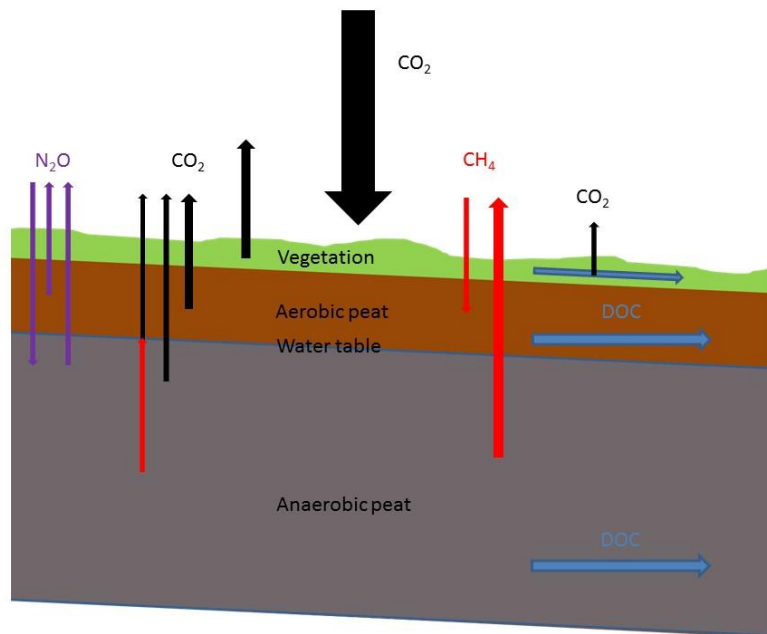
Figure 1.5 Schematic of simplified peatland greenhouse gas exchange and DOC transport, showing inputs, transport and outputs. Living vegetation is shown in green, aerobic peat layer is shown in brown, anaerobic peat layer is shown in grey. CO_2 fluxes are shown in black arrows, CH_4 in red arrows, N_2O in purple and DOC in blue arrows. Where the red arrow goes over into the black arrow, CH_4 is oxidised into CO_2. See text for detail on processes and transport.

1.4 Peatland management and impacts

Many peatlands worldwide have been degraded; in 2009, 15% of the world's peatlands had been drained for agriculture, livestock, peat mining and forestry purposes (Joosten, 2009). There are also concerns that due to climate change some peatlands will dry out (Rowson et al., 2010). Combined with emissions from peat fires, drained peatlands account for almost 6% of global anthropogenic CO_2 emissions, despite only covering 0.3% of the world's land cover (Joosten, 2009). Drainage of peatlands influences the hydrology, which could lead to changes in

the production and consumption processes and fluxes of GHGs. When lowering the water table, aeration is enhanced, peat pores become air filled and cracks could appear in the peat (Lindsay, 2010). This could lead to an increase in decomposition of litter and peat (Clymo, 1984), an increase in mineralisation of nitrogen (Freeman et al., 1996) and net methane emissions could be reduced or completely stopped. In general, drainage will stimulate the growth of vascular plants and reduce the growth of bog mosses (Limpens et al., 2008).

1.4.1   *Afforested peatlands*

Historically in the UK, peatlands were considered to be "unproductive wastelands" (Alan and Macdońald, 1945) and attempts were made to modify them in order to increase their productivity; i.e. their capacity to provide food or fuel for human consumption. The technical ability to plough peatlands to a depth that allowed effective drainage enabled other land uses to derive economic benefit from peatlands, including afforestation with non-native conifers (Lindsay et al., 1988). This has resulted in large areas of northern peatlands being drained and afforested in the 20th century (Huttunen et al., 2003).

In many northern European countries, where peatlands have a naturally sparse and open tree cover, forestry on peat was encouraged by widely spaced drainage which led to these naturally tree covered peatlands to become more productive. In the UK, where the peatlands are naturally largely treeless (Charman, 1994), the ploughing of the peat typically results in a micro topography of closely spaced furrows within a few metres of each other. The peat that is removed during ploughing is pushed up on both sides of the furrow, creating two plough throws. Immediately after ploughing, these are typically up to 50 cm in height, but gradual collapse and oxidation result in reduction of this height over time. In between two plough throws, there could be some original surface left, depending on how widely furrows were spaced or how deep the furrows were ploughed. Trees are usually planted on the plough throws, since these are the driest (Figure 1.6). In addition to the furrows, deeper, wider collector drainage ditches are ploughed, often perpendicular to furrows at intervals of hundreds of metres to collect water from the smaller ditches and furrows (Anderson et al., 2000).
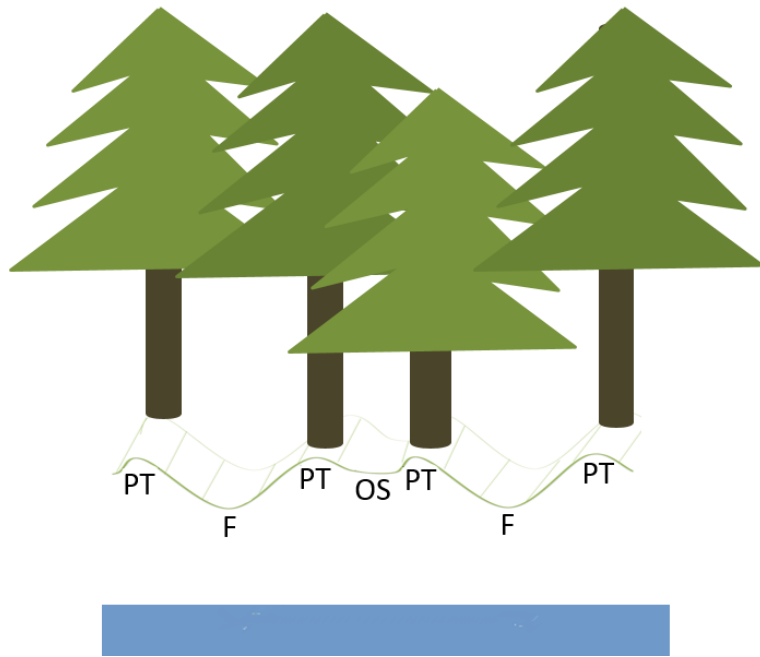
Figure 1.6 Schematic of micro topography of a ploughed and afforested peatland, PT= Plough throw, OS= Original surface and F= Furrow, blue is waterlogged peat.

Forestry plantations on deep peat have proved to be less productive than had been expected, and are now widely considered to have detrimental impacts on ecosystem services that outweigh economic benefits (Andersen et al., 2016). For example, afforestation leads to a loss of unique peatland biodiversity, both within the afforested part of the peat and on open natural peatlands adjacent to the forest plots (Wilson et al., 2014). Afforestation also alters the microbial community which control nutrient cycling (Creevy et al., 2018), and it is generally considered to also impact the GHG fluxes, because the water table is lowered due to deep ploughing and thus a deeper oxygen layer in the peat. Such changes in the decomposition processes have so far not been empirically demonstrated.

1.4.2   *Restored peatlands*

The aim of restoring peatlands is to re-establish peatland ecosystem services. Key measures to improve these ecosystem services in open unafforested peatlands usually include drain or ditch blocking (Armstrong et al., 2009; Holden and Armstrong, 2007) where artificial dams are created of plastic piling, peat or heather bails at intervals in the drains (Armstrong et al., 2009; Holden et al.,

2004). This results in a slowdown of the water flow, allowing the water table to rise and the peat to recover (Holden et al., 2004). Up to about 6 years ago, restoration of afforested, naturally open, peatlands was done by removal of trees, either by felling to waste (i.e. felling trees without removing round wood or harvest residues), harvesting logs, or mulching (Anderson et al., 2016; Hancock et al., 2014), together with drain blocking (Anderson, 2010). However, these limited measures resulted in poor or slow restoration progress and nowadays, due to improved funding options brought about by increased recognition of peatlands as a C store, more advanced restoration techniques are used. On top of the techniques used before, also furrow blocking, in-filling of furrows with plough throws and driving multiple times over the site to restore a more natural topography are executed (N. Cowie, RSPB Scotland, personal communication).

Increasing the water levels reduces peat oxidation, increasing the potential of peatlands to become C sinks again (Chapman et al., 2012). At the same time, CH_4 emission can also be enhanced by a higher water table (Dinsmore et al., 2008; MacDonald and Fowler, 1998), owing to the creation of more anaerobic conditions in peat (see above). Reduced peat aeration can further lead to a decrease in N mineralization and thus a decrease in N availability for plants (Urbanová et al., 2011). To be able to understand how the ecosystem functions and reacts to restoration the hydrology and soil processes together with vegetation structure and their interactions have to be considered (Urbanová et al., 2011). However, it is difficult to detect changes that are due to the restoration by measuring fluxes and processes before and after restoration, because of potentially extreme inter-annual variability. Therefore, the use of paired sites (restored and non-restored sites) under the same weather conditions enables a meaningful comparison. When comparing conditions or processes in paired sites, inter annual variability of climatic conditions provides opportunities for detecting changes caused by restoration. Hence, multiyear studies are important, since the differences between restored and non-restored sites could differ more in some years than others. For example sites could behave very similar in wet years, but be very different in dry years, since the restored site will be able to hold more water and thus stay wetter than the drained site (Bubier et al., 2005).

1.5 GHG fluxes from natural peatlands

It is important to know the GHG fluxes of natural peatlands, so the fluxes of restoration sites can be compared to the fluxes of natural sites in order to find out if restoration is a success from a GHG perspective. Several studies have been undertaken on the GHG fluxes of natural northern peatlands; below a summary is given.

1.5.1 _Carbon dioxide_

1.5.1.1 Net ecosystem fluxes

Saarnio, et al. (2007) performed a literature review on net CO_2 fluxes from pristine boreal ombrotrophic and minerotrophic peatlands. They found wide ranges in CO_2 flux values, indicating peatlands acting as both C sinks and sources; ombrotrophic peatlands range from -67 to +85 g C m^{-2} y^{-1}, with an average of 15 ±53 g C m^{-2} y^{-1} and minerotrophic peatlands range from -98 to +101 g C m^{-2} y^{-1}, with an average of -15 ±63 g C m^{-2} y^{-1} (note that throughout this thesis, gas fluxes have a positive sign when describing net fluxes from soil or vegetation to the atmosphere, and negative sign when describing an uptake from the atmosphere).

Missing in this literature review is a study on an Atlantic blanket bog in Ireland, where Laine et al. (2006) found a net ecosystem exchange (NEE) of -242 to -206 g CO_2 m^{-2} y^{-1}. Further, they found that the drier microforms were more effective CO_2 sinks due to higher C assimilation despite an overall higher respiration rate than in wet microforms. A near pristine blanket bog in the Flow Country, Scotland, was found to be a C sink of -114 g C m^{-2} y^{-1} averaged over 6 years (Levy and Gray, 2015).

Peatlands can thus act as a C source and sink and it is important to know what the NEE of (near) pristine peatlands close to restoration sites is in order to know what the "goal" regarding NEE is.

1.5.1.2 Ecosystem respiration fluxes

The processes behind C uptake by plants and ecosystem respiration (R_{eco}) are very different and thus are likely to have a dissimilar response to changing conditions (Cai et al., 2010); therefore it is useful to look at ecosystem respiration separately.

Salm et al. (2012) found a median soil CO_2 efflux of 150.9 g C m^{-2} y^{-1} in natural bogs in Estonia. The emissions correlated with soil temperature at different depths (0, 10, 20, 30 and 40 cm), and water level. Furthermore, soil temperature at 10 cm from the ground surface explained 68.9% of CO_2 flux.

Yamulki et al. (2013) found a clear seasonal trend, with CO_2 fluxes 4-5 times higher in the summer (May-September) than in winter in a raised bog in Scotland. The average annual flux (measured over 2 years) was 469.4 g C m^{-2} y^{-1}. They found a significant correlation with soil temperature, DOC/DON ratio and pH.

The respiration flux seems very variable as well, which is not surprising giving the variance in NEE for natural peatlands. To fully understand the processes behind GHG fluxes it is important to measure respiration separately.

1.5.2 Methane

Saarnio et al. (2007) also performed a literature review on CH_4 fluxes from ombrotrophic and minerotrophic pristine peatlands. The average flux was 5 ± 4 and 13 ± 10 g CH_4-C m^{-2} y^{-1} respectively, with fluxes ranging from 0.2 to 16.4, and 0.09 to 27.3 g CH_4-C m^{-2} y^{-1} in ombrotrophic and minerotrophic peatlands, respectively.

Not included in this literature review are the fluxes from a blanket bog in Scotland, (MacDonald and Fowler, 1998), which are between 0.16 and 13.5 g CH_4-C m^{-2} y^{-1}. Salm et al. (2012) found a median CH_4 flux of 8.5 g CH_4-C m^{-2} y^{-1} from natural bogs in Estonia, which correlated negatively with water table depth. Further, they found a weak but significant correlation with soil temperature at different depths and with air temperature. Yamulki et al. (2013) found a CH_4 flux of 16.9 g CH_4-C m^{-2} y^{-1} on a raised bog in central Scotland, but found a significant correlation only with soil temperature but not water table depth. Forbrich et al.

(2011) looked at the effect of microforms on the CH_4 flux in an oligotrophic peat complex in Eastern Finland with a flux range from 1.5 ± 1 to 8.9 ± 2.9 mg CH_4 m^{-2} h^{-1}. The highest seasonal variation occurred in the hollows, followed by ridges and then hummocks. Their results are in line with the results from Laine et al. (2006) who found large spatial variation in CH_4 fluxes on a blanket bog in Ireland, with an area-weighted flux of 4.6 g CH_4-C m^{-2} y^{-1}.

A separate literature review (87 studies, from 186 sites) of CH_4 fluxes from northern peatlands by Abdalla et al. (2016) found annual average values of 12 ± 21 g CH_4-C m^{-2} y^{-1}. However, the fluxes were found to be highly variable with a 95% confidence interval of 7.6-15.7 g CH_4-C m^{-2} y^{-1} for the mean and 3.3-6.3 g CH_4-C m^{-2} y^{-1} for the median. The highest emissions where found in fens, and main controllers for CH_4 fluxes were identified to be water table depth, plant community composition and soil pH. Air temperature was not found to be good predictor by itself, but in an interaction with plant community, water table depth and soil pH it was (Abdalla et al., 2016).

The importance of vegetation for CO_2 and CH_4 emissions was also demonstrated by Chanton et al. (2008), who applied natural abundance radiocarbon approaches to determine C partitioning and dynamics in boreal peatlands. They showed that DOC is relatively young compared to the solid peat to a depth of 3 meters. In sedge dominated peatlands (e.g. fens), the ^{14}C content of the emitted CH_4 and CO_2 are both similar to the ^{14}C content of the DOC. However, in *Sphagnum* and woody plant dominated peatlands with few sedges (e.g. bogs), the ^{14}C content of the emitted CH_4 and CO_2 were intermediate between the ^{14}C content of the solid peat and the DOC. Therefore, it seems that CO_2 and CH_4 emissions mainly originate from DOC in fens, whereas in bogs they come from both DOC and the solid peat.

1.5.3 *Nitrous oxide*

Several studies have been conducted on N_2O emissions from natural peatlands, all showing relatively low emissions, 0-0.1 g N_2O-N m^{-2} y^{-1}, and some ombrotrophic mires even show net N_2O consumption (Alm et al., 1999; Martikainen et al., 1995; Minkkinen et al., 2002; Nykänen et al., 1995; Regina et al., 1996).

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Yamulki et al. (2013) found N_2O fluxes of 0.03 g N_2O-N m^{-2} y^{-1} on a near pristine bog in Scotland. They did not find any seasonal patterns and no correlations with measured environmental variables were found. Martikainen et al. (1993) found much lower N_2O fluxes from an ombrotrophic bog in Finland, of less than 0.004 g N_2O-N m^{-2} y^{-1}. Similar results were found by Salm et al (2012) from pristine bogs in Estonia; 0.005 g N_2O-N m^{-2} y^{-1}.

1.6 GHG fluxes from drained and drained and afforested peatlands

1.6.1 *Carbon dioxide*

The improved aeration of drained peat could lead to an increase in decomposition of litter and peat (Clymo, 1984).

Strack et al. (2009) investigated the relationship between *Sphagnum* productivity and CO_2 emissions under extreme droughts by comparing a drained peatland with a natural one. They found a reduction in *Sphagnum* productivity when volumetric water content (VWC) was below 28%, as well as a reduction in the contribution to R_{eco} by Sphagna at drained sites. There was a decline in average seasonal R_{eco} when the water table dropped from 15 to 80 cm. R_{eco} increased when the water table dropped lower than 80 cm, but it stayed lower than the R_{eco} of the natural site. This reduction in R_{eco} is probably due to the fact that the labile C has been used up in the early season, so only the more recalcitrant substrates remain. On top of this is the water content at the surface probably below the optimal for microbial respiration. However all sites with a water table lower than 55 cm were on average a net source of CO_2 under full-light conditions, since *Sphagnum* mosses nearly ceased fixing CO_2 (Strack et al., 2009).

Lab-based studies have found higher CO_2 fluxes from peat soils with lower water table than from soils with high water table (e.g. Dinsmore et al. 2008; Estop-Aragonés et al. 2016; Blodau et al. 2004). However, Salm et al. (2012) did not find a significant correlation between water table depth and CO_2 emissions in the field.

The general view is that forestry-drained peatlands always turn into a C source (e.g. Couwenberg et al. 2011). However, Minkkinen and Laine (1998) and Ojanen et al. (2013) showed that even after afforestation and drainage of nutrient poor, but natural tree covered, peatlands, the soil can act as small C sinks. In fertile peatlands, soils may turn into a C source after drainage and afforestation, but because of the fast tree growth, the ecosystem stays a C sink. The main factors that control this balance were site fertility, water table, and temperature (Ojanen et al., 2013). A drained nutrient poor peatland forest (live tree stand biomass was 3.52 t of dry mass ha^{-1}) in southern Finland was also shown to be an overall C sink, with an NEE of -237.4 ±27.3 g C m^{-2} y^{-1} (Lohila et al., 2011). Mäkiranta et al. (2007) and Lohila et al. (2007) found overall a 30-year old Scots Pine forest on drained bog to be a small source of CO_2 (50 g C m^{-2} y^{-1}). Yamulki et al. (2013) showed that CO_2 fluxes from soil and understorey vegetation in a raised bog increased by 35% due to drainage and afforestation, from 335.7 g C m^{-2} y^{-1} in undrained and planted areas to 453 g C m^{-2} y^{-1} in drained and planted areas. However, they did not find a significant difference between the flux from soil and understorey vegetation from drained and planted areas and the ecosystem flux near pristine peatland.

Hargreaves et al. (2003) conducted a C balance study over a chronosequence of afforested peatlands. They concluded that during the first nine years an afforested peatland was a C source with a total C loss of ~9000 g C m^{-2}, but by the age of 26 the plantations accumulated C, with a total of -5420 g C m^{-2}. When averaging the peat loss over a 60-year rotation they concluded that there may be no more than 100-200 g C m^{-2} y^{-1} lost. This together with the C uptake from the trees means that the system will take up more C than it will lose. Since also methane emissions were decreased to almost zero, because of the lowering of the water table, afforestation of peatlands can have a climate cooling effect. However, they concluded that most peatlands hold a lot more C than can be added by growing trees, since the peat layer can keep on growing and trees will die at a certain age, releasing the C back into the atmosphere. Therefore, whilst continued forestry can be carbon neutral as far as aboveground vegetation is concerned, net loss of soil C means that over time, these systems act as net C sources. They concluded that in

the long run afforestation of peatlands will have a climate warming effect (Cannell et al., 1993). However, Lindsay (2010) has highlighted some problems with their paper. First of all the undrained peatland they use as a baseline for their model is described by Billett et al. (2004) and Dinsmore et al. (2010) as extensively drained and subject to commercial peat mining. This could explain the low C accumulation rate found and has thus impacted their model. Further, they describe the 26 year old plantation as mature, with full canopy closure and with little ground vegetation, but this site is not mature yet and will not be felled until the trees are 60 years of age. Their model ends at 26 years and Lindsay (2010) has used the values of rate of peat loss established until then and made some general predictions of the likely course up to harvesting at 60 years. This results in much more peat lost, up to 700 g C m^{-2} y^{-1} by Year 60 under a steady increase in the rate of loss. The amount of peat lost over 60 years, would than result in no net C benefit from forestry and when C loss via DOC is taken into account it could result in even more C losses (Lindsay, 2010).

This shows that the response of CO_2 fluxes from drained and afforested peatlands can be very different, but in general drainage leads to in increased rate of peat decomposition. To understand fully what happens to the peat under these forest plantations, peat decomposition rate should be measured directly. In order to capture a complete CO_2 balance of drained and afforested peatlands a full rotation has to be measured/modelled.

1.6.2   *Methane*

Drainage of peatlands increases the aerobic layer in the peat (Schrier-Uijl et al., 2010) leading to lower CH_4 fluxes. This is partly because of a lower C input in the methanogenic anaerobic layer (Basiliko et al., 2003; Bergman et al., 1998, 2000) and partly because CH_4 oxidation is increased (Holden, 2005; Sundh et al., 2000).

Several lab peat incubation studies have found lower CH_4 fluxes in low water table treatments than in high water table treatments (Dinsmore et al., 2008; MacDonald and Fowler, 1998; Moore and Dalva, 1993). In northern drained bogs, fluxes range from -0.22 – 7.43 g CH_4-C m^{-2} y^{-1} and in drained fens fluxes range

from -0.91 – 3.54 g CH_4-C m^{-2} y^{-1}, which is lower than from pristine northern peatlands (Salm et al., 2009). In a big literature review drainage was found to significantly reduce CH_4 fluxes in peatlands, on average by 84% (Abdalla et al., 2016).

Minkkinen et al. (2007) showed that in forested peatlands with effective drainage the soil took up CH_4 at a rate of up to 1 g m^{-2} y^{-1}. However, Minkkinen and Laine (2006) estimated that the waterlogged ditches in a forest emit as much or even more CH_4 as is consumed by the rest of the forest. This would mean that most drained afforested peatlands are small sources of CH_4. This is in line with Salm et al. (2012), who found a median CH_4 flux of 2.4 g CH_4-C m^{-2} y^{-1}. There was a negative correlation between CH_4 flux and water table depth, and a significant correlation with soil temperature above 10º C. Additionally there was a weak but significant correlation with soil and air temperature.

Yamulki et al (2013) also found a drained and afforested site to still be a small source of CH_4; 0.11 g CH_4-C m^{-2} y^{-1}. However this was a four time reduction from the undrained and planted site CH_4 flux; 0.48 g CH_4-C m^{-2} y^{-1}, which had a water table depth twice as high as the drained site. CO_2 emissions went up by 35% due to drainage, and the conclusion of the study was that the increase in CO_2 flux outweighed the decrease in CH_4 flux.

In general, therefore, drainage and afforestation leads to a reduction in CH_4 flux, but it is site specific if the net CH_4 flux is positive or negative.

1.6.3 *Nitrous oxide*

Drainage could increase mineralisation of nitrogen (Freeman et al., 1996), leading to a higher N_2O flux. Salm et al. (2009) showed from a literature review on northern peatlands that N_2O fluxes significantly increase with drainage. Fluxes in drained bogs ranged from 0-0.08 g N_2O-N m^{-2} y^{-1} and from drained fens from 0-0.26 g N_2O-N m^{-2} y^{-1}. Drained peatlands in Estonia were found to emit 0.001 g N_2O-N m^{-2} y^{-1}, which is not significant different than what they found for natural peatlands. These emissions correlated negatively with water table depth, but there was no correlation with soil temperature (Salm et al., 2012).

Martikainen et al. (1993) showed that there was no effect of drainage and afforestation on N_2O fluxes of measured peat bogs in Finland, remaining at less than 0.004 g N_2O- N m^{-2} y^{-1}. However, there was a significantly increase in N_2O emissions of drained and afforested fens in Finland; up to 0.14 g N_2O-N m^{-2} y^{-1} (Martikainen et al., 1993). Regina et al. (1996) showed an increase in N_2O fluxes in both minerotrophic and ombrotrophic peatlands. Fluxes from a drained Spruce forest in southwest Sweden are 0.19 ± 0.067 g N_2O- N m^{-2} y^{-1} over a 6 year period (Holz et al., 2016).

This shows that the response of N_2O flux to drainage and afforestation is site specific, with reduced, increased and unchanged fluxes reported in the literature.

1.6.4   *GHG balance over a full forest rotation*

A few studies have looked at the total GHG balance over a full forest rotation; Hommeltenberg et al. (2014) have shown that an afforested drained bog in southern Germany is an overall GHG source of 134 kg C m^{-2} over 44 years. He et al (2016) have modelled the GHG balance of a Norway Spruce forest on a fen in southwest Sweden. They conclude that overall, the forest is a GHG source and when the biomass from the harvested trees is released back into the atmosphere this source becomes even bigger. The Spruce trees take up 413 g C m^{-2} y^{-1} and the peat is decomposed at rate of 399 g C m^{-2} y^{-1}, with N_2O emissions contributing a further 0.7 g N m^{-2} y^{-1}, which is equivalent to 76 g C m^{-2} y^{-1}. They have calculated that the forest takes up 16.0 kg C m^{-2} over 60 years and in this time 26.4 kg C m^{-2} is being emitted to the atmosphere as CO_2 and N_2O.

1.7   Restored peatlands

At this moment, there is only limited data available on long term monitoring of peatland restoration. Post restoration data shows that in a short time frame (2-5 years) water table levels can recover (Worrall et al., 2007), but vegetation restoration of the target mire species may take several decades to achieve (Lunt et al., 2010).

Rowson, et al. (2010) carried out a 2-year carbon budget study on a drained blanket peat bog, immediately after drain blocking. They found that the bog was a small net sink of CO_2 of -17.7 g C m^2 y^{-1} and 2 g CH_4-C m^{-2} y^{-1} was produced. However, when also taking dissolved organic carbon (DOC), particulate organic carbon (POC), and input of C from rainfall into account the peatland was found to be a net source of C.

In a review study, restored peatlands from forestry, cropping, grazing and mining together, from 13 different studies, showed on average an increase on CH_4 flux of 46%. However further statistical analysis did not find a significant difference between the fluxes from sites before and after restoration. This indicates that the different managed sites respond different to restoration and more data is needed to fully identify the changes in CH_4 fluxes (Abdalla et al., 2016).

Urbanova et al. (2011) investigated re-wetting effects on soils from three ombrotrophic (intact, drained and degraded) and two minerotrophic (intact and drained) peatlands in a lab study. They found no change in the phosphorus (P) (soluble reactive phosphorus) concentration in any soil, only in the drained fen the concentration of ammonium and dissolved organic nitrogen (DON) increased. DOC increased significantly in the drained fen and degraded bog, CO_2 production decreased and methane production and the number of methanogens increased in all soils.

On two forest-to-bog restoration sites in the north of Scotland, Hambley (2016) found that a site felled 11 years prior to measuring acted as a C source, with 80 g C m^{-2} y^{-1}. However a site felled 17 years prior to measuring, which was still partially drained (Hancock et al., in press), acted as a C sink of -71 g C m^{-2} y^{-1}. The difference in CO_2 fluxes between these two sites, was partly explained by the difference in soil moisture content, with the younger site being drier. These results show that at least in this example, restoration can be successful in changing these sites back to C stores and that long term measurements are important. However the older restoration site was still a smaller sink than a close by near pristine bog which was a C sink of -114 g C m^{-2} y^{-1} (Levy and Gray, 2015), and verification

across more sites and restoration ages is needed to assess the generality of the trends observed by Hambley (2016).

The recovery of bog vegetation following forest removal and raising of water tables forms an important aspect of peatland restoration work. This reestablishment of mainly mosses, but also sedges, rushes and shrub vegetation are partly responsible to soil moisture conditions, and thus represent an indicator of the progression of sites towards natural bog ecosystems. They also facilitate changes in ecosystem C assimilation and release, as well as potentially affecting the transport of methane from belowground via aerenchyma (see above). Hancock et al. (in press) found that in the first six years after the start of restoration (fell to waste of trees and blocking of collector drains, but not of furrows), vegetation underwent changes towards more bog-like species (e.g. *Sphagnum fallax, Sphagnum capillifolium* and *Eriophorum vaginatum*). However during the eight years after this the overall vegetation change stagnated, but the spatial differences increased, with vegetation in drier and wetter areas moving in different successional directions. They concluded that their findings indicate that whilst the overall moisture levels have recovered, higher, drier areas left after the restoration process ceased to develop towards bog vegetation, and proposed additional management to reduce topographic artefacts from forest removal and drain blocking in these areas is required. They also found that slope impacted the recovery rate of vegetation with flatter areas showing a good development of bog vegetation, whereas sloping ground had an increased frequency of dry indicator species. They concluded that as well as blocking of collector drains, it would be recommended to block the furrows too to bring water tables closer to the surface.

Results from restoration in a forestry drained ombrotrophic bog and a forestry drained minerotrophic fen in Finland found that after ten years the mineral element concentrations (Ca, K, Mg, Mn, and P) of the peat were the same as reported in pristine peatlands (Haapalehto et al., 2011). The increase of K and Mn concentrations show in particular the recovery of the functionality of the ecosystem regarding the nutrient cycling between peat and plants. On both sites, plant communities changed to peatland vegetation of wetter conditions, but many typical species of pristine peatlands were still missing. This is in line with results

reported by Jauhiainen et al. (2002), who found no clear change of vegetation species on the hollows on a restored bog after three years, but on intermediate ridges, species composition was identical to that found in hollows of pristine bogs.

1.8 Flux measurement techniques

Net fluxes of CO_2, CH_4 and N_2O to the atmosphere can either be measured on ecosystem scale, using the eddy covariance (EC) technique, or on small scale, using chambers.

With the chamber technique, small scale variation within an ecosystem and measurements at the process level can be carried out (Griffis et al., 2000), which is very important in a peatland since these consist of hummocks, ridges and hollows (Figure 1.3).

Usually collars are inserted into the soil to a depth of 2-5 cm. During measurement events, chambers are fitted onto these collars with a gas-tight seal for about 2–60 minutes, depending on which gasses are measured and what kind of chambers are being used (Smith and Conen, 2004). During this time the change in concentration of the target gas can be measured, either directly with a gas analyser (closed dynamic chambers), or by taking gas samples over a certain time span (closed static chambers) (Heinemeyer and McNamara, 2011).

When measuring from chambers it is important to make sure that the seal between the collar and soil is maintained. If the seal is not maintained leakage could occur, which could affect the measured fluxes. Leakage depends on the porosity of the soil and the moisture content; leakage is less when the moisture content is high, like for example in peatlands (Heinemeyer and McNamara, 2011). Further, a difference in pressure can occur between the chamber and the atmosphere, since gas is taken out. This can simply be addressed by installing a venting tube (Davidson et al., 2002). Davidson et al. (2002) found that a pressure difference of ±0.1 Pa between the inside and the outside of a chamber caused an error of about 15% in the measured CO_2 flux. Also temperature changes of the soil and air beneath the chamber can occur, which needs to be minimised, e.g. by insulating the chamber thermally (Wagner and Reicosky, 1992). After closing the chamber,

forced external advection and turbulence is prevented, which modifies diffusion resistance of the plant-atmosphere boundary layer. Use of fans inside the chamber can aid mixing within the chamber space, and reduce boundary layers on soil and vegetation surfaces (Denmead and Reicosky, 2003; Hutchinson et al., 2000).

Chamber measurements usually do not measure CH_4 lost via ebullition (Baird et al., 2009). Ebullition bubbles rise quickly from below the water to the surface (Schuldt et al., 2013). This loss can be a steady stream or the bubbles may accumulate and form pockets of gas, which are lost episodically. When a chamber is positioned over a location with a steady stream of ebullition, this will give accurate results since the concentration increases linearly over time. However, the chances of placing a chamber over a location like this are not that big, so when up scaling fluxes to ecosystem level there is a chance of under estimating the fluxes. If ebullition is non-steady, the increase in concentration could be erratic, which could result in a large error in the calculated flux. Ebullition is non-random, with increases in water table and falls in atmospheric pressure being triggers (Strack et al., 2005; Tokida et al., 2007). Commonly, non-chamber based approaches such as floating mat-records and hydraulic heads are used to measure ebullition (Fechner-Levy and Hemond, 1996; Rosenberry et al., 2003), or continuous flux measurements either with EC or with frequent (automated) chamber measurements (Goodrich et al., 2011).

The EC method is useful to measure continuous fluxes on the ecosystem scale (Baldocchi, 2003) over a fairly homogeneous area (Baldocchi et al., 2001). With the EC technique vertical wind speeds and gas concentrations are measured with instruments mounted on a so-called flux tower (Denmead, 2008; Finnigan et al., 2003).

One of the challenges with the EC technique is that it is not always clear where measured fluxes originate. The footprint, i.e. the upwind source area of the flux (Schuepp et al., 1990), is usually estimated with analytical or Langrangian stochastic models (Laine et al., 2006).

Chamber measurements have clear advantages when complex surface conditions mean that assumptions underlying the EC method are violated. This advantage of

greater resolution of spatial heterogeneity by chambers is balanced by the advantages of EC methods in integrating fluxes over space and time, enabling better up-scaling of flux values (Laine et al., 2006). Forbich et al. (2011) compared EC fluxes and closed chamber fluxes from an oligotrophic peatland. They showed that fluxes from the closed chambers had strong within microform variability, but that seasonal trends were similar to the EC data. Laine et al. (2006) also compared the EC and closed chamber fluxes from an Atlantic blanket bog in Ireland. Their data shows a similar agreement for the seasonal trend as Forbich et al. (2011), but less agreement between the two techniques over short (half hour, day) time periods. Further, there was less agreement during the winter than during the summer. In a subarctic mire in Finland, static chamber measurements from different microtopographical areas and drier ecosystems in the landscape, like lichen heath and mountain birch forest, where up-scaled using a high-resolution land cover map and compared to EC measurements. The results from both techniques were in strong agreement (Hartley et al., 2015).

So both techniques have their advantages and disadvantages and it depends on what the main goal of the research is, which technique is most suitable to use.

1.9 Regional focus of this thesis

The Flow Country, in the north of Scotland, holds the largest continuous blanket peat bog of Europe and possibly the world (Figure 1.7). Together with some more scattered areas in west Sutherland the total area of blanket bog is 4000 km^2 (Lindsay et al., 1988). These moorlands are of unique importance in Britain for birds (Avery and Leslie, 1990), with important breeding populations of golden plover, dunlin, greenshank, common scoter and both red- and black-throated divers.
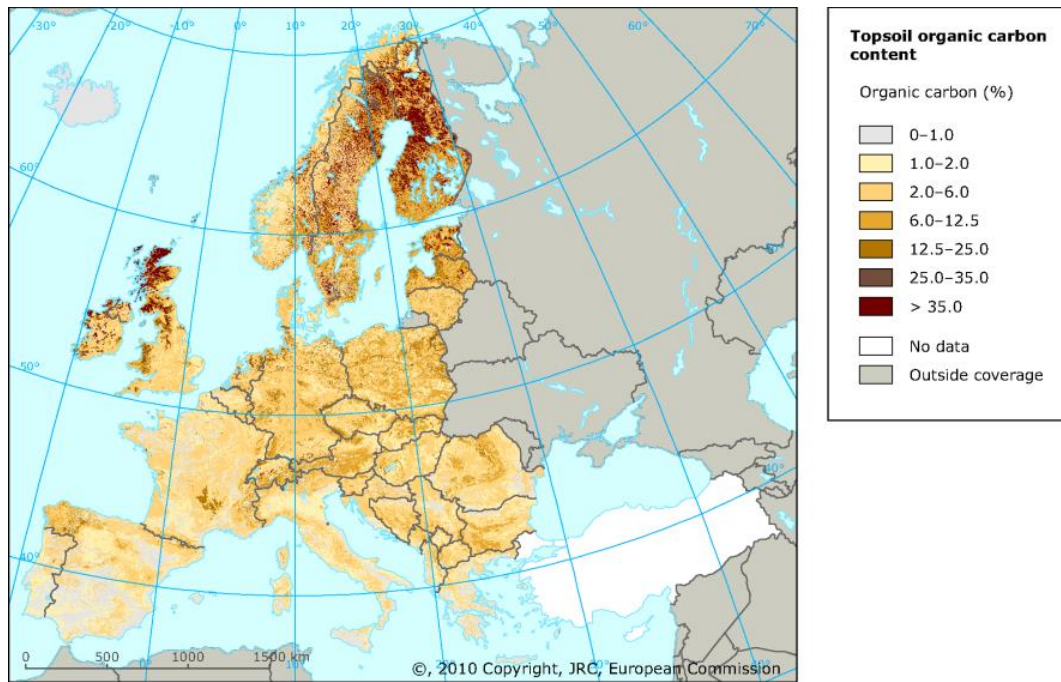
Figure 1.7 The map shows the percentage of organic carbon content in the surface horizon of soils in Europe. The darker regions correspond to soils with high values of organic carbon, with the darkest colours representing peatlands (Joint Research center, European Environment Agency, 2010).

Big parts of the blanket bog were afforested with non-native trees, mainly Sitka Spruce (*Picea sitchensis*) and Lodgepole Pine (*Pinus contorta*), in the 1980s (Lindsay et al., 1988) (Figure 1.8 and Figure 1.9). New forestry ploughing technology made it possible to plough the deep, wet peat for the first time, together with the use of *Pinus contorta* as a nurse crop for *Picea sitchensis*, this was a breakthrough in silviculture (Avery and Leslie, 1990). Combined with tax benefits to make forestry attractive, 67,000 ha, almost 17% of the total peatland area, was afforested (Rydin and Jeglum, 2006). This gave a big boost to the local employment and it helped towards the fulfilment of the government's tree planting target of 33,000 ha per year (Warren, 2000). However the forests are threatening the survival of the moorland breeding birds and at the same time providing good habitat for predators such crows and foxes (Bainbridge et al., 1987).

Figure 1.8 Geographical context of the forest plantations in the red box, in the north of Scotland as shown in Figure 1.9 (Gorelick et al., 2017).

Figure 1.9 Pictures of the appearance and disappearance of the forest plantations in the north of Scotland as seen from space. Pictures are zoomed in on the red square on the picture in Figure 1.8. The first picture is from 1984, where the first few forest plantations are vaguely visible. The second picture is from 1997, when most forest plantations (in dark green) were present. The third picture is from 2016 where large areas of forest have been felled (Gorelick et al., 2017).

With the end of the tax benefits, large scale planting stopped in the late 1980s and a programme to appoint Sites of Special Scientific Interest (SSSIs) began. From the late 1990s onwards, the Royal Society for the Protection of Birds (RSPB) started to restore parts of the peatland to recreate the habitat for native peatland birds. In the UK afforested peatland restoration is also being carried out by wind farm developers (Scottish Power Renewables, 2015) and the Forestry Commission (Anderson, 2010). This has resulted in large afforested blanket bog areas being restored back to open blanket bogs. Since 2000, forest-to-bog restoration was conducted at a rate of 500 ha per year, in the UK (Anderson et al., 2016). Key measures of peatland restoration from forestry include felling of trees and blocking of drains. Since the RSPB started with the restorations in the north of Scotland, the recognition of peatlands as important ecosystems for storing C, and their significance as C sinks in the context of climate change has increased. The peat bogs in Scotland contain about 1620 Mt of carbon (Chapman et al., 2009). Understanding the impact of restoration on the greenhouse gas balance, both in the short and long term, remain under-researched. Given a continued effort to restore more peatland areas, both in the UK and world-wide, there is a clear need to obtain robust estimates of these impacts, which could then inform management methods and restoration policy (e.g. Scottish Government 2016).

1.10 Research aims

The above sections highlighted some clear knowledge gaps in our understanding of the effect of both afforestation of peatlands and forest-to-bog restoration, which need to be addressed. Therefore the aims of this study are to quantify the GHG fluxes on both the short and long term from forest-to-bog restoration sites, to quantify peat decomposition under forest plantations on peat and to understand how peatland afforestation changes the peat quality and its effect on the response of CO_2 and CH_4 fluxes to a rise in water table under similar climatic conditions. These aims are addressed in separate chapters of this thesis:

1. **A study of greenhouse gas fluxes during blanket peat bog restoration from forestry plantations**

To understand the impacts of forest-to-bog restoration on greenhouse gas fluxes CO_2, CH_4 and N_2O fluxes were measured from sites undergoing restoration. Both the short term (months) and long term (years) effects have been investigated. Further environmental variables (soil moisture, soil temperature, vegetation, and micro-topography) were measured, to try to explain the changes in GHG fluxes. I hypothesised that the forest plantation soils have the highest CO_2 and N_2O fluxes, due to the drainage and hence aeration of peat. By contrast, I expected that intact bogs have significantly reduced CO_2 flux to the atmosphere, but higher net CH_4 flux to the atmosphere. For sites that are undergoing forest-to-bog restoration, I expected initially high fluxes of CO_2 to the atmosphere following soil disturbance during restoration. After this, my expectation is that soil respiration fluxes from restoration sites will become increasingly similar to undisturbed peatlands. Further, we expect CO_2 and N_2O fluxes to be mainly driven by soil temperature and CH_4 fluxes mainly by soil moisture and vegetation.

2. **Separating autotrophic and heterotrophic soil CO_2 effluxes in afforested peatlands**

The peat soils under the forest plantations are very important as long-term C stores and this could be compromised by the combined effect of drainage and afforestation. In order to understand how much peat is being lost, direct measurements of the peat decomposition rate have to be made and this is missing from literature. I have conducted a study in which I have separated the soil CO_2 flux into autotrophic (e.g. living plant material) and heterotrophic (e.g. bacteria and fungi) components. I hypothesised that 1) autotrophic respiration has a significant contribution to the total soil C flux, 2) the CO_2 flux from litter decomposition is minimal and 3) interactions between C supply to the rhizosphere by trees result in higher decomposition rates of litter.

3. **An incubation study of the GHG flux responses to a changing water table linked to biochemical parameters across a peatland restoration chronosequence**

Drainage and afforestation has likely changed the biochemical composition of the peat. Due to this the peat soils of different forest-to-bog restoration ages, forest plantation and near pristine bog are likely to respond differently to an increase in water table. In this chapter, I tried to understand how the changes in composition of peat following forest removal respond to a water table rise and investigate how this may be linked to GHG fluxes. I hypothesized that: 1) sites with different vegetation types (determined by time since restoration), show differences in biochemical composition of soil organic matter (SOM), 2) this difference in biochemical composition of the SOM will lead to different GHG fluxes under the same climatic conditions, and 3) the timing (in years post felling) of a rise in water table matters; different restoration ages will respond differently to this rise. Another goal is to determine whether there are generic environmental predictors or site-specific factors of GHG production linked to vegetation cover history under restored peatlands. In this context, being able to understand if there are generic controls is important, as it enables a prediction of fluxes based on more generic information.

2 A study of greenhouse gas fluxes during blanket peat bog restoration from forestry plantations

2.1 Abstract

Large areas of northern peatlands have been drained and afforested in the 20th century. Since the end of the 1990s, a considerable amount of these forest plantations have been felled and drains are blocked in order to restore them back to open peatlands. The impact of these restoration efforts on the greenhouse gas fluxes was unknown until now. We have measured the effects of restoration both on the short (months) and long term (years) by measuring soil CO_2, CH_4 and N_2O fluxes from a chronosequence of restoration sites (0-17 years) in the Flow Country, Scotland. Short term (up to 1.5 years post felling) results show that the CO_2 flux from the driest microform is significantly lower in the felled sites than in the forest plantation and bog control sites, with no further significant differences between microforms. However, some extremely high flux values of CH_4 are observed in the summer following forest removal, which seems to settle back in the second summer post felling and are completely back to average CH_4 fluxes several years post felling. There were no differences found in the CO_2 flux between the long-term restoration sites, near pristine bog control and forest plantation control sites, mean flux over all these sites was 2.27 ±0.079 µmol m^{-2} s^{-1}. However we hypothesise that in the older restoration sites a bigger part of the respiration flux is from plant respiration than from peat respiration compared to the younger restoration sites, since there is more vegetation present in the older restoration sites. Forest soils were weak sinks of CH_4 for part of the season (mean -1.27 ±3.09 nmol m^{-2} s^{-1}), and net CH_4 flux to the atmosphere increased with restoration age, being highest in the near pristine bog (mean 11.83 ±2.83 nmol m^{-2} s^{-1}). N_2O flux is similar over all sites with a mean uptake of -0.17 ±0.028 nmol m^{-2} s^{-1} over all sites.

2.2 Introduction

Natural peatlands are an important carbon (C) sink (Moore, 1994) and are the most efficient carbon store on Earth: about a third of the global terrestrial organic

carbon pool is estimated to be stored in northern peatlands (Gorham, 2010; Turunen et al., 2002; Vitt et al., 2000) and an equivalent of 40-60% of the atmospheric carbon dioxide (CO_2) content is stored in peatlands around the world (Stocker et al., 2013), despite only covering about 3% of the total land area (Joosten et al., 2012). Peatlands store this amount of C by taking up atmospheric CO_2 in their plants via photosynthesis (gross primary productivity (GPP)); after the plants die, the litter gets deposited under anaerobic conditions in the waterlogged peat. Extremely low decomposition rates under these anaerobic conditions mean that these ecosystems act as net C sinks, accumulating dead biomass to form the significant C reservoirs. The decomposition of the peat together with the vegetation respiration gives the ecosystem respiration (R_{eco}). Net ecosystem exchange (NEE) is the sum of GPP and R_{eco}, which gives the net CO_2 flux from these systems, which is negative when C is sequestered and positive when C is lost.

Even though anaerobic decomposition in peatlands is very slow, it produces methane (CH_4) (Zinder, 1993), which is a much stronger GHG than CO_2; over a time span of 100 years it has a potential to warm the atmosphere 28 - 34 times more than CO_2 (depending on the inclusion of climate-carbon feedbacks; IPCC 2013). Another possible GHG emitted from peatlands is nitrous oxide (N_2O), which can be produced under both aerobic (nitrification) and anaerobic (denitrification) conditions; however, in highly anaerobic conditions, denitrification can take up N_2O from the atmosphere (Davidson and Schimel, 1994). N_2O is an even stronger GHG than CH_4; with a warming potential of between 265 and 298 times that of CO_2 over 100 year time span (Stocker et al., 2013). This means that peatlands can on the one hand store large amounts of C, but on the other hand produce the more potent greenhouse gases, CH_4 and N_2O. Therefore, the balance between these three gases determines the role of peatlands in climate change mitigation.

As well as climate regulation through C sequestration, peatlands fulfil a number of other ecosystem services, including supporting unique biodiversity, regulating nutrients and water, preserving ecological and archaeological records and providing recreational spaces (De Groot et al., 2002). However historically they

have been considered less favourably as "unproductive wastelands" (Alan and Macdońald, 1945) and people have sought to modify them to increase their productivity; e.g. their capacity to provide food or fuel for human consumption. The technical ability to plough peatlands to a depth that allowed effective drainage enabled other land uses to derive economic benefit from peatlands, including afforestation with non-native conifers (Lindsay et al., 1988). This has resulted in large areas of northern peatlands being drained and afforested in the 20th century (Huttunen et al., 2003).

In the north of Scotland, approximately 16% of the total blanket bog area (4000 km^2) were afforested in the 1980s, predominantly using the non-native conifer species Sitka Spruce (*Picea sitchensis*) and Lodgepole Pine (*Pinus contorta*) (Fig. 1) (Lindsay et al., 1988). Nevertheless, forestry plantations on deep peat are deemed to have detrimental impacts on ecosystem services that outweigh economic benefits (Andersen et al., 2016). For example, afforestation leads to a loss of unique biodiversity both within the afforested peatland, but also on adjacent sites of open natural peatlands due to edge effects (Wilson et al., 2014) Afforestation alters microbial community which controls nutrient cycling (Creevy et al., 2018). It is generally thought that afforestation would also affect the GHG fluxes, since deep ploughing has led to a lowering of the water table and the aeration of the peat, which results in changes in the decomposition processes; however this has never been empirically demonstrated in Scotland.

From the 1990s onwards, increased awareness of the negative impacts of deep drainage and afforestation of peatlands, and a better understanding of the importance of peatlands for other ecosystem services has led to a shift in land management (Andersen et al., 2016), as well as changes in policy preventing further planting on deep peat in the UK. Restoration of afforested peatlands has been promoted to return vital ecosystem functions and restore peatland habitats and species (Lunt et al., 2010).

Large scale planting ended in the late 1980s in the north of Scotland and a programme to designate Sites of Special Scientific Interest (SSSIs) covering the remaining intact open blanket peatlands began. In the UK, SSSIs are areas of land

and water that are considered to represent the natural heritage best in terms of their flora, fauna, geology and or geomorphology. The wider Flow Country peatlands within Caithness and Sutherland were later brought under the European Natura 2000 network, becoming the largest (143,500ha) terrestrial Special Area for Conservation and Special Protection Area in the UK. From the late 1990's the Royal Society for the Protection of Birds (RSPB) acquired afforested peatlands in the Flow Country (58° 22' N, 3° 53' W). A programme started to restore peatland habitats primarily to improve conditions for the important wetland assemblage. Restoration management has been implemented over a number of stages, due the added complexity of having to remove poorly grown trees before attempts to restore hydrology. Restoration measures aimed at reinstating blanket peatland vegetation in combination with hydrological restoration (i.e. blocking of drains and re-wetting of formerly forested areas) have clear and measurable biodiversity benefits (Hancock et al., in press), but there is so far no assessment of the long term greenhouse gas impact of peatland restoration following afforestation.

Understanding the impact of peatland restoration on the exchange of greenhouse gases with the atmosphere is urgently needed to inform land management strategies. Therefore, the main aim for our study was to measure the greenhouse gas fluxes of sites undergoing peatland restoration from forestry, termed forest-to-bog restoration. The processes behind GPP and R_{eco} are very different and thus are likely to have a dissimilar response to changing conditions (Cai et al., 2010). To be able to distinguish between these processes we have chosen to just look at R_{eco} fluxes (R_{soil} in the forest plantations). We have looked at the short-term effect of forest-to-bog restoration (months) and the long term effect (years) by following a chronosequence of restoration sites. By measuring environmental variables (moisture, temperature, vegetation, and micro-topography) that could explain the changes in GHG fluxes we tried to understand the mechanisms behind these. We hypothesised that the forest plantation soils have the highest CO_2 and N_2O fluxes, due to the drainage and hence aeration of peat. By contrast, we expect that intact bogs have significantly reduced CO_2 flux to the atmosphere, but higher net CH_4 flux to the atmosphere. For sites that are undergoing forest-to-bog restoration, we expect initially high fluxes of CO_2 to the atmosphere following soil disturbance

during restoration. After this, our expectation is that soil respiration fluxes from restoration sites will become increasingly similar to undisturbed peatlands. Further, we expect CO_2 and N_2O fluxes to be mainly driven by soil temperature and CH_4 fluxes mainly by soil moisture and vegetation.

2.3 Methods

2.3.1 Study site

The research area is located in the Flow Country in the north of Scotland, (58° 22' N, 3° 53' W), one of the largest areas of blanket peat bogs in Europe. The average annual precipitation between 1981 and 2010 was 970.5 mm with an average air temperature of 11.4°C, measured at the Kinbrace weather station approximately 20 km from plots (Location: 58º13'89''N, 3º55'1.2''W; Altitude: 103 m amsl; Met Office, n.d.).

2.3.2 Site descriptions

Since the late 1990's, there has been an ongoing programme of forestry removal. This has involved felling trees in-situ, and leaving them on site combined with collector drain blocking to start the process of restoration of peatland habitats. This has resulted in a chronosequence of different restoration ages. For this study, we include a number of sites that span the duration of the restoration process. Restoration sites include plots where restoration was started in 1998 (R98), 2006 (R06), 2012 (R12) and 2015 (R15). Comparable blanket bog sites that were never afforested or drained and existing standing forestry plantation plots were used as control sites (Figure 2.1 and Figure 2.2).
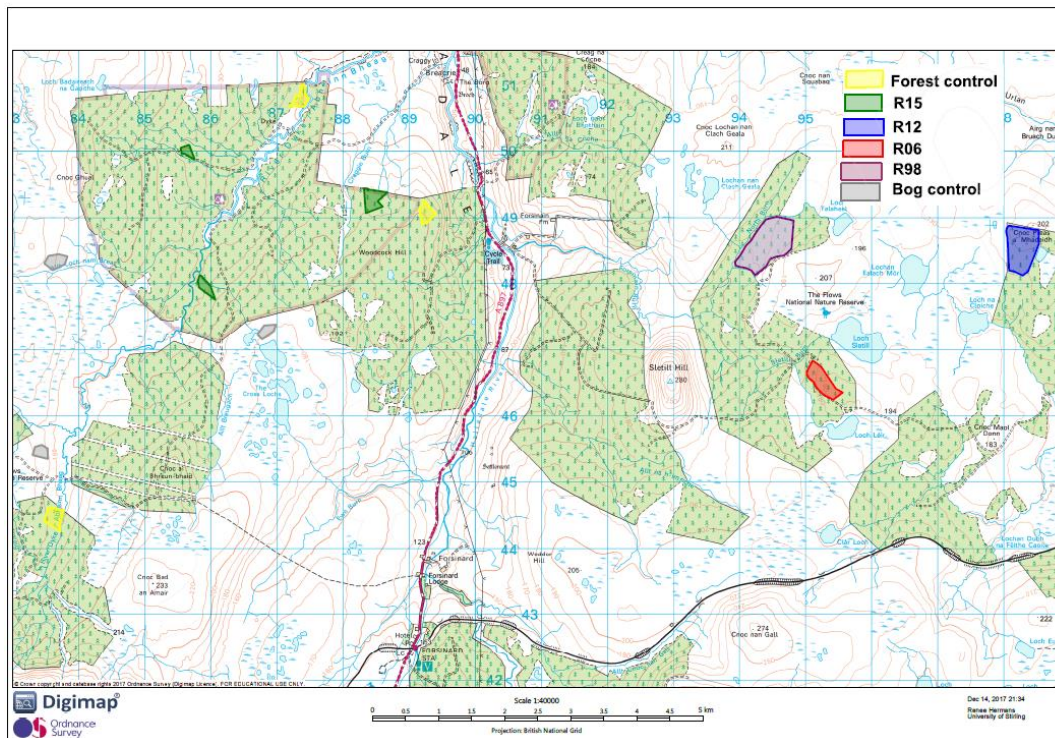
Figure 2.1 Local map with all study sites in the Flow Country, Scotland.

Forest control plots contained a mixture of *Picea sitchensis* and *Pinus contorta*, which were around 30 years old. Stand density was high (about 5000 trees per ha), with no vascular understory, but sporadic patches of moss, predominantly feather e.g. *Hypnum jutlandicum, Hylocomium splendens* and in some instances, *Sphagnum fallax* and *Sphagnum capillifolium* in furrows. The average diameter at breast height (DBH) for *Picea sitchensis* was 13.3 cm (n=22) and for *Pinus contorta* 17.9 cm (n=33), with an average ratio per area of *Picea sitchensis* / *Pinus contorta* of 0.6. Average canopy cover was 76.3%. (RSPB unpublished data, n.d.; Smith et al., 2014; Smith and Hancock, 2016).

At the time of measurements, R15 plots had very little ground cover, partly because a closed canopy prior to felling meant very little ground vegetation was present and partly due to the recent disturbance of felling. There were some patches of *Polytrichum commune, Eriophorum sp., Calluna vulgaris* and in some instances, *Sphagnum fallax* and *Sphagnum capillifolium* in furrows. After felling, the round wood (i.e. tree stems) was extracted, and other harvest residues (branches, needles) left as brash mats to aid forestry operations during felling.

The R12 plots had similar vegetation composition to R15; however, with a higher cover. Trees here were felled and left in the furrows, as the extraction of stems was not economically viable.

In the R06 plots vegetation was also similar to the R12 and R15 plots; however, *Sphagnum spp.* were also present and the ground was completely covered. Trees here were also left in the furrows after felling, but they were smaller than the trees in R12.

R98 plots were dominated by *Eriophorum vaginatum, Sphagnum* spp*., Calluna vulgaris, Erica cinerea* and *Erica tetralix.* There was also re-growth of *Picea sitchensis* at low density throughout the site. During harvest, trees here had also been felled and left in the furrows, but these trees would have been even smaller than the ones in R06.

All restoration sites used have undergone collector drain blocking either with peat or plastic dams. However, the furrows themselves were not managed in any way and continued to provide some element of drainage, especially on more sloping ground.

Bog control plots were located in three different sites and were dominated by *Sphagnum* spp*., Erica tetralix, Calluna vulgaris, Eriophorum vaginatum, Eriophorum angustifolium,* and *Pleurozia purpurea.*

Figure 2.2 Some of the study sites; A) Forest plantation, B) Felling in action of one of R15 sites, C) One of the R15 sites after felling with forest plantations in the back of the picture, D) R06, E) R98 and F) One of the near pristine bog sites. Picture credits: A), D) and E) R. Hermans, B) G. Thompson, C) H. Hermans and F) M. Hancock.

The double-ploughing of the peat at the time of afforestation created a regular micro topography with low lying furrows (c. 1.5 m wide) flanked by high ridges (plough throws; c. 0.75 m wide) on either side. In between two plough throws, there is an area of c. 0.50 m width of the original (unploughed) surface (Figure 2.3). The height from the bottom of the furrow to the top of the plough throw is about 0.5 m and from the original surface to the base of the plough throw is about 0.15-0.2 m. In general, conifer seedlings were planted on the plough throws because of the improved drainage compared to the original surface. All forest-to-bog sites used still have this micro topography.
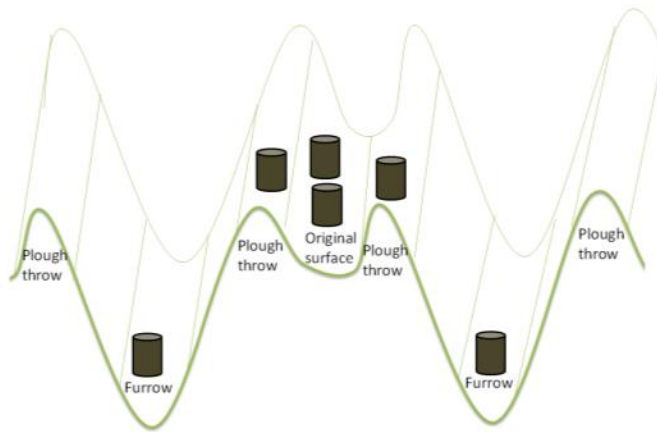
Figure 2.3 Micro topography of restored and forest plantation sites, with location of measurement chambers.

Peat depths were measured at five locations randomly in each plot and average water table was recorded for each site (Table 2.1; RSPB unpublished data, n.d.; Smith et al., 2014; Smith and Hancock, 2016).

Table 2.1 Range of peat depth and mean water table, where negative values mean below the peat surface, (± variance over all seasons and plots) for experimental sites. [1]Water table measured monthly from October 2012-October 2014 (RSPB unpublished data, n.d.), [2]Water table measured in March 2015 and August 2015 (Gaffney, 2016) [3]Water table measured monthly from July 2013-July 2016, [4]Water table measured monthly from May 2015-May 2016 in R98 (RSPB unpublished data, n.d.).

Site	Peat depth	Average water table
Forest[1]	137 – 204	-40.1 (±14.8)
R15[2]	120 – 537	-23.5 (±1.7)
R12[3]	185 – 460	-16.2 (±6.3)
R06	120 – 300	No data
R98[4]	110 - 360	-8.2 (±9.3)
Bog[1]	75 – 280	-10.2 (±8.4)

2.3.3   *Experimental set up*

2.3.3.1   *Short term impact plots*

To capture the short-term effect of tree felling three afforested sites assigned for felling between October 2014 and August 2015 were measured from July 2013 to July 2016; i.e. capturing both pre- and post-felling conditions. R15 plots were located in separate forestry plots, spaced 2-3 km apart. In order to meaningfully measure the impact of tree felling on GHG exchanges, each site undergoing forestry removal was paired with a forest and bog control site of similar peat depth and slope angle (Figure 2.1), which were measured over the same period.

2.3.3.2   *Long term impact plots*

The long-term effect of felling to waste was measured using the chronosequence of forest-to-bog restoration sites (R12, R06 and R98). Plots were located in single forestry blocks (larger than 0.23 km^2), spaced between 2 and 4 km apart. Measurements on these sites were paired with those on the same bog and forest control sites as used for the short-term measurements (Figure 2.1).

2.3.4   *GHG measurements*

Permanent flux collars (20 cm diameter, 10 cm height) were installed to a maximum depth of 3 cm in April 2013. Collars were placed over existing vegetation without removing plant or moss biomass. Plant functional type (with categories: *Sphagnum*, other mosses, sedges, shrubs, grasses, lichens, litter and bare peat) cover inside each collar was estimated at the end of the fieldwork. Two collars were placed on each micro-topographical form (Figure 2.3). In plots in unforested bog sites, these microforms were matched with two collars each located with *Sphagnum*, sedge and heather to represent low, medium and higher micro-topographic locations.

Measurements of soil GHG fluxes where done from July 2013 until July 2016. Approximately every 6 weeks gas exchange was measured in a sub-set of sites ('small' sampling round) consisting of one bog site, one forest site, R15 site and R98. Each site contained three replicate plots, picked randomly by putting dots on

a map. In addition to these campaigns, a total of seven complete sampling rounds including all sites were carried out over the entire sampling period ('big' sampling rounds; Figure 2.1). During the 'big' rounds three forest control, bog control and R15 sites were measured, all with one replicate plot within them, and R12 and R98 sites with three replicate plots within them were measured. The 'small' sampling round was usually spread over two days, and the larger sampling round was usually spread over four days. The reason for having two different sizes of sampling rounds is that, whilst only the 'big' round provides fully replicated flux results, this had to be balanced by logistical constraints in terms of requirements for field personnel. 'Big' rounds required a large number of field assistants, to ensure measurements across as small a time window as possible. 'Small' rounds were logistically more feasible, and allowed a more frequent coverage of selected sites to resolve seasonal GHG flux dynamics.

GHG measurements were taken by fixing dark static chambers, with a height of 20 cm and a diameter of 20 cm to the surface of collars using rubber seals to achieve a gas tight connection. A small fan in the chambers made sure the air inside was mixed. The chambers were insulated with reflective cover to minimize heating from solar radiation. A vent was in place to compensate small pressure differences between the chamber and the ambient atmosphere. Chambers were placed on the permanent collars for thirty minutes, and 20 ml gas samples were collected at 0, 3, 6, 18 and 30 minutes, using 1 m long tubing to avoid disturbance around the chamber (Figure 2.4). The gas samples were stored in 12 ml evacuated exetainers (Labco Limited, Lampeter, UK), which resulted in them being pressurized, and taken back to the lab.

Figure 2.4 Gas sampling for GHG flux calculations in action; chambers are visible, with tubing towards sampler who in this way is able to stay on the platform to avoid disturbance.

2.3.5   *Laboratory analysis of GHG*

All gas samples were run on a Gas Chromatograph 5890 Series II with a HayeSep-Q column, for gas separation, a flame ionisation detector (FID) with methaniser for CO_2 and CH_4 detection and an electron capture detector (ECD) for N_2O detection. Samples were introduced from pressurised gas vials via a custom-built auto sampler (Electronics workshops, University of York) certified standards were used to create calibration curves to determine concentrations from gas samples and within runs to correct for drift. CO_2 standards were 382.3, 818.4 and 1827 ppm, for CH_4 standards were 1.7, 8.8 and 43 ppm and for N_2O standards were 0.3 and 1.0 ppm. The precision of the instrument was determined by calculating the coefficient of variation of the standards analysed at the start of each day, which were always below 5%.

2.3.6   *Soil moisture and soil temperature measurements*

Alongside flux measurements, soil temperature (10 cm thermistor) and -moisture (HH2 moisture meter, Delta-T Devices, Cambridge) were measured by hand held sensors next to each collar. The temperature in the chamber and air temperature outside the chamber were also measured.

At the four sites used for the 'small' sampling round, loggers where installed in one of the three plots in April 2013 to record soil moisture and soil temperature at 5 and 20 cm soil depth at 30-minute intervals. Initially, soil moisture was measured in the original surface, and temperature in all three microforms. From September 2014 onwards, soil moisture was also measured at 5 and 20 cm depth in plough throws and furrows. This was accomplished with a combination of Tinytag loggers (model TGP-4017, Gemini Data Loggers, Chichester, UK) and Hobo micro stations (model H21-002, Onset Computer Corporation, Bourne, MA, USA), using TMB-M002 temperature probes (Onset Computer Corporation, Bourne, MA, USA) and S-SMD-M005 soil moisture sensors (Decagon Devices, Inc., Pullman, WA, USA). Air temperature was recorded by i-Buttons (DS1921G, Maxim integrated, San Jose, USA) at 50 cm above the ground, shielded from direct sunlight.

2.3.7 *Flux calculations and statistics*

Flux rates were calculated using the *HMR* package (Pedersen, 2017) in RStudio (Version 1.0.136). Concentrations are regressed against time since chamber closure to calculate the flux, using either a linear or a non-linear function (see Section 7.1), whichever fits the data best (Pedersen, 2010). Concentrations were checked for outliers by regressing all but one concentration against time and if this improved the fit this was used. Fluxes were expressed as $\mu mol\ m^{-2}\ s^{-1}$ or $nmol\ m^{-2}\ s^{-1}$. Only fluxes based on regressions with a p-value < 0.1 were considered as robust estimates, and considered for further analysis. This led to 8.5% rejection of CO_2 fluxes on 27.5% for CH_4 and 46.6% for N_2O. To eliminate outliers, fluxes with more than 3 times the standard deviation were also eliminated, which led to rejection of 7.3% for CO_2 fluxes, 6.1% of CH_4 and 12.3% for N_2O fluxes.

Data analyses were undertaken in RStudio (RStudio Team, 2016). CO_2 data was log transformed, CH_4 data was transformed using square root and N_2O data did not need to be transformed. Statistically significant differences and correlations were determined using p-values, where the p-value is used to weigh the strength of the evidence against the null hypothesis (no difference/correlation). P-values less than, or equal to, 0.05 (i.e. less than a 5% probability that the null hypothesis

is correct), indicate that the null hypothesis should be rejected in favour of the alternative ('working') hypothesis. P-values between 0.05 and 0.1 (i.e. a 5-10% probability that the null hypothesis is correct) suggest marginal significance and are interpreted as such throughout. P-values greater than 0.1 (i.e. a 10%, or greater, probability that the null hypothesis is correct) are too large to reject the null hypothesis.

A linear model was used to identify differences between the GHG fluxes from R15 plots pre felling and the forest and bog control plots per microform. The same was done over the time span post felling.

To find out if there were differences between sites (excluding R15 sites as these were measured over a different period) and whether fluxes could be explained by climatic factors (soil temperature and moisture), vegetation or microform, a linear mixed-effect model (LMM) using the *nlme* package in R (Pinheiro et al., 2017) was used. *Site* was used as a continuous variable in months post felling, this was done to overcome the problem of pseudo-replication, and because time since felling is the main driver of interest. Forest plantation sites were set to 0 years and bog sites were set to 300 months (25 years). 25 years was chosen since a biodiversity study showed that the R98 site showed restored moisture conditions and stabilised bog vegetation in the wetter areas after 14 years, so getting close to a functioning bog again (Hancock et al., in press). However, outputs were also tested for bog set to 20, 30 and 35 years.

All numerical predictors were standardized to 1 standard deviation prior to statistical analyses, to allow relative effect sizes of predictors to be compared directly (Nakagawa and Schielzeth, 2010). Model selection was based on information theory (Burnham and Anderson, 2002); first the most complex model was built, which included the variables soil moisture and temperature at both 5 and 20 cm depth and months since felling with an interaction between them and microform and presence of sedge and *Sphagnum* as fixed effects; *plot* and *collar* were included as random effects. All possible combinations of this model were identified using the 'dredge' function in the *MuMIn* package (Barton, 2017), set up so that *months since felling* was always kept in the model as a predictor

variable, since our main hypothesis are about differences between sites. Multicollinearity was assessed for all possible models and only the ones without multicollinearity were used. Goodness of model fit was assessed with the small-sample size corrected Akaike's Information Criterion (AICc), which is calculated using the number of parameters and either the maximum likelihood estimate for the model or the residual sum of squares. "Likelihood" here is a measure of the extent to which a sample provides support for particular values of a parameter in a parametric model. AICc values of different models can be compared and the model with the lowest AICc is selected as the "best approximating model" (Burnham and Anderson, 2002). Any of the models with a delta AICc of less than 2 are considered to be as good as the best model (Richards, 2005). 'Dredge' also gives a weight to the models it produces, ranging between 0 and 1; with for example a weight of 0.7 meaning that there is a 70% chance that that model is the best approximating model of the models considered. If the weight of the best model is low, it is not possible to say that that model really is the best model, meaning other models also have to be considered. In this study, the model with the best AICc and highest weight was used, and where the top model had a weight of less than 0.6 the simplest model was used. The marginal R^2, which describes the proportion of variance explained by the fixed factor(s), and the conditional R^2, which describes the proportion of variance explained by both the fixed and random factors (Nakagawa & Schielzeth 2010), was calculated using the function *sem.model.fit*s from the *piecewiseSEM* package.

For the gases that have a significant temperature correlation, the temperature coefficient (Q_{10}) is calculated using the van 't Hoff equation:

$$Q_{10} = (\frac{R_2}{R_1})^{\left(\frac{10}{T_2-T_1}\right)} \tag{2.1}$$

With R_1 the flux at temperature T_1 and R_2 the flux at temperature T_2. Q_{10} gives the factor by which the flux increases for every 10-degree rise in temperature (Ito et al., 2015).

2.4 Results

2.4.1 *Short term effects of forest removal on GHG fluxes*

Prior to felling in 2015, there was no statistically significant difference between any of the GHG fluxes in forest control sites and the to-be-felled sites in any of the microforms (CO_2 p>0.6, CH_4 p>0.8 and N_2O p>0.6), apart from an indication of a difference in N_2O flux from the plough throw (p=0.06). However CH_4 fluxes were significantly lower in the furrow and original surface of the to-be-felled sites than in the bog control sites (original surface p<0.001, furrow p=0.05), but fluxes were not significantly different from the plough throw (p=0.3). CO_2 and N_2O fluxes were not significant different (p>0.9 and p>0.2 respectively).

In the period post felling the CO_2 fluxes from the plough throw where significantly lower in the felled sites than in the forest control sites (p=0.02). CH_4 fluxes were significantly higher from the original surface and plough throw of the felled sites than of the forest control sites (p<0.0001 and p=0.03 respectively). Further there were no significant differences in the CO_2, CH_4 and N_2O fluxes between forest control and post felling sites (CO_2 p>0.8, CH_4 p=0.2, N_2O p>0.1; Figure 2.5). When comparing the fluxes from the felled sites to the bog control sites there are no significant differences in N_2O (p>0.1) and neither in CH_4 (p>0.4) fluxes anymore, but CO_2 fluxes from the plough throw in the felled sites were significantly lower than from the bog (p<0.001). Further there were no significant differences in CO_2 fluxes (p>0.2). Some of the most extreme CH_4 flux values observed during the entire observation period occurred in the wetter microforms (furrow and original surface) of the felled sites during summer months about 2 to 7 months after felling. However, they seem to settle back down in the second summer post felling, even though the soil temperature is similar, but soil moisture levels were lower (Figure 2.5).
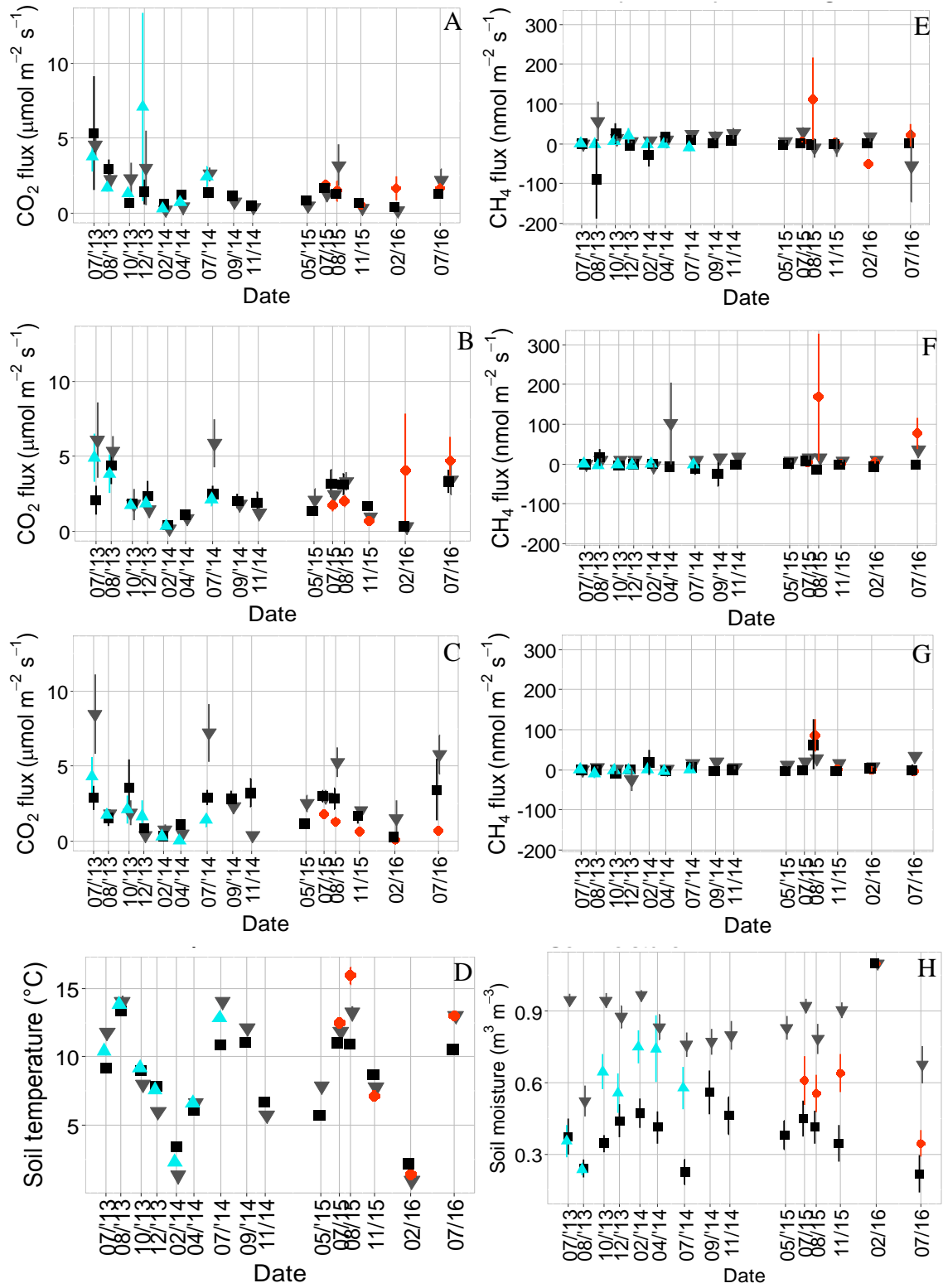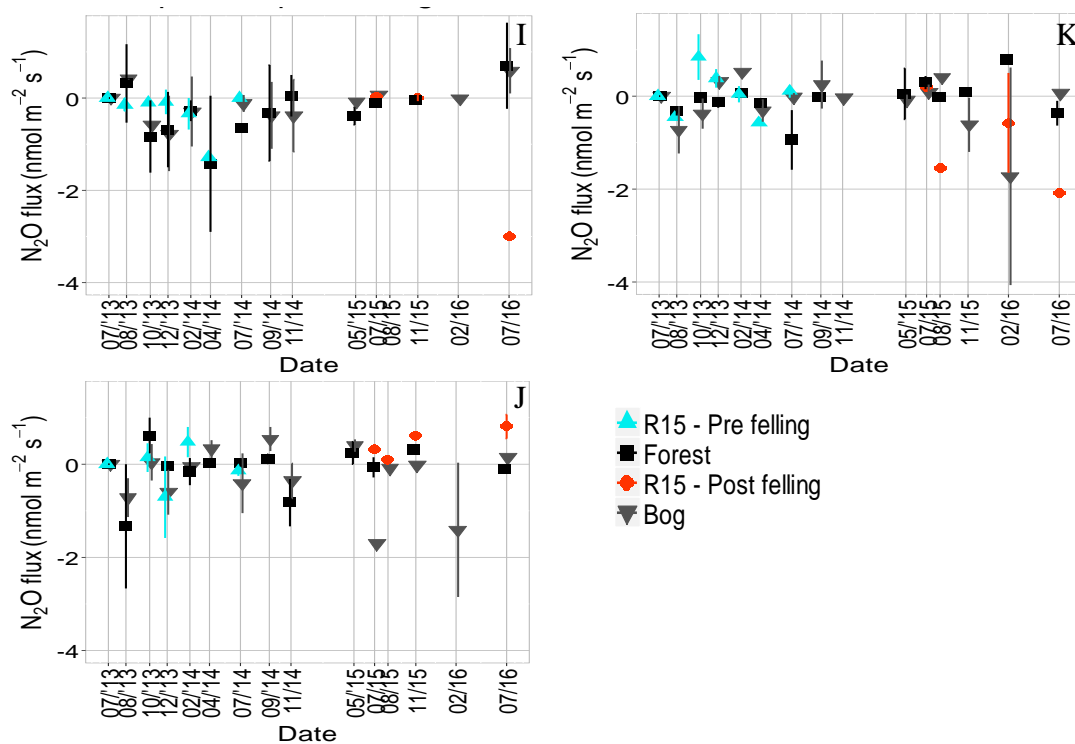
Figure 2.5 Short-term effect of felling on fluxes. Symbols represent mean fluxes in replicate plots (n=6), error bars are standard errors. A) CO_2 from furrow, B) CO_2 from original surface, C) CO_2 from plough throw, of E) CH_4 from furrow, F) CH_4 from original surface, G) CH_4 from plough throw, D) soil temperature at 5 cm depth, H) soil moisture at 5 cm depth, I) N_2O from furrow, J) N_2O from original surface, K) N_2O from plough throw.

2.4.2 *Long term effects of forest removal on GHG fluxes*

The GHG fluxes from the chronosequence of restoration sites show some interesting patterns with different responses between the GHG to restoration (Figure 2.6).
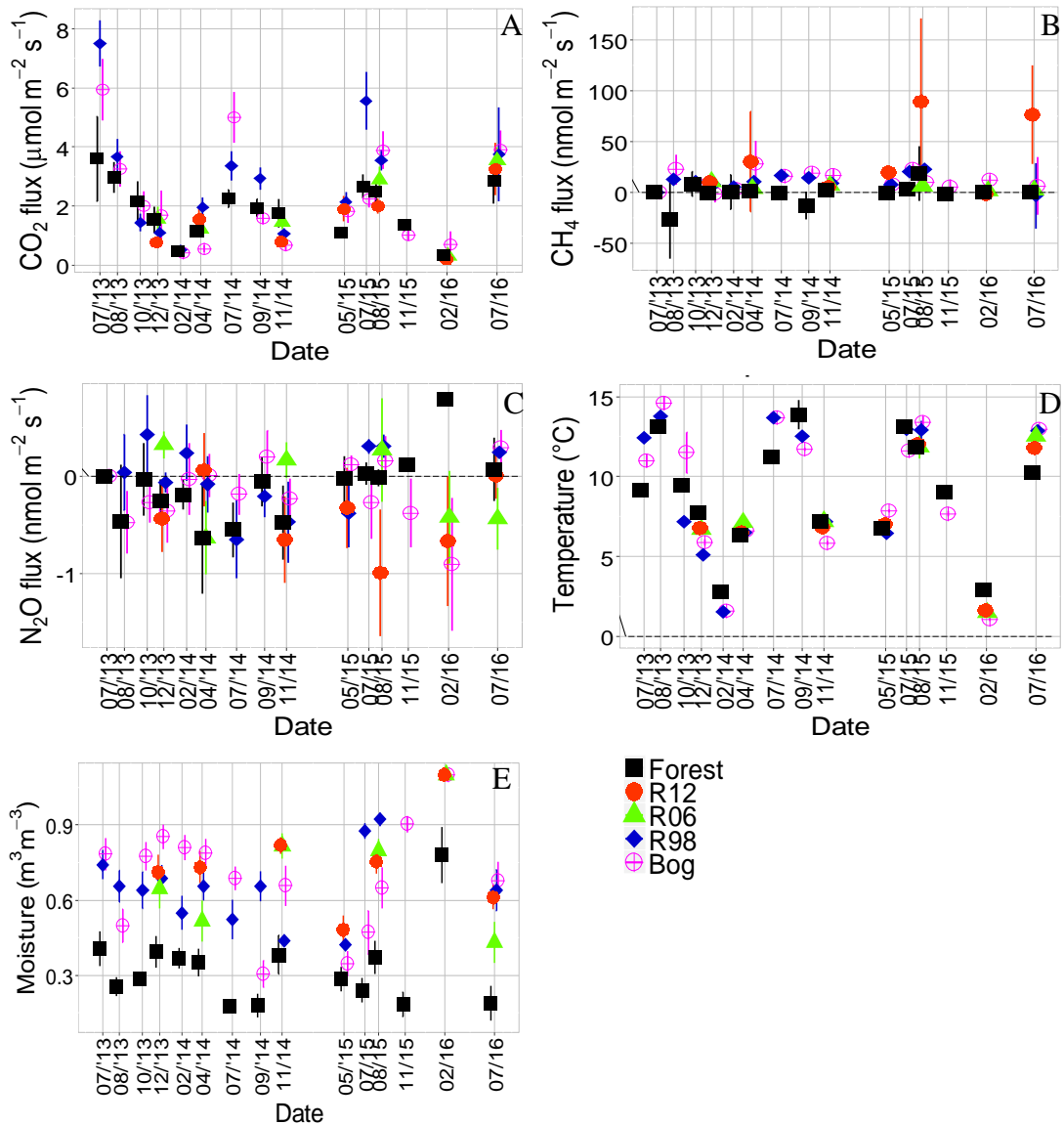
Figure 2.6 GHG fluxes and soil temperature and moisture at 5 cm depth. Symbols are averages across all microforms in three replicate plots (n=18), error bars are standard errors. A) CO_2, B) CH_4, C) N_2O, D) Soil temperature at 5 cm depth, E) soil moisture at 5 cm depth

2.4.2.1 CO_2 flux

There is a clear annual cycle in CO_2 fluxes from all sites, with a mean CO_2 flux of 2.27 ±0.079 µmol m^{-2} s^{-1}. There are no significant differences between sites (p=0.9; Figure 2.6). Setting the age of the bog sites to a different number of

months did not make a difference (20 years p=0.7, 30 years p=0.9 and 35 years p=0.8).

There was only one model in the top set of models, since all other models had a delta AICc of more than 2. CO_2 fluxes were best explained with a combination of *soil temperature* and *microform; Site in months after felling* was kept in all models since this was our main interest (Table 2.2, Table 2.3). The marginal R^2 for the model was 0.4 and conditional R^2 was 0.5.

Table 2.2 Model selection summary. 1 model in top model set with a delta AICc of less than 2. Df= degrees of freedom, LogLik=Log likelihood.

Candidate models	LogLik	AICc	ΔAICc	Weight
Soil temperature + Microform + Site in months after felling	-1027.0	2072.2	0	1

Table 2.3 Model coefficients with standard error

Fixed effects	Estimate	Standard error
Intercept	0.0069	0.087
Site in months after felling	-0.0046	0.069
Microform – Original surface	0.34	0.093
Microform – Plough throw	0.45	0.093
Soil temperature at -5 cm	0.68	0.029

CO_2 fluxes were significantly different between microforms, with significantly higher fluxes from plots in plough throw and original surface than in furrow ($p < 0.001$). However, there is no significant interaction between site and microform, meaning that within each microform there is no significant difference between the sites (Figure 2.7). Since the area of each microform in the forest plantations and restored sites are not equal, but 0.43 for the furrow and plough throw and 0.14 for

the original surface, the CO_2 flux is scaled by area, giving a better representation of the mean flux of the whole site (Table 2.4). Temperature was the strongest predictor. The temperature response corresponds to an apparent Q_{10} of 7.0 for a 5 cm temperature measurement depth (Figure 2.8).

Table 2.4 Scaled CO_2 fluxes (μmol m^{-2}s^{-1}) to forest plantation plot level by microform area ($\pm$ standard error).

Microform	Fractional area	Unweight Forest plantation	Area weighted Forest plantation	Unweight R12	Area weighted R12
Original surface	0.14	2.09 (±0.19)	0.29 (±0.03)	1.36 (±0.23)	0.19 (±0.03)
Plough throw	0.43	2.15 (±0.26)	0.92 (±0.11)	1.40 (±0.23)	0.60 (±0.10)
Furrow	0.43	1.50 (±0.31)	0.65 (±0.13)	2.02 (±0.46)	0.87 (±0.20)
Total	1	1.91 (±0.15)	1.86 (±0.18)	1.60 (±0.19)	1.66 (±0.22)

Microform	Fractional area	Unweight R06	Area weighted R06	Unweight R98	Area weighted R98
Original surface	0.14	1.70 (±0.24)	0.24 (±0.03)	3.19 (±0.36)	0.45 (±0.05)
Plough throw	0.43	2.63 (±0.40)	1.13 (±0.17)	3.68 (±0.45)	1.58 (±0.19)
Furrow	0.43	1.40 (±0.24)	0.60 (±0.10)	2.31 (±0.25)	0.99 (±0.11)
Total	1	1.88 (±0.18)	1.97 (±0.20)	3.07 (±0.21)	3.02 (±0.23)
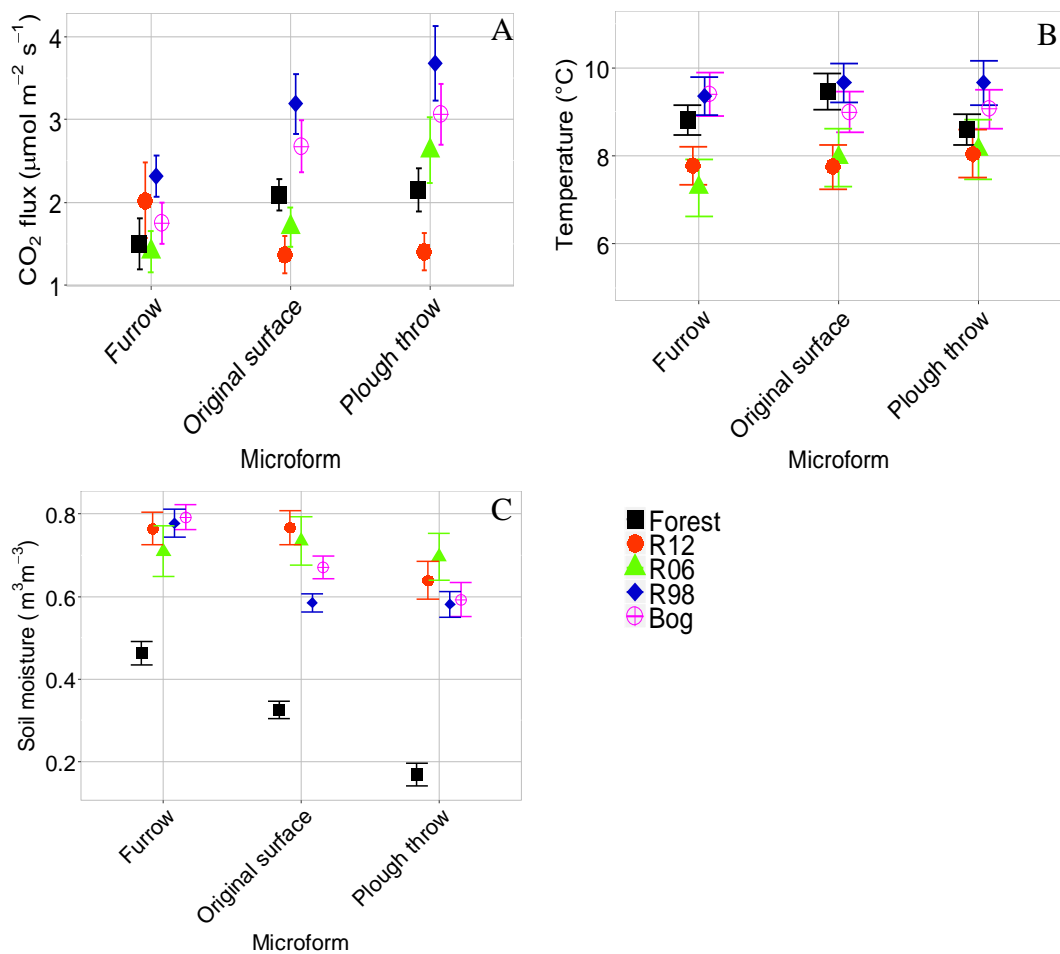
Figure 2.7 CO_2 fluxes per microform (A) with the corresponding soil temperature at 5 cm depth (B) and soil moisture at 5 cm depth (C) per microform. Symbols are averages over all sampling campaigns (3 years) split by site, error bars are standard errors.
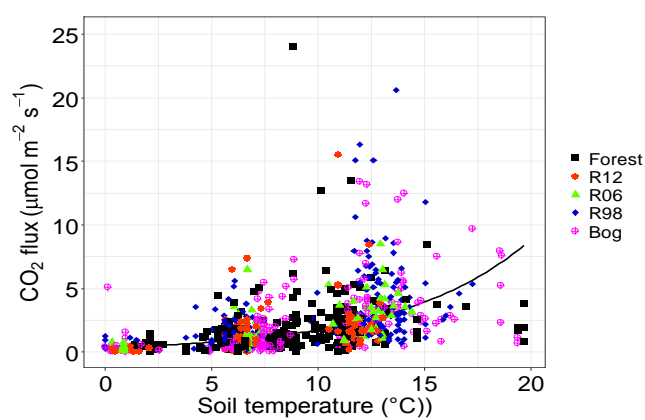
Figure 2.8 Temperature response of all measured CO_2 fluxes across all sites. Regression line is mixed effect model prediction.

2.4.2.2   CH₄ flux

Mean CH_4 flux over all sites was 10.19 ±1.54 nmol m^{-2} s^{-1}. All sites emitted CH_4 through the year, except the forest plantations, which on average took up CH_4 through parts of the year (Figure 2.6). There were signs of an annual cycle with forest plantations in the summer of 2013 and 2014 uptaking CH_4 while other sites emitted CH_4. However in the summer of 2015 forest plantations also emmitted CH_4, coinciding with unusually high summer moisture contents compared to summers in 2013 and 2014 (Figure 2.6).

There are two models with an AICc difference of less than 2 and they are as good as each other in explaining the variance in the CH_4 flux. Since the first model is the simplest, this model is used. CH_4 fluxes were best predicted with soil temperature at 5 cm depth, and Site (Table 2.5, Table 2.6). The marginal R^2 was 0.09 and conditional R^2 was 0.2. This means that these variables do not explain the variance in CH_4 flux well.

Table 2.5 Model selection summary. Models are ranked by AICc and weight; where higher weighted models have more support. Df= degrees of freedom, Loglik=Log likelihood.

Candidate models	Df	LogLik	AICc	ΔAICc	Weight
Soil temperature at - 5 cm + Site in months after restoration	6	-1848.5	3709.2	0	0.51
Soil temperature at - 5 cm + Soil moisture at -5 cm + Site in months after restoration + Soil moisture at 5 cm x Site in months after restoration	8	-1846.5	3709.2	0.0	0.49

Table 2.6 Model coefficients with standard error

Fixed effects	Estimate	Standard error
Intercept	1.88	0.33
Site in months after felling	1.02	0.33
Soil temperature at -5 cm	0.33	0.13

CH_4 fluxes increase with increasing months after restoration (p = 0.007, Figure 2.9) and this stayed significant when changing the set age of the bog sites (20 years p=0.005, 30 years p=0.01 and 35 years p=0.01). CH_4 flux to the atmosphere were positively significant but weakly correlated with soil temperature, with an apparent Q_{10} of 0.26 (p = 0.01; Figure 2.10). In contrast to CO_2, there are no significant differences between microforms.
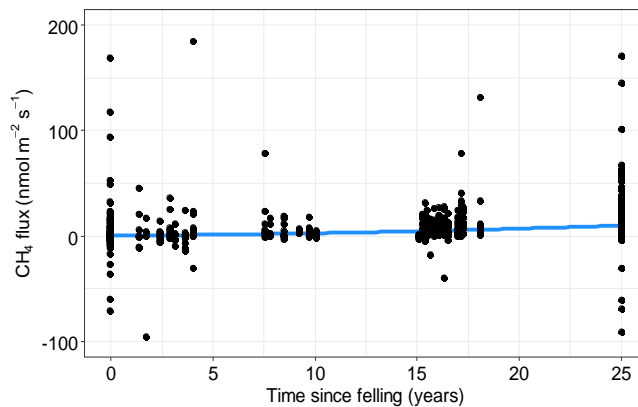
Figure 2.9 CH_4 flux as a fuction of time since restoration (forest = 0 year and bog = 25 years), from mixed effect model.
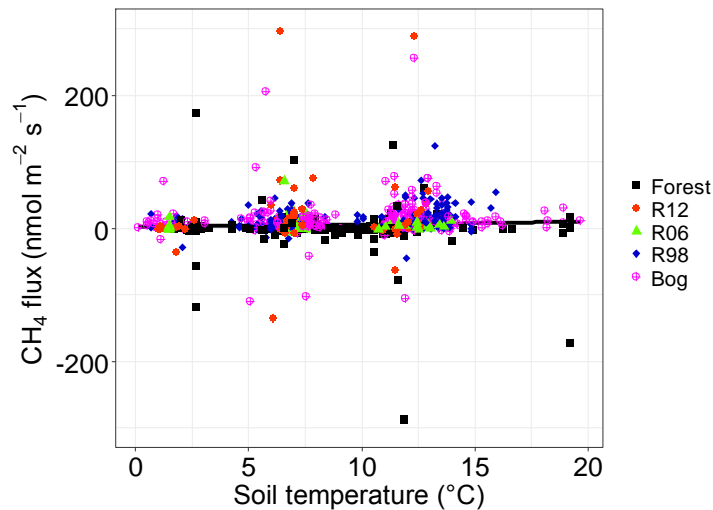
Figure 2.10 Temperature response of all measured CH$_4$ fluxes across all sites. Regression line is mixed effect model prediction.

2.4.2.3 N$_2$O flux

N$_2$O fluxes from all sites are very close to 0, with a mean uptake of -0.17 ±0.028 nmol m^{-2} s^{-1} over all sites (Figure 2.6). Linear mixed effects model results indicate that there are no variables that correlate significantly with N$_2$O flux, meaning that none of the variables could explain the variation in N$_2$O flux.

2.4.2.4 Soil temperature and soil moisture

All sites had a similar seasonal pattern for soil temperature and soil moisture at 5 cm depth. However the forest plantation sites have the highest soil temperatures in winter and lowest in summer. There were significant differences between the soil temperatures of the sites; the bog and R98 sites had signifcantly higher soil temperatures than R06 and R12 (p<0.05; Figure 2.6). For soil moisture the magnitude of differences between measurement dates within bog sites was much bigger than in forest plantation sites. The soil moisture at -5 cm in the forest plantations was significantly lower than from all other sites (p<0.001; Figure 2.6).

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2.5 Discussion

2.5.1 *Long term effect*

Based on flux results collected over three years, the removal of forestry and drain blocking, but with no furrow blocking, had no significant influence on the CO_2 flux, as we found no significant difference between any of the sites. This is in contrast with our hypothesis that a higher water table (Table 2.1) would reduce organic matter decomposition and thus reduce CO_2 flux, as found in lab studies by Dinsmore et al. (2008), Estop-Aragonés et al. (2016), Blodau et al. (2004). The proposed mechanism behind this reduction in CO_2 flux is called the enzymic latch mechanism; in anaerobic peat the oxygen limitation on the enzyme phenol oxidase can minimize peat decomposition, since phenol oxidase is one of the only enzymes that can attack phenolics (polyphenols, tannins and humics) (Freeman et al., 2001). However drainage of a peatland can open the "latch" and significantly reduce phenolics, since phenol oxidase will not be oxygen limited anymore. Rewetting can then accelerate carbon loss to the atmoshpere and water, since the amount of nutrients and labile C have increased due to drainage (Fenner and Freeman, 2011). However there are more mechanisms working in these sites, which can have an influence on the CO_2 fluxes; a big part of the CO_2 fluxes from the restoration and bog sites is respiration by vegetation, in contrast to the soil respiration from the forest plantations. More vegetation on the older restoration and bog sites, could result in higher respiration fluxes (Waddington and Price, 2000), which may compensate for the reduced CO_2 flux from the reduction in peat decompostion. Hambley (2016) has shown that in the R98 sites, a near pristine bog and a site felled in 2004 in the Flow Country, CO_2 uptake by the vegetation outweighs plant respiratation and peat decomposition, meaning that these sites in total assimilate CO_2. Therefore the vegetation is very active and will thus respire more. Another source of CO_2 in restored sites are dead tree roots left in the soil after the removal of conifers, which, if the water table is not high enough, will decompose and thus release CO_2 to the atmosphere. With restoration of the peatland hydrology, by blocking drains etc., these roots will not decompose, so in the older restoration sites (which have a higher water table) the contribution of root decomposition to the CO_2 flux will be minimal. In a separate root trenching

study conducted in adjacent forestry plantations, we have shown that newly created dead root biomass can contribute about 27% of the total soil CO_2 flux of forest plots in the first year of decomposition (Chapter 3), so this could be a significant contribution to the CO_2 flux from restored areas. As shown there are complex interactions and many sources of CO_2, where contrasting source dynamics can mask inherent peat decomposition differences. However, our results show that CO_2 respiration flux is not a major factor for the greenhouse gas impact of restoration.

The biggest driver of CO_2 flux was soil temperature at 5 cm depth. We have found a very strong temperature response, with an apparent Q_{10} of 7.0. As mentioned earlier CO_2 flux can be broken up into three major parts; vegetation respiration, peat decomposition and in the restoration sites root decomposition. Temperature has a positive influence on all three mechanisms. Our Q_{10} is higher than found in the literature, where for peatlands it ranges from $1.9 - 6.1$ (Chapman and Thurlow, 1996; Juszczak et al., 2012; Lafleur et al., 2005; Silvola et al., 1996), possibly because the temperature response of drained peat decomposition is higher than the response of pristine peat and our Q_{10} is averaged over all our sites.

We have found no significant difference between the soil CO_2 flux from the forest plantation and the ecosystem CO_2 flux from the bog sites. However in this comparison, respiration by aboveground tree biomass is not taken into account, whilst bog fluxes represent complete ecosystem respiration, making the comparison for CO_2 exchange between ecosystem and the atmosphere incomplete (Artz et al., 2013). Including tree respiration in the CO_2 flux from forest plantations is likely to result in higher ecosystem respiration compared to other sites. To understand the forest plantation fluxes completely they should be measured at the ecosystem level, for example with the eddy covariance technique.

Yamulki, et al. (2013) investigated the impact of drainage on planted (*Pinus contorta*) sites on a lowland ombrotrophic raised bog in mid Scotland, showing an increase of 35% in CO_2 flux from soil and understorey vegetation in the drained and planted areas, compared to the undrained and planted areas. This shows that aerated peat under a forest plantation does emit more CO_2 than water logged peat

under a forest plantation. However, similar to our findings, they did not find a significant difference between the drained and planted site and a near pristine site. Minkkinen and Laine (1998), Lohila et al. (2011) and Ojanen et al. (2013) showed that even after drainage for forestry of nutrient poor naturally forested peatlands, they still are a small C sink. This is in contrast with the more general view that forestry-drained peatlands become a C source (e.g. (Couwenberg et al., 2011). However, Ojanen et al. (2013) showed that in fertile sites, the soil turns into a C source after drainage and afforestation, but because of the fast tree growth, the ecosystem stays a C sink. The main factors that control this balance were site fertility, water table, and temperature (Ojanen et al., 2013).

CH_4 fluxes increase significantly from the forest plantation sites to the bog control sites, with the restoration sites having intermediate mean values. This is likely to relate to the higher water table in these sites (Table 2.1), which increases methanogenesis near the soil surface, and provides conditions that inhibit the oxidation of generated methane before it is exchanged with the atmosphere (Zinder, 1993). Lab studies have found a similar result of higher CH_4 fluxes in high water table treatments than in low water table treatments (Dinsmore et al., 2008; MacDonald and Fowler, 1998; Moore and Dalva, 1993). Surprisingly, there are no significant differences between microforms for CH_4 fluxes within sites. The soil moisture data (Figure 2.7C) shows that all microforms in the forest plantations are much drier than in the other sites. Therefore, we think that this lack of difference in flux between microforms is likely to be caused by a reduced water table across all microforms in forest plantations, leading to a strong impact of site conditions that dominates flux magnitudes, with only a minor impact from within-site, micro-topography related conditions.

We did not find a significant relation between vegetation and CH_4 flux. This in contrast to what has been found in several other studies, which show a direct effect of some vegetation species, by transporting CH_4 through plant tissue to the atmosphere (aerenchyma species) and by providing suitable substrate for CH_4 production. Furthermore, an indirect effect of vegetation on CH_4 flux has been shown, since plant species are a good indicator of environmental conditions like water level, pH etc. (Levy et al., 2012). Greenup et al. (2000) and Couwenberg et

al. (2011) have shown a good statistical relationship between aerenchyma species and CH_4 emission at sites in the UK and Germany, whilst Bubier et al. (1995) found a strong relationship between bryophyte abundance and CH_4 emissions at sites in Canada. In an analysis of a large data set of CH_4 from soils in the UK, Levy et al. (2012) have found that vegetation species composition is the best single predictor of mean CH_4 fluxes and Gray et al. (2013) have shown that both species composition and functional groups are good predictors of CH_4 flux. We hypothesise that the reason why there was no significant relationship found in our sites is due to the disturbance that most of these sites have undergone. In the restoration sites the water table is high, which as shown leads to higher CH_4 fluxes, but the vegetation is still recovering towards bog vegetation. Therefore, there is no clear relationship between vegetation and CH_4 flux.

The CH_4 fluxes measured over all sites were positively significantly correlated with soil temperature. This is in line with what was found in the literature where it is proven that methanogenesis is temperature dependent (Westermann et al., 1989; Zinder, 1993). Yvon-Durocher et al. (2014) have shown in a meta-analyses that on an ecosystem level CH_4 emissions are also temperature dependent and that this dependency is similar to the dependency found in pure cultures of methanogens in lab studies.

In accordance with our results, Minkkinen et al. (2007) show that afforested peatlands with effective drainage take up CH_4. However, Minkkinen and Laine (2006) estimated that the waterlogged ditches in a forest emit as much or even more CH_4 as is consumed by the rest of the forest. This could mean that most drained afforested peatlands are small sources of CH_4. The furrows in our forest plantation sites were usually not waterlogged, and on average even took up CH_4; -3.79 ±7.63 nmol m^{-2} s^{-1}. However the collector drains around the forest plots were waterlogged, but no measurements were done here. Yamulki et al. (2013) also found a clear difference between their drained and planted site and the near pristine bog site, with CH_4 fluxes from the near pristine site the highest. Fluxes from the undrained and planted site were in between those of the other two sites.

The measured N_2O fluxes have a mean uptake of -0.068 ±0.014 nmol m^{-2} s^{-1} from all sites and there is no significant difference between any of our sites or microforms. There are several studies of N_2O emissions from natural peatlands, all showing relatively low emissions, with some ombrotrophic mires showing net N_2O consumption like ours (Martikainen et al., 1993; Regina et al., 1996; Yamulki et al., 2013). Martikainen (1993) measured very low N_2O fluxes of below 0.009 nmol m^{-2} s^{-1} from an ombrotrophic bog in Finland with no effect of drainage and afforestation on N_2O fluxes. In contrast to our results, Regina et al. (1996) showed an increase in N_2O fluxes after afforestation in both minerotrophic and ombrotrophic peatlands. Similar to our results Yamulki et al. (2003) found no significant differences between near pristine bog and drained and planted sites, but they found a small N_2O emission of 0.014-0.065 nmol m^{-2} s^{-1}.

2.5.2   *Short term effect*

The short-term (up to 1.5 years) effect of felling was different than hypothesised, which was that the disturbance would lead to higher soil CO_2 efflux. However, we found significantly lower CO_2 fluxes in the felled sites than in the forest control sites from the plough throw locations, whilst for other microforms there was no significant difference in CO_2 fluxes between sites. This might be explained by a decrease in CO_2 fluxes due to a reduction in root respiration, combined with an increase in CO_2 flux due to soil disturbance during felling. In contrast to our results clear felling of a Spruce plantation on a blanket bog in Ireland led to a reduction of CO_2 emissions by 55 to 63%, which was explained by the lack of root respiration after felling (Byrne and Farrell 2005).

Prior to felling, CH_4 fluxes were significantly lower in the to-be-felled sites than in the bog control sites (in the furrow and original surface, Figure 2.6), but post felling there was no significant difference. This indicates an increase in CH_4 fluxes following tree felling, which is also shown in the significant difference between the harvested sites and the forest control sites (in the original surface and plough throw), which was not there prior to felling. Some of the most extreme CH_4 flux values observed during the entire study period occurred in the two summers, up to 1.5 years, post felling. We saw similar outbursts of CH_4 in the

summer months in the R12 sites coinciding with the R15 ones, but in the R06 and R98 sites we do not see them anymore. This shows that the extreme CH_4 fluxes settle back down in the longer-term post felling, indicating the importance of long-term measurements.

Huttunen et al. (2003) investigated the effect of clear felling of a nutrient rich peatland on CH_4 and N_2O fluxes. They measured only in the growing season, 6 months after clear felling until 3 years after. They found no significant difference in CH_4 and N_2O fluxes between their control plantation site and the clear felled site. However, they did find a significant interaction between "time" and "cutting treatment", which they explained with the higher emissions from the clear-cut sites during the first two summers.

2.6 Conclusion

This paper shows that when restoring blanket bog from forestry plantation, the change in CH_4 flux is the most important and CO_2 respiration and N_2O fluxes do not change. In the long-term plots there was no significant difference between sites in CO_2 and N_2O fluxes. However CH_4 fluxes increased with restoration age and are highest in the near pristine bog sites. The biggest emissions of CH_4 are observed up to 4 years post felling, and these outbursts were not visible anymore in sites felled 7 years ago. In order to understand if these sites have a positive or a negative climate forcing the CO_2 uptake needs to be measured.

3 Separating autotrophic and heterotrophic soil CO₂ effluxes in afforested peatlands

3.1 Abstract

In order to quantify peat decomposition, soil respiration under 30 year old forest plantations on naturally treeless blanket bogs in the north of Scotland was partitioned into autotrophic (e.g. living plant material) and heterotrophic (e.g. bacteria, fungi) respiration. Peatlands are a very important C store, which can be compromised by drainage and afforestation; therefore, it is important to know the rate at which peat is lost. Partitioning was done using the trenching technique, where a trench is dug around a small area of intact peat, cutting through all living tree roots, then CO_2 fluxes are compared from trenched plots to intact (control) plots. Litter input, litter decay rate (measured by comparing fluxes from collars with and without litter) and soil temperature and moisture where measured in all plots. The contribution to the CO_2 flux of decaying roots killed in the trenched plots was accounted for. A mixed effect model was used to model the fluxes from the experimental plots. CO_2 flux was best explained by a combination of soil moisture, soil temperature, trenching treatment, microform (due to ploughing of the peat) and litter treatment. Using this model the annual peat decomposition (heterotrophic flux) was calculated at 126.8 ± 14.7 g C m^{-2} y^{-1}, which is 44% of the total soil respiration. Hence, 56% of the total soil respiration came from the tree roots (autotrophic flux). Decomposition of needle litter appears to be faster when an active rhizosphere (control plots) is present than when the rhizosphere is not active (trenched plots), hinting at an interaction between tree root C input and heterotrophic decomposition of organic matter. At this stage the surface litter C input into the soil alone is more than is leaving as CO_2, meaning even without taking root turnover into account, there is seemingly a soil C sink. However, the litter input over the total rotation of the forest plantation has to be taken into account to know if the soil is a C sink or source overall.

3.2 Introduction

Large areas of peatlands in the boreal and temperature zone have been drained and afforested primarily by conifer species, in the 20th century. For instance, up until 1995, about 15 million hectares of peatlands in boreal and temperature zone were drained for forestry (Paavilainen and Paivanen, 1995) and the growth of peatland forests has significantly increased in the years after (Huttunen et al., 2003). This has led to habitat loss and changes in the greenhouse gas balance of these systems. Since natural peatlands are an important carbon sink, with an estimated third of the global terrestrial carbon pool stored in northern peatlands (Gorham, 2010; Turunen et al., 2002; Vitt et al., 2000) this can have a big impact on the global greenhouse gas (GHG) balance. An equivalent of 40-60% of the atmospheric carbon dioxide (CO_2) is stored in peatlands around the world (Stocker et al., 2013), despite only covering about 3% of the total land area (Joosten et al., 2012). In the British uplands, deep peats (> 45 cm depth) contain about 0.47 kg C m^{-2} per centimetre depth (Cannell et al., 1993). Scottish peat soils cover about 1.7M ha (22.7% of Scotland) and it is estimated that they store 1620Mt of C (56% of Scottish soil C; Chapman et al. 2009).

Drainage of peatlands influences the hydrology, which is known to lead to changes in the production and consumption processes of organic matter and fluxes of greenhouse gases (Silvola et al., 1996). When lowering the water table, aeration is enhanced which leads to an increase in decomposition of litter and peat (Hargreaves et al., 2003) and an increase in mineralisation of nitrogen (Freeman et al., 1996). Methane emissions can be reduced, stopped or uptake could take place (Ojanen et al., 2010b). On the other hand, carbon fixation is increased by the vegetation, which can be a considerable C sink depending on the effectiveness of drainage and nutrient availability (Minkkinen et al., 2001; Yamulki et al., 2013). However, most peatlands hold considerably more C in the soil than can be added by growing trees. The peat layer can keep on growing for millennia, but trees will die at a certain age or be harvested, releasing the C back into the atmosphere, which new trees will take up again. This means there is a limit to the amount of C a forest can sequester, and a different timescale involved in the residency time of the C. Of course, the residency time is dependent on the timber's fate if it is

harvested (Hargreaves et al., 2003). In the UK, where commercial plantations have been established on deep peat, the majority of the timber is destined for biofuel (personal communication N. Cowie), hence any C stored during the plantation's lifetime would be released back as CO_2 within years.

The peat soils under these forestry plantations are thus very important as a long-term C store, which could be compromised by the combined effect of drainage and afforestation. It is therefore important to know how the peat is altered by afforestation and how much C is released into the atmosphere as a result. Knowing this can help us understand and model the effects of drainage in afforested peatlands on peat oxidation rates in boreal peatlands.

To be able to separate the peat CO_2 flux, from the CO_2 flux coming from the tree roots, fluxes have to be partitioned into autotrophic (e.g. living plant material) and heterotrophic (e.g. bacteria, fungi) components. There are several techniques to do this in the forest (Subke et al., 2006): 1) Trenching; a treatment plot is set up by separating living roots by digging a trench deeper than the main rooting depth and lining this with impenetrable material. 2) Girdling; by removing several centimetres of bark and phloem around a tree, the transport of assimilates from the crown to the roots is stopped, which eventually leads to the roots dying. 3) Gap; comparing the flux from a gap in the forest (e.g. a clear felled gap) with the soil flux from a forest stand. 4) Radiocarbon; organic matter can be dated because of the radioactive decay of the ^{14}C isotope. The $\Delta^{14}C$ value of the organic matter reflects the atmospheric value at the time of photosynthetic assimilation. All of these methods have specific uncertainties associated with artefacts induced by the techniques and accuracy of measurements (Subke et al., 2006). For example, trenching, gap and girdling approaches all result in an increase of dead root biomass, and the flux from these dead roots contributes to the heterotrophic respiration. When comparing soil CO_2 fluxes between control and treatment plots, this leads to an under-estimation of autotrophic respiration. The lack of an active rhizosphere in these approaches could also lead to a difference in the decomposition rate of litter; with smaller decomposition rates in the absence of an active rhizosphere than when one is present. This leads to an underestimation of the heterotrophic flux (Subke et al., 2004). Trenching and gap studies also lead to

an increase of soil water content, since there are no living roots to take up water. This could result in a decreased CO_2 flux. The radiocarbon method allows the flux to be split into recent (up to 1 year) assimilated C and a proportion representing older assimilated C by measuring the $\Delta^{14}C$ value of respired soil CO_2. However there are significant uncertainties associated with the assumptions underlying the age of C in measured fluxes, with significant overlap of recent "autotrophic" CO_2 and relatively recent "heterotrophic" CO_2 fluxes (Subke et al., 2006).

In this study, we aimed to quantify the heterotrophic flux contributions to CO_2 flux from the soil surface underneath coniferous forest plantations. In order to obtain peat decomposition rates, we use a trenching approach to separate autotrophic and heterotrophic CO_2 sources in the soil. By including a detailed capture of C inputs and decomposition rates of dead roots, we aim to constrain artefacts associated with this method, in order to obtain a best estimate of the C budget in organic soils under conifer plantations. We hypothesise that 1) that autotrophic respiration has a significant contribution to the total soil C flux and 2) that the CO_2 flux from litter decomposition is minimal. We further hypothesise that 3) interactions between C supply to the rhizosphere by trees result in higher decomposition rates of the litter.

3.3 Methods

3.3.1 *Study site*

The research area is located in the Flow Country in the north of Scotland, (58° 22' N, 3° 53' W), the largest area of blanket peat bog in Europe. Four paired plots were established in the beginning of June 2014 in three separate forestry plantation blocks of identical age containing a mixture of Sitka Spruce (*Picea sitchensis)* and Lodgepole Pine (*Pinus contorta)* (Figure 3.1). The forests are around 30 years old and very dense (about 5000 trees per ha), with no vascular plant understory. Average diameter at breast height (DBH) for Sitka Spruce was 13.3 cm and for Lodgepole Pine 17.9 cm, with an average ratio per area of *P. sitchensis* : *P. contorta* of 0.6. Average canopy cover was 76.3%. The peat depths in these three forest plots are between 30 and 260 cm, with depths at research

plots between 137 and 204 cm (RSPB unpublished data, n.d.; Smith et al., 2014; Smith and Hancock, 2016). The average annual precipitation in the research area between 1981-2010 was 970.5 mm with an average air temperature of 11.4°C measured at the Kinbrace weather station approximately 20 km from the plots (Location: 58º13'89''N, 3º55'1.2''W; Altitude: 103 m amsl) (Met Office, n.d.). Seasonal averaged water table relative to ground surface is -349.5 ($\pm$20.2) mm in spring (March-May), -456.6 ($\pm$33.5) mm in summer (June-August), -403.9 ($\pm$48.7) mm in autumn (September-November) and -243.8 ($\pm$14.0) mm in winter (December-February).

3.3.2 *Experimental set up*

Candidate locations for trenched and control areas in each plot were initially identified and soil surface respiration measured. Based on respiration results, two closely matched plots were selected, and randomly allocated a treatment (trenching or control). Paired plots were no more than 10 metres apart from each other.

Figure 3.1 Local map showing locations of experimental plots in yellow.

The double ploughing of the peat at the time of afforestation created a regular micro topography with low lying furrows (c. 1.5 m wide) flanked by high ridges (plough throws; c. 0.75 m wide) on either side. In between two plough throws, there is an area of 0.50 m width of the original (unploughed) surface (Figure 3.2). The height from the bottom of the furrow to the top of the plough throw is about 0.5 m and from the original surface to the plough throw is about 0.15-0.2 m. In general, conifer seedlings were planted on the plough throws because of the improved drainage compared to the original surface.

Figure 3.2 Micro topography in forest plantations, with location of measurements for flux chambers.

3.3.3 *Trenching*

In 'trenched' plots, carbon supply to roots from trees was prevented by digging a c. 40 cm deep below variable ground level, 30 cm wide trench to just below the main rooting depth of the trees, cutting through all roots present. The trench was double-lined using polypropylene gardening cloth, and re-filled with peat soil in between the two layers of cloth to prevent in-growth of roots (Figure 3.3). The dimensions of each trench plot were about 3.5 x 1.5 meters and included all three micro topographic forms. These dimension maximised the space between trees, with closest trees located about 30 cm from trenches. Following trenching, the assumption is that all roots inside the trenched plots dies over subsequent months.

Figure 3.3 Left: trenching plot dug and all living tree roots are sawn trough. Right: finished trench plot; trenches double lined with polypropylene gardening cloth and filled in with peat.

3.3.4   *CO$_2$ measurements*

In each plot, three pairs of PVC collars of 10 cm height with a diameter of 20 cm where installed to a depth of 3 cm within the three microforms (Figure 3.2). CO_2 measurements were taken using custom-built dark dynamic flow through chambers, with a height of five cm and a diameter of 20 cm, which were placed on the permanent collars for three minutes. The chamber was connected to an EGM 4 Infrared Gas Analyser (PP-Systems, Amesbury, MA, USA), recording CO_2 concentrations every 4-5 seconds. Fluxes were calculated from increases in CO_2 concentration within the chamber over 3 minutes. Measurements were carried out ten times between August 2014 and July 2016.

3.3.5   *Litter*

Six litter traps (0.07 m^2 each) were located close to each plot, and litter (falling needles and twigs) collected at each sampling visit. Litter was allowed to fall onto the soil surface within collars for the duration of the experiment. To be able to

distinguish peat respiration from litter respiration, surface litter was removed manually from of one (always the same) of the two paired collars in each microform before measuring respiration. The litter present in the collar with litter was weighed after a respiration measurement and then placed back in the collar. Litter from close to the collar was collected and weighed in the field, then taken back to the lab, dried and weighed again to establish the wet to dry mass ratio of litter and calculate litter dry mass within each collar.

3.3.6 _Roots_

Root biomass was determined from soil cores (0-20 cm deep and 6.5 cm diameter) taken from each microform in all plots, at the start (June 2014) and end (July 2016) of the experiment. Roots from each core were carefully separated and sorted into three root diameter classes: smaller than 2 mm, 2 to 5 mm, and greater than 5 mm. All roots and the root-free soil were dried at 50°C for 7 days, and weighed to establish percentage roots per gram of soil.

To estimate root decomposition, roots were taken from soil collected in each plot, dried (50°C for 7 days) and separated in the same size classes as described previously. Between 0.36 and 0.69 g of dried root material (separately for each size class) were placed in polyester mesh bags (10 x 10 cm; mesh size of 0.5 mm) for field incubations. Bags were soaked in water for 2 days prior to field placement, to mimic field conditions. Four replicate bags of each size class where buried at 5-10 cm depth in all three microforms in all plots four weeks after trenching. To account for any weight loss that may have occurred prior to field incubation, five bags of each size class where taken into the field and not buried, but taken back to the lab; the proportional mass loss of litter in these bags was used to correct the initial root mass of all other bags.

One bag per root class per microform was collected from all sites in November 2014, March 2015, July 2015 and July 2016. After retrieval, bags were dried for seven days at 50°C, and root dry mass recorded.

Root decay was fitted to an exponential decay function:

$$M_t = M_0 e^{-kt} \qquad (3.1)$$

With M_t the remaining amount of root biomass after collection from the field, M_0 the initial root biomass, t time and k the decay constant. Data fits were performed separately for root size and microform.

3.3.7 *Soil moisture and temperature*

Between June 2014 and July 2016, soil moisture and soil temperature at 5 and 20 cm soil depth were recorded at 30-minute intervals in all three microforms in a nearby plot, using 12-bit smart temperature sensors, S-TMB-M002 (Onset Computer Corporation, Bourne, MA, USA) and 10HS soil moisture smart sensors, S-SMD-M005 (Decagon Devices, Inc., Pullman, WA, USA combined with Onset's smart sensor technology) connected to a Hobo micro station (Onset Computer Corporation, Bourne, MA, USA).

In addition to this, soil temperature (10 cm thermistor) and moisture (HH2 moisture meter, Delta-T Devices, Cambridge) were measured at 5 cm depth next to each collar during sampling. Air temperature was also measured at 1 m above the ground during sampling.

3.3.8 *Statistics and flux calculations*

Data were analysed using R (RStudio Team, 2016). All CO_2 data was log transformed to meet the criteria of normality. A linear mixed-effect model (LMM) using the *nlme* package in R (Pinheiro et al., 2017) was used to predict CO_2 fluxes in between measurement campaigns. All numerical predictors were standardized to 1 standard deviation prior to statistical analyses, to allow relative effect sizes of predictors to be compared directly (Nakagawa and Schielzeth, 2010). Model selection was done based on information theory (Burnham and Anderson, 2002). First the most complicated model was built, with interactions between soil moisture, soil temperature, trench treatment and microform plus interactions between trench treatment, microform and litter treatment, with plot as a random effect. After this all possible combinations of this model were identified using the

dredge function in the *MuMIn* package (Barton, 2017). The best-performing model ("top model") was identified with the small-sample size corrected Akaike's Information Criterion (AICc). Models with a delta AICc of less than 2 are considered to be as good as the top model (Richards, 2005). In this study, just the top model was used, since all predictors in this model, except the interaction, were present in at least over half of the models in the top model set (delta AICc of less than 4). The interaction was present in 5 out of the 11 top models, so this term was included in the model as well. P-values for the mixed effect model were calculated using the package *lmerTest* (Kuznetsova et al., 2016).

Annual fluxes were calculated using the predict function over the mixed effects model from library *lme4* in R (Bates et al., 2015). Thus trench treatment, microform and litter treatment, and the interaction between soil moisture and soil temperature were taken into account with plot as a random effect. The predictions were made over half-hourly measurements of soil moisture and soil temperature at 5 cm soil depth in all three microforms just outside the plots. As soil moisture was significantly higher in trenched plots, predictions are made on soil moisture levels outside of the trench plot, to minimize the impact of this artefact. The control and trenched plots both have the same soil moisture and soil moisture x soil temperature effects, which justifies this approach. There was no difference in soil temperature between trenched and control plots.

From these predictions, partitioned fluxes were calculated from the collars without litter as:

$$F_{auto} + \varepsilon = (F_{control} + \varepsilon) - (F_{trench} + \varepsilon) \tag{3.2}$$

With F_{auto} being autotrophic fluxes, $F_{control}$ being fluxes from the control plots, F_{trench} fluxes from the trench plots, and thus being heterotrophic fluxes, and ε the associated error terms.

The annual flux coming from the litter was calculated from the difference in the modelled annual fluxes between the collars with and without litter.

3.4 Results

3.4.1 *Temporal trends in soil CO$_2$ fluxes*
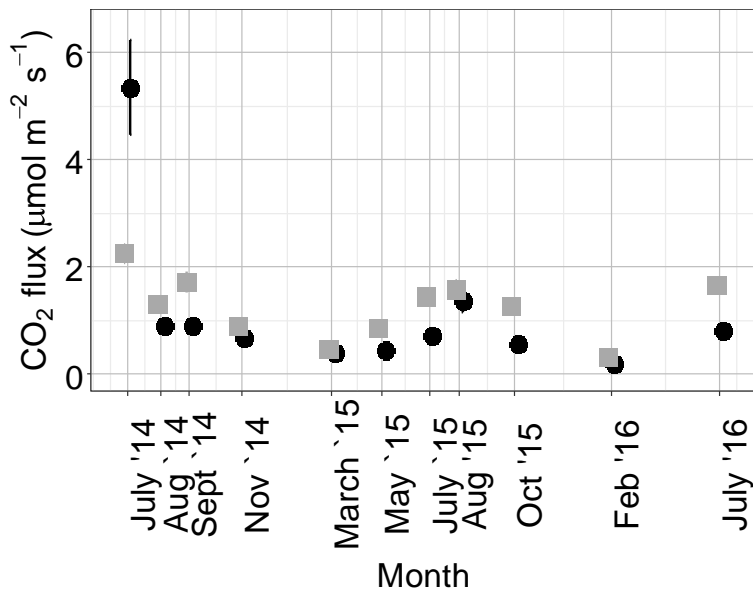
Figure 3.4 Mean CO$_2$ fluxes from control (grey squares) and trenched (black circles) plots over time, averaging across all microforms (n = 12). Error bars are standard errors, and are often smaller than symbols.

Trenching initially led to an increase in soil respiration, followed by a significant reduction in soil CO$_2$ flux. Soil respiration fluxes from both control and trenched plots showed a clear annual cycle, with highest fluxes in summer. Trenched fluxes are significantly lower than fluxes from control plots (p<0.001) and this difference is bigger in the summer (Figure 3.4).

Soil CO$_2$ fluxes were best explained with a combination of soil moisture, soil temperature, trenching treatment, microform and litter treatment, with an interaction between soil moisture and soil temperature, including 'plot' as a random effect. Table 3.1 shows model estimates for each variable, with their standard error and p-value. The marginal R^2 was 0.40 and conditional R^2 was 0.41. The set of models with a ΔAICc of less than 4 is shown in Table 3.2. The predictors of the 'top model', except the interaction, were present in at least over half of the models in the top model set and the interaction term was present in 5 out of the 11 top models.

Table 3.1 Model estimates with standard errors and p-value for best-fit model.

Fixed effect	Estimate	Std. Error	p-value
Intercept	-0.22	0.10	0.05
Trench - Trenched	-0.50	0.07	<0.001
Microform - Original surface	0.42	0.12	<0.001
Microform - Plough throw	0.35	0.13	0.006
Soil moisture	-0.12	0.06	0.03
Soil temperature	0.35	0.03	<0.001
Litter - No Litter	-0.17	0.06	0.008
Soil moisture x Soil temperature	-0.11	0.04	0.008

Table 3.2 Model selection summary, showing the 11 best ranked models with a delta AICc of less than 4. Models are ranked by AICc and weight, where higher weighted models have more statistical support. Df= degrees of freedom, Loglik=Log likelihood, and ΔAICc is the differece in AICc to the 'top model'.

Candidate models	Df	LogLik	AICc	ΔAICc	Weight
Treatment + Microform+ Litter + Soil moisture + Soil temperature + Soil moisture x Soil temperature	10	-402.65	825.87	0.00	0.22
Treatment + Microform+ Litter + Soil moisture + Soil temperature	9	-403.89	826.24	0.37	0.18

Candidate models	Df	LogLik	AICc	ΔAICc	Weight
Treatment + Microform+ Soil moisture + Soil temperature + Soil moisture x Soil temperature	9	-404.31	827.08	1.21	0.12
Treatment + Microform+ Soil moisture + Soil temperature	8	-405.40	827.17	1.30	0.12
Treatment + Microform+ Litter + Soil temperature	8	-405.81	827.98	2.11	0.08
Treatment + Litter + Soil moisture + Soil temperature	7	-407.04	828.36	2.49	0.06
Treatment + Litter + Soil moisture + Soil temperature + Soil moisture x Soil temperature	8	-406.14	828.64	2.78	0.05
Treatment + Soil moisture + Soil temperature	6	-408.32	828.86	2.99	0.05
Treatment + Microform + Soil temperature	7	-407.51	829.30	3.44	0.04
Treatment + Microform+ Litter + Soil moisture + Soil temperature + Soil moisture x Soil temperature + Microform x Treatment	12	-402.26	829.33	3.46	0.04
Treatment + Soil moisture + Soil temperature+ Soil moisture x Soil temperature	7	-407.54	829.37	3.50	0.04

3.4.2   *Spatial trend in soil CO₂ flux*

Soil respiration fluxes were significantly different between microforms for both control and trenched plots. Plots in plough throw (p=0.01) and original surface (p<0.001) had significantly higher fluxes than plots in furrow (Figure 3.5). Fluxes from collars with litter were significantly higher than fluxes from collars without litter (p=0.008).
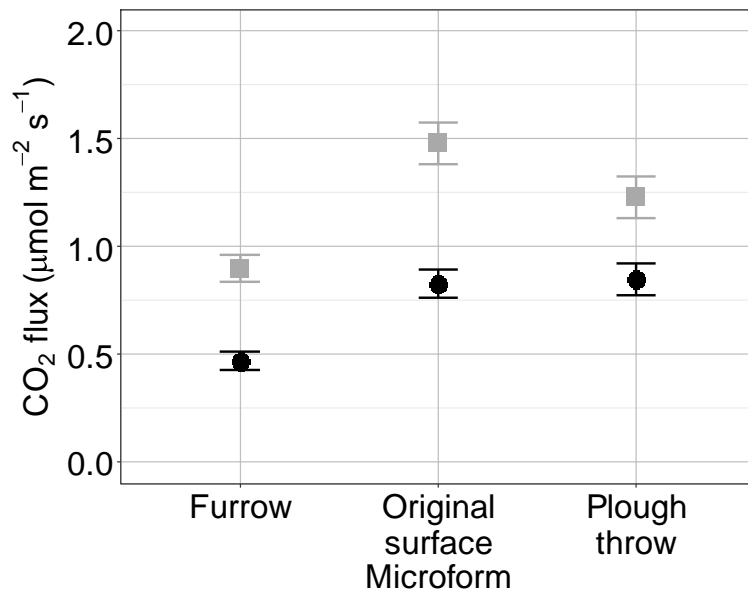
Figure 3.5 Mean soil respiration differences between microforms, over entire study period in trenched (black circles) and control (grey squares) plots. Error bars are standard errors (n=44).

3.4.3   *Role of environmental drivers in modulating CO₂ flux*

A higher soil temperature correlated with a higher soil respiration flux, whilst soil moisture showed an inconsistent correlation with flux values; this significant (p=0.008) interaction between soil temperature and soil moisture means that at high temperatures CO_2 flux decreases with increasing soil moisture, but at low temperatures flux increases when soil moisture increases (Figure 3.6).
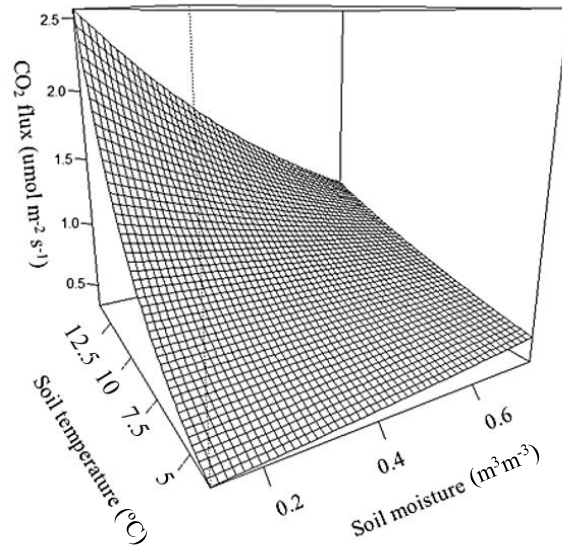
Figure 3.6 Combined effect of soil temperature and soil moisture at 5 cm depth on soil CO_2 flux from the control sites using the 'top model'.

3.4.4 *Partitioned fluxes*

Heterotrophic fluxes and autotrophic fluxes were not statistically different on all sampling campaigns, except in August 2015, where autotrophic fluxes were significantly lower than heterotrophic fluxes ($p<0.01$, Figure 3.7).
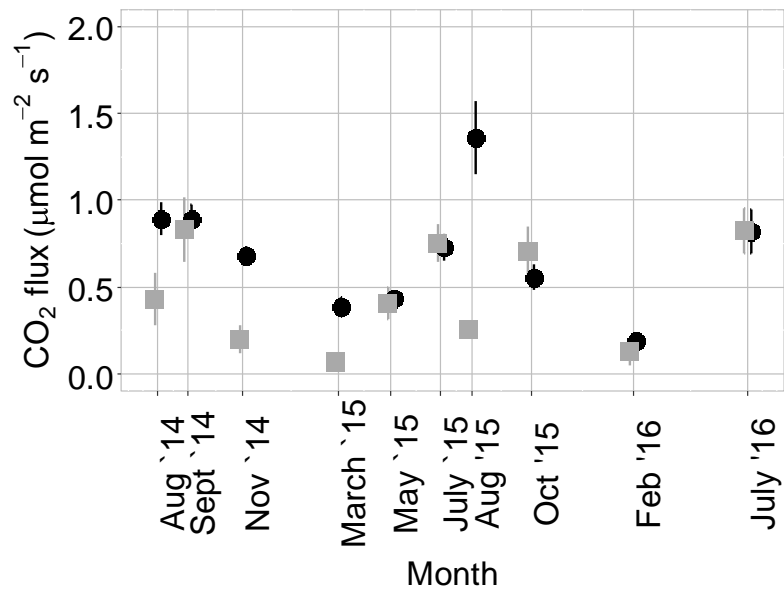
Figure 3.7 Mean partitioned fluxes over time (n=12). Heterotrophic fluxes (black circles) are total CO_2 efflux from soils in trenched plots, while autotrophic fluxes (grey squares) are calculated from the difference in soil CO_2 efflux between control and trenched plots. Error bars are standard errors.

Flux simulations based on the soil model details indicate significantly lower autotrophic fluxes than heterotrophic fluxes (p=0.01, Figure 3.8). Across all microforms, heterotrophic fluxes represented 61% and autotrophic fluxes represented 39% of the total fluxes. From these predictions, annual sums for autotrophic and heterotrophic fluxes have been calculated, giving an average peat decomposition flux of 183.7 ± 21.2 g C m^{-2} y^{-1} (Table 3.3).
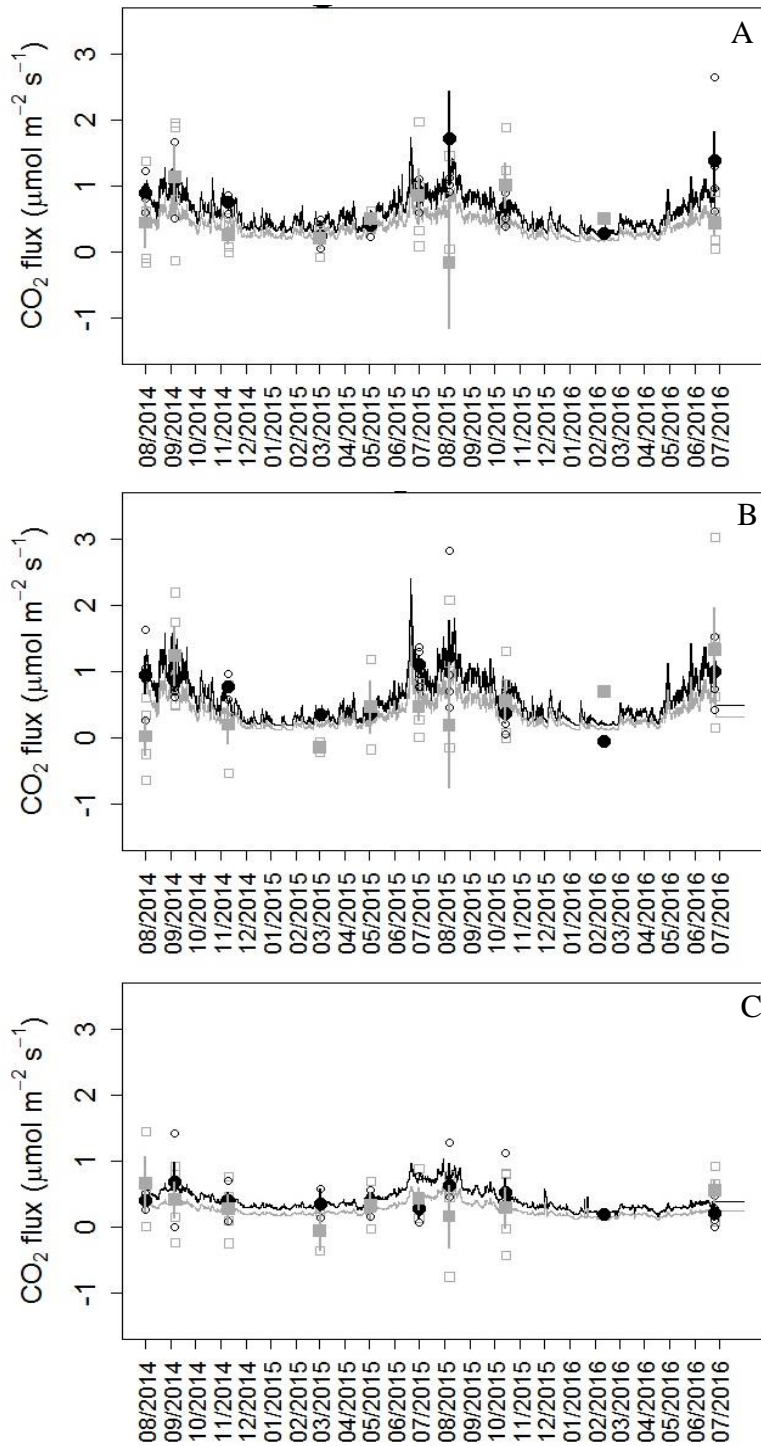
Figure 3.8 Modelled and measured fluxes of heterotrophic (grey) and autotrophic soil CO_2 efflux from the three topographic microforms. Open symbols are individual measured fluxes from n =4 plots, closed symbols are average fluxes with error bars. Connecting lines are the predicted fluxes using soil temperature and moisture at 5 cm depth. A) Original surface, B) Plough throw and C) Furrow.

Table 3.3 Mean C flux (as CO_2) (in g m^{-2} y^{-1}) emitted from heterotrophic (F_h) or autotrophic (F_a) sources during the first year (August 2014 – August 2015), second year (August 2015 – August 2016) of the study, and average fluxes for both years (standard error in brackets). Total soil CO_2 efflux (F_{soil}) is shown for average fluxes only.

Microform	Year 1		Year 2		Average		
	F_h	F_a	F_h	F_a	F_h	F_a	F_{soil}
Original surface	221.0 (20.4)	141.7 (14.4)	195.8 (19.2)	126.1 (13.2)	209.9 (19.8)	134.5 (13.8)	342.5 (34.0)
Plough throw	200.6 (25.2)	129.7 (14.4)	197.0 (25.2)	126.1 (14.4)	198.2 (25.2)	127.3 (14.4)	326.2 (42.1)
Furrow	157.3 (20.4)	100.9 (8.4)	128.5 (16.8)	82.9 (7.2)	142.9 (18.6)	91.3 (7.8)	234.2 (26.4)
Average of all microforms	193.0 (22)	124.1 (12.4)	173.8 (20.4)	111.7 (11.6)	183.7 (21.2)	117.7 (12.0)	301.3 (34.2)

3.4.5   *Impact of litter and roots*

There was no detectable difference in litter fall between trenched and control plots. Litter fall per year was 718.8 grams of litter per m^{-2} y^{-1}, and assuming 50% of this is C (Mathews, 1993), this represents a C input to the soil of 359.4 g m^{-2} y^{-1} via litter fall.

CO_2 flux from surface litter is calculated from the difference in the modelled annual fluxes between the collars with and without litter. C emitted by litter in the control plots appears to be higher than in trenched plots, but the average amount of litter in the collars of the trenched plots is higher than in the collars of the control plots (Table 3.4).

Table 3.4 Mean amount of C (in g m^{-2} y^{-1}) emitted as CO_2 by just the litter, for both years (standard error in brackets).

Microform	Litter trench (g)	CO_2 flux Trench	Litter Control (g)	CO_2 flux Control
Original surface	14.84	34.4 (32.4)	7.66	62.5 (50.4)
Plough throw	11.03	36.0 (40.8)	7.47	60.1 (61.3)
Furrow	18.53	26.4 (28.8)	17.54	43.2 (40.8)

For both the control and the trench plots, roots smaller than 2 mm declined in total biomass from the start of the experiment to the end of the experiment and there was no significant difference between the control and trenched plots at the end of the experiment. There are also no significant differences between control and trenched plots or between the beginning and end of the experiment for root classes 2-5mm and >5mm. However, there is a trend of lower root biomass in most of the trenched plots compared to the control plots at the end of the experiment, indicating that there are no roots growing in the trenched plots (Figure 3.9).

With an assumed rooting depth of 25 cm (found during trenching), root biomass per m^2 in August 2014 is 1.26 ± 0.32 kg, 0.60 ± 0.11 kg and 0.71 ± 0.25 kg for <2 mm roots, 2-5mm roots and >5 mm roots, respectively.
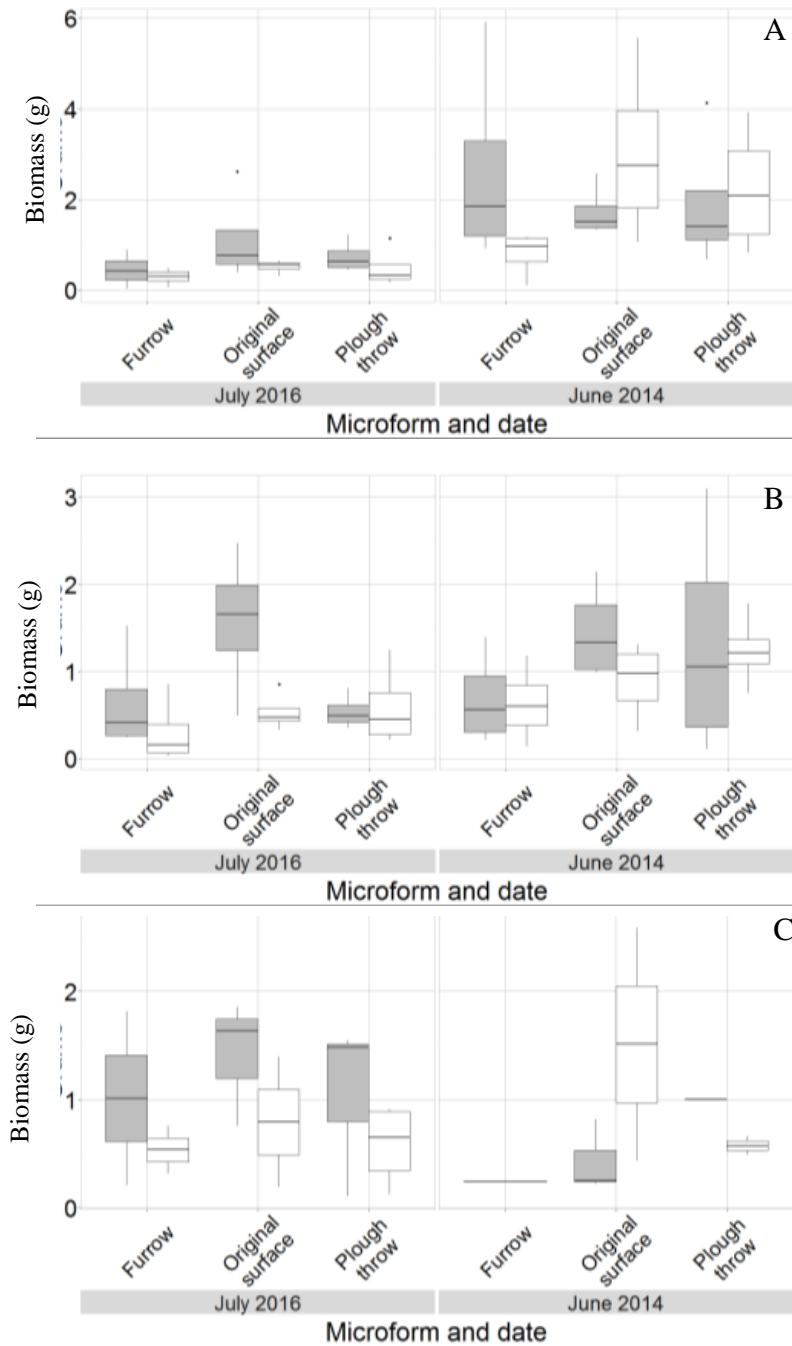
Figure 3.9 Root biomass in soil cores of control (grey) and trenched (white) plots at the beginning of the experiment (June 2014) and end of experiment (July 2016), split into three root size classes, per microform. A) root size <2 mm, B) root size 2-5 mm, C) root size >5 mm. Hinges correspond to the first and third quartiles, the upper whisker goes to the largest number that is less than or equal to quartile 3 plus 1.5 * inter-quartile range and the lower whisker goes to the smallest number that is less than or equal to quartile 1 plus 1.5 * inter-quartile range.

3.4.6   *Root decomposition*
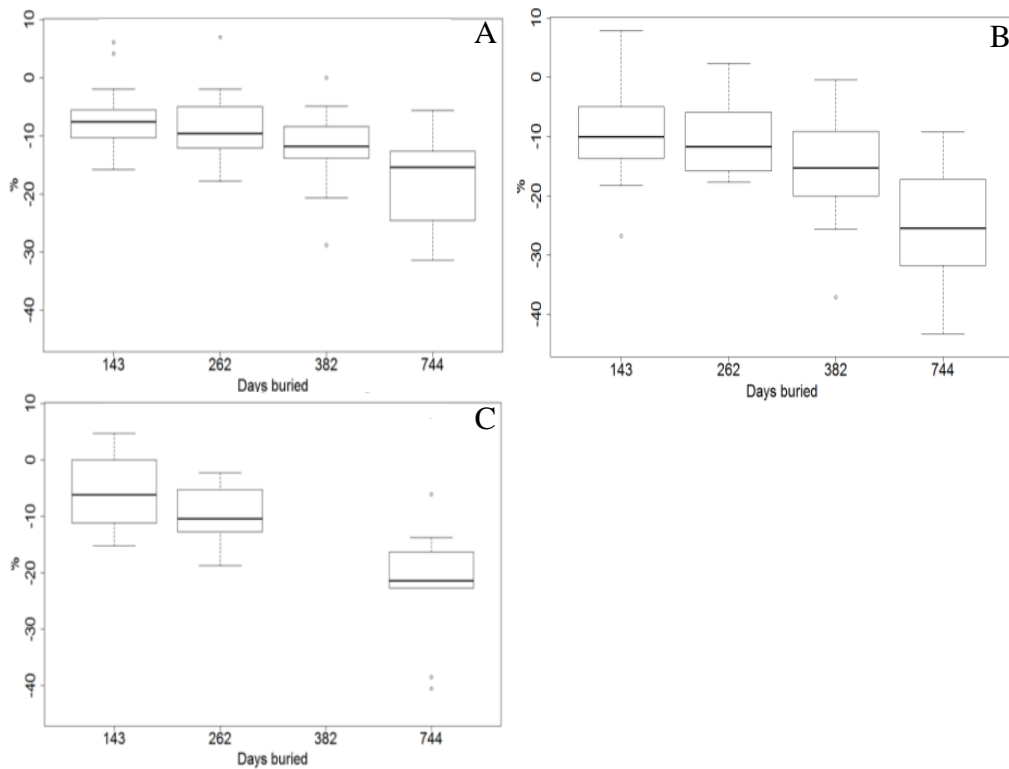
Figure 3.10 Percent lost in root bags over number of days buried, for each root size class.

Decay constants (k) calculated based on the percent biomass lost in the root bags (Figure 3.10 and Table 3.5) showed no significant differences for any of the root size classes.

Table 3.5 Decay constant (k) of roots in year^{-1} by root size class, standard error in brackets.

Root size	k
<2 mm	0.11 (0.01)
2-5 mm	0.11 (0.02)
>5 mm	0.19 (0.04)

3.4.7 *C flux from dead roots*

From the biomass of roots per m^2 in the trenched plots at the beginning of the experiment, the amount of C emitted from the decaying roots is calculated, using the exponential decay function (Table 5). It is assumed that all biomass lost is emitted as CO_2 and that 50% of roots is C, as conservative assumptions, meaning that estimates are maximum possible CO_2 flux from dead roots (Mathews, 1993).

Table 3.6 Root decay (standard error in brackets) in trenched plots and associated C emissions in $g\ m^{-2}\ y^{-1}$.

Root class	C emitted in first year	Decay in roots in second year	C emitted in second year
<2 mm	65.6 (16.7)	117.6 (29.9)	58.8 (14.9)
2-5mm	31.2 (5.7)	56.0 (10.3)	28.0 (5.1)
>5 mm	61.4 (21.6)	101.6 (35.8)	50.8 (17.9)
Total	158.2 (27.9)	275.2 (47.8)	137.6 (23.8)

The carbon emitted by the dead roots in the trenched plots needs to be subtracted from the heterotrophic flux, since this is actually autotrophic respiration that has taken place in the trenched plots as an artefact of the trenching technique. The autotrophic flux is calculated as fluxes from control plot minus fluxes from trenched plot, and the heterotrophic flux in trenched plot was overestimated, the autotrophic fluxes need to be corrected by adding the root decay flux. Since there are no significant differences in the root biomass in the soil cores between the microforms, C emitted by decaying roots is spread evenly over the three microforms (Table 3.7).

Table 3.7 Corrected from heterotrophic (F_h) or autotrophic (F_a) fluxes (standard error in brackets) in g C m^{-2} y^{-1} for dead root decay in trenched plots for both first (August 2014 – August 2015) and second year (August 2015 – August 2016) of the study. Total soil CO_2 efflux (F_{soil}) is shown for average fluxes only.

Microform	Year 1		Year 2		Average		
	F_h	F_a	F_h	F_a	F_h	F_a	F_{soil}
Original surface	168.3 (22.4)	194.4 (17.1)	149.9 (20.8)	172.0 (15.4)	159.1 (21.6)	183.2 (16.3)	342.5 (34.0)
Plough throw	147.9 (26.9)	182.4 (17.1)	151.1 (26.4)	172.0 (16.4)	149.5 (26.6)	177.2 (16.8)	326.2 (42.1)
Furrow	104.6 (22.4)	153.6 (12.5)	82.6 (18.6)	128.8 (10.7)	93.6 (20.5)	141.2 (11.6)	234.2 (26.4)
Average of all microforms	140.3 (23.9)	176.8 (15.6)	127.9 (21.9)	157.6 (14.2)	134.1 (22.9)	167.2 (14.9)	301.3 (34.2)

With this correction, heterotrophic fluxes represents approximately 46% and autotrophic fluxes 54% of the total soil fluxes in the original surface and plough throw, and 40% and 60%, respectively, in the furrow.

3.4.8 *Weighted average for Flow Country forest plantations*

In order to scale fluxes measured on the respective microforms to the entire forest stand flux, estimates were scaled according to their spatial contributions (Table 3.8). This results in a slight shift in proportion of heterotrophic and autotrophic CO_2 flux sources to 44% and 56%, respectively.

Table 3.8 Microform area weighted heterotrophic (F_h) and autotrophic (F_a) fluxes (standard error in brackets) in g C m^{-2} y^{-1} averaged over both years measured.

Microform	Fractional area	Unweight annual F_h	Unweight annual F_a	Area weighted annual F_h	Area weighted annual F_a
Original surface	0.14	159.1 (21.6)	183.2 (16.3)	22.3 (3.02)	25.6 (2.3)
Plough throw	0.43	149.5 (26.6)	177.2 (16.8)	64.3 (11.4)	76.2 (7.2)
Furrow	0.43	93.6 (20.5)	141.2 (11.6)	40.2 (8.8)	60.7 (5.0)
Total	1			126.8 (14.7)	162.5 (9.1)

The C balance of the soil under these forest plantations is visualised in Figure 3.11, with the annual CO_2 fluxes of the forest plantation based on the area-weighted fluxes.
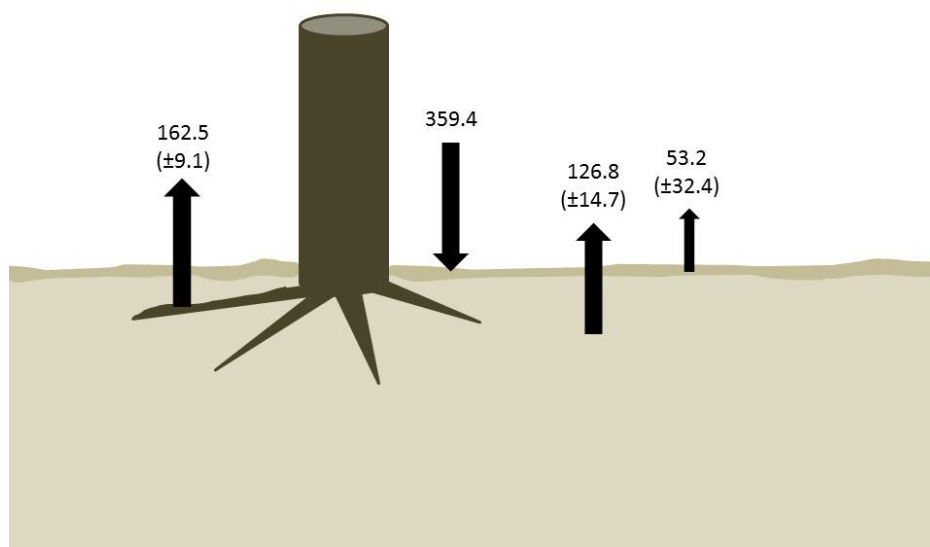
Figure 3.11 C emissions of the soil under a forest plantation on peat, CO_2 flux in g C m^{-2} y^{-1}. The area-weighted flux for the whole forest plantation is shown, with the CO_2 flux from the living roots, the peat, and needle litter and the C input from the needle litter.

3.5 Discussion

Average soil efflux corrected for microform area over the two measurement years was 289.3 ± 12.3 g C m^{-2} y^{-1} from which 162.5 ± 9.1 g C m^{-2} y^{-1} is autotrophic and 126.8 ± 14.7 g C m^{-2} y^{-1} is heterotrophic. Bond-Lamberty and Thomson (2010) have created an online dynamic database of published soil respiration data, including data from 1953 to 2015. The annual heterotrophic flux against the annual soil respiration flux of all boreal forests included in the database (91 sites from 62 studies, see Figure 3.13 and Table 7.1) is plotted, with forests on peat in grey triangles. Our study is included with a red square (Figure 3.12). Average annual soil respiration from all boreal forests included in the database is 542.8 ± 24.5 g C m^{-2} y^{-1} and average heterotrophic flux is 330.4 ± 15.3, compared to our 301.3 ± 25.4 and 134.1 ± 22.9 g C m^{-2} y^{-1} respectively. Our site also has a significantly lower soil respiration and heterotrophic respiration rate than the forests on peat in this database. The average annual soil respiration from the boreal forests on peat is 692.3 ± 39.5 g C m^{-2} y^{-1} and average heterotrophic flux is 347.4 ± 15.3 g C m^{-2} y^{-1}. Average heterotrophic flux from all boreal forests in this database is 61% and autotrophic 39% and for boreal forests on peat 50% heterotrophic and 50% autotrophic, compared to our 44% and 56% respectively. So our results are not only lower in the amount of CO_2 coming from them but also the relative heterotrophic flux is smaller. However our study is right on the regression line over all studies in the database, meaning it does have similar fluxes to other boreal forests, but it is at the lower end (Figure 3.12). This might be because the forest plantations in Scotland are planted on peatlands that are naturally treeless, where the forests in this database are either natural forests or drained, but existing forests. Therefore, the processes going on in these ecosystems might not be similar, which could potentially explain why our results are on the lower end of the graph.

When comparing our results to a study in a similar forest plantation in Ireland, a 39-year old drained *Sitka Spruce* plantation on naturally treeless blanket bog, our total soil respiration of 301.3 ± 25.4 g C m^{-2} y^{-1} is similar but a slightly higher than what they found; 260 g C m^{-2} y^{-1} (Byrne and Farrell, 2005). Our peat oxidation rates, 126.8 ± 14.7 g C m^{-2} y^{-1}, are higher than found by Hargreaves et

al. (2003), who found <100 g C m^{-2} y^{-1} in a mature Spruce stand on peat in Scotland. However, they point out that their estimate is the difference between two large uncertain numbers; total net C exchange and net tree gain.
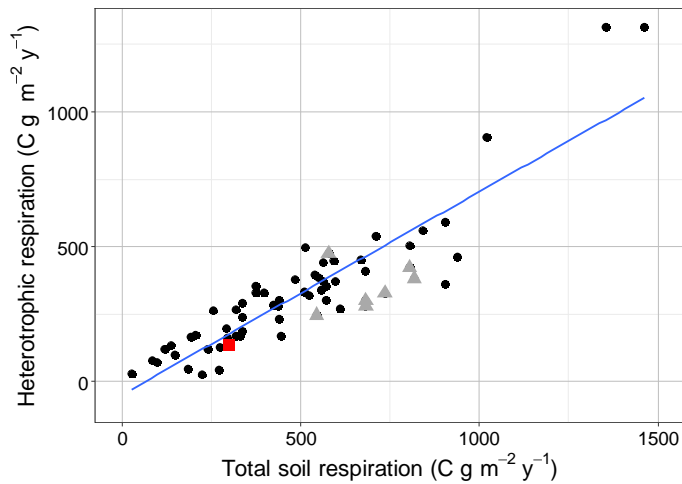
Figure 3.12 Heterotrophic annual flux against soil respiration annual flux (g C m^{-2} y^{-1}) in Boreal forests, peat soils in grey triangles, from Bond-Lamberty and Thomson (2010) dynamic database. This study included in the red square.

Figure 3.13 Locations of research sites used in Figure 3.12 (Bond-Lamberty and Thomson 2010).

Our root decay constants of between 0.11 and 0.19 year^{-1}, for root sizes <2 mm, 2-5 mm and >5 mm respectively are lower than those published in the meta-analytical review by Subke et al. (2006) where a range from 0.21-0.93 year^{-1} was found. However none of the sites used in their meta-analysis were located in the boreal zone, and decay constants of litter in northern peatlands were found to be between 0.02 and 0.45 year^{-1} (Moore et al., 2008), our results fall within this range.

To calculate the root biomass at the start of the experiment one soil core per microform was taken and assumed this was representative for the whole microform. It was not possible to distinguish between living and dead roots in the soil cores, so initial living root biomass might have been overestimated. The total root biomass was used to estimate living root biomass per m^2 and the assumption was made that all of this was killed by trenching and the amount of C emitted from it was calculated. All biomass lost was assumed to be decomposed and thus emitted as CO_2. This is probably an overestimation, since fine roots are a key energy source and heterotrophic microorganisms in the soil use the dead roots as substrate for their metabolism, absorbing some of the C in their biomass and releasing the rest as CO_2 into the atmosphere (Gougoulias et al., 2014; Yuan and Chen, 2010). The dead root emission correction made a big difference to the ratio of heterotrophic to autotrophic flux, going from 61% and 39% respectively over all microforms to 46% and 54% respectively in the original surface and plough throw and 40% and 60% respectively in the furrow, so a decrease in heterotrophic flux of 15% and 21%. This is in line with the corrections used in other studies; Subke et al. (2006) found in there meta-analysis a range from 2% to 24%, with an average of 12%. This big difference in the fraction heterotrophic : autotrophic flux shows that even two years after trenching the dead roots still have a major contribution to the CO_2 flux, so this is something that should be taken into account when carrying out experiments like this.

The observed difference in the CO_2 flux from just the litter between the control and trenched plots (Table 3.4) indicates (at least as a trend) that heterotrophic processes are reduced under trenching. In presence of an active rhizosphere (control plots), decomposition of needle litter appears to be faster than when the rhizosphere is not active (trenched plots). Therefore, in the control plots a slightly larger proportion of the total CO_2 flux is heterotrophic decomposition than the trenched plots suggest, which means there is a slight underestimation of heterotrophic flux in our results. This is in line with results from literature (Subke et al., 2004, 2011).

Using our litter traps and interpolating between sampling days, we found a C input of 359.4 g C m^{-2} y^{-1} via litter fall. This is in line with other Sitka Spruce

forests of similar age to our forest plantations in the UK, which range from 272.9 to 573.1 g C m^{-2} y^{-1} (www.forestry.gov.uk/fr/INFD-67MEVC in Morison et al. 2012). As the total modelled soil efflux is only 289.3 ± 12.3 g m^{-2} y^{-1}, this would mean there is more C entering the soil as surface litter alone than there is C leaving as CO_2 meaning that even without taking root turnover into account, there is seemingly a soil C sink.

The average peat depth in these forest plots is 126.2 (±15.5) cm, with 0.47 kg C m^{-2} per centimetre depth (Cannell et al., 1993) this means that there is about 59.3 (±7.3) kg C m^{-2} stored in the peat under these forests. In order to find out if peat is being lost under these plantations, the total soil C input from roots and litter should be quantified over the lifespan of the trees. This minus the C lost via peat oxidation will show if the peat layer is getting thinner or not.

4 An incubation study of the GHG flux responses to a changing water table linked to biochemical parameters across a peatland restoration chronosequence

4.1 Abstract

Large areas of northern peatlands have been drained and afforested with conifer trees in the 20th century. This has led to changes in the hydrology, chemical quality and quantity of organic matter inputs and soil microbial communities, which are all likely to impact the greenhouse gas fluxes from these sites. Since the 1990s, considerable areas of these forest plantations have been felled and drains are blocked, in order to restore them back to open peatlands. The aim of this study was to understand how the changes in composition of peat following forest removal respond to a water table rise and investigate how this may be linked to GHG fluxes. Therefore, we conducted an incubation study, where vegetation free cores from a near pristine bog, three different restoration sites, felled in 1998, 2006 and 2012 and a forest plantation have been incubated at 8° Celsius with either a low, a high or a changed from low to high water table. CO_2 and CH_4 fluxes have been measured, pore water is analysed for DOC, nitrate, phosphate and sulphate, and the peat quality was measured using fibre analysis, C:N ratio and soil pH. Results show that the peat quality and nutrient availability in the pore water have been altered by the forest plantations and this has resulted in different CO_2 fluxes between the sites under the same temperature and water table conditions. Higher CO_2 fluxes were found in the peat cores retrieved from forest plantation plots than from cores from sites that have undergone restoration and near pristine bog. However, there were very few differences in CH_4 fluxes from the different sites, indicating that on its own (and in absence of biotic interactions under field conditions), forestry effects on CH_4 flux are limited.

4.2 Introduction

Natural peatlands are an important carbon sink. About a third of the global terrestrial carbon (C) pool is estimated to be stored in northern peatlands (Joosten et al., 2012; Stocker et al., 2013) and an equivalent of 40-60% of the atmospheric

carbon dioxide (CO_2) is stored in peatlands around the world (Stocker et al., 2013), despite only covering about 3% of the total land area (Joosten et al., 2012). In Scotland, peat soils cover about 1.7M ha (equivalent 22.7% of Scottish land surface area) and it is estimated that they store 1620Mt of C, or c. 56% of Scottish soil C (Chapman et al., 2009). However, large areas of peatlands in Scotland have been drained and afforested primarily with conifer species, in the 20th century (Huttunen et al., 2003). Consequential changes include altered soil hydrology, shifts in chemical quality and quantity of organic matter inputs and impacts on soil microbial associations (Andersen et al., 2010; Bellamy et al., 2012; Creevy et al., 2018). These changes in turn mean that processes governing organic matter formation and greenhouse gas exchange are likely to be impacted.

The quality of dead organic matter entering organic soils is an important factor in determining its rates of stabilisation and decomposability (Conant et al., 2011). De Deyn et al. (2008) have shown that in some environments the vegetation can be a good proxy for soil C dynamics, since the quality of the litter is controlled by the vegetation. The peat of bogs is recalcitrant (Bridgham et al., 1998) and thus is it likely that recent C inputs from plants drive the CO_2 and CH_4 fluxes (Chanton et al., 2008; Joabsson and Christensen, 2001; Ström et al., 2003). In peatlands undergoing afforestation, drainage of the soil also influences litter decay and soil organic matter (SOM) transformations (Wickland et al., 2010).

From the 1990s onwards, increased awareness of the negative impacts of deep drainage and afforestation of peatlands and a better understanding of the importance of peatlands for other ecosystem services has led to a shift in land management in the UK (Anderson et al., 2016). Large areas are already undergoing restoration with plans to restore more. However, there is not much known about the legacy of forested areas on the soil environments. Whether previous forest cover has had an impact on soil C stocks, the quality of organic matter found within the peat body, and consequently microbial decomposability and greenhouse gas production remain largely unknown.

Soil carbon cycling in peatlands depends on the soil temperature, water table depth, plant community composition, chemical characteristics of the peat and the

microbial activity in the peat (Whiting and Chanton, 1993; Yavitt, et al., 1997). Previous studies on the effects of water table depth on CO_2 and CH_4 fluxes show that in general decreasing the depth of the water table increases CH_4 fluxes and decreases CO_2 fluxes from the peat (Blodau et al., 2004; Dinsmore et al., 2008; Estop-Aragonés et al., 2016). However, there are so far no assessments of the chemical legacy of the trees in the pore water and of the chemistry of the peat. Neither is there an assessment of whether this has an influence on the CO_2 and CH_4 fluxes and if their response to an increasing water table is the same in sites that are restored in different years.

In the north of Scotland, restoration measures are aimed at reinstating blanket peatland vegetation in combination with hydrological restoration (i.e. blocking of drains and re-wetting of formerly forested areas). Hydrological restoration was initially done by only blocking the collector drains around the plots. This however does not lead to the desired high water table, unless the ground was almost flat. Therefore, additional furrow blocking is done now at around the same time as felling and additional blocking of the furrows of earlier felled sites is also now being carried out. The impact of higher water tables generally leads to an altered GHG balance, with reduced aerobic decomposition of organic matter to CO_2, and general increases in anaerobic methane production (Dinsmore et al., 2008). Interaction of these changes with altered biochemical composition as a consequence of land use change have however not been explored. The goal of this experiment is therefore to understand how the changes in composition of peat following forest removal influence the GHG fluxes and investigate how they respond to a water table rise. We hypothesize that: 1. Sites with different vegetation types (determined by time since restoration started), show differences in biochemical composition of soil organic matter (SOM), 2. This difference in biochemical composition of the SOM will lead to different GHG fluxes under the same climatic conditions, and 3. The timing (in years post felling) of a rise in water table matters; different restoration ages will respond differently to this rise. Another goal is to determine whether there are generic environmental predictors or site-specific factors of GHG production linked to vegetation cover history under restored peatlands. In this context, being able to understand if there are

generic controls is important, as it enables a prediction of fluxes based on more generic information.

4.3 Methods

4.3.1 *Study site*

The research area is located in the Flow Country in the north of Scotland, (58° 22' N, 3° 53' W), one of the largest areas of blanket peat bogs in Europe. Large areas of the Flow Country were drained and planted with non-native trees (*Picea sitchensis* and *Pinus contorta)* in the 1980's. The average annual precipitation between 1981-2010 was 970.5 mm with an average air temperature of 11.4°C, measured at the Kinbrace weather station approximately 20 km from the research sites (Location: 58º13'89''N, 3º55'1.2''W; Altitude: 103 m amsl) (Met Office, n.d.).

Ongoing felling of trees and blocking of collector drains to restore the peatlands has resulted in a chronosequence of different restoration ages. For this study, we used soil cores from a number of sites that span the duration of the restoration process, cores from blanket bog sites that were never afforested or drained and forest plantation plots. Restoration sites include plots felled in 1998 (R98), 2006 (R06) and 2012 (R12).

Forestry plantation control plots contained a mixture of *P. sitchensis* and *P. contorta*. The plantations are around 30 years old and very dense (about 5000 trees per ha), with no vascular understory, but sporadic patches of *Hypnum jutlandicum* and *Sphagnum* mosses (e.g. *S. fallax*). Average diameter at breast height for *P. sitchensis* was 13.3 cm and for *Pinus contorta* 17.9 cm, with an average distribution of 60% *P. sitchensis* and 40% *P. contorta* based on stem area. Average canopy cover was 76.3%. (RSPB unpublished data, n.d.; Smith et al., 2014; Smith and Hancock, 2016).

The R12 plots had patches of *Polytrichum commune, Eriophorum* spp.*, Calluna vulgaris* and in some instances, *Sphagnum fallax* and *Sphagnum capillifolium* in

furrows. However, three years after restoration there was still a lot of bare peat visible. After felling, the trees were left in the furrows.

In the R06 plots, the ground was almost completely covered with vegetation and the species were similar to the R12 plots. Trees here were felled and left in the furrows.

R98 plots were dominated by *Deschampsia flexuosa, Eriophorum, Sphagnum* spp*., Calluna vulgaris, Erica cinerea* and *Erica tetralix.* On the whole site, individual natural regeneration of *P. sitchensis* was present. Trees were younger and therefore smaller than the other restoration sites, and had also been felled and left in furrows.

Bog control plots were located in three different sites and were dominated by *Sphagnum* spp*., Erica tetralix, Calluna vulgaris, Eriophorum vaginatum, Myrica gale* and *Pleurozia purpurea.*

4.3.2 Soil sampling

A total of 175 soil cores of 10 or 20 cm depth and a diameter of 6.5 cm, were collected from the original surface of all plots in March 2015. 150 short cores were taken from two different depths; 75 from 0-10 cm, 75 from 10-20 cm and 25 'long' cores were taken from 0-20 cm. Within each site, 5 sampling locations, spaced about 10 m apart, were chosen to capture spatial variations. At each location, three shallow and deep cores as well as one long core were taken. Each within-site location acted as one experimental block, such that each of the three water table treatments (see below) was allocated to each of the three replicate 10-cm cores per depth. The sampling was done in that way to differentiate between top soil processes and slightly deeper processes in the upper layers of peat with the short cores, while the tall ones would give an overall picture of the upper soil processes. Samples were taken by hammering a PVC pipe of the right length into the soil and extracting a core. Cores were kept in their PVC pipe and sealed in plastic bags for transport to the lab. In the laboratory, the pipes with the cores were placed in plastic tubs (short cores: 9.5 cm diameter and 11 cm tall, long cores: 9 cm diameter and 26.5 cm tall; Figure 4.1). Distilled water was added to a

set level and topped up every few days during the experiment. Soils were maintained at 3° C for 10 weeks before adjusting temperature to 8° C, close to the seasonal average. CO_2 and CH_4 flux measurements started 5 days after the temperature adjustment.

Three water table treatments were set up, where shallow and deep cores from each sampled site/block had water tables adjusted at either a low level (8.5 cm below the surface), high water table (1 cm below soil surface) or had water tables at first set to the lower level for two weeks from start of flux measurements, before water tables were increased to the 'high' level. The long cores only had a changed water table treatment, changing from low (-11 cm) to high (-1 cm) after the first measurement round.

Figure 4.1 Peat cores in their plastic tubs in the incubator. Rhizon samplers are inserted here with evacuated glass vials attached.

4.3.3   *Flux measurements*

Four CO_2 and CH_4 flux measurement rounds were carried out between the beginning of June and mid-October 2015. During each round, CO_2 and CH_4 fluxes were measured from every soil core. Measurements were done by closing the containers with an airtight lid and two tubes connected to a fast greenhouse gas analyser (FGGA-24EP, Los Gatos, San Jose, CA, USA) which measured CO_2 and CH_4 concentrations every 5 seconds. Concentrations were recorded for 10 minutes under dark conditions.

Flux were calculated using the *HMR* package (Pedersen, 2017) in RStudio (Version 1.0.136). Concentrations are regressed against time since container closure to calculate the flux, using either a linear or a non-linear function (see Section 7.1), whichever fits the data best (Pedersen, 2010). Fluxes were expressed in units of mole CO_2 evolved per mass of C in soil cores (determined after flux experiments had finished). Only fluxes based on regressions with a p-value < 0.1 were considered as robust estimates, and considered for further analysis. This led to rejection of 2.4% of CH_4 fluxes, whilst none of the CO_2 fluxes were rejected. To eliminate outliers, fluxes with more than 3 times the standard deviation of average fluxes per gas species were also eliminated, which led to 0.9% rejection of CH_4 fluxes and 1% for CO_2 fluxes.

4.3.4   *Pore water chemistry*

Pore water samples were taken with Rhizon MOM samplers (Rhizosphere Research Products B.V., Wageningen, the Netherlands) for the first and last sampling rounds. These samplers have a diameter of 2.5 mm and a mean pore size of 0.15 μm, and the porous area of the sampler is 10 cm long. The samplers were inserted vertically in the middle of the core immediately after flux measurements, and samples were obtained 24 hours after flux measurements by connecting an evacuated glass vial (Exetainer; Labco Limited, Lampeter, UK; Figure 4.1). About 10 ml of sample was collected each time, which was stored in a dark fridge at 8° C.

A range of biochemical properties was determined in three replicates per treatment of pore water samples. Nitrate, phosphate and sulphate were determined using an ion chromatograph (DX-120, Dionex Corporation, Sunnyvale, USA) and Dissolved Organic Carbon (DOC) concentrations were measured on a Total Organic Carbon analyser (TOC-V CSN, Shimadzu Corporation, Kyoto, Japan). Instrument downtime meant that most samples were analysed up to 5 months after collection. In order to quantify any changes in concentration for all parameters, one batch of 60 samples was analysed repeatedly after 2 to 4 weeks and after 5 months.

4.3.5   Soil chemistry

After the flux measurements were completed, all soil cores were dried at 80°C for 72 hours and weighed. Soil chemistry measurements were taken on the dried peat as follows:

4.3.6   Soil pH measurements

3 g of homogenized dried soil was suspended in 54 ml of distilled water (1:19 dilution) and pH measured after 30 minutes (FiveEasy pH meter, Mettler Toledo, Columbus, USA).

4.3.7   Fibre analysis

Fibre analyses were carried out at Aberdeen university in April 2016 on a sub set of cores of which the pore water had also been analysed (n = 3 per site for each depth increment).

Shallow cores (0-10 cm) were divided into two smaller depth increments to improve resolution of superficial peat layers. Top layers were those which comprised of litter and moss, and the lower layer was consisting of amorphous peat. Where no distinct layers were evident, cores were halved. Dried samples were homogenized with a mortar and pestle, resulting in grain size suitable for mesh bags used in fibre analysis. Roots were extracted from dried samples.

The fibre analysis followed the Carnegie protocol: Carbon extractions to determine hemicellulose, cellulose and lignin in leaf tissue (Carnegie Institution for Science, Stanford, CA, USA) with a few alterations. As this protocol is designed for leaves, not peat, there was a risk of losing some material through the mesh of the sampling bags. To account for this, an additional step was added to the protocol, where bags were submerged in boiling de-ionized water and agitated for 1-2 minutes 5 times. After this, the neutral detergent fibre (NDF) extraction step was carried out in which carbohydrates, lipids, pectin, starch, soluble proteins and non-protein nitrogen are extracted. Then the acid detergent fibre (ADF) step in which hemicellulose and membrane-bound proteins are extracted, then the acid determined lignin (ADL) step to extract cellulose and leave lignin and recalcitrant

materials behind and finally the ashing step to determine the percentage of mineral soil. The other alteration to the Carnegie protocol was to rinse the samples in acetone after the NDF and ADF step as suggested by Ankom Technology. This was done since some of the NDF and ADF solution could stick to the fibres, which would be left in the sample when just rinsing with de-ionized water. The NDF and ADF step were done in an Ankom 2000 fibre analyser (Ankom technology NY, USA).

4.3.8 *C:N ratio*

C and N content of the same cores that were used for fibre analysis were determined on a Flash Combustion Elemental analyser (CE Instruments (Carlo Erba) NA2500, Wigan, UK). Materials were dried at 105°C overnight and ball milled prior to analysis.

4.3.9 *Statistical analysis*

All statistical analysis were done in RStudio (RStudio Team, 2016). Fluxes were analysed using linear mixed effect models for each core depth, using the *nlme* package (Pinheiro et al., 2017). Both CO_2 and CH_4 fluxes were square root transformed, to meet normality requirements. Model selection was based on information theory (Burnham and Anderson, 2002); first the most complex model was built, which included *site*, *water table and time since start of experiment* as fixed effects, with an interaction between them and *incubator* and *plot within site* as a random effect. All possible combinations of this model were identified using the 'dredge' function in the *MuMIn* package (Barton, 2017). Goodness of model fit was assessed with the small-sample size corrected Akaike's Information Criterion (AICc), which is calculated using the number of parameters and either the maximum likelihood estimate for the model or the residual sum of squares. "Likelihood" here is a measure of the extent to which a sample provides support for particular values of a parameter in a parametric model. AICc values of different models can be compared and the model with the lowest AICc is selected as the 'best approximating model' (Burnham and Anderson, 2002).

Peat quality data was analysed using linear models, with *site* and *core depth* as fixed effects and an interaction between them. The pore water chemicals were also analysed with linear models, where the most complex model used *site, core depth, water table* and *time since start of experiment* as fixed effects with interactions between them. Then 'dredge' was used again to find the 'best approximating model'.

Linear models per core depth were used to find parameters that could predict CO_2 and CH_4 fluxes, with peat properties and *site* as fixed effects with an interaction between them.

Principal components analysis was done on the peat properties, using the 'rda' function in the *Vegan* package (Oksanen et al., 2017). The variables nitrate, soluble cell component and lignin and recalcitrant materials were log transformed to meet normality requirements. Post hoc testing against *site* was done using the 'adonis' function.

4.4 Results

4.4.1 *CO₂ fluxes*

Overall, CO_2 fluxes from peat cores varied between -0.20 nmol g^{-1} C s^{-1} and 0.27 nmol g^{-1} C s^{-1}, the negative fluxes are most likely due to a measurement error; however, no correction for this was found. There are some consistent patterns between sites and significant influences of water table treatments. Mean fluxes from shallow (0.038 ±0.003 nmol g^{-1} C s^{-1}) and long (0.028 ±0.004 nmol g^{-1} C s^{-1}) peat cores were significantly greater than from deeper depth (0.0072 ±0.002 nmol g^{-1} C s^{-1}, p<0.0001; Figure 4.2).
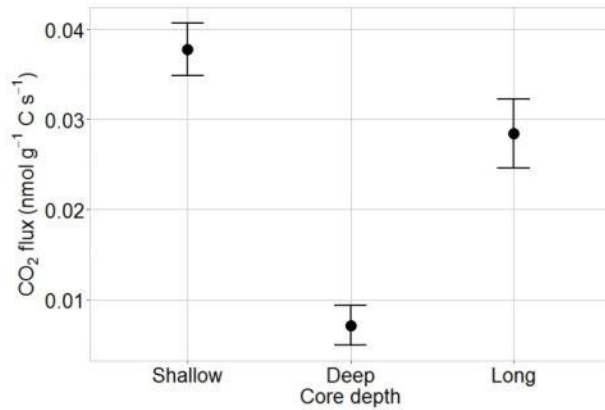
Figure 4.2 Mean CO_2 flux per core depth, averaged over all sites, all water table treatments and all measurement rounds. With shallow 0-10 cm depth (n=300), deep 10-20 cm depth (n=300) and long 0-20 cm depth (n=100).

4.4.1.1 Shallow soil cores

CO_2 flux from forest plantation showed highest flux rates (0.064 ±0.009 nmol g^{-1} C s^{-1}), significantly higher than those from restored sites R12 (0.029 ±0.005 nmol g^{-1} C s^{-1}, p=0.02) and R06 (0.025 ±0.004 nmol g^{-1} C s^{-1}, p=0.02) and from bog cores (0.027 ±0.005, p=0.05), with no further significant differences between sites (p > 0.3; Figure 4.4).

At 0.061 ±0.005 nmol g^{-1} C s^{-1}, the low water table treatment resulted in significantly higher CO_2 fluxes than for either high (0.025 ±0.004 nmol g^{-1} C s^{-1}) or changed (0.016 ±0.004 nmol g^{-1} C s^{-1}) water level treatments (p < 0.001). There was no significant difference between the latter two water level treatments, however. A slight trend of decreasing CO_2 fluxes over the time of the incubation (Figure 4.3) was statistically significant (p <0.001).

4.4.1.2 Deep soil cores

CO_2 fluxes measured from deep cores showed less differentiation between sites than what was observed for shallow peat cores. Fluxes were generally lower compared to more superficial peat cores, irrespective of water table, with several sites showing average fluxes not significantly different from zero. Highest fluxes were observed for forest plantation cores (0.018 ±0.007 nmol g^{-1} C s^{-1}), and lowest rates for cores from R98 (-0.0025 ±0.003 nmol g^{-1} C s^{-1}). The mean flux

difference between these sites was significant ($p<0.0001$). Fluxes from forest plantation cores are also significantly higher than from R06 cores (0.0049 ± 0.004 nmol g^{-1} C s^{-1}, $p=0.04$) and marginally significantly higher than from bog cores (0.0065 ± 0.004 nmol g^{-1} C s^{-1}, $p=0.06$). Fluxes from R12 are marginally significantly higher than from R98 cores (0.0090 nmol g^{-1} C s^{-1}, $p=0.06$), with no further significant differences between sites ($p>0.9$; Figure 4.3). Across all sites, water table treatments did not produce a significant effect in deep cores ($p>0.1$). A trend of decreasing fluxes over time is significant ($p<0.001$, Figure 4.3) with no detectable interaction between time and water table treatments.

4.4.1.3 Long soil cores

Despite differences in CO_2 production in shorter cores from either 0-10 and 10-20 cm, long soil cores, which integrate CO_2 production across the depth from 0 to 20 cm, showed no consistent differences between sites ($p>0.4$; Figure 4.4), or between low and changed water table treatments ($p=0.1$). However, time since the start of the experiment was highly significant, with a decline in CO_2 flux over the three-month period ($p<0.001$; Figure 4.3). The lower level of replication compared to shallow and deep soil cores meant that no interaction between sites and treatments could be tested.
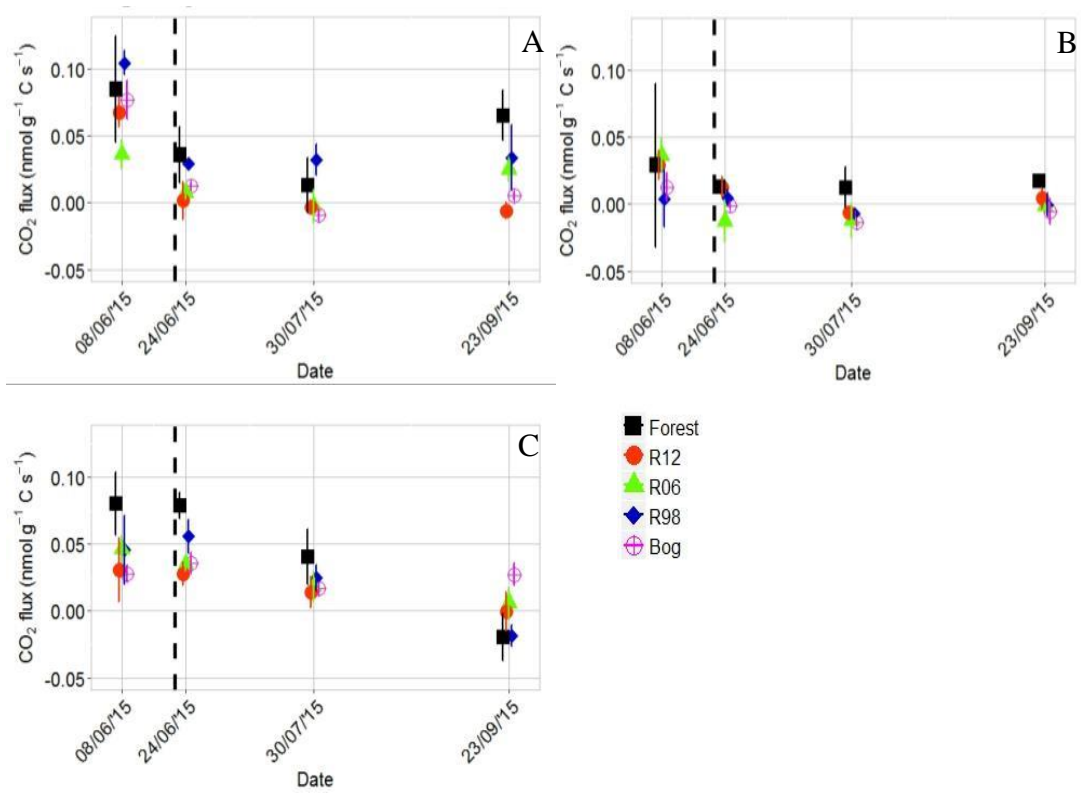
Figure 4.3 CO_2 fluxes for changed water table levels (n=5); error bars are standard error. Dotted line is timing of water table change, from low to high. A) Shallow cores, B) Deep cores, C) Long cores.
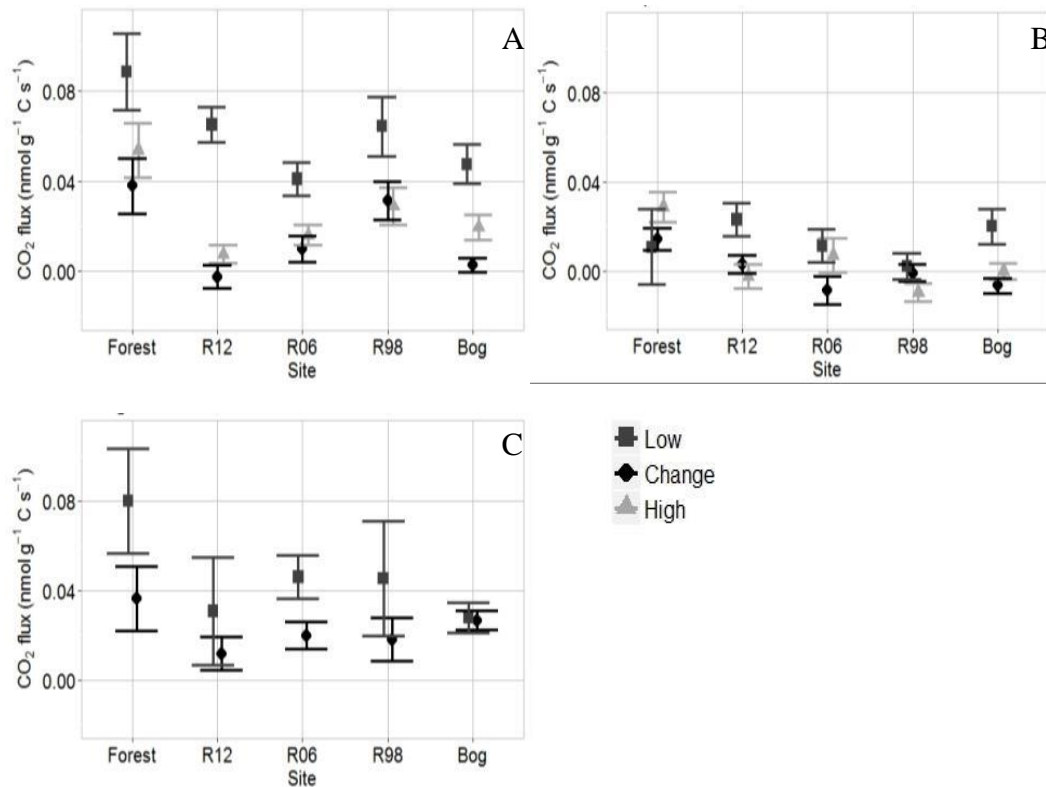
Figure 4.4 CO_2 fluxes per site, points are averages over all measurement rounds (n=20), error bars are standard errors. A) Shallow cores, B) Deep cores, C) Long cores.

4.4.2 *CH₄ fluxes*

Absolute CH_4 fluxes from peat cores varied between -1.11 pmol g^{-1} C s^{-1} and 0.89 pmol g^{-1} C s^{-1}. There was no consistent pattern between sites and water table treatments. Across all sites and water tables, mean fluxes from shallow peat cores (0.0098 ±0.007 pmol g^{-1} C s^{-1}) were significantly higher than from deep cores (-0.010 ±0.005 pmol g^{-1} C s^{-1}, p=0.05). The mean fluxes from the long cores are not significantly different from either of the shorter depth increments (0.0092 ±0.009 pmol g^{-1} C s^{-1}, p>0.3; Figure 4.5).
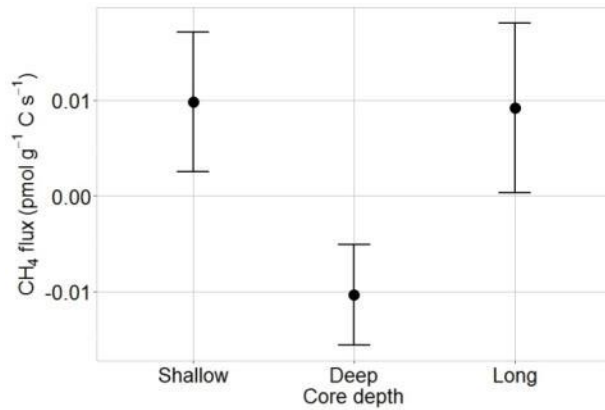
Figure 4.5 Mean CH_4 fluxes averaged over all sites, all water table treatments and all measurement rounds. With shallow 0-10 cm depth (n=300), deep 10-20 cm depth (n=300) and long 0-20 cm depth (n=100).

4.4.2.1 Shallow soil cores

There were no significant differences in CH_4 flux between sites (p>0.7), water table treatments (p>0.5) or time since the start of the experiment (p=0.3) across all shallow peat cores (Figure 4.6, Figure 4.7).

4.4.2.2 Deep soil cores

A similar result was found for deep peat cores; with only a marginally significant difference between Forest and R06 (p=0.07) was found and no further differences between sites (p>0.13). There were no significant differences between water table treatments (p>0.3) or time since the start of the experiment (p=0.3) (Figure 4.6, Figure 4.7).

4.4.2.3 Long soil cores

For the long cores there are no significant differences between sites (p> 0.2, Figure 4.7), water table treatment (p=0.99) and time since the start of the experiment (p=0.9, Figure 4.6, Figure 4.7).
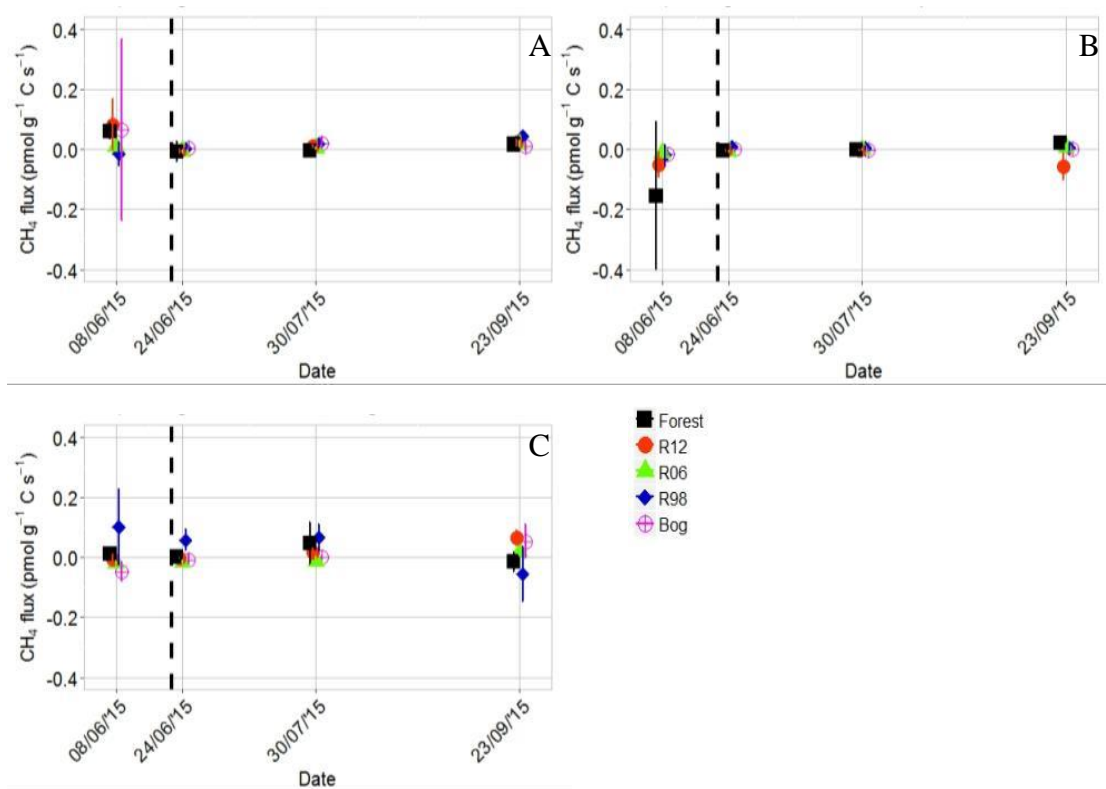
Figure 4.6 CH$_4$ fluxes for the changed water level over the running time of the experiment (n=5), error bars are standard errors. Dotted line is timing of water table change, from low to high. A) Shallow cores, B) Deep cores, C) Long cores.
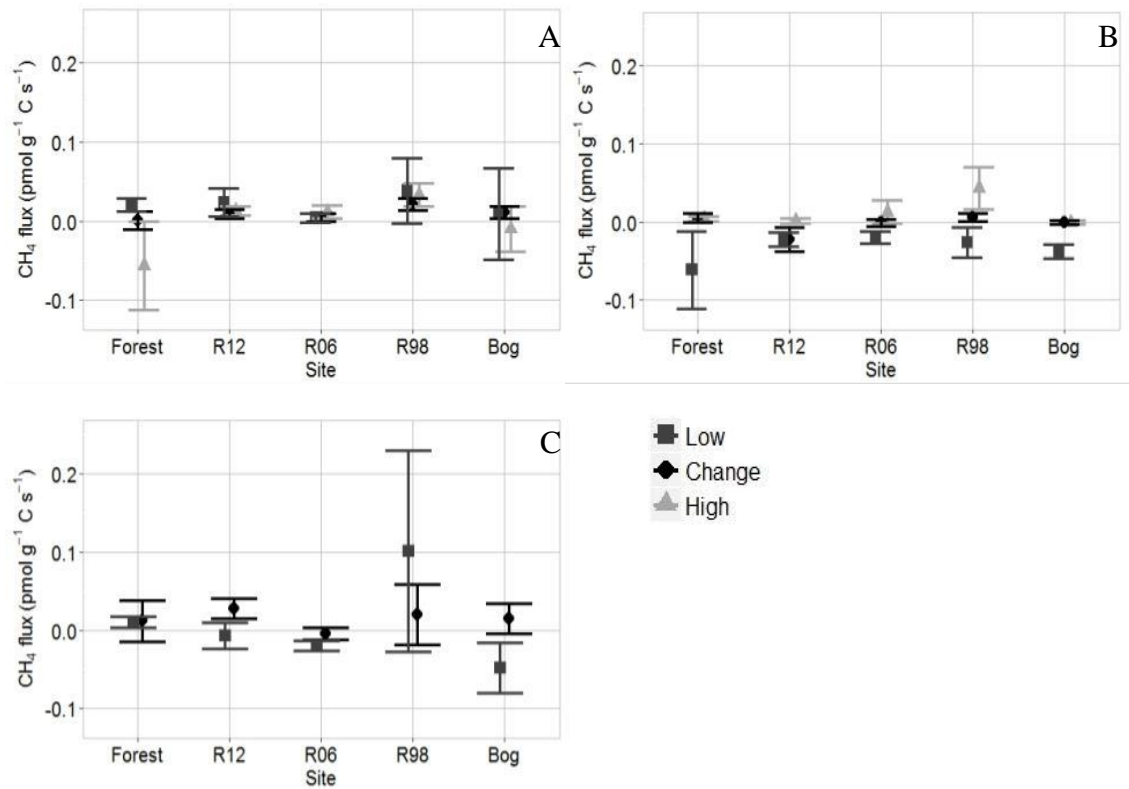
Figure 4.7 CH$_4$ fluxes from the different core depths, points are averages over all measurement rounds (n=20), error bars are standard errors. A) Shallow cores, B) Deep cores, C) Long cores.

4.4.3 *Pore water chemistry*

The 5 months storage of the water samples did not have a significant effect on DOC, (p=0.9), Nitrate (p=0.3), Sulphate (p=0.7) or Phosphate (p=0.5).
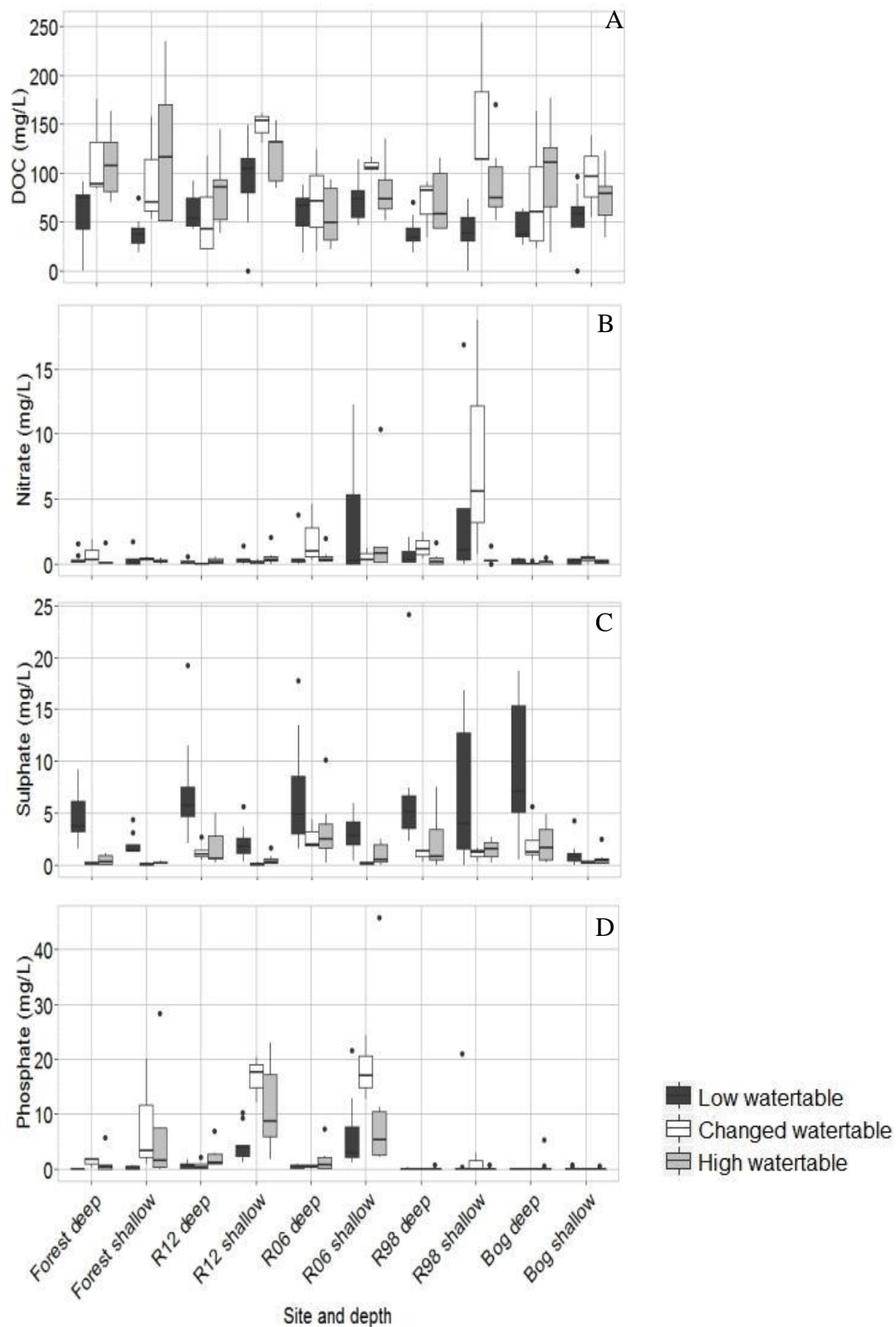
Figure 4.8 Concentrations of A) DOC, B) Nitrate, C) Sulphate and D) Phosphate in the pore water of the different water table treatments, per site split into core depth. Hinges

correspond to the first and third quartiles, the upper whisker goes to the largest number that is less than or equal to quartile 3 plus 1.5 * inter-quartile range and the lower whisker goes to the smallest number that is less than or equal to quartile 1 plus 1.5 * inter-quartile range.

4.4.3.1 DOC

DOC levels in the pore water of the peat cores ranged from 0 to 253.2 mg/L. There is no difference between sites in DOC levels in the pore water (p> 0.1). Over all sites and all depths, the level of water table has a significant influence on DOC concentrations, with low water table showing lower mean values than changed water table treatments (60.6 ±3.2 mg/L and 113.5 ±9.1 mg/L respectively, p<0.001) and significantly lower than high water table (89.9 ±5.4 mg/L, p<0.0001), but no significant difference between the changed and high water table (p>0.9). However, the depth that cores were taken from does not have a significant impact on the DOC concentration in pore water (p=0.3). The interaction between depth and site does show a significant difference only between R12 shallow cores and the shallow cores from the bog (108.6 ±3.4 mg/L and 68.3 ±7.7 mg/L respectively, p=0.02; Figure 4.8). Time since the start of the experiment was significant (p=0.01), and the adjusted R^2 for the model used is 0.29.

4.4.3.2 Nitrate

Nitrate concentration in the pore water is very low in most cores except in cores from R98 and R06, ranging from 0 to 40.3 mg/L. There are some significant differences between the sites; nitrate concentrations in the pore water of the forest plantation (0.3 ±0.08 mg/L) cores are significantly lower than in pore water of cores from R98 (2.7 ±0.03, p=0.01). The concentrations in the pore water of the R12 (0.2 ±0.06 mg/L) and bog (0.2 ±0.03) cores are significantly lower than the cores from R06 (3.2 ±1.1, p=0.02 and 0.004 respectively) and R98 (p=0.002 and 0.0003 respectively). Across all sites, deep cores have significantly lower concentrations than shallow cores (0.4 ±0.08 mg/L and 2.0 ±0.7 mg/L, respectively; p < 0.01). The interaction between sites and depth of the cores shows a significant difference between the shallow cores of R98 and the forest plantation

(p=0.004) and R12 (p=0.004), and the shallow cores of the bog sites and R06 (p=0.03) and R98 (p=0.0007, Figure 4.8B). The adjusted R^2 for the model used is 0.16.

4.4.3.3 Sulphate

Concentrations of sulphate across all samples range from 0 to 24.1 mg/L. Across all core depths and water table treatments the forest plantation (2.1 ±0.4 mg/L) cores had significantly lower concentrations of sulphate than in R06 (4.3 ±0.7, p=0.02) and R98 (4.1 ±0.8, p=0.003) with no further differences between sites. The shallow cores (1.8 ±0.3 mg/L) have significantly less Sulphate in the pore water than the deep cores (4.2 ±0.5, p<0.0001). The interaction between sites and depth of the cores result in significant differences for the deep cores between forest plantation and bog cores (p=0.03) and for the shallow cores between R98 and forest plantation (p=0.04) and bog cores (p=0.02). Within sites there is a significant difference between the deep and shallow cores for R12 (p=0.004), R06 (p=0.01) and the bog cores (p<0.0001). Water table also has a significant influence on the Sulphate concentrations in the pore water; low water table (4.9 ±0.5 mg/L) is significantly higher than cores with the changed (2.1 ±0.6 mg/L, p=0.0001) and high (1.4 ±0.2, p<0.0001), and there is no difference between the high and the changed water table (p=0.9, Figure 4.8C). Time since the start of the experiment has a significant influence on the concentration of sulphate (p=0.003). The adjusted R^2 for the model used is 0.49.

4.4.3.4 Phosphate

Phosphate concentrations in the pore water ranged from 0 to 45.8 mg/L. There is hardly any phosphate in the pore water of most of the cores, except in the shallow cores from R06, R12 and there is some in the shallow core of the forest plantations (Figure 4.8D). Concentrations in the pore water from the forest plantations (2.8 ±1.2 mg/L) is significantly higher than in the cores from R98 (0.7 ±0.5 mg/L, p=0.005) and the bog (1.2 ±1.1 mg/L, p=0.0002) and significantly lower than in the cores from R12 (4.8 ±0.9 mg/L, p=0.003) and R06 (5.8 ±1.6 mg/L, p=0.003). The phosphate concentrations in cores from R06 and R12 are

significantly higher than in cores from R98 (p<0.0001) and bog (p<0.0001). Over all sites and all depths, the concentrations in cores with low water table (1.4 ±0.3 mg/L) are significantly lower than in cores with high water table (3.6 ±1.0 mg/L, p=0.007) and there is no difference between low and changed water table (6.7 ±1.9, p=0.2) and changed and high water table (p=0.9). Over all sites and all water tables phosphate concentrations in the pore water of the deep cores (0.6 ±0.1 mg/L) are significantly lower than in the shallow cores (4.9 ±0.9 mg/L, p<0.0001). The interaction between site and depth of the cores shows for the shallow cores the same significant differences as for the sites overall, showing that these differences are driven in the top layer of the soil, there are no significant differences for the deep cores. There are significant differences between the deep and shallow cores for sites R12 (p<0.0001) and R06 (p<0.0001). Time since the start of the experiment had a significant influence on the concentration (p=0.005), although the difference is very small. The adjusted R^2 for the model used is 0.57.

4.4.3.5 Soil pH

The soil pH measured in all cores ranges from 3.8 to 5. Over all depths, the pH of the bog (4.3 ±0.02) and forest (4.3 ±0.05) soil are significantly higher than of the soil in sites R06 (4.1 ±0.02, p<0.001 and p<0.001 respectively) and R12 (4.2 ±0.03, p=0.02 and p=0.01 respectively). The pH of the soil in site R98 (4.3 ±0.02) is significantly higher than in R06 (p=0.04). The deep cores have a marginally lower pH than the shallow cores (4.2 ±0.02 and 4.3 ±0.03 respectively, p=0.04), but there is no significant difference between the deep and long cores (4.2 ±0.03, p=0.6) and long and shallow cores (p=0.7). The interaction between site and depth of the cores leads to significant differences between sites for the shallow cores, but not for the deep cores; the pH of forest shallow cores is significantly higher than in the bog shallow (p=0.01), R06 shallow (p<0.0001), R12 shallow (p<0.0001) and R98 shallow (p=0.0007). The only significant difference within a site is in the forest plantation where shallow cores have significantly higher pH than the deep cores (p<0.0001; Figure 4.9). The adjusted R^2 for the model used is 0.3.
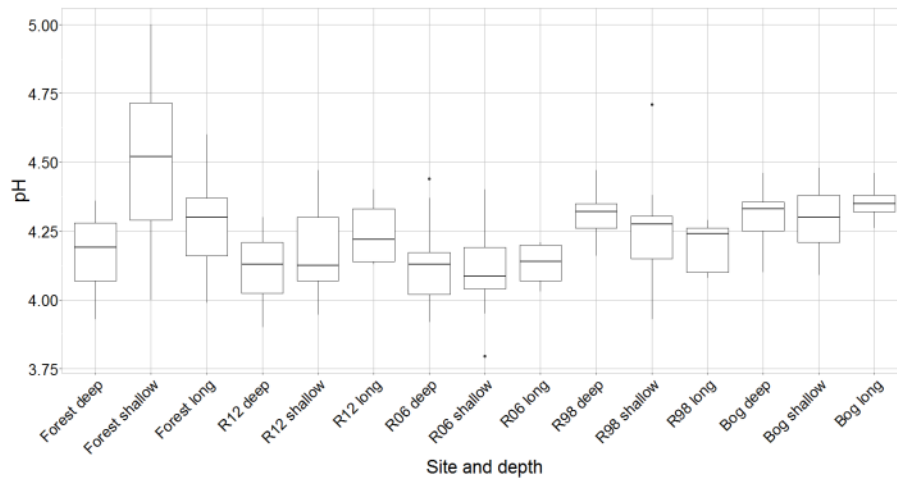
Figure 4.9 Soil pH for the different sites, split per depth of the soil core.

4.4.4 *Fibre analysis of the soil*

4.4.4.1 *Soluble components*

Soluble components of peat biomass include carbohydrates, lipids, pectin, starch, soluble proteins and non-protein nitrogen. In general, the percentage of soluble cell components increases towards the deeper layers and there is a gradient from forest plantation cores towards the bog cores across the age of restoration sites. Forest plantation cores (18.2 ±1.3%) have a significantly lower percentage of soluble cell components than R06 (23.0 ±1.3%, p=0.01), R98 (25.2 ±1.5%, p=0.0001) and bog (22.3 ±1.0%, p=0.05) and R12 has a significantly lower percentage than R98 (p=0.004). Across all sites, the deep cores (24.4 ±0.9%) contain the most soluble cell components, compared to the upper part of shallow cores (19.0 ±1.0%, p<0.001) and the lower part of shallow cores (21.8 ±1.1%, p=0.05). The difference in soluble cell components between lower and upper parts of shallow cores was statistically significant (p=0.03; Figure 4.10A).

4.4.4.2 *Hemicellulose*

Hemicellulose contents show increases from the forest plantation towards bog cores and from the shallow to the deep cores. Forest plantation (14.7 ±1.8%), R12 (13.4 ±1.5%) and R06 (14.9 ±1.5%) cores have significantly less hemicellulose than R98 (20.3 ±1.5%, p=0.03, p=0.007 and p=0.05 respectively) and bog cores (21.8 ±1.0%, p=0.005, p=0.0007 and p=0.006 respectively). The shallow top

cores (15.2 ±1.2%) have significantly less hemicellulose than the deep cores (18.9 ±1.0%, p=0.03). When comparing sites by depth of the cores there are a few significant differences; the forest shallow bottom cores (10.0 ±1.5%) have significantly less hemicellulose than the R98 (23.7 ±2.2%, p=0.01) and bog shallow bottom cores (24.5 ±1.6%, p=0.006) and the R12 shallow bottom cores (12.7 ±1.5%) have significantly less hemicellulose than bog shallow bottom (p=0.05; Figure 4.10B).

4.4.4.3   Cellulose

Across all sites there is a higher percentage of cellulose in the shallow top (22.8 ±0.5%) and shallow bottom (20.5 ±0.8%) layers compared to the deep layers (18.7 ±0.8% p=0.0001 and p=0.02 respectively). Bog cores (23.9 ±0.9%) have significantly higher percentages of cellulose than restored sites (18.6-20.7%; p<0.05), but are only marginally and not significantly higher than forest cores (Figure 4.10C).

4.4.4.4   Lignin and recalcitrant materials

Percentages of lignin and recalcitrant material levels show an apparent decrease from forest plantation towards bog and from the top to the deeper layers in the restored sites, with significantly higher levels in forest plantation (44.9 ±2.2%), R12 (44.2 ±2.1%) and R06 (41.3 ±1.8%) than R98 (34.1 ±0.9%, p≤0.01) and bog (31.0 ±1.5%, p≤0.0001). The deep cores (36.4 ±1.2%) have significantly lower levels of lignin and recalcitrant material than the shallow top cores (41.4 ±1.9%, p=0.01), whilst the shallow bottom cores (39.5 ±2.5%) are not significantly different from either deep or shallow top cores (p≥0.2).

When comparing sites by depth of the cores there are a few significant differences; for the shallow top cores: R12 (49.8 ±1.7%) has significantly higher levels of lignin and recalcitrant materials than R98 (33.9 ±1.6%, p=0.007) and bog (34.0 ±3.8%, p=0.007). For the shallow bottom cores: R12 (43.0 ±3.5%), R06 (42.4 ±3.7%) and forest plantation cores (p=51.5 ±1.7%) have significantly higher levels than bog cores (27.3 ±0.9, p=0.008, p=0.01 and p<0.0001 respectively) and

forest plantation cores have significantly higher levels than R98 (33.3 ±2.5%, p=0.001; Figure 4.10D).

4.4.4.5 Mineral soil

There is very little mineral soil material in all peat cores, ranging from 0 to 7.8%, with no significant differences between sites or soil core depth Figure 4.10E).
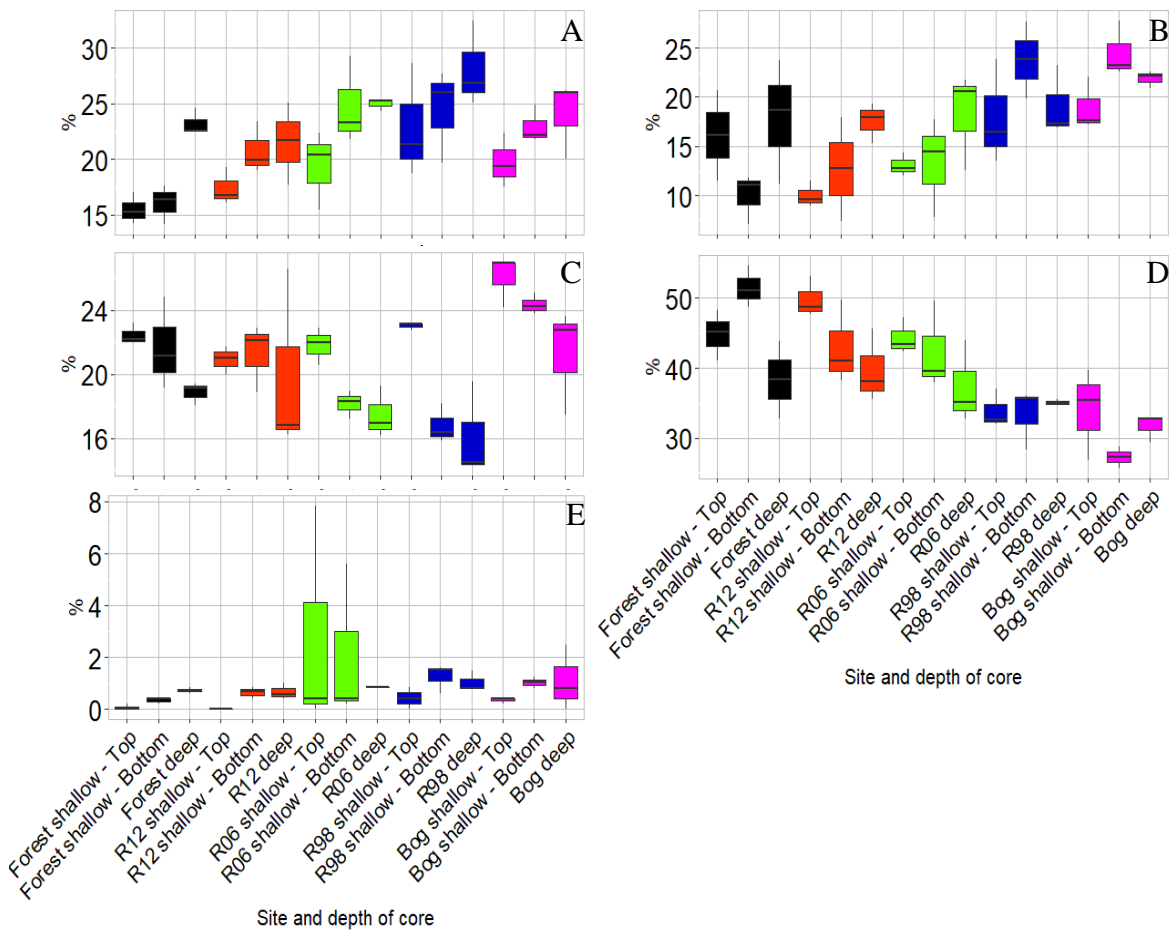
Figure 4.10 Peat quality per site split into core depth, with the shallow cores also split in a top and bottom part. A) % Soluble cell component, B) % Hemicellulose and bound proteins, C) % Cellulose, D) % Lignin and recalcitrant material and E) % Mineral soil.

C:N ratio ranges from 24.2 to 54.4, with an apparent downward trend from the forest plantation cores to the bog cores (Figure 4.11). R98 cores (28.4 ±1.0) have significantly lower C:N ratio than forest plantation (36.8 ±2.7, p=0.002) and R12 (36.2 ±1.3, p=0.003) cores, but no other significant differences between sites were detected. Across all sites, the deep cores (31.6 ±1.5) have a significantly lower C:N ratio than the shallow top cores (35.7 ±1.6, p=0.03). At 32.6 ±1.1, shallow bottom cores are of intermediate mean C:N ratios, which did not however differ significantly from the other core depths.
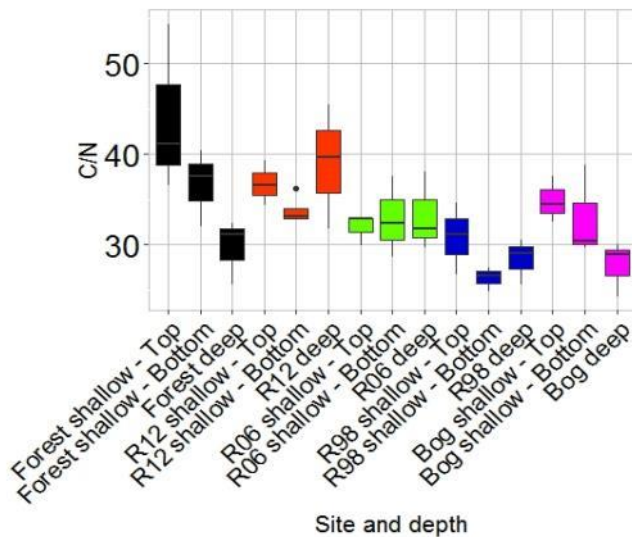
Figure 4.11 C:N ratio per site split into core depth, with the shallow cores also split in a top and bottom part.

4.4.6 <u>Fluxes against pore water chemistry and peat quality</u>

4.4.6.1 CO_2 fluxes

4.4.6.1.1 Shallow cores

In shallow cores, CO_2 flux shows negative correlations with both DOC (p=0.0002) and phosphate (p=0.001) concentrations in the pore water, and a positive correlation with soil pH (p<0.001; Figure 4.12). No other significant correlations across all sites were found. Within sites, however, one relationship

emerged in R12 cores; increasing levels of sulphate (p=0.02) are associated with higher CO_2 fluxes. None of the other chemical variables are significantly related to CO_2 fluxes for the shallow cores (p>0.2).
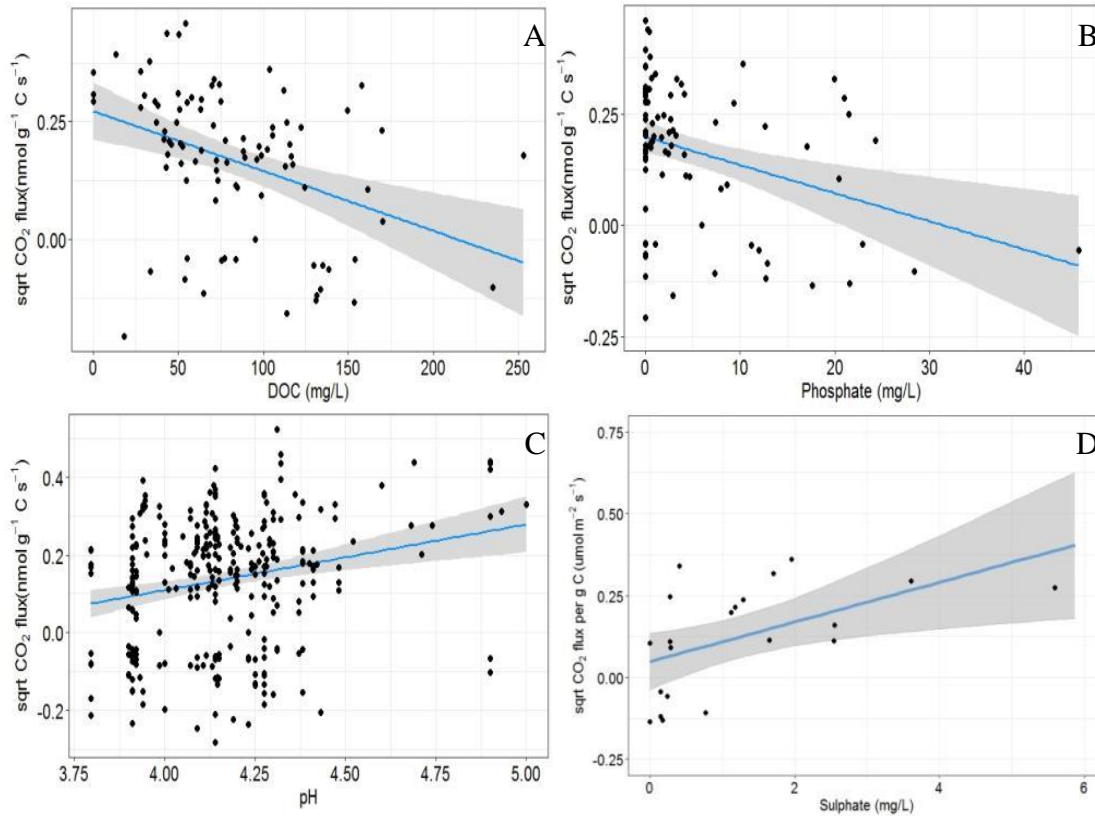
Figure 4.12 Correlations of CO_2 fluxes with biochemical parameters in the shallow cores. A), B) and C) in all sites, and D) in site R12.

4.4.6.1.2 Deep

For the deep cores a few of the chemicals have a marginally significant relationship with CO_2 fluxes; increasing CO_2 fluxes were associated with increasing levels of sulphate in all sites (p=0.07) and nitrate in sites R98 (p=0.06) and Bog (p=0.09). None of the other chemicals had a significant relationship with CO_2 fluxes (p>0.2).
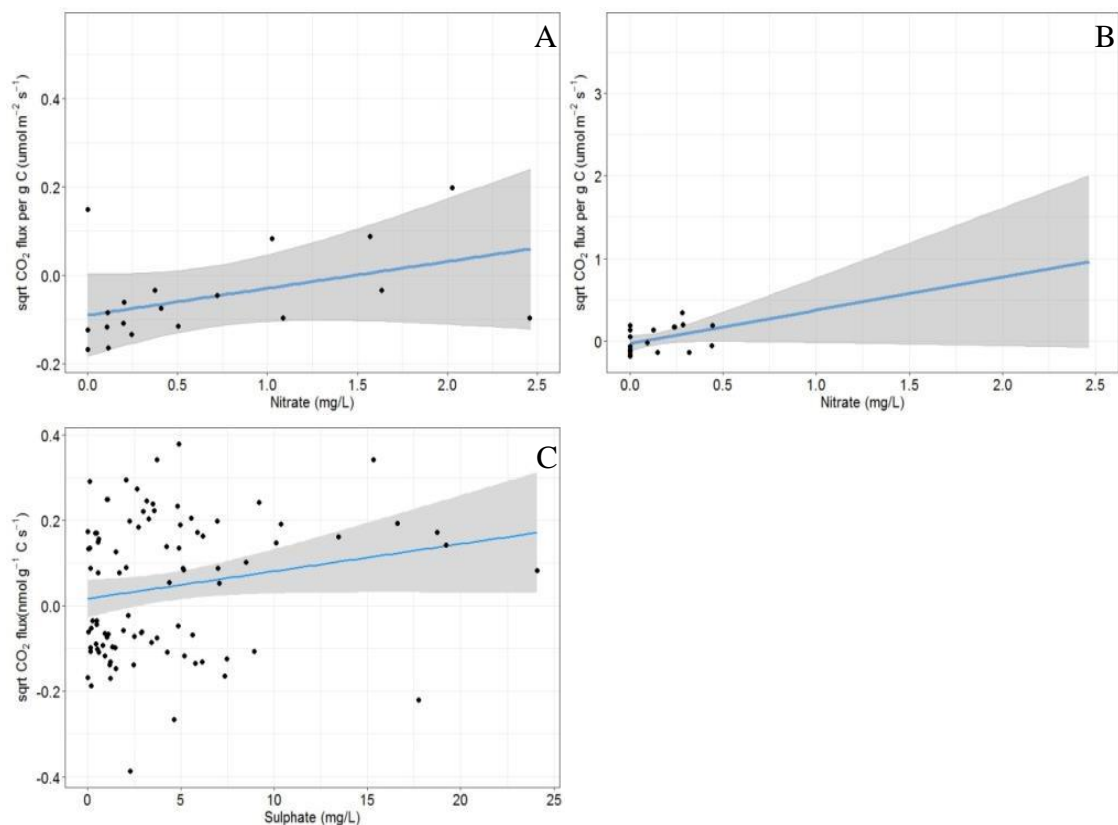
Figure 4.13 Correlations of CO_2 fluxes with biochemical parameters in the deep cores. A) in site R98, B), in site Bog and C) in all sites.

4.4.6.1.3 Long

Increasing levels of DOC (p=0.006) and nitrate (p=0.03) were associated with decreasing CO_2 fluxes in the long cores. A similar relationship was found for phosphate, although this was only marginally significant (p=0.07; Figure 4.14). There are no site-specific relationships, and none of the other pore water chemicals or pH were significantly related (p>0.5) to the CO_2 fluxes, no fibre analysis was done on the long cores.
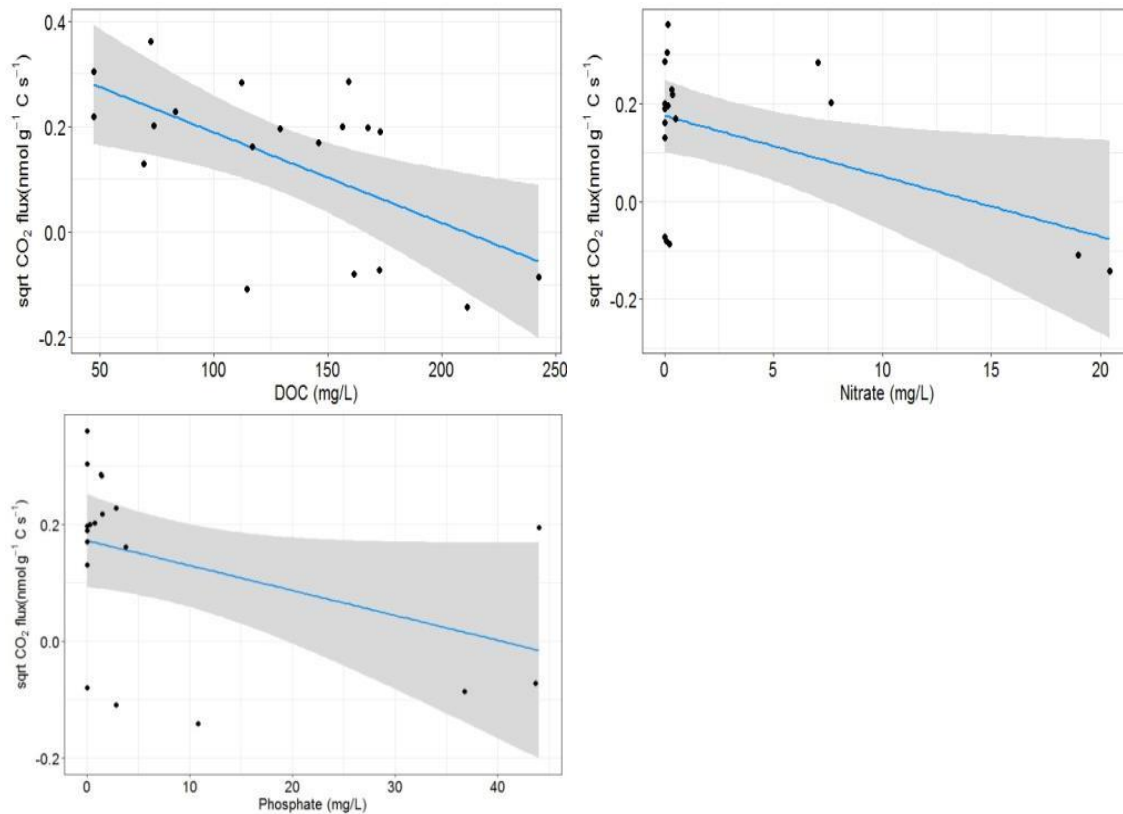
Figure 4.14 Correlations of CO_2 fluxes with biochemical parameters in the long cores. Correlations in all graphs are in all sites.

4.4.6.2 CH₄ fluxes

4.4.6.2.1 Shallow cores

In shallow cores, increasing CH_4 fluxes were marginally significantly associated with increasing percentages of lignin and recalcitrant material in the peat ($p=0.06$); in contrast, decreasing fluxes were significantly associated with increasing percentages of mineral soil ($p=0.03$). However, when looking at individual sites, there is a significant relationship between pH levels and CH_4 fluxes in cores from R98; increasing pH levels were associated with decreasing fluxes ($p<0.001$; Figure 4.15). The other chemicals did not have a significant relationship with CH_4 fluxes in the shallow cores ($p>0.6$).
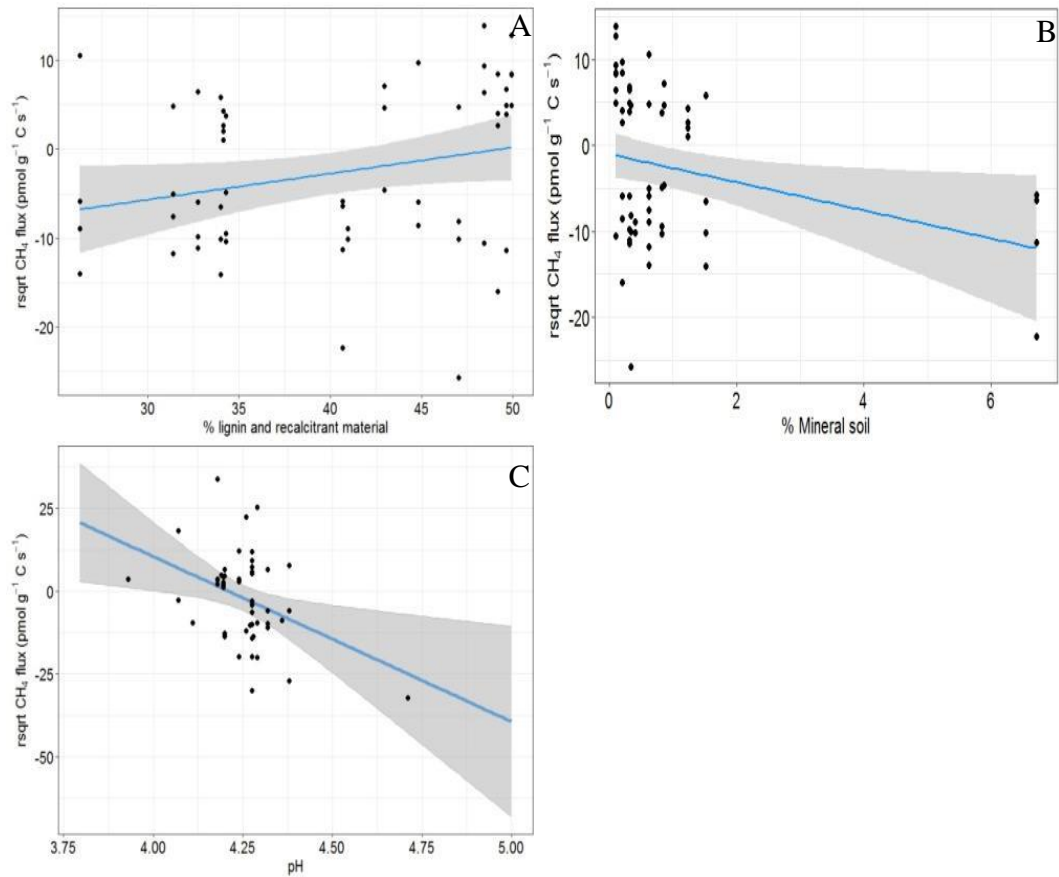
Figure 4.15 Correlations of CH$_4$ fluxes with biochemical parameters in the shallow cores. A) and B) in all sites, and C) in site R98.

4.4.6.2.2 Deep cores

In the deep cores, CH$_4$ fluxes correlated positively with C:N ratio (p=0.05), DOC (p=0.03) and lignin and recalcitrants (p=0.02), and had a weak, only marginally significant, negative correlation with concentration of sulphate (p=0.09; Figure 4.16). Further, there are no significant relationships between the measured chemicals and the CH$_4$ fluxes (p>0.1).
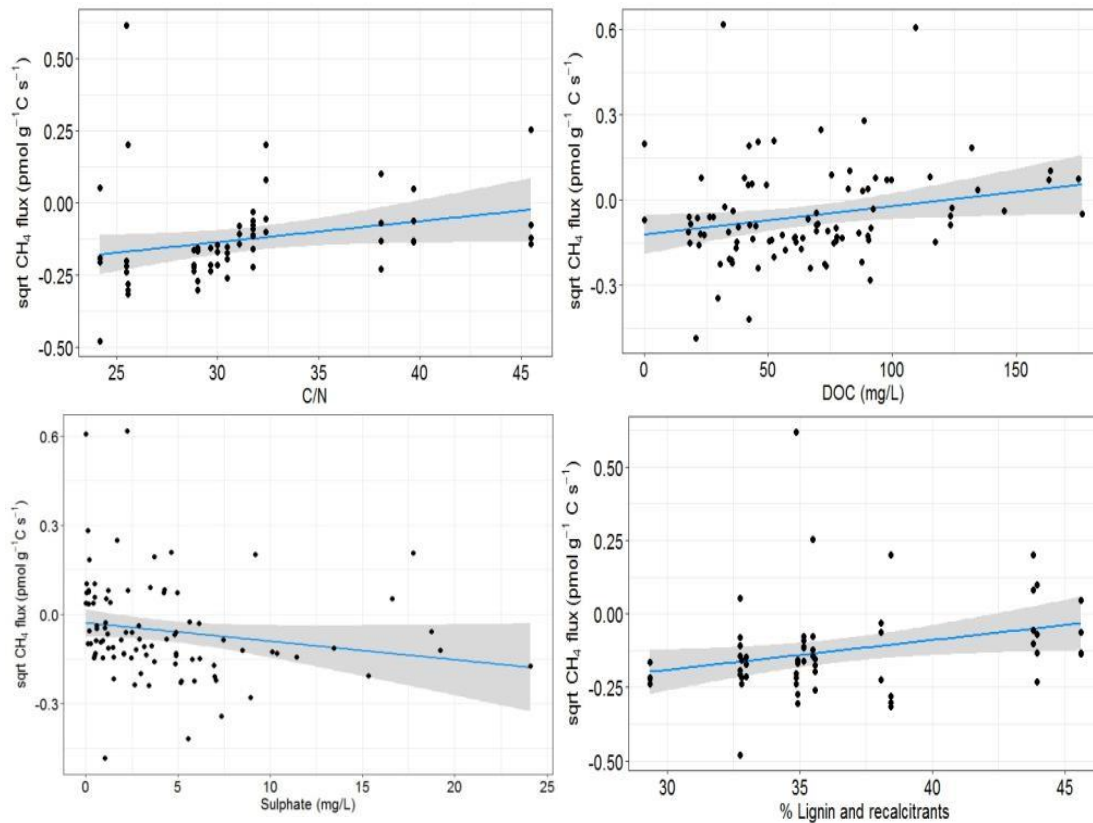
Figure 4.16 Correlations of CH$_4$ fluxes with biochemical parameters in the deep cores. All correlations are in all sites.

4.4.6.2.3 Long cores

None of the biochemical peat properties showed a significant relationship with CH$_4$ fluxes in the long cores (p>0.2).

4.4.6.2.4 Principal component analysis

The principal component analysis indicates some consistent patterns, which separate the soil quality components according to sites. For shallow cores, there is a continuous transition from forest to bog sites via restoration sites of increasing age that are both influenced by PC1 and PC2 (Figure 4.17A). This consistent trend disappears in deep cores (Figure 4.17B). The trend observed in the PCA of shallow cores is significant (p=0.001); the sites do differ in overall peat quality and pore water chemicals between sites, in contrast to the deep cores (p=0.27).
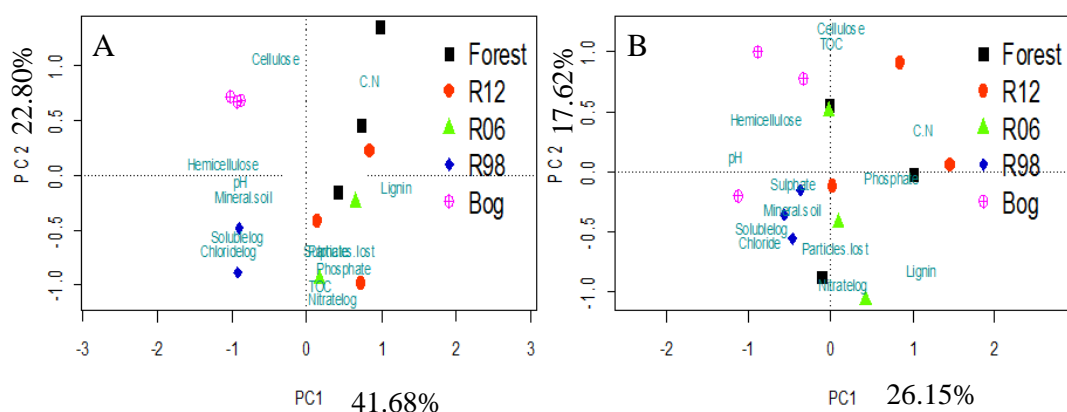
Figure 4.17 PCA A) shallow cores. B) deep cores

4.5 Discussion

The findings of this study indicate that, under identical temperature and moisture conditions, there are significant differences in both CO_2 and CH_4 fluxes from peat along a restoration chronosequence. CO_2 production in peat cores retrieved from forest plots was higher than that measured on cores from sites that have undergone restoration and where no forest had been planted. CH_4 production by contrast showed no direct influence of peat quality in shallow depths, but some trends in deeper layers. This indicates an important impact of forest plantations on the biochemical peat constituents, and consequently the potential to produce greenhouse gases.

4.5.1 *CO₂ flux*

Over all cores CO_2 fluxes varied between -0.20 nmol g^{-1} C s^{-1} and 0.27 nmol g^{-1} C s^{-1} (-0.41 to 0.57 µmol m^{-2} s^{-1}). Field flux measurements from these sites with soil temperature between 7.5 and 8.5 °C range from 0.023 to 5.46 µmol m^{-2} s^{-1}, with a mean flux of 1.29 ±0.13 µmol m^{-2} s^{-1} (Chapter 2). In a similar incubation study of fen soils from grassland, cropland and forest from 0-30 cm, 30-60 cm and 60-100 cm depth, from Switzerland, Bader et al. (2017) found slightly higher CO_2 fluxes at 10 °C; 0.075 ±0.0032 nmol g^{-1} C s^{-1}. They did not find any differences between

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the sites, but they found, similar to us, higher CO_2 fluxes from the top soils (0-30 cm) than the deeper layers (30-60 cm).

4.5.2 *CH$_4$ flux*

CH_4 fluxes from peat cores varied between -1.11 pmol g^{-1} C s^{-1} and 0.89 pmol g^{-1} C s^{-1} (-2.81 to 2.62 nmol m^{-2} s^{-1}). Measurements of the same sites in the field with soil temperature between 7.5 and 8.5 °C range from -103.13 to 75.53 nmol m^{-2} s^{-1}, with a mean of 5.53 ±2.30 nmol m^{-2} s^{-1} (Chapter 2). Similar to the CO_2 fluxes, the mean of the field CH_4 fluxes is thus considerably higher than the fluxes measured in the laboratory, but they are within the range of the field fluxes. This could indicate a reduction in microorganism activity in the incubated cores, potentially due to long storage.

4.5.3 *Role of chemistry in regulating CO$_2$ and CH$_4$ fluxes*

4.5.3.1 *Pore water chemicals*

We did not find any statistical differences in DOC levels between sites. The DOC concentrations in our sites (low water table 60.6 ±3.2 mg/L, changed water table 113.5 ±9.1 mg/L and high water table 89.9 ±5.4 mg/L) are similar to field pore and surface DOC concentrations found by Gaffney (2016) in the Flow Country. However, our concentrations are higher than found by Dinsmore et al. (2008) in a grass dominated, lowland ombrotrophic peatland in Scotland (43 ±2.1 mg/L) where, in contrast to our results, they found no significant differences between water table treatments. However our results fall in the same range as found by Clark et al. (2012) in cores from UK peatlands and they found lower DOC levels in their dry cores than in their wet cores (6.1 to 39.3 mg/L for their dry cores and 39.6 to 276.0 mg/L for their wet cores). Nitrate concentration in the pore water is lower in cores from forest plantation, R12 and bog (0.23 ±0.10 mg/L), than in cores from R98 and R06 (2.7 ±0.03 and 3.2 ±1.1 respectively). However, all concentrations are higher than found by Dinsmore et al (2008) of 0.03± 0.01 mg/L and by Proctor (2006) 0.017 ±0.012 mg/L in a blanket bog in England. The high levels in sites R06 and R98 could be explained by the fact that sites had been fertilised before planting, and that trees where left in furrows after felling. Thus,

higher levels of nitrate in the pore water of these sites could be due to breaking down of tree material. Hancock et al. (in press) have also found higher nitrogen levels in the vegetation of the R98 site than would be expected in bogs. However R12 also had tree material breaking down in the furrows, but had lower levels of nitrate, it is possible that this site got fertilised less when planted, since we know fertilisation was often very patchy. In forest sites, where continuous needle input and higher microbial activity (as indicated by CO_2 flux results) would be likely to transform organic nitrogen into mineral forms (including nitrate in oxygenated layers), lower levels may result from higher nitrate uptake by roots.

Mean sulphate levels (3.30 ±0.16 mg/L) are similar to those found by Proctor (2006) in a blanket bog in England, 4.71 ±1.17 mg/L. They show significant differences between sites, with forest plantation cores having significantly lower concentrations of sulphate than in R06 and R98 and the shallow cores have significantly less sulphate in the pore water than the deep cores. Sulphate reduction is fast in the periodically aerobic layers of the peat (Clymo, 1965), which could possibly explain the low concentrations in the forest plantation cores. Phosphate concentrations are highest in cores from R06, R12 and forest plantations. The range of phosphate levels, 0 to 45.8 mg/L, in our cores is much bigger than found by White et al (2008), 0 and 1.69 mg/L, although mean concentrations from R98 and bog cores fall within their range, suggesting that forest plantations have a big influence on the levels of phosphate.

4.5.3.2   Peat quality

As hypothesised, the forest plantations have altered the quality of the peat; in general there were trends of increasing percentages of soluble cell components and hemicellulose and a decreasing trend in lignin and recalcitrant material levels and C:N ratio from the forest plantation towards the bog cores. The turnover rates of these components go from fast to slow for soluble cell component, hemicellulose, cellulose and lignin and recalcitrant material (Berg and McClaugherty, 2008).

The shallow cores have less soluble cell components and hemicellulose than the deep cores and they have more cellulose and lignin and recalcitrant material and a higher C:N ratio than the deep cores. This is partly in contrast with what we expected since according to Clymo (1984) more recalcitrant material is accumulated during peat formation, since the easily decomposable organic matter is lost in the process. This would mean that the deeper layers of peat should have more recalcitrant materials than more superficial layers. However, the higher levels of recalcitrant material near the soil surface of forest plantation and younger restoration sites could be an indication of advanced peat decomposition (Klavins et al., 2008; Leifeld et al., 2012; Wüst-Galley et al., 2016), but lower C:N ratios would then be expected in the top soil layers, since peat mineralization appears to increase the relative nitrogen content of the soil (Krüger et al., 2015; Kuhry and Vitt, 1996; Malmer and Holm, 1984). However, we found higher C:N ratios in the top layers than in the deeper layers. Our results are similar to those of Bader et al. (2017) and they argued that the higher levels of lignin and recalcitrant materials in the top layers of the forest soils is due the higher abundance of lignin rich (wood derived) plant residues and not due to advanced peat decomposition.

4.5.3.3 *CO_2 flux explained by biochemical parameters*

Alternative analyses could have been conducted to test the relationships between gas fluxes and biochemical parameters. Multiple correlations were used to determine this relationship which may have the potential for Type I statistical error, in which a true null hypothesis may be incorrectly rejected, also known as a "false positive" finding. A Type I error may lead to the conclusion that a relationship between the flux and the biochemical parameter exists, when actually there is none (Whitlock and Schluter, 2009). With a p-value of 0.05 there is a 5% chance that the null hypothesis is incorrectly rejected, and thus when using multiple correlation tests there is a reasonable chance of a Type I error, simply because of the amount of correlations tested for. A possible "fix" for this problem is to reduce the threshold value for rejecting the null hypothesis to a lower value (e.g. $\alpha = 0.01$). However, this would increase the chance of a Type II error, also known as a "false negative" finding, where the null hypothesis is false, but not rejected (Whitlock and Schluter, 2009). A more robust method would be multiple

linear regression, which accounts for the variance explained by multiple predictors within the model. Standardising predictors can identify the relative weight of individual parameters in affecting variation in the response variable. This is important to keep in mind when interpreting the results.

DOC, phosphate and pH emerged as generic predictors of CO_2 flux in the shallow cores. As levels of DOC are not significantly different between sites, these cannot explain the observed differences in CO_2 fluxes. The negative correlation between phosphate concentration and CO_2 flux in the shallow cores is in contrast with what was expected, as the higher availability of a macronutrient such as P could plausibly lead to higher microbial activity and hence higher decomposition rates (Amador and Jones, 1993). Conversely, it is possible that under certain conditions, demand for phosphate is reduced, which then results in an accumulation of phosphate. This has been shown in several studies for accumulation of a similar chemical compound; acetate (Avery et al., 1999; Duddleston et al., 2002; Hoehler et al., 1999; Shannon, and White, 1996). Soil pH was positively correlated with CO_2 flux. pH is known to affect soil microbial communities in wetlands (Hartman et al., 2008), which in their turn affect the CO_2 flux.

In the shallow cores, CO_2 flux from forest plantation cores was significantly higher than those from restored sites R12, R06 and from bog cores. This could partly be explained with the biochemical results: Phosphate concentrations in the pore water of the forest plantations are lower than in the pore water of R12 and R06, but higher than the pore water of the bog cores. The soil pH in the forest plantation cores is significantly higher than in R12, R06 and bog. These correspond with the higher CO_2 flux from the forest plantation cores than from the R12, R06 and only for pH the bog cores. However, phosphate was also significantly different between the forest plantation cores and R98 cores and between the cores from R06 and R12 and the R98 and bog cores. pH was also significantly different between the R06 cores and the R98 and bog cores. However, these differences did not lead to a significant difference in fluxes.

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There is one site-specific predictor for CO_2 flux in the shallow cores; in R12 cores increasing levels of sulphate (p=0.02) are associated with higher CO_2 fluxes. A similar relationship is found in the deep cores from all sites. In general, sulphate is a good indicator of oxidation, since under aerobic conditions sulphur is being oxidised to sulphate (Toivonen et al., 2013). This is supported by our results despite some exceptions, such as the drained forest plantations, which have significantly lower concentrations of sulphate in their pore water than restoration sites, but higher rates of CO_2 production. Sulphate serves as a nutrient, and thus increases microbial activity (Blagodatskaya et al., 2010), which can explain the positive correlation with CO_2 flux. In addition to the general predictive power of sulphate, nitrate also indicates a more site-specific influence on CO_2 fluxes from the deep cores. In R98 and bog cores, increasing CO_2 fluxes are associated with increasing levels of nitrate. Nitrate also serves as a nutrient and thus higher levels of nitrate can lead to higher CO_2 fluxes (Blagodatskaya et al., 2010).

Overall, the results show that there are some biochemical constituents of peat (and of soil solution in peat) that emerge as good correlators for peat decomposability (measured as CO_2 flux). However, there is no clear-cut pattern by which peat decomposition can be explained by one or only a few parameters alone. We hypothesise that this is due to different management of the forest plantations, e.g. different amounts of fertiliser, and the different ages of the trees when felled, resulting in much smaller trees in the older restoration sites than in the younger ones and resulting in different ground vegetation at the time of felling. This will have resulted in different microbial communities, which are now re-adjusting after felling. Creevy et al. (2018) have shown a difference in the communities of the dominant microbial consumers, testate amoebae, between the forest plantations and the near pristine bogs in the Flow Country. They have also shown that the microbial communities in the R98 site are more similar to the forest plantations than the near pristine bog, so even though we see the peat quality recovering with restoration age, the microbial communities seem to recover slower. This could explain why it is so difficult to find good biochemical predictors for our sites. However, the complicated results could also be a statistical artefact and more robust statistical testing is needed to determine the relationships between

biochemicals and fluxes. Two recent studies on SOM parameters and decomposition rates in peatlands also could not find strong relationships between CO_2 flux and chemicals (Bader et al., 2017; Säurich et al., 2017). Bader et al. (2017) focused on soil organic carbon (SOC) content, soil pH and C:N ratios and Säurich et al. (2017) focused on top of that also on total nitrogen content, calcium carbonate content, bulk density, texture, oxalate extractable iron oxide content, calcium acetate lactate, extractable phosphorus content, $\delta^{13}C$ and $\delta^{15}N$.

4.5.3.4 *CH₄ flux explained by chemicals*

In shallow cores, there are two generic predictors; increasing CH_4 fluxes, like CO_2 fluxes in some shallow cores, are associated with increasing percentages of lignin and recalcitrant material in the peat. In contrast, decreasing fluxes are associated with increasing percentages of mineral soil, so an increase in percentage of organic soil. Since the response is similar for both CH_4 and CO_2 fluxes this hints at a general stimulation of microbial activity in some cores. This could be because there might be more useful substrate in the organic soil than in the mineral soil, which microorganisms use and thus emit more CH_4 and CO_2.

Additional to these, there is also one site specific predictor of CH_4 in the shallow cores. In cores from R98, increasing pH levels are associated with decreasing fluxes. pH is known to affect soil microbial communities in wetlands (Hartman et al., 2008); however, we only found a relationship between pH and CH_4 flux in the R98 cores. This could be because both methanogens (produce CH_4) and methanotrophs (consume CH_4) have a different response to pH levels, which could lead to a zero net effect (Dedysh et al., 1998).

In the deep cores increasing net CH_4 flux is generally associate with increasing levels of DOC, lignin and recalcitrant material, and C:N ratio. CH_4 fluxes from the deep cores of the forest plantation were higher than from the R06 cores, but there are no significant differences in the levels of the biochemical predictors, so these cannot explain the differences in CH_4 flux between these two sites. Similar to our result, White et al. (2008) also found a positive relationship between DOC and CH_4 flux, but this correlation was only significant when they considered both the bog and fen mesocosms together and in their fen mesocosms separately, but

not in their bog mesocosms. However, in contrast to our results they also report a negative relationship with pore water phosphate and ammonium (not measured by us) in their bog mesocosms. Similar to DOC, nitrate and sulphate concentrations in the pore water where only significant over all mesocosms and in the fen mesocosms, but not in the bog ones. They explained these inconsistencies by the fact that the concentrations of many of the pore water parameters are very low in the bog and have therefore a low predictive power. This is likely the case in our peat cores as well, and could explain why we see correlations with some parameters in some sites and not in others.

4.5.4 *Role of water table*

The water table treatment had, as expected, a significant effect on the CO_2 flux from shallow cores; fluxes from cores with a low water table where higher than those from cores with a high water table. However, in the deep cores there was no significant effect of water table treatment. This could be because the C in these deeper layers has become highly recalcitrant, due to the drainage of the sites which has led to long term aeration in the field (Laiho, 2006). Fluxes from the long cores were also not significantly different between the low and changed water table treatments. Other studies have also shown higher CO_2 fluxes from cores with lower water table than from cores with high water table, however these studies did not look at different core depths (e.g. Dinsmore et al. 2008; Estop-Aragonés et al. 2016; Blodau et al. 2004; Moore & Roulet 1993). The contrasting flux response to water table depth (and hence aeration of pore spaces in peat) indicate some fundamental differences in peat from superficial or deeper soil layers. Particularly at our sites, where trees had been present over preceding years (or in case of forestry sites where still present), bulk density has been affected by layers of needle litter on the surface. This lower bulk density in superficial peat depths is likely to allow a much stronger aeration effect from lowered water table compared to higher peat bulk density at greater depth, so that the oxygenation of peat pores in response to a lower water table may have a much smaller effect here.

There were no significant differences in CH_4 flux across all three core depths between any of the water table treatments. This is in contrast with what was

expected and with the literature where studies have found higher CH_4 fluxes in high water table treatments than in low water table treatments (Aerts and Ludwig, 1997; Dinsmore et al., 2008; MacDonald and Fowler, 1998; Moore and Dalva, 1993) and where a change in water table from low to high has led to a pulse of CH_4 flux (Dinsmore et al., 2008). It is possible that a short-term flush of CH_4 was missed in our study (1-2 days after water table change), but overall, the lack of CH_4 flux response is surprising. This could potentially be because the average water table depth in the field for the forest plantations is -40 cm and -10 cm in the bog (Table 2.1), this means that the low water table in the incubation study is not really that low and this could have led to the lack of water table treatment response in the CH_4 fluxes. White et al. (2008) also did not find a significant effect of water table treatment in their bog mesocosms, but they did find a significant effect in their fen mesocosms. Field results from the same sites show increasing CH_4 fluxes from the forest plantation to the near pristine bog, with the restoration sites in-between. Here we hypothesised that this was due to the increasing water table from the forest plantations to the near pristine sites (chapter 2), but this lab incubation study shows that most likely there are different drivers as well.

4.6 Conclusion

We show that forest plantations have altered the quality of the peat and nutrient availability in the pore water. Different CO_2 fluxes between sites under the same temperature and water table indicate that the chemical and physical legacies of the forest plantations shape the biogeochemical processes in peatlands. For CH_4 fluxes only very few differences between sites emerged, with only two of the restoration sites displaying significant differences, which indicates that on its own (and in absence of biotic interactions under field conditions), forestry effects on CH_4 flux are limited. We have found both generic and some site-specific predictors for both CO_2 and CH_4 fluxes, but it was difficult to interpret consistent changes in peat composition and water table depth in light of flux responses. It appears that site-specific conditions, possibly linked to detailed management during periods of forestry, or linked to the method of forest removal seem to override global controls, which makes prediction of the data challenging.

However, the complicated results could also be a statistical artefact and more robust statistical testing is needed to determine the relationships between biochemicals and fluxes.

5 General discussion

Peatlands are a globally important C store (Stocker et al., 2013), which can be compromised by drainage and afforestation (Lindsay, 2010). A better understanding and awareness of the importance of peatlands for ecosystem services has led to a change in land management (Andersen et al., 2016; Anderson et al., 2016), and an increasing number of afforested peatlands are now being restored to enable recolonization of peatland species and a return to ecosystem functioning (Andersen et al., 2016; Lunt et al., 2010).

There is only very limited data on GHG fluxes of peatland restoration sites in the literature (e.g. Rowson et al. 2010; Abdalla et al. 2016), and only one study from a forest-to-bog restoration site, which focuses on CO_2 fluxes only (Hambley, 2016). There is also very limited knowledge on how afforestation alters the peat biochemically and how this in itself influences the GHG fluxes of restored sites. The rate of peat decomposition under forest plantations on naturally treeless peatlands is also unknown and knowing this can help us understand and model the effects of drainage in afforested peatlands on peat oxidation rates in boreal peatlands.

The work presented here attempts for the first time to produce a GHG flux balance of forest-to-bog restoration in the UK, addressing an important land use policy question. GHG emissions are reported for the UK under the terms of the United Nations Framework Convention on Climate Change (UNFCC). GHG emissions have to be reported in climate change mitigation reports to show what kind of attempts are made to achieve the targets of GHG emissions to reduce global warming, agreed on by countries around the world in the Kyoto protocol (Morison, 2012). Large areas of afforested peatlands are undergoing restoration in the UK; since 2000, forest-to-bog restoration was conducted at a rate of 500 ha per year and more will be restored in the future (Anderson et al., 2016) as government-funded grant schemes are now in place to restore peatland habitats impacted mainly by drainage and afforestation. However, until now the UK was unable to provide net GHG numbers for the forest-to-bog restoration sites.

The main findings of this thesis are:

1) Forest-to-bog restoration impacts mainly on CH_4 flux, while both CO_2 respiration and N_2O fluxes are unchanged over a chronosequence of restoration sites. Net CH_4 fluxes are lowest in forest plantations and increase with restoration age, being highest in the near pristine bog.

2) Peat decomposition rate under the forest plantations is 126.8 ± 14.7 g C m^{-2} y^{-1}, which is 44% of the total soil respiration. Hence, 56% of the total soil respiration came from the tree roots (autotrophic flux).

3) Forest plantations have altered the quality of the peat and nutrient availability in the pore water. Different CO_2 fluxes between vegetation free peat cores from different sites for the same climatic conditions show that this shapes the biogeochemical processes in the peatlands. However there were very few differences in CH_4 fluxes between vegetation free peat cores from the different sites under the same temperature and water table level, indicating that on its own (and in absence of biotic interactions under field conditions), forestry effects on CH_4 flux are limited.

5.1 Main impact of forestry on blanket bog

Results presented in Chapter 2 show that there is only a significant difference in CH_4 flux and not in N_2O flux and CO_2 respiration between the forest plantations and near pristine blanket bogs. On average, over the three years measured, the forest plantation soils take up CH_4 from the atmosphere (-1.27 ± 3.09 nmol m^{-2} s^{-1}) and the near pristine blanket bog emits CH_4 (11.83 ± 5.57 nmol m^{-2} s^{-1}). This is in line with the results from Yamulki et al. (2013) and Minkkinen et al. (2007), which indicates that CH_4 is the most important GHG when comparing forest plantations and near pristine blanket bogs. Due to the measurement technique used, forest plantation soil respiration is compared with ecosystem respiration in the blanket bog in this study, which is not a fair comparison, therefore more information is needed.

Blanket bogs can potentially store more C than forests (over decennia) (Clymo, 1984) and thus the main question about the forest plantations is how quickly peat decomposes (heterotrophic respiration) and whether forest plantations add more C to the peat than is being decomposed. Chapter 3 shows that the peat decomposition rate under the 30-year old forest plantations was 126.8 ± 14.7 g C m^{-2} y^{-1}; this is the first quantification of this flux under drained and afforested peatlands in the UK. This means that forest plantations have to sequester, at least 126.8 g C m^{-2} y^{-1} over the length of a rotation in order to act as a C sink. The total C input from above ground of these 30 year old forest plantations was about 360 g C m^{-2} y^{-1} and the total soil efflux measured was only about 290 g C m^{-2} y^{-1}, indicating that these forest plantations are a C sink at the moment. However, the C input when the trees are younger, and thus smaller, will be much lower and this means that the input over a full rotation has to be measured. Lindsay (2010) used Hargreaves et al. (2003) C balance model of an afforested peatland in Scotland and concluded that over its lifespan, the forest plantations have no net C benefit and when C loss via DOC is taken into account it could result a net C loss. The peat decomposition rate Hargreaves et al. (2003) used over the first 26 years of the forest plantation was similar in magnitude to ours, but relatively poorly constrained, ranging from 100-200 g C m^{-2} y^{-1}. Lindsay (2010) showed that when the trees are 60 years old, the peat decomposition rate could be as high as 700 g C m^{-2} y^{-1}. A study that has looked at the total GHG balance of a full rotation of forest plantations on a fen in Sweden shows that these plantations are GHG sources. However they report a much higher peat decomposition rate of 399 g C m^{-2} y^{-1} (He et al. 2016).

Altered patterns of input of organic matter between forests and naturally vegetated bogs also manifests itself in the physical and biochemical quality of organic matter. The active *Sphagnum* moss layer in the bog is replaced with needle litter in the forest plantations, which in contrast to *Sphagnum* moss, holds almost no water and is aerated. Tree litter has a different chemical composition than the litter from the bog vegetation, which alters the peat chemistry. However, needle litter is only deposited on the surface and thus only influences the shallow layers, while the deeper layers are potentially impacted by tree roots. These differences are

indirect effects of afforestation and are independent of drainage, but will interact under field conditions. In Chapter 4, the impacts of these differences on CO_2 and CH_4 fluxes were studied in the laboratory under similar temperature and water table levels of vegetation free peat cores from, among others, forest plantations and near pristine blanket bogs. The results show that there is a difference in CO_2 flux between the two, with forest plantation soil respiration in both the shallow (0-10 cm) and deep cores (10-20 cm) being higher than near pristine bog soil respiration. The forest plantation peat thus decomposes faster than the peat from the near pristine blanket bog under the same temperature and water table. This is probably because the different biochemical composition of the peat has different decomposition rates, which may have led to a difference in microbial communities (Creevy et al., 2018), resulting in different decomposition rates. When comparing the fluxes from the more realistic high water table treatment of the bog cores with the fluxes from the low water table treatment of the forest plantation cores, this difference only increases. This suggests that the bog vegetation is a major part of the field measured CO_2 respiration.

However, in the same incubation study there was no significant difference in CH_4 flux between the forest plantation cores and near pristine bog cores, under the same climatic conditions. Since the field study did show a difference in CH_4 flux, this indicates that the vegetation probably has a big influence also on the CH_4 fluxes. Both direct, by transporting CH_4 in aerenchyma plants and thus inhibiting CH_4 oxidation which leads to a higher CH_4 emission, and indirect, since vascular plants considerably change the microbial community structure. Removal of vascular plants is shown to reduce potential CH_4 production and increase potential CH_4 oxidation (Robroek et al., 2015). However, there was no direct effect of vegetation on CH_4 flux in the field. This analysis was done over the CH_4 fluxes of all sites together and we hypothesised that the lack of vegetation effect was due to the disturbance of most sites, which interfered with the correlation, since vegetation is at different recovering phases towards bog vegetation in all restoration sites.

Thus, afforestation increases the peat decomposition rate and the change in vegetation and water table combined is likely the driver of the difference in CH_4 fluxes from the forest plantations and near pristine bog in the field.

5.2 Restoration impacts on GHG fluxes

Chapter 2 shows the impact of forest-to-bog restoration on GHG fluxes in the field. There was no difference in ecosystem respiration and N_2O flux between the near pristine bog and any of the restoration sites. However, CH_4 fluxes increase significantly with restoration age and are highest in the near pristine bog. To be able to inform site managers and policy makers it is important to understand the processes behind these fluxes and what is driving them.

When combining the results of the field (Chapter 2) and incubation study (Chapter 4), an explanation for the lack of the difference in CO_2 respiration between sites can be found. In the incubation study (Chapter 4) there were no significant differences in the soil respiration flux of the shallow (0-10 cm) and long (0-20) cores between any of the restoration sites and the near pristine bog cores under the same climatic conditions. There were only marginally significantly higher CO_2 fluxes in deep (10-20 cm) cores from the most recently restored site compared to the oldest restoration site (R12 and R98, respectively). This shows that potentially all restoration sites and the near pristine bog site have a similar peat decomposition rate under similar temperature and water table and that probably the microbial community is becoming more similar. In the incubation study it was shown that the water table had a significant influence on the CO_2 fluxes from the shallow cores, with lower fluxes in the high water table treatment than in the low water table treatment. This is in line with what is found in literature (Blodau et al., 2004; Dinsmore et al., 2008; Estop-Aragonés et al., 2016). In the field the water table of R12 is lowest and increases towards the near pristine bog (Table 2.1); therefore, in the field a lower CO_2 flux from the older restoration sites and the near pristine bog is expected than from the younger restoration sites, but this was not observed. This gives evidence for our hypothesis that the higher vegetation respiration in the older restoration sites and near pristine bog, due to more

vegetation present, is compensating the reduced peat decomposition. This is an important finding and helps us understand the processes of these restoration sites.

When the CH_4 flux results of the field and incubation study are combined, this gives a more complex picture. The incubation study did also not show any significant differences in CH_4 fluxes between the sites under controlled conditions of temperature and water table. This finding indicates that the observed changes in peat in terms of physical structure and biochemical composition (Chapter 4) cannot explain the differences in net CH_4 fluxes in the field. The increase in CH_4 fluxes with restoration age and towards the near pristine bog in the field was linked to the increase in water table in the same direction (Table 2.1). However, there was no significant influence of water table treatment on the CH_4 fluxes in the lab incubation study, contrasting with field results as well as findings in the scientific literature (Dinsmore et al., 2008; MacDonald and Fowler, 1998). This means that water table alone also cannot explain the difference in CH_4 fluxes in the field. As mentioned above, the lack of vegetation in the cores in the incubation experiment could potentially explain in part the difference in response to water table. This because vegetation can act as transporters of CH_4 in aerenchymatous plants, inhibiting CH_4 oxidation, and vascular plants also change the microbial communities, with reduced potential of CH_4 production and increased potential of CH_4 oxidation due the removal of vascular plants (Robroek et al., 2015). The shift in vegetation and the increased water table combined are probably the reason for the differences in CH_4 fluxes between sites in the field. The other possible explanation for the difference in response to water table, could be the difference in peat depth in the cores (10 to 20 cm) and in the field (several meters), where consequently in the field potentially more CH_4 can be produced. In addition, the average water table depth in the field for the forest plantations is -40 cm and -10 cm in the bog (Table 2.1), which means that the low water table in the incubation study is not really that low and this could potentially explain the lack of water table treatment response in the CH_4 fluxes as well.

Taken together, a picture emerges that forest-to-bog restoration reduces peat decomposition and increases vegetation respiration, hinting at a recovery of the C sink. N_2O fluxes are not influenced and all sites remain a small sink of this strong

GHG. However, the emission of CH_4 increases due to restoration and it will depend on the size of the C sink if the restoration of these sites can be a climate mitigation tool.

5.3 Management implications

In this thesis, I have shown that in the long-term restoration is successful regarding GHG fluxes, since the fluxes of the restoration sites, with time since felling, become more similar to the fluxes from the near pristine bog. Hancock et al. (in press) have also shown that the vegetation of the R98 site is recovering back to bog vegetation, although in the drier plough throws this recovery has stopped after about 6 years, showing the importance of raising the water table high enough with additional management like blocking furrows with peat dams.

Only the CH_4 flux changes with restoration, and not the CO_2 respiration and N_2O flux, but as shown above peat decomposition is reduced with restoration. Since CH_4 is a much stronger GHG gas than CO_2 (28-34 times stronger than CO_2 over 100 years), this is an important finding. In order to get a complete picture if restoration is successful, and that restored sites act as C sinks again, CO_2 uptake needs to be known. The net ecosystem exchange of a near pristine blanket bog close to our sites averaged over 6 years was -114 g C m^{-2} y^{-1} (Levy and Gray, 2015) and the R98 site was a net C sink of -71 g C m^{-2} y^{-1} measured from March 2014 till April 2015 (Hambley, 2016). However a younger restoration site, felled in 2004, was still a C source of 80 g C m^{-2} y^{-1} measured from May 2014 till May 2015 (Hambley, 2016), showing that it takes time before these restored sites recover regarding CO_2 fluxes. In order to gain a complete understanding of the greenhouse gas balance, all fluxes need to be converted to CO_2 equivalents (CO_2e; Gohar and Shine, 2007) as a common unit, which takes the global warming potential into account. Using these numbers together with our CH_4 and N_2O fluxes, we can calculate a GHG balance for the near pristine bog and R98 site. For the near pristine bog, this gives a CH_4 flux of 167 ($\pm$40) g CO_2e m^{-2} y^{-1} and N_2O flux of -58 ($\pm$28) g CO_2e m^{-2} y^{-1} together with the net CO_2 flux (in g CO_2 m^{-2} y^{-1}) this gives a sink of -307.80 ($\pm$50) g CO_2e m^{-2} y^{-1}. For the R98 site CH_4 flux is 155 ($\pm$30) g CO_2e m^{-2} y^{-1}, N_2O flux -25 ($\pm$29) g CO_2e m^{-2} y^{-1} together with the net CO_2

flux this gives a smaller sink than the near pristine bog, of -130 (±42) g CO_2e m^{-2} y^{-1} (Figure 5.1).
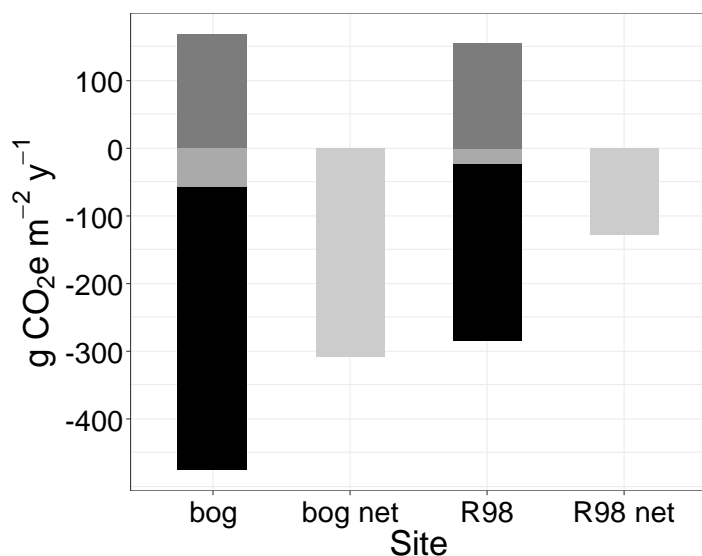
Figure 5.1 Global warming potential in CO_2 equivalent. Black is net CO_2 flux (from Levy and Gray (2015) for near pristine bog and Hambley (2016) for R98), dark grey is CH_4 flux, lighter grey is N_2O flux and lightest grey is the net GHG balance of each site.

This shows that the restoration of R98 is successful from a GHG perspective and that both R98 and the near pristine bog have an overall climate cooling effect. The site R98 was felled when the trees were still relatively small (around 20 years of age) and since harvesting was not economically viable they were left in the furrows, with no blocking of the furrows. This is not normal practice any longer, and most forest-to-bog restoration sites in the UK are harvested in recent years (Anderson et al., 2016), with additional measures to raise the water table like furrow blocking, in-filling of furrows with plough throws and cross tracking the site to restore a more natural topography (N. Cowie, RSPB Scotland, personal communication). Trees in forest plantations on peat hold a lot of nutrients (Anderson et al., 2016), and these can leach, mainly from harvest residue (brash) left on site after felling (Asam et al., 2014). A higher fertility in R98 than in near pristine bog, but lower than in the forest plantations was found by Hancock et al. (in press). The key peat-forming species, *Sphagnum capillifolium*, is sensitive to nitrogen (Gunnarsson and Rydin, 2000), so restoration sites that are harvested (with removal of the brash material) could potentially recover quicker. On the

other hand, the R98 site had a ground cover of about 10% of *Sphagnum* mosses when this site was felled. Forest plantations felled at a more mature age have a greater degree of canopy closure, which leads to a significant reduction in ground cover of *Sphagnum*. Hancock et al. (in press) show that forest plantations of roughly 30 years of age, with a closed canopy, have a *Sphagnum* ground cover of only about 5%, a more severe reduction in moss cover is likely to slow down the recovery of mosses after forest removal. The restoration sites used in this study were felled in different ways and had different levels of canopy closure; therefore, it is difficult to say with certainty what the total GHG balance is of the younger restoration sites of this study. Our results however indicate a change in CO_2 and CH_4 fluxes of the restoration sites towards near pristine bog, indicating a gradual recovery of these sites.

5.4 Conclusions and key outstanding questions

This study has provided some important insights in the processes taking place in afforested peatlands and forest-to-bog restoration sites. In conclusion, I show that forest-to-bog restoration can be successful from a GHG perspective, leading to a reduction in peat decomposition, but an increase in CH_4 emission, with, at least, the oldest restoration site having an overall climate cooling effect. However, a number of key questions remain. Firstly, in order to close the GHG flux balance of the younger restoration sites and forest plantations the CO_2 uptake has to be measured. In the restoration sites, this could be done either with clear chambers that enable measurement of ecosystem gas exchange, or with the EC technique. In the forest plantation, this has to be done with the EC technique, as no chamber based ecosystem exchange measurements are feasible. EC flux measurements measuring the net exchange over forested peatlands are ongoing (since 2016) in the Flow Country, and in combination with results reported in this thesis, will provide a more complete insight into the greenhouse gas balance of forest-to-bog restoration.

Secondly, results based on the statistical model used to explain the differences in CH_4 flux (Chapter 2) show that additional parameters to those measured in this study are likely to be relevant. The main information missing seems to be the

water table and adding this will most likely improve the explanatory power of the model (Abdalla et al., 2016; Salm et al., 2012). Another parameter that could be used is the slope of the sites, as this partly links with the water table and could be an important parameter for the amount of runoff water.

Thirdly, the focus of this study is on gas exchange, but it is clearly acknowledged that also aquatic transport of C sequestered from the atmosphere are significant (e.g. Billett et al., 2006). Gaffney (2016) conducted an in-depth study of the effects of bog restoration on the aquatic C fluxes. Linking his results with my study and Hambley's (2016) NEE study of R98 and an older restoration site will give a very important full GHG flux balance of forest-to-bog restoration sites, which is needed to be able to report correct numbers to the UNFCC.

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7 Appendices

7.1 *HMR* approach for flux calculations

The *HMR* approach is used to calculate greenhouse gas fluxes from the concentrations measured from the closed static chambers. This approach offers a transparent way to fit non-linear data when appropriate, as well as linear data and data representing no flux. The model is implemented as a package (Pedersen, 2017) in the open source software R. Concentrations are regressed against time since chamber closure using either a linear or a non-linear function to calculate the flux based on chamber volume and ground surface area.

The starting point of the approach is, if possible, to apply the non-linear extended *HM* model to the data. This model is a modification of the *HM* model by Hutchinson and Mosier (1981), and it accounts for horizontal gas transport through chamber leaks and transport through the soil under the chamber by using a first-order diffusion model. This first-order model is based on two assumptions: 1) concentration gradients drive horizontal gas transport and the gas concentration is changed at a rate proportional to the concentration difference and 2) at some point after chamber closure, the gas concentration in the soil under the chamber changes linearly with depth up to some depth, d, below which the gas concentration is constant and not affected by the presence of the chamber. The chamber concentration C_t at time $t > 0$ after closure is given by:

$$C_t = \varphi + f_0 \frac{\exp(-\kappa t)}{-\kappa h} \qquad (7.1)$$

Where φ represents the assumed constant source concentration located at depth d below the soil surface, f_0 the initial flux, $h = V/A$ and V is chamber volume and A cross-sectional area, κ is a model parameter depending on soil characteristics and chamber design, calculated as $\kappa = D_p/hd$, where D_p represents the effective gaseous diffusion coefficient in the soil. The model parameters $\varphi > 0$, $\kappa > 0$ and $-\infty < f_0 > \infty$ are estimated by the least squares method (Seber and Wild, 1989), by minimizing the mean squared errors (MSE) criterion.

If the estimation procedure of the revised *HM* model indicates a lack of fit, the linear model is used or a flux below the detection limit (no flux) is identified. The software makes a recommendation of which model fits the data best and the user then decides which model to use based on three graphs displayed: 1) the data and all three fitted model lines, 2) a visualisation of finding the estimate of κ, by plotting the MSE_c function over the maximal range of κ to provide an overview of the optimization task for the recommended model, and 3) the expanded view of the MSE_c function near the unique optimal value of κ.

The calculated flux is independent of the degree of non-linearity, which greatly reduces the restriction of deployment time common in earlier models. A 95% confidence interval for the calculated flux and a p-value for the null hypothesis of no flux are also calculated, which can be used to show how confident the user is in the calculated flux (Pedersen, 2010).

7.2 Articles used in Figure 3.12

Table 7.1 List of articles used in Figure 3.12.

Authors	Year	Title
Bokhorst, Stef, Daniel B. Metcalfe, and David A. Wardle	2013	Reduction in Snow Depth Negatively Affects Decomposers but Impact on Decomposition Rates Is Substrate Dependent
Bond-Lamberty, B, C Wang, and ST Gower	2004	Contribution of Root Respiration to Soil Surface CO2 Flux in a Boreal Black Spruce Chronosequence
Bond-Lamberty, Ben, Dustin Bronson, Emma Bladyka, and Stith T. Gower	2011	A Comparison of Trenched Plot Techniques for Partitioning Soil Respiration
Cleveland, Cory C., Alan R. Townsend, and Steven K. Schmidt	2002	Phosphorus Limitation of Microbial Processes in Moist Tropical Forests: Evidence from Short-Term Laboratory Incubations and Field Studies
Domisch, T., L. Finér, M. Ohashi, A. C. Risch, L. Sundström, P. Niemelä, and M. F. Jurgensen	2006	Contribution of Red Wood Ant Mounds to Forest Floor CO2 Efflux in Boreal Coniferous Forests

Ernfors, M., U. Sikström, M. Nilsson, and L. Klemedtsson	2010	Effects of Wood Ash Fertilization on Forest Floor Greenhouse Gas Emissions and Tree Growth in Nutrient Poor Drained Peatland Forests
Fang, H J, G R Yu, S L Cheng, T H Zhu, Y S Wang, J H Yan, M Wang, M Cao, and M Zhou	2010	Effects of Multiple Environmental Factors on CO2 Emission and CH_4 Uptake from Old-Growth Forest Soils
Gaumont-Guay, D., T. A. Black, A. G. Barr, T. J. Griffis, R. S. Jassal, P. Krishnan, N. Grant, and Z. Nesic.	2014	Eight Years of Forest-Floor CO2 Exchange in a Boreal Black Spruce Forest: Spatial Integration and Long-Term Temporal Trends
Gaumont-Guay, David, T. Andrew Black, Tim J. Griffis, Alan G. Barr, Rachhpal S. Jassal, and Zoran Nesic	2006	Interpreting the Dependence of Soil Respiration on Soil Temperature and Water Content in a Boreal Aspen Stand
Gaumont-Guay, David, T. Andrew Black, Tim J. Griffis, Alan G. Barr, Kai Morgenstern, Rachhpal S. Jassal, and Zoran Nesic	2006	Influence of Temperature and Drought on Seasonal and Interannual Variations of Soil, Bole and Ecosystem Respiration in a Boreal Aspen Stand

Gaumont-Guay, David, T. Andrew Black, Harry McCaughey, Alan G. Barr, Praveena Krishnan, Rachhpal S. Jassal, and Zoran Nesic   2009   Soil CO_2 Efflux in Contrasting Boreal Deciduous and Coniferous Stands and Its Contribution to the Ecosystem Carbon Balance

Gaumont-Guay, David, T Andrew Black, Alan G Barr, Rachhpal S Jassal, and Zoran Nesic   2008   Biophysical Controls on Rhizospheric and Heterotrophic Components of Soil Respiration in a Boreal Black Spruce Stand

Glukhova, T V, S E Vompersky, and A G Kovalev   2013   Emission of CO_2 from the Surface of Oligotrophic Bogs with Due Account for Their Microrelief in the Southern Taiga of European Russia

Grogan, P., and F. S. Chapin   1999   Arctic Soil Respiration: Effects of Climate and Vegetation Depend on Season

Hagedorn, F., Martin, M., Rixen, C., Rusch, S., Bebi, P., Zürcher, A., Siegwolf, R. T. W., Wipf, S., Escape, C., Roy, J., Hättenschwiler, S.   2010   Short-Term Responses of Ecosystem Carbon Fluxes to Experimental Soil Warming at the Swiss Alpine Treeline

Havas, P, and E. Mäenpää   1972   Evolution of Carbon Dioxide at the Floor of a Hylocomium Myrtillus Type Spruce Forest

Hermle, Sandra, Michael B. Lavigne, Pierre Y. Bernier, Onil Bergeron, and David Paré 2010 Component Respiration, Ecosystem Respiration and Net Primary Production of a Mature Black Spruce Forest in Northern Quebec

Högberg, Peter, Anders Nordgren, Nina Buchmann, Andrew F. S. Taylor, Alf Ekblad, Mona N. Högberg, Gert Nyberg, Mikaell Ottosson-Löfvenius, and David J. Read 2001 Large-Scale Forest Girdling Shows That Current Photosynthesis Drives Soil Respiration

Howard, Erica A., Stith T. Gower, Jonathan A. Foley, and Christopher J. Kucharik 2004 Effects of Logging on Carbon Dynamics of a Jack Pine Forest in Saskatchewan, Canada

Ilvesniemi, H, J Levula, R Ojansuu, P Kolari, L Kulmala, J Pumpanen, S Launiainen, T Vesala, and E Nikinmaa 2009 Long-Term Measurements of the Carbon Balance of a Boreal Scots Pine Dominated Forest Ecosystem

Kane, E. S., D. W. Valentine, G. J. Michaelson, J. D. Fox, and C. L. Ping 2006 Controls over Pathways of Carbon Efflux from Soils along Climate and Black Spruce Productivity Gradients in Interior Alaska

Khomik, Myroslava, M. Altaf Arain, and J. H. McCaughey 2006 Temporal and Spatial Variability of Soil Respiration in a Boreal Mixedwood Forest

Kim, Yongwon, Seong Deog Kim, Hiroyuki Enomoto, Keiji Kushida, Miyuki Kondoh, and Masao Uchida 2013 Latitudinal Distribution of Soil CO_2 Efflux and Temperature along the Dalton Highway, Alaska

Kim, Yongwon, Masahito Ueyama, Fumiko Nakagawa, Urumu Tsunogai, Yoshinobu Harazono, and Noriyuki Tanaka 2007 Assessment of Winter Fluxes of CO_2 and CH_4 in Boreal Forest Soils of Central Alaska Estimated by the Profile Method and the Chamber Method: A Diagnosis of Methane Emission and Implications for the Regional Carbon Budget

Kolari, Pasi, Liisa Kulmala, Jukka Pumpanen, Samuli Launiainen, Hannu Llvesniemi, Pertti Hari, and Eero Nikinmaa 2009 CO_2 Exchange and Component CO_2 Fluxes of a Boreal Scots Pine Forest

Laganière, Jérôme, David Paré, Yves Bergeron, and Han Y.H. Chen 2012 The Effect of Boreal Forest Composition on Soil Respiration Is Mediated through Variations in Soil Temperature and C Quality

Lukeno, J. O., and W. D. Billings | 1985 | The Influence of Microtopographic Heterogeneity on Carbon Dioxide Efflux from a Subarctic Bog

Lyuri, D. I., D. V. Karelin, A. V. Kudikov, and S. V. Goryachkin | 2013 | Changes in Soil Respiration in the Course of the Postagrogenic Succession on Sandy Soils in the Southern Taiga Zone

Mahli, Y, D D Baldocchi, and P G Jarvis | 1999 | The Carbon Balance of Tropical, Temperate and Boreal Forests

Mäkiranta, Päivi, Kari Minkkinen, Jyrki Hytönen, and Jukka Laine | 2008 | Factors Causing Temporal and Spatial Variation in Heterotrophic and Rhizospheric Components of Soil Respiration in Afforested Organic Soil Croplands in Finland

Mallik, A. U., and D. Hu | 1997 | Soil Respiration Following Site Preparation Treatments in Boreal Mixedwood Forest

Moilanen, M., J. Hytönen, and M. Leppälä | 2012 | Application of Wood Ash Accelerates Soil Respiration and Tree Growth on Drained Peatland

Molchanov, A. G. | 2009 | CO_2 Emission from the Surface of Dark Gray Forest Soils of the Forest Steppe and Sandy Soddy-Podzolic Soils of the Southern Taiga

Morén, Ann Sofie, and Anders Lindroth   2000 CO_2 Exchange at the Floor of a Boreal Forest

Nakane, Kaneyuki, Takahiro Kohno, Takao Horikoshi, and Takayuki Nakatsubo   1997   Soil Carbon Cycling at a Black Spruce (Picea Mariana) Forest Stand in Saskatchewan, Canada

Ohashi, Mizue, Timo Domisch, Leena Finér, Martin F. Jurgensen, Liselotte Sundström, Jouni Kilpeläinen, Anita C. Risch, and Pekka Niemelä   2012   The Effect of Stand Age on CO_2 efflux from Wood Ant (Formica Rufa Group) Mounds in Boreal Forests

Ojanen, Paavo, Kari Minkkinen, Jukka Alm, and Timo Penttil   2010   Soil-Atmosphere CO_2, CH_4 and N_2O Fluxes in Boreal Forestry-Drained Peatlands

Ojanen, Paavo, Kari Minkkinen, Annalea Lohila, Tiina Badorek, and Timo Penttilä   2012   Chamber Measured Soil Respiration: A Useful Tool for Estimating the Carbon Balance of Peatland Forest Soils?

Pajari, Brita   1995   Soil Respiration in a Poor Upland Site of Scots Pine Stand Subjected to Elevated Temperatures and Atmospheric Carbon Concentration

Payeur-Poirier,   Jean   2012 CO_2 Fluxes of a Boreal Black Spruce
Lionel, Carole Coursolle,   Chronosequence   in   Eastern   North
Hank A. Margolis, and   America
Marc André Giasson

Pearson, Meeri, Markku   2012   Short-Term Impacts of Soil Preparation
Saarinen, Kari Minkkinen,   on Greenhouse Gas Fluxes: A Case Study
Niko Silvan, and Jukka   in Nutrient-Poor, Clearcut Peatland Forest
Laine

Pumpanen, Jukka, Hannu   2003   Seasonal Patterns of Soil CO_2 Efflux and
Ilvesniemi,   Martti   Soil Air CO_2 Concentration in a Scots
Perämäki, and Pertti Hari   Pine Forest: Comparison of Two Chamber
                                        Techniques

Pumpanen,   Jukka,   Carl   2004   Soil CO_2 Efflux from a Podzolic Forest
Johan   Westman,   and   Soil before and after Forest Clear-Cutting
Hannu Ilvesniemi   and Site Preparation

Rayment, M B, and P G   2000   Temporal and Spatial Variation of Soil
Jarvis CO_2 Efflux in a Canadian Boreal Forest

Repnevskaya, M.A.   1967   Liberation of CO_2 from Soil in the Pine
                                        Stands of the Kola Peninsula

Ruess, RW, RL Hendrick,   2003   Coupling   Fine   Root   Dynamics   with
AJ Burton, KS Pregitzer,   Ecosystem Carbon Cycling in Black
B   Sveinbjornsson,   ME   Spruce Forests of Interior Alaska
Allen, and GE Maurer

Russell, C A, and R P Voroney 1998 Carbon Dioxide Efflux from the Floor of a Boreal Aspen Forest. I. Relationship to Environmental Variables and Estimates of C Respired

Rütting, Tobias, Robert G. Björk, Astrid Meyer, Leif Klemedtsson, and Ulf Sikström 2014 Reduced Global Warming Potential after Wood Ash Application in Drained Northern Peatland Forests

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Wang, Wei, Shushi Peng, Tao Wang, and Jingyun Fang | 2010 | Winter Soil CO_2 Efflux and Its Contribution to Annual Soil Respiration in Different Ecosystems of a Forest-Steppe Ecotone, North China

Wickland, Kimberly P., Robert G. Striegl, Jason C. Neff, and Torsten Sachs | 2006 | Effects of Permafrost Melting on CO_2 and CH_4 Exchange of a Poorly Drained Black Spruce Lowland

Wickland, P.K., Jason C. Neff, and Jennifer W. Hardenc — 2010 — The Role of Soil Drainage Class in Carbon Dioxide Exchange and Decomposition in Boreal Black Spruce (Picea Mariana) Forest Stands

Widén, Britta, and Hooshang Majdi — 2001 — Soil CO_2 Efflux and Root Respiration at Three Sites in a Mixed Pine and Spruce Forest: Seasonal and Diurnal Variation

Zha, Tianshan, Zisheng Xing, Kai Yun Wang, Seppo Kellomaki, and Alan G. Barr — 2007 — Total and Component Carbon Fluxes of a Scots Pine Ecosystem from Chamber Measurements and Eddy Covariance

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