Separating autotrophic and heterotrophic soil CO₂ effluxes and net soil carbon balance in afforested peatlands

Renée Hermans[1][5], Rebecca McKenzie[2][6], Roxane Andersen[2], Yit Arn Teh[3], Neil Cowie[4] and Jens-Arne Subke[1]

[1]Department of Biological and Environmental sciences, University of Stirling, Stirling, UK
[2]Environmental Research Institute, University of Highlands & Islands, Thurso, UK
[3]School of Natural and Environmental Sciences, Newcastle University, Newcastle, UK
[4]Centre for Conservation Science, Royal Society for the Protection of Birds Scotland, Edinburgh, UK
[5]IUCN UK Peatland Programme, Edinburgh, UK
[6]Geography Department, Loughborough University, Loughborough, UK

Correspondence to: renee.kerkvliet-hermans@iucn.org.uk

Abstract. Peatlands are a significant global carbon (C) store, which can be compromised by drainage and afforestation. Quantifying the rate of C loss from peat soils under forestry is challenging, as soil CO_2 efflux includes both CO_2 produced from heterotrophic peat decomposition and CO_2 produced by tree roots and associated fungal networks (autotrophic respiration). We experimentally terminated autotrophic belowground respiration in replicated forest plots by cutting through all living tree roots ("trenching"), and measured soil surface CO_2 flux, litter input, litter decay rate and soil temperature and moisture over two years. Decomposition of cut roots was measured and CO_2 fluxes were corrected for this, this resulted in a big change in the fraction heterotrophic : autotrophic flux, suggesting that even two years after trenching decaying root biomass make significant contributions to the CO_2 flux. Annual peat decomposition (heterotrophic CO_2 flux) was 115 ± 16 g C m^{-2} y^{-1}, representing c. 40% of total soil respiration. Decomposition of needle litter is accelerated in the presence of an active rhizosphere, indicating a priming effect by labile C inputs from roots. This suggests that our estimates of peat mineralization in our trenched plots are conservative, and underestimate overall rates of peat C loss. Considering also input of litter from trees, our results indicate that the soils in these 30 year-old drained and afforested peatlands are a net sink for C, since substantially more C enters the soil as organic matter, than is decomposed heterotrophically. This study doesn't account for fluvial C fluxes, which represents is shown to be a small flux compared to the CO_2 soil efflux; further, r (Gaffney et al., 2020). Root litter and exudate deposition could be a significant C source that is only partially sampled by our approach, and this could be a significant C input, adding to these plantations being a potential carbon sink. However, the C balance for these soils should be taken over the lifespan of the trees, in order to determine if the soils under these drained and afforested peatlands are a sustained sink of C, or become a net source over longer periods of forestry.

1 Introduction

Large peatland areas in the boreal and temperate zone have been drained and afforested, in Western Europe, especially in the UK, Ireland and the Fennoscandia region, with conifers replacing native peatland vegetation (Andersen et al., 2016). In the UK alone, >800,000 ha (approximately 20%) were affected by this land-use change (Anderson et al., 2016). As well as causing habitat loss, drainage and afforestation of peatlands influences peatland hydrology, biogeochemistry, and carbon (C) storage. In Fennoscandia, drainage to improve tree growth on naturally ~~forested~~ treed peatlands has been shown to cause significant changes in decomposition and greenhouse gas (GHG) fluxes (Ojanen et al., 2013). However, the effects of drainage and afforestation on temperate peatlands that were previously dominated by smaller-statured vegetation (e.g. blanket bogs, moorland, heathland) are more uncertain (Sloan et al., 2018). While changes in hydrology and soil redox potential are anticipated to accelerate soil C loss and alter the composition of GHG emissions, there is ~~a~~ very little quantitative data on how this shift in land-use changes soil C dynamics and GHG emissions in temperate peatlands (Hermans et al., 2018). Since northern hemisphere peatlands are estimated to store a third of global terrestrial carbon (Gorham, 2010), changes linked to drainage and afforestation of temperate peatlands could have significant impacts on regional C dynamics and GHG balances.

There is a broad consensus that peatland drainage accelerates the loss of endogenous peat C stocks, but the impacts of drainage and afforestation on total soil C stocks and soil respiration are less certain (Hargreaves et al., 2003; Mayer et al., 2020; Simola et al., 2012; Vanguelova et al., 2019; Zerva & M. Mencuccini, 2005). ~~This is because our conceptual and numerical models of peat C dynamics are based on studies where drainage is assumed to be the principal human intervention, and there is no effective functional shift in plant community composition linked to land-use change (e.g. bogs drained to improve the productivity of the existing plant community to increase the quantity of forage for livestock).~~ Afforestation of previously open peatlands in the British Isles (e.g. Mazzola et al., 2020) and Fennoscandia (e.g. Tolvanen et al., 2020) differ from other types of drained peatlands because this land-use change involves a wholesale shift in the functional composition of the plant community (i.e. replacement of short-statured vegetation with trees), leading to potential interactions or synergistic effects arising from changes to both soil hydrology and plant community composition.

The comparatively high rates of net primary production and larger stature of the trees on drained and afforested peatlands can represent a significant net ecosystem C sink, and consequently represent a large source of detrital material to soil (Yamulki et al., 2013). Thus, it is possible that this input of C from more highly productive trees could partially or wholly offset or outstrip some of the losses of C derived from mineralization of the ~~original~~ peat. Moreover, changes to soil organic matter (SOM) chemistry due to a shift towards inputs of more recalcitrant and nutrient-poor coniferous litter could further enhance soil C storage in afforested peatlands in the British Isles and Fennoscandia. This is because the trees planted in these regions (e.g. Sitka spruce) produce tissues that are less readily decomposed ~~are of poorer quality~~ than the organic matter (OM) generated by the short-statured vegetation that they have replaced (i.e. larger proportion of woody debris generated with higher C:N ratios and greater proportion of recalcitrant compounds like lignin) (Hermans et al., 2018). This may affect soil C stocks by inhibiting

or slowing overall rates of decay due to the tree litter's ~~chemical~~ recalcitrance (Liski et al., 2002), but has not been studied in tree plantations on deep peat so far.

65   In order to close these knowledge gaps, we need to determine the C balance of drained and afforested peatland soils, tracking C inputs from tissue turnover (e.g. litterfall and rhizodeposition), as well as C losses from SOM decay. However, separating the direct and indirect effects of trees on peat mineralization is methodologically challenging (Subke et al., 2006). Soil CO_2 efflux includes both CO_2 released from peat mineralization (heterotrophic CO_2 flux) and CO_2 produced from root-rhizosphere (i.e. autotrophic) respiration; experimental manipulation of autotrophic C supply to the

70   rhizosphere allows a separation of these two main component fluxes, but introduces a number of potential artefacts (see Subke et al., 2006 for a methods overview including method-related assumptions and artefacts). Root trenching, where roots are severed throughout the depth of the rooting zone to create areas of forest floor with no recent C input from trees to roots or associated mycorrhizas, has been used across many forest sites, and provides useful insights into relative contributions of autotrophic and heterotrophic soil CO_2 efflux and the respective temporal dynamics. This disruption of root exudation

75   and continuous root turnover could influence peat decay through processes such as microbial priming effects (Kuzyakov, 2006; Subke et al., 2006), where microbial activity (linked with an active rhizosphere) in the soil is stimulated by the addition of easily accessible C from roots (Kuzyakov, 2006). Further experiments are required to evaluate the effects of these other plant-facilitated processes on peat decay, to better constrain estimates of heterotrophic activity in soil.

       In this study, we experimentally determined the C budget of a drained and afforested peat soil. Carbon inputs were

80   tracked by quantifying litterfall, while C outputs were determined using a trenching technique to partition root-rhizosphere and heterotrophic respiration. In addition, we conducted a root decomposition study in rhizosphere and living root-free (i.e. trenched) soil, to constrain artefacts associated with the trenching and in order to determine if rhizosphere-linked processes (e.g. priming effects) facilitated OM decay. We hypothesised that 1) the soils under these forestry plantations are a net C source, 2) soil CO_2 efflux is dominated by autotrophic respiration and 3) interactions between C supply to the rhizosphere

85   by trees and surface litter decomposition result in higher decomposition rates of the litter due to rhizosphere priming effects.

2 Methods

2.1 Study site

The research took place in RSPB's Forsinard Flows National Nature Reserve in the north of Scotland (58° 22' N, 3° 53' W). Four paired plots were established in the beginning of June 2014 in three separate forestry plantation blocks of identical age

90   containing a mixture, 3:5 (on average), of Sitka Spruce (*Picea sitchensis)* and Lodgepole Pine (*Pinus contorta).* The plantations were drained, around 30 years old and very dense (about 5000 trees per ha), with no vascular plant understory, but sporadic patches of moss, predominantly feather moss, e.g. Hypnum jutlandicum, Hylocomium splendens and in some instances, Sphagnum fallax and S. capillifolium in furrows. The 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 Sitka Spruce : Lodgepole Pine of 0.6.~~ The average canopy

95 cover was 76.3% (Smith and Hancock, 2016). Peat depths in these three forestry blocks varied between 30 and 260 cm, with depths at research plots between 137 and 204 cm (Smith et al., 2014). The average annual precipitation in the research area between 1981-2010 was 970.5 mm with an average maximum air temperature of 11.4°C and average minimum air temperature of 3.3°C measured at the Kinbrace weather station approximately 20 km from the plots (Location: 58º13'89''N, 3º55'1.2''W; Altitude: 103 m above mean sea level; Met Office, 2018). Seasonal averaged water table relative to ground surface is -350

100 (±20) mm in spring (March-May), -457 (±34) mm in summer (June-August), -404 (±49) mm in autumn (September-November) and -244 (±14) mm in winter (December-February).

2.2 Experimental set up

Candidate locations for the four paired trenched and control areas in each plot were initially identified at random and soil surface respiration measured. Based on respiration results, two closely matched plots were selected, and randomly allocated a

105 treatment (trenching or control). Paired plots were no more than 10 metres apart from each other.

The double-mouldboard 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 1Figure 1). The height from the bottom of the furrow to the top of the plough throw is on average 0.5 m and from the original surface to the plough throw is about 0.15 - 0.2

110 m. In general, conifer seedlings were planted on the plough throws because of the improved drainage compared to the original surface. For our study, each plot encompassed the three types of micro-topography.

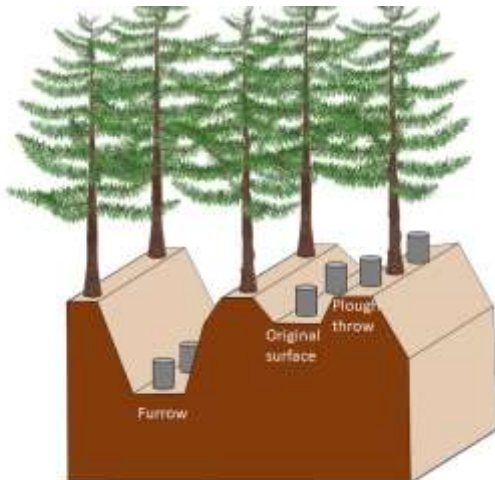



Figure 1 Micro topography in forest plantations, with location of measurements for flux chambers (not to scale).

115

2.3 Trenching

A 40 cm deep and 30 cm wide trench was cut 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 2). The dimensions of each trench plot were about 3.5 x 1.5 meters and included

120 all three micro topographic forms. These dimensions maximised the space between trees, but did not represent ground within 60 cm of trees.~~with closest trees located about 30 cm from trenches.~~

Figure 2 Left: trenching plot dug and all living tree roots are sawn trough. Right: finished trench plot; trenches double lined

125 with polypropylene gardening cloth and filled in with peat.

2.4 CO$_2$ measurements

Three pairs of PVC collars of 10 cm height with a diameter of 20 cm where installed to a depth of three cm within the three microforms (Figure 1~~Figure 1~~) of both trenched and control plots. CO$_2$ measurements were taken using custom-built dark dynamic closed chamber with a height of five cm and a diameter of 20 cm, which were placed on the permanent collars for

130 three minutes. Elasticated rubber material placed over the joint of chambers and collars for the duration of the measurement

provided an air-tight seal. 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.

2.5 Litter

135 Six litter traps (0.07 m² each) were located close to each plot, and litter (falling needles and twigs) collected at each sampling visit. Dry weight of all litter was recorded as area-based averages for each plot separately.

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 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

140 measurement and then placed back in the collar. Litter adjacent to the collar was also 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.

2.6 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

145 the start (June 2014) and end (July 2016) of the experiment. Both dead and living Rroots 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. Root depth was found to be 25 cm when digging trenches and root density for 0-20 cm was assumed to be representative for 0-25 cm.

To estimate root decomposition directly, roots were taken from soil collected in each plot, dried (50°C for 7 days)

150 and separated into 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

155 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 (except root class >5 mm, since there was not enough material for four bags) 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:

160 $$M_t = M_0 e^{-kt} \tag{1}$$

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.

2.7 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, measuring m³/m³ (volumetric water content)) 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, measuring m³/m³ (volumetric water content)) were measured at 5 cm depth next to each collar during sampling. Air temperature was also measured one meter above the ground during sampling.

2.8 Statistical analyses and flux calculations

Data were analysed using R (RStudio Team, 2016). All CO_2 data was log transformed to meet the criteria of normality, and a linear mixed-effect model (LMM) using the ~~nlme~~ lme4 package in R (Bates et al., 2015)~~(Pinheiro et al., 2017)~~ was used to predict CO_2 fluxes based on environmental drivers. All numerical predictors were standardized to one standard deviation prior to statistical analyses, to allow relative effect sizes of predictors to be compared directly (Nakagawa & Schielzeth, 2010). Model selection was done based on information theory (Burnham & Anderson, 2002). First a model of maximum complexity 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 (lmer(CO_2 flux ~ (soil moisture *soil temperature * treatment * microform + treatment * microform * litter treatment) + (1|plot))). Then, 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', hereafter called 'top model' (Burnham & 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. Significance (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), and predictions and error terms where back transformed. 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.

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

$$F_a + \varepsilon = (F_{control} + \varepsilon) - ((F_{trench} + \varepsilon) - (F_{dead\ roots} + \varepsilon)) \tag{2}$$

Where F_a is autotrophic CO_2 flux, $F_{control}$ is the CO_2 flux from the control plots, F_{trench} is the CO_2 flux from trenched plots, $F_{dead\ roots}$ is the CO_2 flux coming from the dead roots in the trenched plots created by the trenching technique and ε the associated

200 error terms, error terms where propagated.

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

3 Results

205 ### 3.1 Temporal trends in soil CO_2 fluxes

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. After the initial perturbation fluxes from trenched plots are significantly lower than fluxes from control plots ($p<0.001$) and this difference is greater in the summer (Figure 3Figure 3).

210

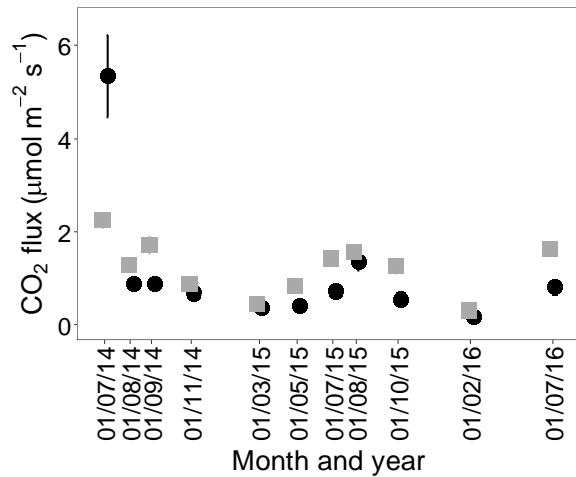



Figure 3 Mean CO_2 fluxes from control (grey squares) and trenched (black circles) plots over time, averaging across all microforms (n = 12) and both litter treatments. Error bars are standard errors and are in most instances smaller than symbols.

215   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 1~~Table 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 on the log -scale, since predictions are made in the original units all uncertainties reinflate. The set of models with a ΔAICc of less than 2 is shown in Table 2. The predictors of the 'top model' were present in ~~at least~~

220 over half of the models in the top model set, so this model was used.

Table 1 Model estimates with standard errors and p-value for best-fit model. All numerical predictors were standardized to one standard deviation prior to analysis.

Fixed effect	Estimate	Std. Error	p-value
Intercept	-0.22	0.10	0.05
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
No Litter	-0.17	0.06	0.008
Soil moisture x Soil temperature	-0.11	0.04	0.008

225 Table 2 Model selection summary, showing the 4 best ranked models with a delta AICc of less than 2. 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'.

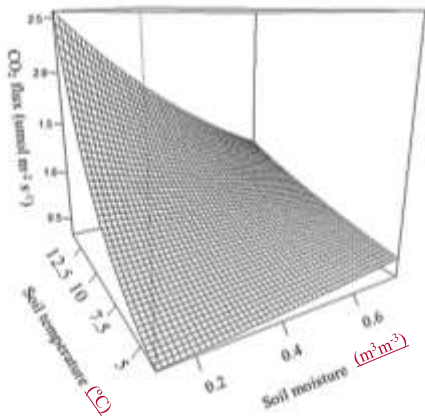
Candidate models	Df	LogLik	AICc	ΔAICc	Weight
Trenched + Microform+ No Litter + Soil moisture + Soil temperature + Soil moisture x Soil temperature	10	-403	826	0.00	0.34
Trenched + Microform+ No Litter + Soil moisture + Soil temperature	9	-404	826	0.37	0.29
Trenched + Microform+ Soil moisture + Soil temperature + Soil moisture x Soil temperature	9	-404	827	1.21	0.19
Trenched + Microform+ Soil moisture + Soil temperature	8	-405	827	1.30	0.18

3.2 Spatial trends and litter contributions to soil CO_2 flux

230 In both control and trenched plots, fluxes from plough throw (control: 1.23 ± 0.10; trenched: 0.85 ± 0.07 µmol m^{-2} s^{-1} ; p=0.01) and original surface (control: 1.48 ± 0.10; trenched: 0.83 ± 0.06 µmol m^{-2} s^{-1} ; p<0.001) were significantly higher than fluxes from furrow (control: 0.90 ± 0.06; trenched: 0.47 ± 0.04 µmol m^{-2} s^{-1}). Across all microforms fluxes from collars with litter (1.03 ± 0.05 µmol m^{-2} s^{-1}) were significantly higher than fluxes from collars without litter (0.91 ± 0.05 µmol m^{-2} s^{-1}, p=0.008).

3.3 Role of environmental drivers in modulating CO_2 flux

235 Observed soil CO_2 efflux values correlated positively with ~~higher~~ soil temperatures, whilst soil moisture showed an inconsistent correlation with flux values; a 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, with an inflection between positive and negative moisture dependence between 6 and 7 °C (Figure 4~~Figure 4~~).

240   There was no difference in soil temperature between trenched and control plots, but soil moisture was significantly higher in trenched plots than in control plots (p<0.001). To account for the artificially elevated soil moisture in trenched plots, CO_2 fluxes were corrected using the global relationship between soil moisture and CO_2 flux (Figure 4~~Figure 4~~) to calculate fluxes expected to occur under moisture conditions in control plots.

245 Figure 4 Combined effect of soil temperature and soil moisture at 5 cm depth on soil CO_2 flux from the control sites, estimated from the 'top model'.

3.4 Partitioned fluxes

Soil CO_2 efflux was partitioned into component fluxes for all measuring dates from August 2014 onwards to remove disturbance related artefacts observed immediately after trenching. The model prediction of heterotrophic respiration is
250 calculated by subtracting the autotrophic flux from the total soil flux and includes emissions from decomposition of cut roots. Flux simulations based on the soil model details indicate significantly lower autotrophic fluxes than heterotrophic fluxes (p=0.01, Figure 5). 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 184 ± 21 g C m^{-2} y^{-1}. Total soil respiration without needle litter is 301.3 ± 34.2 g C m^{-2} y^{-1}, with needle decomposition adding 41.2 ± 53.5 g C m^{-2} y^{-1} to annual fluxes, giving a total soil respiration including needle litter of 343 ± 35 g C m^{-2} y^{-1}.

255

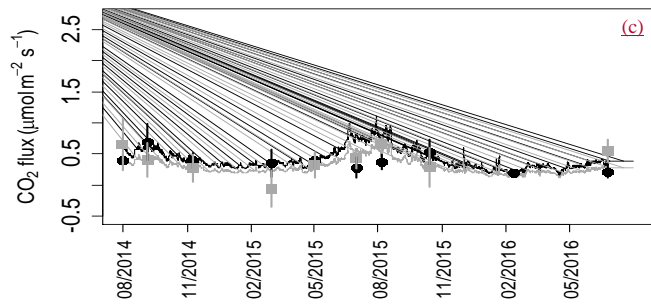
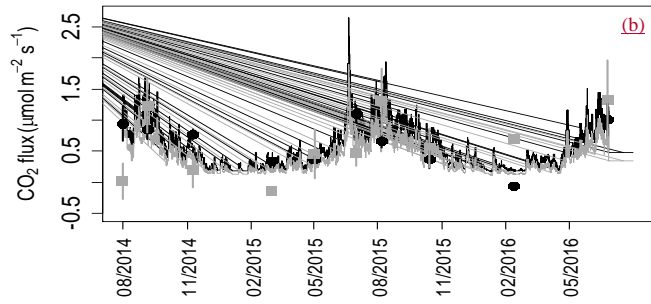
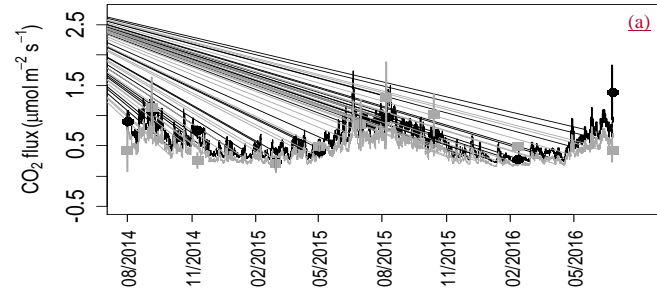
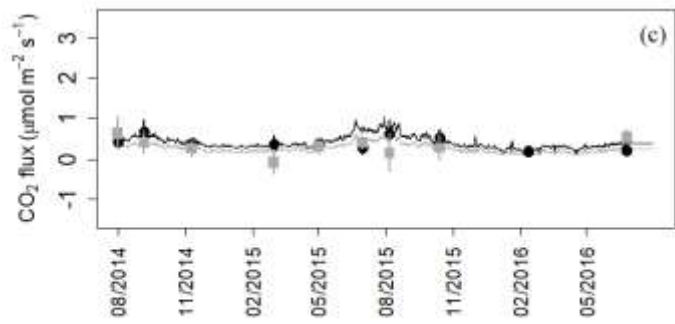
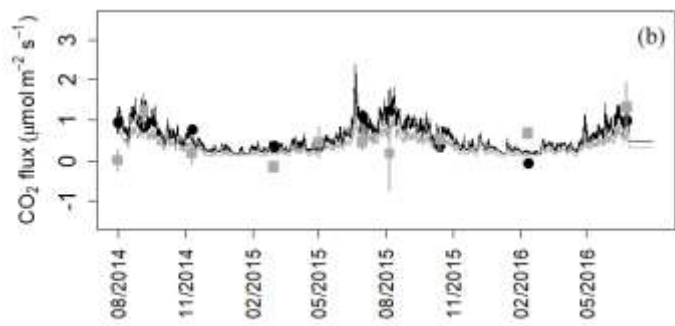
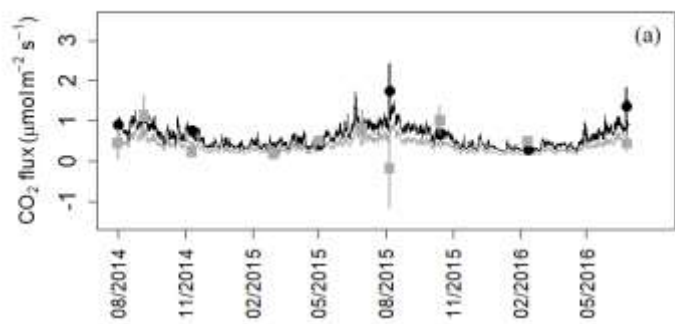



Figure 5 Modelled and measured fluxes of heterotrophic (black) and autotrophic (grey) soil CO_2 efflux from the three topographic microforms. Closed symbols are average fluxes with error bars (n = 4 plots). Connecting lines are the predicted fluxes using soil temperature and moisture at 5 cm depth. a) Original surface, b) Plough throw and c) Furrow.

265

3.5 Impact of litter and roots

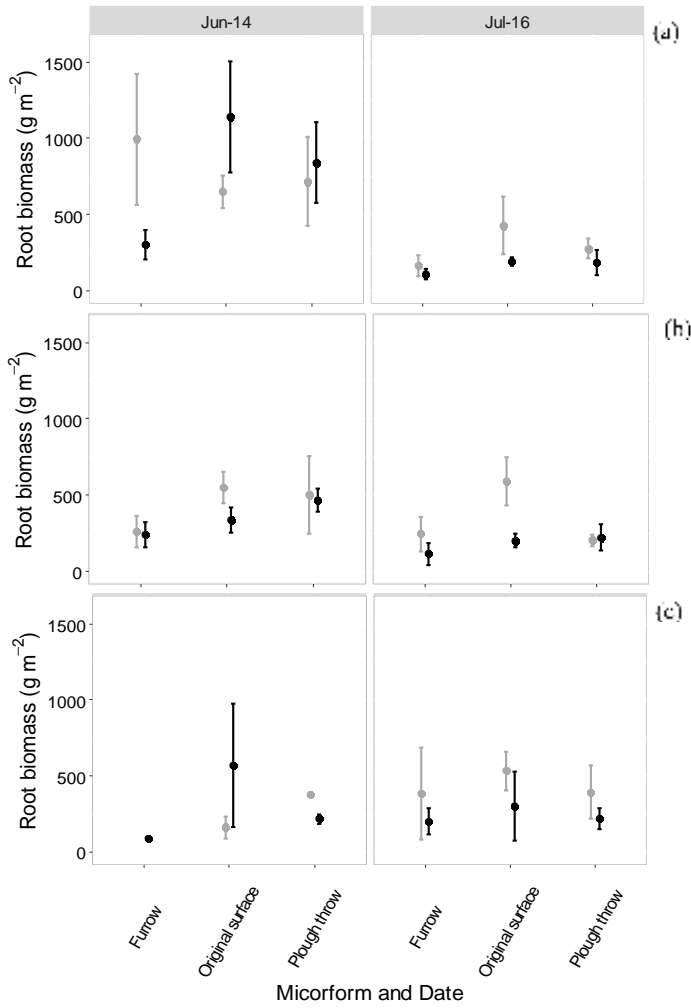
Litter fall was 719 ± 71.3 grams of litter per $m^{-2} y^{-1}$, with no detectable difference between trenched and control plots. Assuming a C fraction of biomass of 50% (Mathews, 1993), this represents an input to the soil of 359 g C $m^{-2} y^{-1}$ via litter fall.

CO_2 flux from surface litter is calculated from the difference in the modelled annual fluxes between the collars with
270 and without litter, with the fluxes from collars with litter significantly higher than the CO_2 flux from the collars without litter (p = 0.008, Table 1~~Table 1~~). C emitted by litter in the control plots appears to be higher than in trenched plots~~. Further, the average amount of litter in the collars (per m⁻²) of the trenched plots is higher than in the collars of the control plots,~~ and the CO_2 flux per gram of litter is ~~resulting in a~~ 1.7 to 3.6 times higher ~~CO_2 flux per gram of litter~~ from the control plots than from the trenched plots (Table 3~~Table 3~~).

275

Table 3 Mean amount of C emitted as CO_2 by surface needle litter in 'litter collars', for both years (standard error in brackets).

Microform	Litter		CO_2 flux		CO_2 flux per g litter	
	[g m⁻²]		[g C m⁻² y⁻¹]		[mg C (g litter)⁻¹]	
	Trench	**Control**	**Trench**	**Control**	**Trench**	**Control**
Original surface	472.4 (174.0)	237.8 (61.0)	34.4 (32.4)	62.5 (50.4)	72.8 (73.6)	263 (222)
Plough throw	351.1 (125.2)	263.5 (85.4)	36.0 (40.8)	60.1 (61.3)	103 (122)	228 (244)
Furrow	589.8 (288.8)	558.4 (256.2)	26.4 (28.8)	43.2 (40.8)	44.8 (53.5)	77.4 (81.2)

Root biomass per m^2 with an assumed rooting depth of 25 cm in August 2014 was 761 ± 324 g, 603 ± 110 g and 715 ± 257 g for < 2 mm roots, 2-5 mm roots and > 5 mm roots, respectively. For both the control and the trench plots, roots smaller
280 than 2 mm declined in total biomass from the start of the experiment to the end of the experiment, but there ~~was~~ were no significant difference between the control and trenched plots at the start and end of the experiment. Despite an apparent trend towards higher root biomass in control plots in July 2016, these differences were not statistically significant. There was also no significant differences between the beginning and end of the experiment for root classes 2-5 mm and >5 mm (Figure 6).

285 Figure 6 Root biomass per square meter to 25 cm in control (grey) and trenched (black) 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. Symbols are average fluxes with error bars representing standard errors (n = 4 plots).

3.6 Root decomposition

290 Root mass in decomposition bags showed a consistent decline over the duration of the experiment (Figure 7). The calculated decay constant (k) showed systematic differences by microform, with highest decay rates tending to occur for incubations at "original surface" (Table 4).

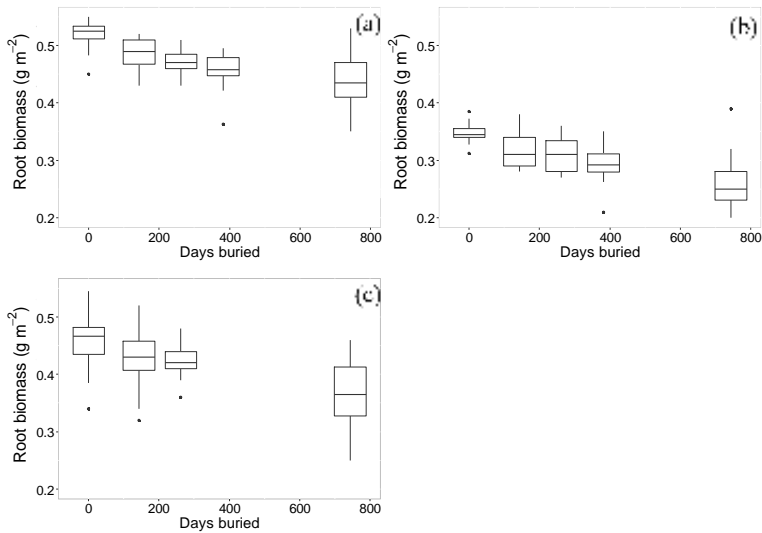



Figure 7 Root mass remaining in root bags over number of days buried, for each root size class averaged across all microforms.
295 a) root size <2 mm, b) root size 2-5 mm, c) root size >5 mm.

Table 4 Root decay constants and associated C emissions in trenched plots by microform and root size classes (standard error in brackets).

	Root diameter mm	Decay constant y^{-1}	C emitted year 1 $g\ C\ m^{-2}\ y^{-1}$	C emitted year 2 $g\ C\ m^{-2}\ y^{-1}$
Original surface	<2	0.106 (0.019)	57 (18)	52 (17)
	2-5	0.180 (0.027)	28 (7)	23 (6)
	>5	0.190 (0.027)	50 (25)	41 (21)
	Total	**269 (63)**	**135 (32)**	**116 (27)**
Plough throw	<2	0.097 (0.015)	39 (12)	35 (11)
	2-5	0.153 (0.026)	33 (6)	28 (5)
	>5	0.100 (0.022)	10 (1)	9 (1)
	Total	**164 (27)**	**82 (13)**	**73 (12)**
Furrow	< 2	0.068 (0.015)	10 (3)	9 (3)
	2-5	0.097 (0.018)	11 (4)	10 (3)
	>5	0.065 (0.023)	3 (/)	3 (/)
	Total	**48 (10)**	**24 (5)**	**22 (5)**

3.7 C flux from dead roots

300   The amount of C emitted from the decaying roots is calculated using the exponential decay function (1), with the biomass of roots per m^2 to a depth of 20 cm in the trenched plots at the beginning of the experiment as M_0. It is assumed that all biomass lost is emitted as CO_2 and that 50% of roots is C (Mathews, 1993), as conservative assumptions, meaning that estimates are maximum possible CO_2 flux from decaying roots in trenched plots. To correct for soil CO_2 efflux generated in trenched plots as an artefact of creating dead root biomass, annual estimated CO_2 emissions were corrected by subtracting root-decay based

305   estimates from trenched plot CO_2 emissions (Table 5).

Table 5 Corrected for dead root decay in trenched plots, heterotrophic soil CO_2 efflux (excluding litter) (peat only; F_h) and 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.

	Year 1		Year 2		Average		
	F_h	F_a	F_h	F_a	F_h	F_a	F_{soil}
Original surface	86.5 (37.7)	276 (35)	80.2 (33.2)	242 (30)	83.3 (35.4)	259 (33)	342 (48)
Plough throw	118 (29)	212 (20)	124.1 (28.0)	199 (19)	121 (28)	206 (19)	327 (34)
Furrow	134 (21)	125 (10)	107 (17)	105 (9)	120 (19)	115 (9)	235 (21)

Heterotrophic fluxes represents approximately 24% and autotrophic fluxes 76% of the total soil fluxes in the original surface, 37% and 63% respectively in the plough throw, 51% and 49% respectively, in the furrow and 38% and 62% respectively averaged over all microforms.

3.8 Weighted average for soil CO_2 flux in Flow Country forest plantations

In order to scale soil CO_2 fluxes (excluding litter) from different microforms to the level of an entire forest stand, fluxes from individual microforms were weighted by their fractional area (Table 6). This results in a slight shift in proportion of heterotrophic and autotrophic CO_2 flux sources to 40% and 60% respectively and a total area weighted soil CO_2 flux of 289.4 ± 18.6 g C m^{-2} y^{-1}.

Table 6 Area-weighted heterotrophic (peat decomposition only) (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	Area-weighted F_h	Area-weighted F_a
Original surface	0.14	12 (5)	36 (5)
Plough throw	0.43	52 (13)	88 (8)
Furrow	0.43	52 (8)	49 (4)
Total	1	115 (16)	174 (10)

Formatted Table

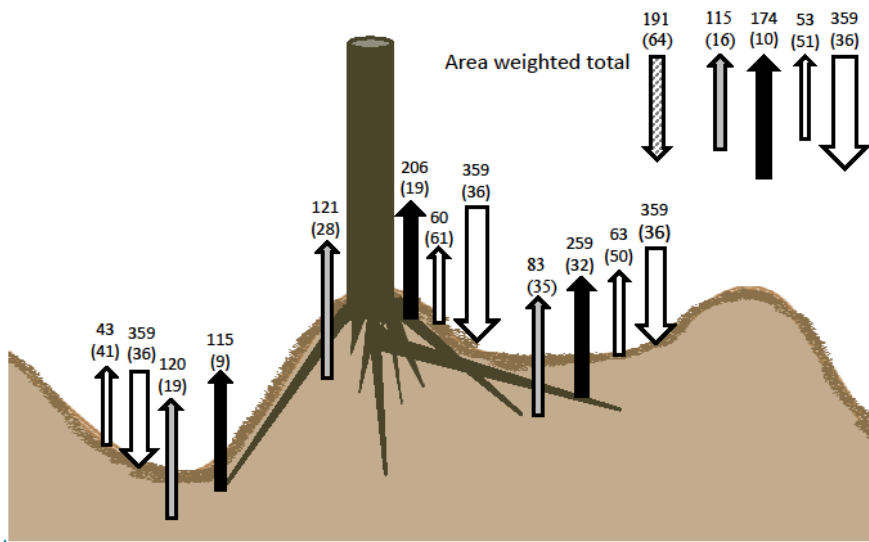
4 Discussion

Our results Mass balance calculations indicate that the soils in these 30 year old drained and afforested peatlands are a net sink

325   for C, as substantially more C enters the soil as organic matter, than is decomposed heterotrophically. The soil surface C

balance of the soil under these forest plantations is visualised in Figure 8, with the annual CO_2 fluxes of the forest plantation

based on the area-weighted fluxes. Based on these fluxes, we tentatively estimate the soil C sink (the difference between litter

C input and total heterotrophic soil CO_2 efflux) to be 191 ± 64 g C m^{-2} y^{-1} for our site.

330

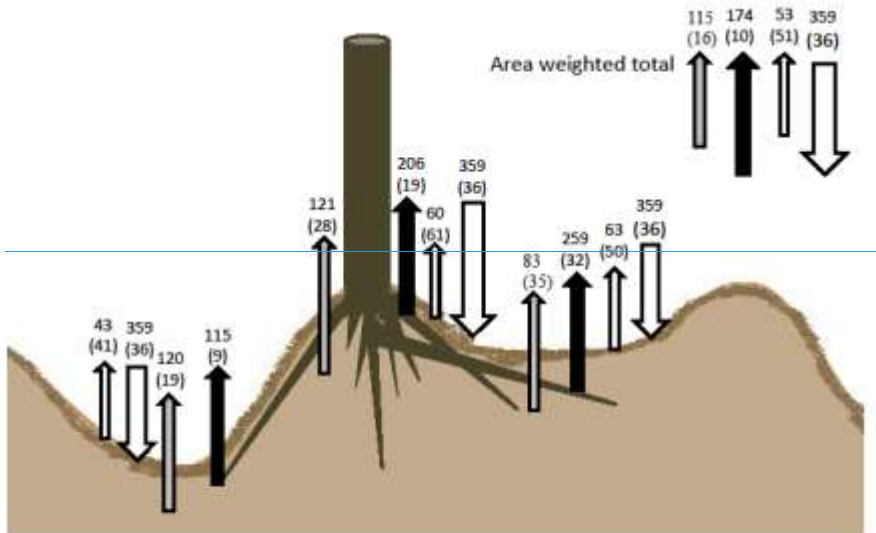



Figure 8 8 Summary of soil C budget (in g C m^{-2} y^{-1}) under the canopy of a Sitka spruce and Lodgepole pine plantation on deep peat. Downward arrows indicate litterfall, whilst upward fluxes show autotrophic (F$_a$) (black), peat decomposition fluxheterotrophic (peat only; F$_h$) (grey), and surface needle litter (white) across the three main microforms. Total forest soil fluxes with area weighted values are visualised in the top right corner, including the estimated soil C sink (grey and white
335 diagonal striped).

We found a C input of 359 g C m^{-2} y^{-1} via litter fall, similar to other Sitka Spruce forests of similar age to these forest plantations in the UK, which range from 273 to 573 g C m^{-2} y^{-1} (Morison et al. 2012). This is balanced by total soil efflux including litter-derived CO_2 of 342.5 ± 34.7 g C m^{-2} y^{-1}, i.e. the amount of C entering the soil as surface litter alone falls within a similar range
340 to C leaving as CO_2. Missing in the C budget in Figure 8 are the input of C from root exudates that remain in the soil C pool (net rhizodeposition), potential losses through aquatic C export, and root growth and turnover. Gaffney, et al. (2020) have measured the aquatic C flux (DOC, DIC, POC) from similar forest plantations in the north of Scotland and have found a flux of 13.9 g C m^{-2} y^{-1}, which is a small flux compared to the CO_2 soil efflux. Root:shoot allocation in forest ecosystems is usually in the order of 1:3 (Laiho & Laine, 1997), so it is possible that belowground litter and exudate deposition belowground
345 productivity could account for a significant C input only partially sampled by our approach (i.e. excluding large root stocks), which means that our tentative soil C sink estimate is conservative. adding to these plantations being a potential carbon sink.

The rate of peat decomposition in these drained and afforested peatlands is substantial, but overall soil CO_2 efflux and ratio of heterotrophic/autotrophic respiration falls within boreal averages for forested ecosystems (Figure 9; Bond-Lamberty and Thomson, 2010).

350

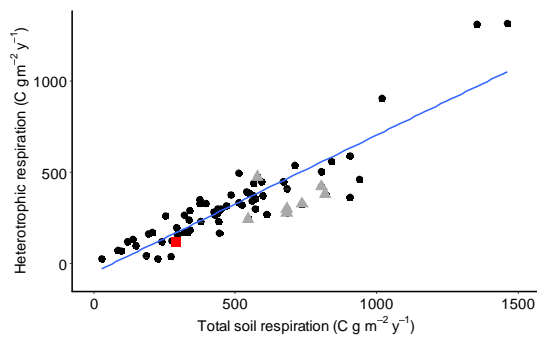



Figure 89 Heterotrophic annual flux against soil respiration annual flux (g C m^{-2} y^{-1}) in Boreal forests in black dots, Boreal forests on peat soils in grey triangles, from Bond-Lamberty and Thomson (2010) dynamic database downloaded on 19/04/2020. Our study is included in the red square. See Table 7 in Appendix for references to

355 studies used to create this graph.

Average soil efflux corrected for microform area without litter (to determine the peat decomposition rate) over the two measurement years was 289 ± 19 g C m^{-2} y^{-1} of which 174 ± 10 g C m^{-2} y^{-1} is autotrophic and 115 ± 16 g C m^{-2} y^{-1} is

360 heterotrophic.

Results from other drained temperate peatland sites under conifer plantationOur total soil respiration (including litter) of 342.5 ± 34.7 g C m^{-2} y^{-1} is vary from around 260 g C m^{-2} y^{-1} at a 39-year old drained Sitka spruce plantation in Ireland on naturally treeless blanket bog (Byrne & Farrell, 2005) to values of 972 g C m^{-2} y^{-1} on average across 18 to 44 year old Sitka spruce plantations on poorly drained Dystric Histosols in the south of Ireland (Jovani-Sancho et al., 2018), with similar annual

365 fluxes of slightly higher than values of around 260 g C m^{-2} y^{-1} reported for a similar forest plantation in Ireland, a 39-year old drained Sitka spruce plantation on naturally treeless blanket bog (Byrne & Farrell, 2005)453 g C m^{-2} y^{-1} reported from under a 43-year old lodgepole pine plantation in central Scotland (Yamulki et al., 2013). Afforested boreal peatlands also show generally higher soil CO_2 flux values, ranging from 577 to 705 g C m^{-2} y^{-1} (e.g. Mäkiranta et al., 2008; Minkkinen et al., 2018; Ojanen et al., 2010). Also taking into account possible measurement bias associated with the chemical absorption method used

370 by Byrne & Farrell (2005), which generally underestimates fluxes compared to more reliable infrared gas analysis based methods (Janssens & Ceulemans, 1998), our results of of 342.5 g C m^{-2} y^{-1} sit at the low end of total soil respiration fluxes.

These low rates are corroborated by independent chamber flux measurements across forest sites in the Flowcountry (Hermans et al., unpublished), and are likely to relate to poor site fertility and specific biochemical properties of the peat at these sites (Hermans et al., 2019).

375   Our peat oxidation rates of 115 ± 16 g C m^{-2} y^{-1} are also low compared to temperate afforested peatlands, which have been reported to vary between 211 and 407 g C m^{-2} y^{-1} for Sitka spruce sites in Ireland (Jovani-Sancho et al., 2018), whilst boreal peatlands show an even larger range of heterotrophic flux sums (145 to 670 g C m^{-2} y^{-1} ; Ojanen et al., 2010). Our low estimates result in part from the root decomposition correction, which reduced heterotrophic flux estimates by around 60 g C m^{-2} y^{-1}, and is not routinely applied across other studies. higher than found by Hargreaves et al. (2003), who found <100 g C

380   m^{-2} y^{-1} in a 26-year old Sitka spruce plantation on drained deep (> 2 m) peat in Scotland. However, they point out that their estimate has a big uncertainty, since it was calculated from the difference between total net C exchange and net tree gain, which both have a large uncertainty.

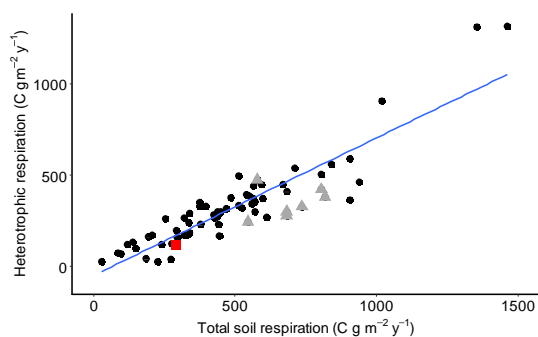
       Comparing our results to a study in 18 to 44 year old Sitka spruce plantations on poorly drained Dystric Histosols in Southern the south of Ireland, our results of total soil respiration is much lower than their 972 g C m^{-2} yr^{-1}. This could be due

385   the difference in age of the trees. Our results do show a similar percentage of peat-only respiration of 38% of the total soil respiration minus the litter flux, compared to their 35% (Jovani-Sancho et al., 2018).

       Minkkinen et al (2018) measured carbon fluxes of a drained, naturally forested peatland (Kalevansuo peatland forest) in the south of Finland over 4 years. They found that the ecosystem was a strong sink of CO_2 in all studied years, with an average NEE for the 4 years of -234 g C m^{-2} y^{-1}. By subtracting the carbon sink of the tree stand from eddy-covariance derived

390   NEE the authors show that the soil was a carbon sink of -60 g C m^{-2} y^{-1}. However, By modelling their forest soil respiration fluxes from chamber measurements, they found the peat only respiration alone made up 53% of the total forest floor respiration flux, litter 22%, roots 16% and autotrophic respiration of above-ground vegetation 8%, with soils representing a weak C source. Our results show a lower percentage of peat only respiration of 38% of the total soil respiration minus the litter flux. The higher percentage found by Minkkinen et al (2018) could possibly be explained by them not applying a dead root correction to their

395   fluxes, which as we show could lead to a big difference in fluxes. For forestry-drained boreal peatlands, Ojanen et al (2013) report a range of soil C balances from weak source to sinks depending on site fertility. Accounting for belowground litter production and fine root turnover is an important source of uncertainty in soil C balance estimates (Ojanen et al., 2014), and whilst our soil C balance focuses on surface litter only, our calculations indicate a weak C sink even before belowground litter input is considered.

400

~~Figure 9 Heterotrophic annual flux against soil respiration annual flux (g C m^{-2} y^{-1}) in Boreal forests in black dots, Boreal forests on peat soils in grey triangles, from Bond-Lamberty and Thomson (2010) dynamic database downloaded on 19/04/2020. Our study is included in the red square. See Table 7 in Appendix for references to studies used to create this graph.~~

405

Trenching is likely to underestimate heterotrophic respiration and rates of peat mineralization since this approach does not account for rhizosphere effects such as priming (Walker et al., 2016). Therefore, it is likely that the estimated rate of peat oxidation from trenching is conservative. The observed difference of 1.7 to 3.6 times higher CO_2 flux per gram of litter from the control plots than from ~~and~~ the trenched plots (Table 3~~Table 3~~) indicates that heterotrophic processes are reduced

410 under trenching. In presence of an active rhizosphere (control plots), decomposition of needle litter and/or soil organic matter (SOM) appears to be faster than when the rhizosphere is not active (trenched plots). This priming of organic matter decomposition is likely to be the result of microbial activity in the soil stimulated by the addition of easily accessible C from roots (Kuzyakov, 2006). Friggens et al. (2020) recently demonstrated the accelerated loss of organic soil under coniferous and deciduous forest plantations on peaty podzols in Scotland, which is consistent with soil priming through the elevated input of

415 C from treesin the rhisosphere. ~~Further, s~~Several studies have shown that mycorrhizal fungi are involved in soil priming (Kuyper, 2017; Paterson et al., 2016), further underlining the interaction between plant-associated biotic activity and decomposition in underlying peat. Therefore, in the control plots a slightly larger proportion of the total CO_2 flux could be heterotrophic decomposition than the fluxes from the trenched plots suggest, which means there could be an underestimation of heterotrophic flux in our results, in line with results from literature (Subke et al., 2004; Subke et al., 2011).

420 To calculate the root biomass at the start of the experiment, one soil core per microform was taken and since trees were standing close to each other (1.5 to 2 m apart) this was assumed to be representative for the whole microform. It was not possible to distinguish between living and dead roots in the soil cores, so our results ~~living root biomass~~ might ~~have been~~ overestimate the living root biomass~~d~~. 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 38% and 62% respectively (without area-

425 weighting of fluxes), so a decrease in heterotrophic flux of 23%. This is in line with the corrections used in other studies; a

comparison of corrections used in trenching studies indicates a range from 2% to 24%, with an average of 12% (Subke et al., 2006). This big difference in the fraction heterotrophic : autotrophic flux suggests that even two years after trenching, decaying root biomass make significant contributions to the CO_2 flux.

That soils under a 30-year old conifer plantation on deep peat are a C sink is an interesting finding. However, in order to determine if these soils are a long-term sink or source of carbon, the balance between soil C input from roots and litter and C loss via oxidation should be quantified over the lifespan of the plantation. The average peat depth in these forest plots is 126 ($\pm$16) cm, with 0.47 kg C m^{-2} per centimetre depth (Cannell et al., 1993), which represents ca. 59.3 ($\pm$7.3) kg C m^{-2} stored in the peat under these plantations. The largest carbon losses most likely occurred in the initial planting phase of afforestation (Simola et al., 2012; Vanguelova et al., 2019; Zerva & M. Mencuccini, 2005), but fluxes have not been measured through this phase and cannot be quantified as new policy prevents planting on deep peat (Forestry Commission, 2016). In other parts of the world, peatland drainage is still actively happening and studies from these sites show very high rates of peat oxidation during the first 5-10 years of conversion (e.g. (Cooper et al., 2020; McCalmont et al., 2021; Minkkinen et al., 2018; Prananto et al., 2020)(McCalmont et al., 2021). In the UK forest plantations on deep peat usually end in clear felling of the site and restoration of the peat. The results of this study could also help inform what the CO_2 fluxes will be when timber is harvested and large quantities of felling residues are left above ground as well as whole root systems below ground. However, we note that changes in water table and soil moisture conditions created by the soil rewetting associated with clear-felling will have significant and separate impacts beyond the conditions of active drainage under which we took our measurements.However, the water table and soil moisture conditions created by the soil rewetting associated with clear-felling and restoration will be different to this study where active drainage was present.

5 Code and data availability

The R code and datasets analysed in this paper are not publicly available. Requests to access the datasets should be directed to renee.kerkvliet-hermans@iucn.org.uk.

6 Author contribution

Funding acquisition and initial conceptualization of the whole PhD project was done by J-A Subke, R. Andersen, Y. Teh and N. Cowie. Further in-depth conceptualization of this particular work was done by R. Hermans and J-A Subke, with support from R. Andersen, Y Teh and N. Cowie. Investigation, methodology, project administration, data curation, formal analysis, software, visualization and writing was done by R. Hermans with supervision and guidance of J-A Subke, R. Andersen, Y. Teh and N. Cowie.

7 Competing interests

The authors declare that they have no conflict of interest.

8 Acknowledgements

We are grateful for the PhD studentship that enabled this work, jointly funded by the University of Stirling and the Royal Society for the Protection of Birds. Trenching of plots was supported by volunteers working at the RSPB Forsinard reserve and the Environmental Research Institute of the University of the Highlands and Islands. We thank Rebecca McKenzie, Paul Gaffney, Peter Gilbert and Nathalie Triches for help with field measurements. Further we gratefully acknowledge Daniela Klein, Norrie Russell, Trevor Smith (RSPB), Graeme Findlay (Forestry Commission Scotland), Fountains Forestry and Donald MacLennan (Brook Forestry) for guidance and land access.

9 References

Andersen, R., Farrell, C., Graf, M., Muller, F., Calvar, E., Frankard, P., Caporn, S., & Anderson, P. (2016). An overview of the progress and challenges of peatland restoration in Western Europe. *Restoration Ecology*, 1–12. https://doi.org/10.1111/rec.12415

Anderson, R., Vasander, H., Geddes, N., Laine, A., Tolvanen, A., O'Sullivan, A., & Aapala, K. (2016). Afforested and forestry-drained peatland restoration. In A. Bonn, T. Allott, M. Evans, H. Joosten, & R. Stoneman (Eds.), *Peatland restoration and ecosystem services - science, policy and practise* (pp. 213–233). Cambridge University press.

Barton, K. (2017). MuMIn: Multi-Model Inference. *R Package Version 1.40.0*. https://cran.r-project.org/package=MuMIn

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed)*. Springer, New York, USA.

Byrne, K. A., & Farrell, E. P. (2005). The effect of afforestation on soil carbon dioxide emissions in blanket peatland in Ireland. *Forestry*, *78*(3), 217–227. https://doi.org/10.1093/forestry/cpi020

Cannell, M. G. R., Dewar, R. C., & Pyatt, D. G. (1993). Conifer plantations on drained peatlands in Britain: A net gain or loss of carbon? *Forestry*, *66*(4), 353–369. https://doi.org/10.1093/forestry/66.4.353

Cooper, H. V., Evers, S., Aplin, P., Crout, N., Dahalan, M. P. Bin, & Sjogersten, S. (2020). Greenhouse gas emissions resulting from conversion of peat swamp forest to oil palm plantation. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-14298-w

Forestry Commission. (2016). Supplementary guidance to support the FC forests and peatland habitats guideline note (2000). *Scottish Forestry Publications*, 1–5.

Friggens, N. L., Hester, A. J., Mitchell, R. J., Wookey, J. S. P. A., & Parker, T. C. (2020). Tree planting in organic soils does not result in net carbon sequestration on decadal timescales. *Global Change Biology*, *April*, 1–11. https://doi.org/10.1111/gcb.15229

Gorham, E. (2010). Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications*, *1*(2), 182–195.

Hargreaves, K. J., Milne, R., & Cannell, M. G. R. (2003). Carbon balance of afforested peatland in Scotland. *Forestry*, *76*(3), 299–317.

Hermans, R., Zahn, N., Andersen, R., Teh, Y. A., Cowie, N., & Subke, J. A. (2018). An incubation study of GHG flux responses to a changing water table linked to biochemical parameters across a peatland restoration chronosequence. *Mires and Peat*, *23*, 1–18. https://doi.org/10.19189/MaP.2018.DW.354

Janssens, I. A., & Ceulemans, R. (1998). Spatial variability in forest soil CO_2 efflux assessed with a calibrated soda lime technique. *Ecology Letters*, *1*(2), 95–98.

Jovani-Sancho, A. J., Cummins, T., & Byrne, K. A. (2018). Soil respiration partitioning in afforested temperate peatlands. *Biogeochemistry*, *141*(1), 1–21. https://doi.org/10.1007/s10533-018-0496-0

Kuyper, T. W. (2017). Carbon and Energy Sources of Mycorrhizal Fungi: Obligate Symbionts or Latent Saprotrophs? In *Mycorrhizal Mediation of Soil: Fertility, Structure, and Carbon Storage* (pp. 357–374). Elsevier Inc. https://doi.org/10.1016/B978-0-12-804312-7.00020-6

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). lmerTest: Tests in Linear Mixed Effects Models. *R Package Version 2.0-33*. https://cran.r-project.org/package=lmerTest

Kuzyakov, Y. (2006). Sources of CO_2 efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry*, *38*(3), 425–448. https://doi.org/10.1016/j.soilbio.2005.08.020

Laiho, R., & Laine, J. (1997). Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. *Forest Ecology and Management*, *93*(1–2), 161–169. https://doi.org/10.1016/S0378-1127(96)03916-3

Liski, J., Perruchoud, D., & Karjalainen, T. (2002). Increasing carbon stocks in the forest soils of western Europe. *Forest Ecology and Management*, *169*(1–2), 159–175. https://doi.org/10.1016/S0378-1127(02)00306-7

Mäkiranta, P., Minkkinen, K., Hytönen, J., & Laine, J. (2008). Factors causing temporal and spatial variation in heterotrophic and rhizospheric components of soil respiration in afforested organic soil croplands in Finland. *Soil Biology and Biochemistry*, *40*(7), 1592–1600. https://doi.org/10.1016/j.soilbio.2008.01.009

Mathews, G. (1993). *The carbon content of trees. Forestry Commission Technical Paper 4*. 21.

Mayer, M., Prescott, C. E., Abaker, W. E. A., Augusto, L., Cécillon, L., Ferreira, G. W. D., James, J., Jandl, R., Katzensteiner, K., Laclau, J. P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J. A., Vanguelova, E. I., & Vesterdal, L. (2020). Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. *Forest Ecology and Management*, *466*, 118127. https://doi.org/10.1016/j.foreco.2020.118127

Mazzola, V., Perks, M. P., Smith, J., Yeluripati, J., & Xenakis, G. (2020). Seasonal patterns of greenhouse gas emissions from

520   a forest-to-bog restored site in northern Scotland: Influence of microtopography and vegetation on carbon dioxide and methane dynamics. *European Journal of Soil Science*, *August*, 1–22. https://doi.org/10.1111/ejss.13050

McCalmont, J., Kho, L. K., Teh, Y. A., Lewis, K., Chocholek, M., Rumpang, E., & Hill, T. (2021). Short- and long-term carbon emissions from oil palm plantations converted from logged tropical peat swamp forest. *Global Change Biology*, *27*(11), 2361–2376. https://doi.org/10.1111/gcb.15544

525   Met Office. (2018). *Kinbrace climate*. https://www.metoffice.gov.uk/public/weather/climate/gfm5qbgxz

Minkkinen, K., Ojanen, P., Penttilä, T., Aurela, M., Laurila, T., Tuovinen, J. P., & Lohila, A. (2018). Persistent carbon sink at a boreal drained bog forest. *Biogeosciences*, *15*(11), 3603–3624. https://doi.org/10.5194/bg-15-3603-2018

Morison, J., Matthews, R., Miller, G., Perks, M., Randle, T., Vanguelova, E., White, M., & Yamulki, S. (2012). Understanding the carbon and greenhouse gas balance of forests in Britain. *Research Report - Forestry Commission, UK*.

530   Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, *85*(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Ojanen, P., Lehtonen, A., Heikkinen, J., Penttilä, T., & Minkkinen, K. (2014). Soil CO_2 balance and its uncertainty in forestry-drained peatlands in Finland. *Forest Ecology and Management*, *325*, 60–73. https://doi.org/10.1016/j.foreco.2014.03.049

535   Ojanen, P., Minkkinen, K., Alm, J., & Penttilä, T. (2010). Soil–atmosphere CO_2, CH_4 and N_2O fluxes in boreal forestry-drained peatlands. *Forest Ecology and Management*, *260*(3), 411–421. https://doi.org/10.1016/j.foreco.2010.04.036

Ojanen, P., Minkkinen, K., & Penttilä, T. (2013). The current greenhouse gas impact of forestry-drained boreal peatlands. *Forest Ecology and Management*, *289*, 201–208. https://doi.org/10.1016/j.foreco.2012.10.008

Paterson, E., Sim, A., Davidson, J., & Daniell, T. J. (2016). Arbuscular mycorrhizal hyphae promote priming of native soil
540   organic matter mineralisation. *Plant and Soil*, *408*(1–2), 243–254. https://doi.org/10.1007/s11104-016-2928-8

Prananto, J. A., Minasny, B., Comeau, L.-P., Rudiyanto, R., & Grace, P. (2020). Drainage increases CO_2 and N_2O emissions from tropical peat soils. *Global Change Biology*, *26*(8), 4583–4600. https://doi.org/https://doi.org/10.1111/gcb.15147

Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, *86*(10), 2805–2814.

545   RSPB unpublished data. (n.d.). *No Title*.

RStudio Team. (2016). *RStudio: Integrated Development Environment for R* (1.0.136). RStudio, Inc. http://www.rstudio.com/

Simola, H., Pitkänen, A., & Turunen, J. (2012). Carbon loss in drained forestry peatlands in Finland, estimated by re-sampling peatlands surveyed in the 1980s. *European Journal of Soil Science*, *63*(6), 798–807. https://doi.org/10.1111/j.1365-2389.2012.01499.x

550   Sloan, T. J., Payne, R. J., Anderson, A. R., Bain, C., Chapman, S., Cowie, N., Gilbert, P., Lindsay, R., Mauquoy, D., Newton, A. J., & Andersen, R. (2018). Peatland afforestation in the UK and consequences for carbon storage. *Mires and Peat*, *23*, 1–17. https://doi.org/10.19189/MaP.2017.OMB.315

Smith, T., & Hancock, M. (2016). *Interim report on monitoring of forest to bog restoration, Dyke and Forsinain forests:*

baseline forest characteristics and vegetation.

555 Smith, T., Hancock, M., & Stagg, P. (2014). *The RSPB Forest to Bog Restoration Project Forsinard Flows Interim Report – July 2012 – Sept 2013*. *April*.

  Subke, Inglima, I., & Francesca Cotrufo, M. (2006). Trends and methodological impacts in soil CO2 efflux partitioning: A metaanalytical review. *Global Change Biology*, *12*(6), 921–943. https://doi.org/10.1111/j.1365-2486.2006.01117.x

  Subke, J.-A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., & Cotrufo, M. F. (2004). Feedback interactions between
560 needle litter decomposition and rhizosphere activity. *Oecologia*, *139*(4), 551–559. https://doi.org/10.1007/s00442-004-1540-4

  Subke, Voke, N. R., Leronni, V., Garnett, M. H., & Ineson, P. (2011). Dynamics and pathways of autotrophic and heterotrophic soil CO2 efflux revealed by forest girdling. *Journal of Ecology*, *99*(1), 186–193. https://doi.org/10.1111/j.1365-2745.2010.01740.x

565 Tolvanen, A., Tarvainen, O., & Laine, A. M. (2020). Soil and water nutrients in stem-only and whole-tree harvest treatments in restored boreal peatlands. *Restor Ecol*, *28*(6), 1357–1364.

  Vanguelova, E. I., Crow, P., Benham, S., Pitman, R., Forster, J., Eaton, E. L., & Morison, J. I. L. (2019). Impact of Sitka spruce (Picea sitchensis (Bong.) Carr.) afforestation on the carbon stocks of peaty gley soils- A chronosequence study in the north of England. *Forestry*, *92*(3), 242–252. https://doi.org/10.1093/forestry/cpz013

570 Walker, T. N., Garnett, M. H., Ward, S. E., Oakley, S., Bardgett, R. D., & Ostle, N. J. (2016). Vascular plants promote ancient peatland carbon loss with climate warming. *Global Change Biology*, *22*(5), 1880–1889. https://doi.org/10.1111/gcb.13213

  Yamulki, S., Anderson, R., Peace, a., & Morison, J. I. L. (2013). Soil CO_2 CH_4 and N_2O fluxes from an afforested lowland raised peatbog in Scotland: implications for drainage and restoration. *Biogeosciences*, *10*(2), 1051–1065.
575 https://doi.org/10.5194/bg-10-1051-2013

  Zerva, A., & M. Mencuccini. (2005). Carbon stock changes in a peaty gley soil profile after afforestation with Sitka spruce (Picea sitchensis). *Annals of Forest Science*, *62*, 873–880. https://doi.org/10.1051/forest

 10 Appendix

Table 7 List of articles used in ~~Figure 9~~

Authors	Year	Title
Bond-Lamberty, B, C Wang, and ST Gower	2004	Contribution of Root Respiration to Soil Surface CO_2 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
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 CO_2~~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, 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
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
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
Ma, Y., Piao, S., Sun, Z., Lin, X., Wang, T., Yue, C., and Yang, Y.	2014	Stand ages regulate the response of soil respiration to temperature in a Larix principis-rupprechtii plantation
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
Mahli, Y, D D Baldocchi, and P G Jarvis	1999	The Carbon Balance of Tropical, Temperate and Boreal Forests
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
Mustamo, P., Maljanen, M., Hyvärinen, M., Ronkanen, A. K., and Kløve, B.	2016	Respiration and emissions of methane and nitrous oxide from a boreal peatland complex comprising different land-use types.
O'Conell, K. E. B., Gower, S. T., & Norman, J. M.	2003	Net Ecosystem Production of Two Contrasting Boreal Black Spruce Forest Communities
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?
Pumpanen, J., Kulmala, L., Lindén, A., Kolari, P., Nikinmaa, E., and Hari, P.	2015	Seasonal dynamics of autotrophic respiration in boreal forest soil estimated by continuous chamber measurements
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

Ryan, M. G., M. B. Lavigne, and S. T. Gower — 1997 — Annual Carbon Cost of Autotrophic Respiration in Boreal Forest Ecosystems in Relation to Species and Climate

Sawamoto, Takuji, Ryusuke Hatano, Masato Shibuya, Kunihide Takahashi, Alexander P. Isaev, Roman V. Desyatkin, and Trofim C. Maximov — 2003 — Changes in Net Ecosystem Production Associated with Forest Fire in Taiga Ecosystems, near Yakutsk, Russia

Vogel, JG;, DW; Valentine, and RW Ruess — 2005 — Soil and Root Respiration in Mature Alaskan Black Spruce Forests That Vary in Soil Organic Matter Decomposition Rates

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