



Separating autotrophic and heterotrophic soil CO₂ effluxes in afforested peatlands

Renée Hermans¹⁵, Rebecca McKenzie²⁶, Roxane Andersen², Yit Arn Teh³, Neil Cowie⁴ and Jens-Arne Subke¹

5 ¹Department of Biological and Environmental sciences, University of Stirling, Stirling, UK

²Environmental Research Institute, University of Highlands & Islands, Thurso, UK

³School of Natural and Environmental Sciences, Newcastle University, Newcastle, UK

⁴Centre for Conservation Science, Royal Society for the Protection of Birds Scotland, Edinburgh, UK

10 ⁵IUCN UK Peatland Programme, Edinburgh, UK

⁶Geography 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 CO₂ efflux includes both CO₂ produced from heterotrophic peat decomposition and CO₂ 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 CO₂ flux, litter input, litter decay rate and soil temperature and moisture over two years. Annual peat decomposition (heterotrophic CO₂ flux) was $115 \pm 16 \text{ g C m}^{-2} \text{ y}^{-1}$, representing c. 40% of total soil respiration. Decomposition of needle litter is accelerated in the presence of an active rhizosphere, indicating a priming effects 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. 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 (Andersen 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 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 and 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 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 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.

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), 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 CO₂ efflux includes both CO₂ released from peat mineralization (heterotrophic CO₂ flux) and CO₂ produced from root-rhizosphere (i.e. autotrophic) respiration; experimental manipulation of autotrophic C supply to the 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 CO₂ efflux and the respective temporal dynamics. This disruption of root exudation 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 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 forest plantations are a net C source, 2) soil CO₂ efflux is dominated by autotrophic respiration and 3) interactions between C supply to the rhizosphere by trees 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 containing a mixture 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 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 air temperature of 11.4°C measured at the Kinbrace weather station approximately 20 km from the plots (Location: 58°13'89''N, 3°55'1.2''W; Altitude: 103 m above mean sea level; Met Office, 2018). Seasonal averaged water table relative to ground surface is -350 (±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 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 treatment (trenching or control). Paired plots were no more than 10 metres apart from each other.

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

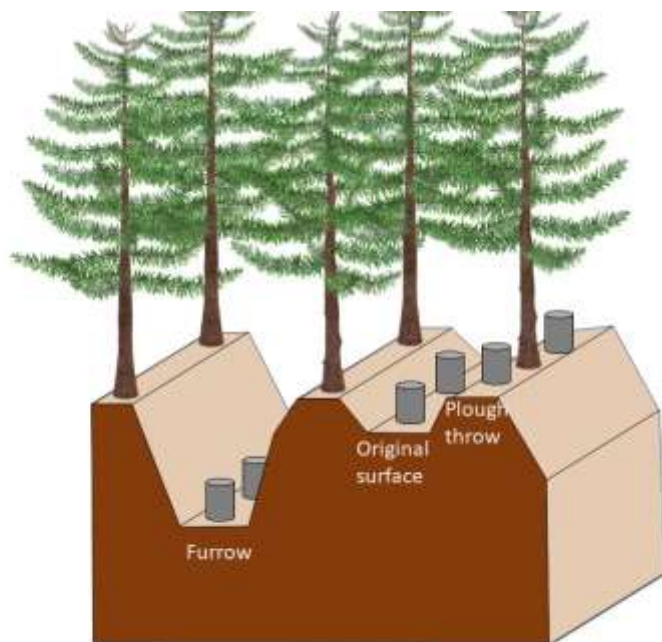


Figure 1 Micro topography in forest plantations, with location of measurements for flux chambers (not to scale).

110 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



all three micro topographic forms. These dimensions maximised the space between trees, with closest trees located about 30
115 cm from trenches.



Figure 2 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.

120 **2.4 CO₂ 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) of both trenched and control plots. CO₂ 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 three minutes. Elasticated rubber material placed over the joint of chambers and collars for the duration of the measurement provided
125 an air-tight seal. The chamber was connected to an EGM 4 Infrared Gas Analyser (PP-Systems, Amesbury, MA, USA), recording CO₂ concentrations every 4-5 seconds. Fluxes were calculated from increases in CO₂ concentration within the chamber over 3 minutes. Measurements were carried out ten times between August 2014 and July 2016.

2.5 Litter

Six litter traps (0.07 m² each) were located close to each plot, and litter (falling needles and twigs) collected at each sampling
130 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 measurement and then placed back in the collar. Litter adjacent to the collar was also collected and weighed in the field, then
135 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 the start (June 2014) and end (July 2016) of the experiment. Roots from each core were carefully separated and sorted into
140 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.

To estimate root decomposition directly, 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
145 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 were 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 were 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.
150 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:

$$M_t = M_0 e^{-kt} \quad (1)$$

155 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
160 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 one meter above the ground
165 during sampling.

2.8 Statistical analyses and flux calculations

Data were analysed using R (RStudio Team, 2016). All CO₂ data was log transformed to meet the criteria of normality, and a linear mixed-effect model (LMM) using the *nlme* package in R (Pinheiro et al., 2017) was used to predict CO₂ fluxes based on environmental drivers. All numerical predictors were standardized to one standard deviation prior to statistical analyses, to
170 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 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. 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
175 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 and Anderson, 2002). Any of the models with a delta AICc of less than 2 are considered to be as good
180 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).

185 Annual fluxes were calculated using the predict function over the mixed effects model from library *lme4* in R (Bates et al., 2015). 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.

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

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

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Where F_a is autotrophic CO₂ flux, $F_{control}$ is the CO₂ flux from the control plots, F_{trench} is the CO₂ flux from trenched plots, $F_{dead\ roots}$ is the CO₂ flux coming from the dead roots in the trenched plots created by the trenching technique and ε the associated error terms.

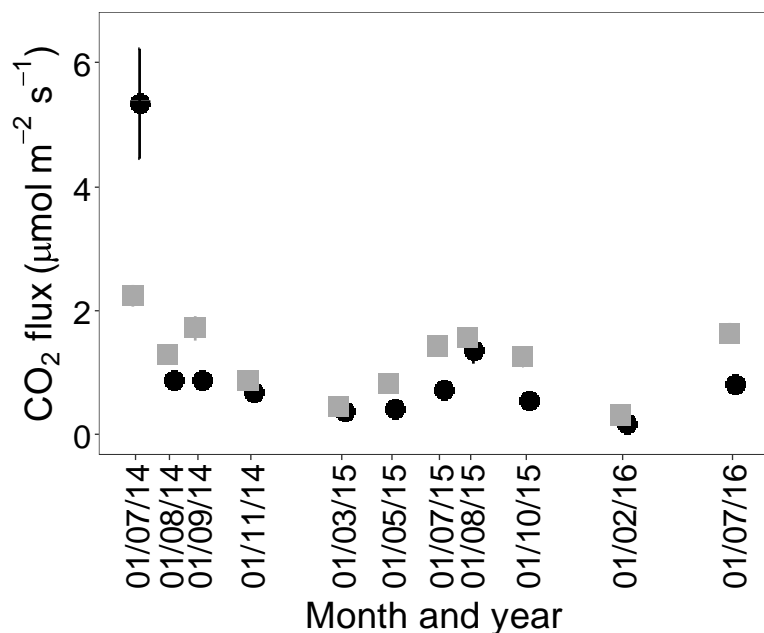


195 The annual flux from litter was calculated from the difference in modelled annual fluxes between collars with and without litter.

3 Results

3.1 Temporal trends in soil CO₂ fluxes

200 Trenching initially led to an increase in soil respiration, followed by a significant reduction in soil CO₂ 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 3).



205 Figure 3 Mean CO₂ 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.

210 Soil CO₂ 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 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 $\Delta AICc$ of less than 2 is shown in



Table 2. The predictors of the ‘top model’ were present in at least over half of the models in the top model set, so this model was used.

215 Table 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
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

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 Δ AICc is the difference 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
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3.2 Spatial trends and litter contributions to soil CO₂ flux

In both control and trenched plots, fluxes from plough throw (control: 1.23 ± 0.10 ; trenched: $0.85 \pm 0.07 \mu\text{mol m}^{-2} \text{s}^{-1}$; $p=0.01$) and original surface (control: 1.48 ± 0.10 ; trenched: $0.83 \pm 0.06 \mu\text{mol m}^{-2} \text{s}^{-1}$; $p<0.001$) were significantly higher than fluxes from furrow (control: 0.90 ± 0.06 ; trenched: $0.47 \pm 0.04 \mu\text{mol m}^{-2} \text{s}^{-1}$). 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, $p=0.008$).

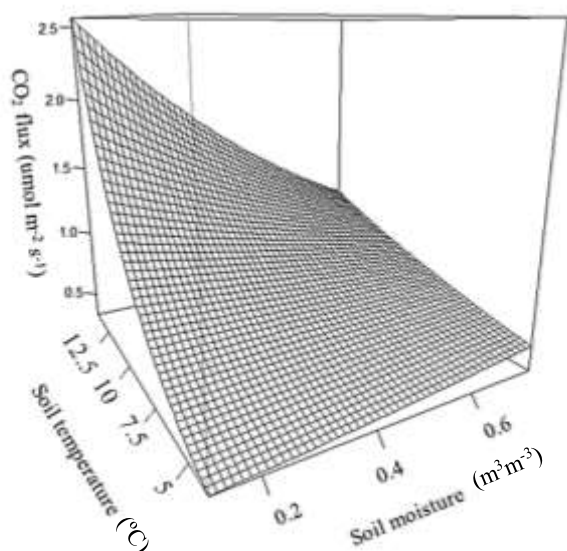
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3.3 Role of environmental drivers in modulating CO₂ flux

Observed soil CO₂ 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 CO₂ flux decreases with increasing soil moisture, but at low temperatures flux increases when soil moisture increases (Figure 4).

230

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, CO₂ fluxes were corrected using the global relationship between soil moisture and CO₂ flux (Figure 4) to calculate fluxes expected to occur under moisture conditions in control plots.



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Figure 4 Combined effect of soil temperature and soil moisture at 5 cm depth on soil CO₂ flux from the control sites, estimated from the ‘top model’.

3.4 Partitioned fluxes

240 Soil CO₂ efflux was partitioned into component fluxes for all measuring dates from August 2014 onwards to remove disturbance related artefacts observed immediately after trenching. 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 $184 \pm 21 \text{ g C m}^{-2} \text{ y}^{-1}$.
245 Total soil respiration without needle litter is $301.3 \pm 34.2 \text{ g C m}^{-2} \text{ y}^{-1}$, with needle decomposition adding $41.2 \pm 53.5 \text{ g C m}^{-2} \text{ y}^{-1}$ to annual fluxes, giving a total soil respiration including needle litter of $343 \pm 35 \text{ g C m}^{-2} \text{ y}^{-1}$.

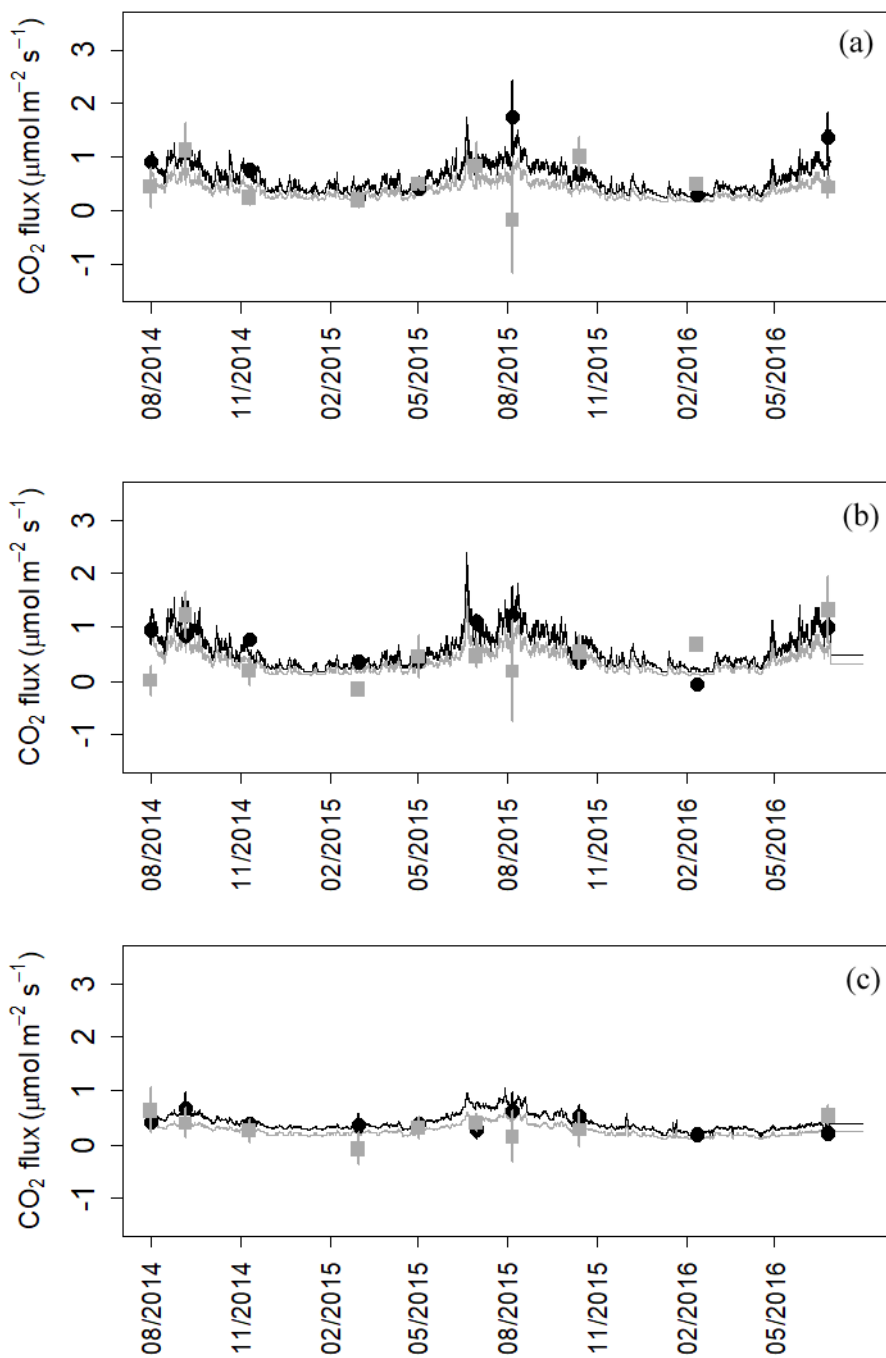




Figure 5 Modelled and measured fluxes of heterotrophic (black) and autotrophic (grey) soil CO₂ efflux from the three topographic microforms. Closed symbols are average fluxes with error bars (n = 4 plots). Connecting lines are the predicted fluxes using soil temperature and moisture at 5 cm depth. a) Original surface, b) Plough throw and c) Furrow.

3.5 Impact of litter and roots

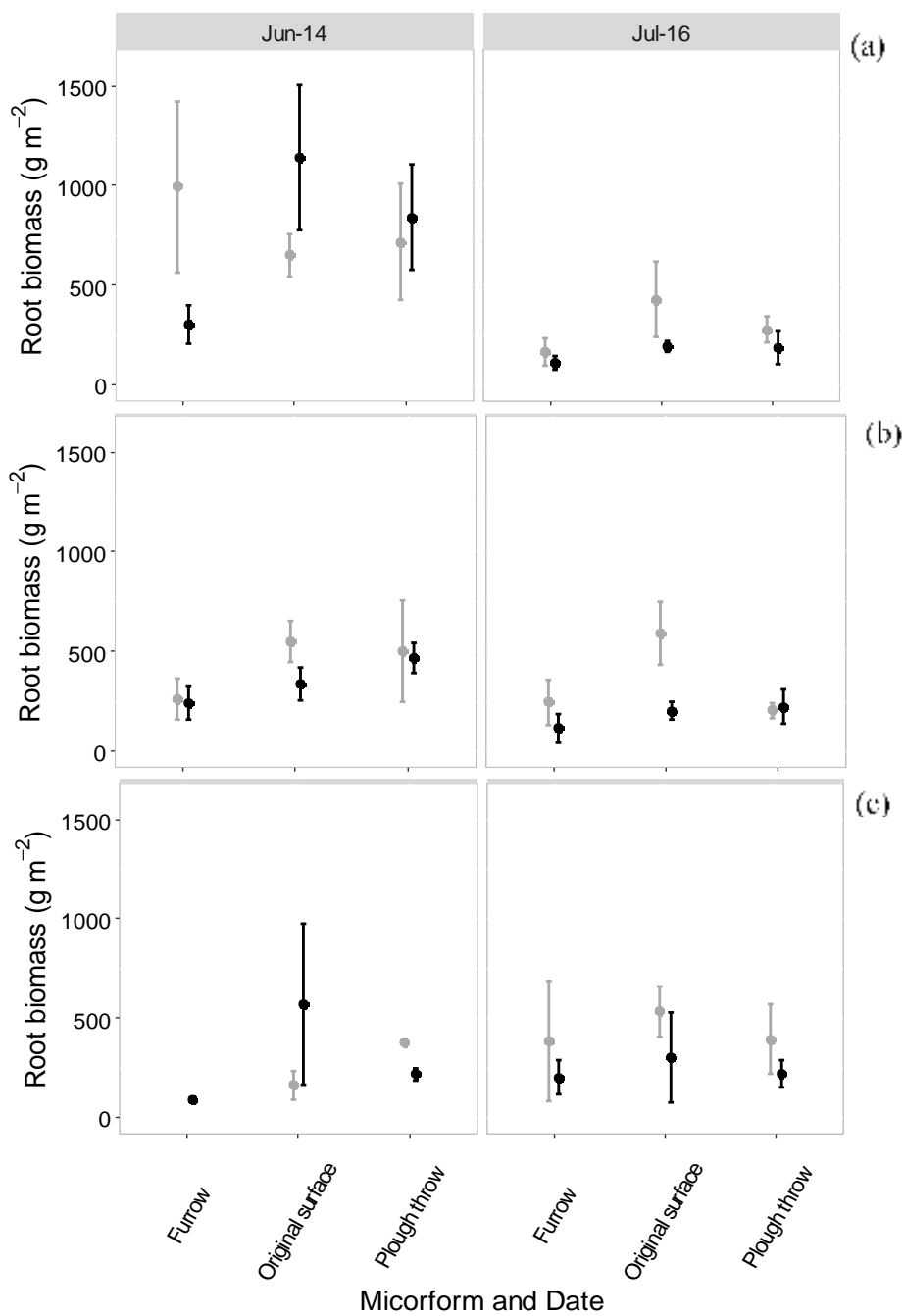
Litter fall was 719 ± 71.3 grams of litter per $\text{m}^2 \text{y}^{-1}$, with no detectable difference between trenched and control plots. Assuming a C fraction of biomass of 50% (Mathews, 1993), this represents an input to the soil of $359 \text{ g C m}^{-2} \text{y}^{-1}$ via litter fall.

CO₂ flux from surface litter is calculated from the difference in the modelled annual fluxes between the collars with and without litter, with the fluxes from collars with litter significantly higher than the CO₂ flux from the collars without litter ($p = 0.008$, 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, resulting in a 1.7 to 3.6 times higher CO₂ flux per gram of litter from the control plots than from the trenched plots (Table 3).

Table 3 Mean amount of C emitted as CO₂ by surface needle litter in ‘litter collars’, for both years (standard error in brackets).

Microform	Litter [g m ⁻²]		CO ₂ flux [g C m ⁻² y ⁻¹]		CO ₂ flux per g litter [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 $761 \pm 324 \text{ g}$, $603 \pm 110 \text{ g}$ and $715 \pm 257 \text{ g}$ for < 2 mm roots, 2-5 mm roots and > 5 mm roots, respectively. 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, but there was 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).

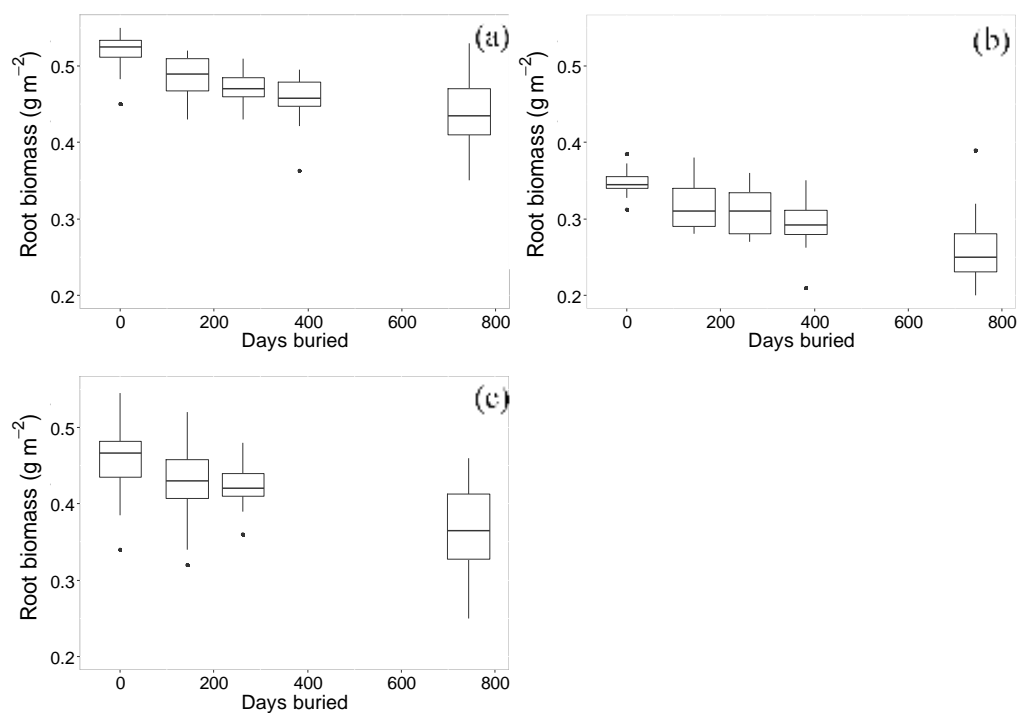




270 Figure 6 Root biomass per square meter to 25 cm in control (grey) and trenched (black) plots at the beginning of the experiment (June 2014) and end of experiment (July 2016), split into three root size classes, per microform. a) root size <2 mm, b) root size 2-5 mm, c) root size >5 mm. Symbols are average fluxes with error bars representing standard errors ($n = 4$ plots).

3.6 Root decomposition

275 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).



280 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	Decay constant	C emitted year 1	C emitted year 2
	mm	y ⁻¹	g C m ⁻² y ⁻¹	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

285 The amount of C emitted from the decaying roots is calculated using the exponential decay function (1), with the biomass of roots per m² to a depth of 20 cm in the trenched plots at the beginning of the experiment as M₀. It is assumed that all biomass lost is emitted as CO₂ and that 50% of roots is C (Mathews, 1993), as conservative assumptions, meaning that estimates are maximum possible CO₂ flux from decaying roots in trenched plots. To correct for soil CO₂ efflux generated in trenched plots as an artefact of creating dead root biomass, annual estimated CO₂ emissions were corrected by subtracting root-decay based
 290 estimates from trenched plot CO₂ emissions (Table 5).



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Table 5 Corrected heterotrophic (peat only; F_h) and autotrophic (F_a) fluxes (standard error in brackets) in $\text{g C m}^{-2} \text{y}^{-1}$ 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.

300 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 weighed soil CO_2 flux of $289.4 \pm 18.6 \text{ g C m}^{-2} \text{y}^{-1}$.

305

Table 6 Area-weighted heterotrophic (peat only) (F_h) and autotrophic (F_a) fluxes (standard error in brackets) in $\text{g C m}^{-2} \text{y}^{-1}$ 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)



4 Discussion

Mass balance calculations indicate that the soils in these 30 year old drained and afforested peatlands are a net sink for C, as substantially more C enters the soil as organic matter, than is decomposed heterotrophically. The C balance of the soil under these forest plantations is visualised in

Figure 8, with the annual CO₂ fluxes of the forest plantation based on the area-weighted fluxes.

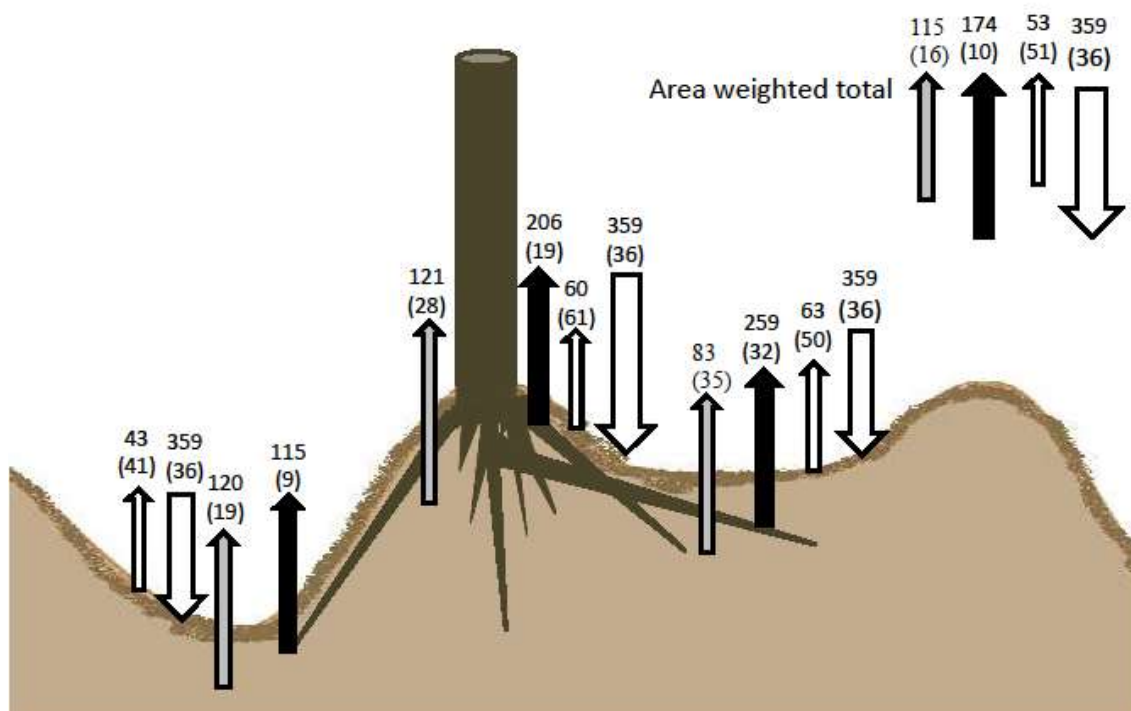


Figure 8 Summary of soil C budget (in g C m⁻² y⁻¹) under the canopy of a Sitka spruce and Lodgepole pine plantation on deep peat. Downward arrows indicate litterfall, whilst upward fluxes show autotrophic (F_a) (black), heterotrophic (peat only; F_h) (grey), and surface needle litter (white) across the three main microforms. Total forest soil fluxes with area weighted values are visualised in the top right corner.

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 CO₂ 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 to C leaving as CO₂. 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 CO₂ soil efflux. Root:shoot allocation in forest ecosystems is usually in the order of 1:3 (Laiho and Laine, 1997), so it is possible that belowground productivity could account for a significant C input only partially sampled by our approach (i.e. excluding large root stocks), adding to these plantations being a potential carbon sink.

330 The rate of peat decomposition in these drained and afforested peatlands is substantial, but overall soil CO₂ efflux and ratio of heterotrophic/autotrophic respiration falls within boreal averages for forested ecosystems (Figure 9; Bond-Lamberty and Thomson, 2010). Average soil efflux corrected for microform area without litter (to determine the peat decomposition rate) over the two measurement years was $289 \pm 19 \text{ g C m}^{-2} \text{ y}^{-1}$ of which $174 \pm 10 \text{ g C m}^{-2} \text{ y}^{-1}$ is autotrophic and $115 \pm 16 \text{ g C m}^{-2} \text{ y}^{-1}$ is heterotrophic.

335 Our total soil respiration (including litter) of $342.5 \pm 34.7 \text{ g C m}^{-2} \text{ y}^{-1}$ is slightly higher than values of around $260 \text{ g C m}^{-2} \text{ y}^{-1}$ reported for a similar forest plantation in Ireland, a 39-year old drained Sitka spruce plantation on naturally treeless blanket bog (Byrne and Farrell, 2005). Our peat oxidation rates of $115 \pm 16 \text{ g C m}^{-2} \text{ y}^{-1}$ are also higher than found by Hargreaves et al. (2003), who found $<100 \text{ g C m}^{-2} \text{ y}^{-1}$ in a 26 year old Sitka spruce plantation on drained deep ($> 2 \text{ m}$) 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.

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

345 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 CO₂ in all studied years, with an average NEE for the 4 years of $-234 \text{ g C m}^{-2} \text{ y}^{-1}$. By subtracting the carbon sink of the tree stand from NEE the authors show that the soil was a carbon sink of $-60 \text{ g C m}^{-2} \text{ y}^{-1}$. By modelling their forest soil respiration fluxes from chamber measurements they found the peat only respiration made up 53% of the total forest floor respiration flux, litter 22%, roots 16% and autotrophic respiration of above-ground vegetation 8%. 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 350 them not applying a dead root correction to their fluxes, which as we show could lead to a big difference in fluxes.

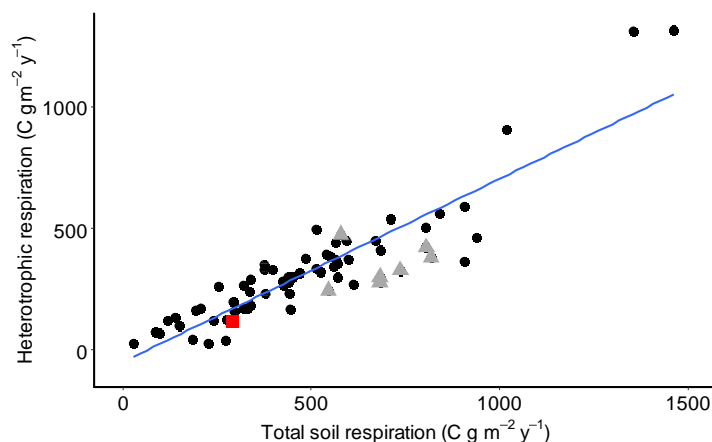


Figure 9 Heterotrophic annual flux against soil respiration annual flux ($\text{g C m}^{-2} \text{y}^{-1}$) in Boreal forests in black dots, Boreal
355 forests on peat soils in grey triangles, from Bond-Lamberty and Thomson (2010) dynamic database downloaded on
19/04/2020. Our study is included in the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

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
360 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 trenched plots (Table 3) indicates that heterotrophic processes are reduced 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).
365 Further, several studies have shown that mycorrhizal fungi are involved in soil priming (Kuyper, 2017; Paterson et al., 2016).
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, 2011).

To calculate the root biomass at the start of the experiment, one soil core per microform was taken and since trees
370 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 living root biomass might have been overestimated.
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-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
375 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 (±16) cm, with 0.47 kg C m⁻² per centimetre depth (Cannell et al., 1993), which represents ca. 59.3 (±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 and 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. McCalmont et al., 2021).

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.

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10 Appendix

505 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. Nestic.	2014	Eight Years of Forest-Floor CO ₂ 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 Nestic	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 Nestic	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 Nestic	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, Mikael 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 CO₂ 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'Connell, 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 CO₂, CH₄ and N₂O 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 CO₂ 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