



Heterotrophic soil respiration in three forestry-drained boreal peatlands dominated by Downy birch (*Betula pubescens* Ehrh.)

Md Rezaul Karim, Jani Anttila, Katja T. Rinne-Garmston & Sakari Sarkkola

To cite this article: Md Rezaul Karim, Jani Anttila, Katja T. Rinne-Garmston & Sakari Sarkkola (28 Oct 2025): Heterotrophic soil respiration in three forestry-drained boreal peatlands dominated by Downy birch (*Betula pubescens* Ehrh.), Scandinavian Journal of Forest Research, DOI: [10.1080/02827581.2025.2578181](https://doi.org/10.1080/02827581.2025.2578181)

To link to this article: <https://doi.org/10.1080/02827581.2025.2578181>



© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group



Published online: 28 Oct 2025.



Submit your article to this journal [↗](#)



View related articles [↗](#)



View Crossmark data [↗](#)

Heterotrophic soil respiration in three forestry-drained boreal peatlands dominated by Downy birch (*Betula pubescens* Ehrh.)

Md Rezaul Karim, Jani Anttila, Katja T. Rinne-Garmston and Sakari Sarkkola

Natural Resources Institute Finland (Luke), Helsinki, Finland

ABSTRACT

Boreal peatlands contain a significant terrestrial carbon storage. Many of the boreal mire sites support tree growth naturally, and tree stands largely affect their carbon dynamics controlling the decomposition and new carbon inputs. Most research has focused on the conifer stands, with limited attention given to carbon emissions from peatland sites dominated by stands of deciduous tree species and how the emissions change along stand succession. We studied heterotrophic soil respiration (CO₂) using site-specific temperature and water table interaction models and simulations at half-hourly intervals over two growing seasons (May–September 2021–2022) in three downy birches (*Betula pubescens* Ehrh.)-dominated drained nutrient-rich peatland sites in Finland. The stand represented three developmental classes: young stand (stand age 10 years), middle-aged stand (50 years), and mature stand (80 years). Instantaneous CO₂ fluxes ranged from 0.09 to 1.37 g CO₂ m⁻² h⁻¹, and mean cumulative fluxes ranged 11.6–30.3 g m⁻² d⁻¹. For the summer period, the cumulative fluxes showed to decrease along the stand age being highest (2927 g CO₂ m⁻²) in young stand, and lowest (1113 g CO₂ m⁻²) in mature stand. These results highlight how stand development influences soil carbon emissions, with key implications for peatland management and climate mitigation.

ARTICLE HISTORY

Received 2 May 2025
Accepted 13 October 2025

KEYWORDS



Deciduous tree; soil temperature; water table; interaction effect; CO₂ efflux

Introduction

Peatlands are important carbon (C) reservoirs and play a major role in the global C cycle. According to the latest estimate, the total northern peatland C stocks is 1,055 Gt of C (Nichols and Peteet 2019). The accumulation of C in peatlands results from elevated water table levels (WL) and associated anoxic conditions, which facilitate the accumulation of partially decomposed organic matter as peat. After management practices such as drainage for forestry, the top layer of peat potentially decomposes faster because of water-level drawdown and consequent increase in the thickness of the oxic unsaturated layer in peat (Straková et al. 2012). This phenomenon has historically been widespread both regionally and globally. In Finland, nearly 5 million hectares of peatlands have been drained for forestry purposes. Understanding soil-atmosphere greenhouse gas (GHG) fluxes in these drained areas is imperative for annual GHG reporting and to devise strategies to mitigate climate change. Many studies have investigated seasonal and annual GHG emissions from drained peatlands, identifying soil temperature, WL, and site type—which delineates the nutrient status of the site—as the primary explanatory

variables for soil CO₂ efflux (von Arnold et al. 2005a, 2005b; Minkkinen et al. 2023). Moreover, research on peatlands emphasize the importance of temperature in driving temporal variations in soil and ecosystem respiration (Updegraff et al. 2001; Lafleur et al. 2005) and heterotrophic respiration (Mäkiranta et al. 2007, 2008; Minkkinen et al. 2007). Up to 96% of the temporal variation in heterotrophic respiration within a specific peatland site can be attributed to soil temperature (Mäkiranta et al. 2008). However, studies have shown that large spatial variation exists within and between sites in the temperature sensitivity of heterotrophic respiration due to variations in nutrient status of the sites (Minkkinen et al. 2007; Mäkiranta et al. 2008).

Anaerobic decomposition in soils occurs much slower than aerobic decomposition (Bergman et al. 1999; Šantrůčková et al. 2005). Subsequently, WL depth usually contributes as a main factor controlling the organic matter decomposition rate in peatlands by directly regulating the volume of the oxic peat layer (Waddington et al. 2015; Obradović et al. 2023). Laboratory studies have shown that CO₂ emission from peat samples rises with increased WL depth demonstrating the influence of

CONTACT Md Rezaul Karim  ext.rezaul.karim@luke.fi  Natural Resources Institute Finland (Luke), Latokartanonkaari 9, Helsinki, 00790, Finland

© 2025 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

water level on decomposition (Moore and Dalva 1993, 1997; Blodau et al. 2004). However, *in situ* studies have showed considerable variability in the relationship between WL and measured peat soil CO₂ emissions (Silvola et al. 1996a; Lafleur et al. 2005). On the other hand, challenges in predicting the decomposition rate of peat layers in response to climate change have led to significant uncertainties in peatland C pool studies (Laiho 2006). Detailed information on the dependence of heterotrophic respiration on soil temperature and WL is required to improve current methods for estimating decomposition rates in drained peatlands.

Downy birch (*Betula pubescens* Ehrh.) is an ecologically and economically highly important tree species in northern Europe, particularly in Finland. Significant areas of birch-dominated forests are growing on organic soils i.e. peatlands. Peatlands constitute 12% of the total volume of the growing stock in Finland (Niemistö and Korhonen 2008). Downy birch stands have a noteworthy role in forestry, as well as in the pulp and paper industry. According to the Finnish National Forest Inventory data (NFI11, measured in 2009–2013), the total area of birch-dominated stands on drained peatlands is 572 000 ha. However, the present knowledge on the actual and temporal CO₂ efflux of downy birch stands in Finland is extremely poor. The birch forests deviate ecologically significantly from coniferous forests where most of the GHGs research is concentrated. To our knowledge, no previous studies have investigated the interaction effect of soil temperature and WL depth on heterotrophic soil respiration on downy birch-dominated drained peatlands despite the wide natural distribution area of this species on the Eurasian continent.

Our aim of this study was to estimate the heterotrophic soil respiration at different stages of the succession of downy birch stands on drained forested peatlands. The stand succession was categorized to three developmental classes: young stand (stand age approximately 10 years), middle-aged stand (app. 50 years) and mature stand (app. 80 years). Additionally, we aimed to model the response of heterotrophic soil respiration to soil temperature and water level.

Materials and methods

Study sites

Heterotrophic soil respiration was measured in three forestry-drained peatlands sites in Juupajoki, Central Finland (N 61° 50' 36.542", E 24° 17' 37.010", 180 m above sea level, and sites are in close proximity to each other). The study sites were selected from the network of permanent sample plots connected to the long-term study sites

Table 1. General description of the study sites (mean ± standard deviation).

| | DB-10 (Young stand) | DB-50 (Middle-aged stand) | DB-80 (Mature stand) |
|---|--------------------------------------|--|--------------------------------------|
| Coordinates (WGS84) | 61° 50' 55.65" N 24° 19' 14.52" E | 61° 51' 13.75" N 24° 17' 14.83" E | 61° 53' 10.70" N 24° 24' 07.34" E |
| Site type ¹ | Rhtkg (herb-rich type) | Mtkg II (<i>Vaccinium myrtillus</i> - type) | Rhtkg (herb-rich type) |
| Stand age (years) | 10 | 50 | 80 |
| Peat depth (n = 30), (cm) | 85.2 ± 3.2 | 74.6 ± 2.5 | 115.1 ± 3.5 |
| Bulk density (n = 15) (g cm ⁻³) | 0.13 ± 0.04 | 0.12 ± 0.03 | 0.16 ± 0.02 |
| Drainage year | 1936 | 1950 | 1909 |

(1) Vasander and Laine 2008.

maintained by Hyytiälä Forestry Field Station. The mean ages of the trees within the stands were 10, 50, and 80 years, representing a chronology of young, middle-aged, and mature stands, respectively (Table 1). According to Hynynen et al. (2010), the upper limit for the rotation period of downy birch is 70–80 years due to biological aging, resulting in decreased growth and an increased risk of rot. Therefore, in our study, an 80-year-old birch stand is considered as mature. The Nälkärasinsuo site (10-year-old young stand) was initially drained for forestry purposes in 1936, and the tree stand was regenerated through clearcutting in 2006. The Rajasuo site (50-year-old middle-aged stand), was drained in 1950, and managed by a light thinning in 1970s. The Loukaskorpi site (80-year-old mature stand), was initially drained in 1909. The drainage network was expanded in the 1920s, and ditch network maintenance was completed in 1964. The current tree stand of the sites consists mostly of downy birch (88%), while the remainder comprises Norway spruce (*Picea abies*) as an understorey species, exhibiting varying densities. The management and succession history of all sites and their tree stands are well known because of the long-term monitoring of the stands. According to the Finnish classification system for drained peatland forests (Vasander and Laine 2008), all the sites can be categorized as either nutrient-rich Herb-rich or *Vaccinium myrtillus* types (Rhtkg, MtkgII) (Table 1). As per the Finnish classification system of drained peatland forests, the suffix II includes sites that were treeless or sparsely treed mires before drainage operation. At the time of the study, peat depth in the area varies from 71 cm to 120 cm (Table 1). In early summer 2021, soil samples from the study area were collected at depths of 0–10, 10–20, 20–30, 30–40, and 40–50 cm, with five samples per site, totaling fifteen samples, for analysis. Bulk density was measured by drying peat samples of known volume at 105 °C overnight (Blake and Hartge 1986).

Site preparation and measurements

On each study site, four measurement points were established for heterotrophic soil respiration measurements between six to eight months prior to the actual measurements to reduce the impacts of soil disturbance and fresh litter decomposition on the heterotrophic flux. The plots were trenched to a depth of 20 cm using chainsaw (Patelo PT998 Chainsaw, M[®] Made-in-China) with the intention of excluding root respiration, and the further growth of new roots. The size of each measurement points was 60 × 60 cm. Geotextile fabric made of polypropylene was inserted into each measurement point to insulate roots, separating them from the adjacent soil (Minkkinen et al. 2007). After trenching, ground vegetation and litter layers were removed, and the plots were kept free of litter. By implementing these measures, we aimed to exclude the decomposition of new litter from the measurements of heterotrophic soil respiration. As most of the roots in drained peatlands are situated in the topmost peat layers (Laiho and Finér 1996), we assumed that the trenching and removing above ground part of ground vegetation terminated all roots within the plots.

The heterotrophic soil respiration was measured every 2 weeks during June and September in 2021 and 2022 (Figure 1). Respiration measurements were taken by a portable trace gas analyzer (LICOR-7810, The Optical Feedback – Cavity Enhanced Absorption Spectroscopy (OF-CEAS) technique), which was attached to an opaque closed metallic chamber (Ø 31.5 cm, *h* 30 cm). The metallic chamber was equipped with a fan and a thermometer to maintain the chamber's inner temperature within ±2 of the ambient temperature



Figure 1. Heterotrophic soil respiration measurement setup using a LI-COR 7810 gas analyzer connected to a closed dynamic chamber. The setup also includes a foliage litter collection container.

(Alm et al. 2007) and was placed on the sample plot for a measurement period of 180 s. The efflux was corrected for atmospheric pressure and air temperature. Simultaneously with the CO₂ efflux measurement, soil temperature at a depth of 5 cm was measured in the space between the chamber and the edge of the fabric. The groundwater table level was monitored with an accuracy of one cm.

Soil temperature and water level logging

Temperature data loggers (iButton, model 1921G, Dallas Semiconductor Corp.) were installed at each site in autumn 2020 to the depth of 5 and 30 cm. Soil temperature was logged at 3-h intervals. The mean temperature of the two heterotrophic respiration points was calculated and then linearly interpolated for every half hour. The soil temperature at 5 cm depth was chosen to predict the soil CO₂ efflux since it has been observed to be the best single depth for predicting soil CO₂ efflux (Minkkinen et al. 2007).

Water table data loggers (Odyssey[®] capacitance water logger, Dataflow Systems Limited © 2022) were installed at each site in autumn 2020 to a depth of 2 m. The groundwater table was logged every 30 min from October 2020 to October 2022. Here, we report the soil temperature and WL results during the heterotrophic soil respiration measurement period (June–September in 2021 and 2022). These datasets were then used in simulations of the seasonal CO₂ efflux. At the DB-80 site in 2022, the water table data showed unusually stable values with minimal fluctuation. While the exact cause is uncertain, the anomaly may be due to sensor malfunction, logger drift, or local hydrological conditions. As the data still provide contextual information, they were retained in the analysis but clearly noted in the figure caption and interpreted with appropriate caution.

Calculations

Fluxes were calculated from the linear change in CO₂ concentration in the chamber headspace over time using the following equation:

$$\text{flux} = \text{slope} \cdot \left(\frac{M}{V_m} \right) \cdot \left(\frac{T_0}{T_0 + T} \right) \cdot \left(\frac{V}{A} \right) \cdot c \quad (1)$$

In the equation, slope is the change of CO₂ concentration (ppm s⁻¹), *M*, *V_m* are molar mass (g mol⁻¹) and molar volume (m³ mol⁻¹) of CO₂, *V*, *A* are chamber volume (m³) and chamber area (m²), *T*₀ is the temperature at 0 °C (273.15 K), and *T* is the chamber temperature (°C), *c* (= 3600) is the conversion factor from s⁻¹ to h⁻¹. The slopes for the equation were estimated by linear

regression between elapsed measurement time and measured ppm in chamber headspace. Linear fit was deemed appropriate because of the short measurement times. Close to the LICOR detection limit (0–1000 ppm), random measurement errors of small fluxes sometimes resulted in negative values. Some measurement points showed a strange fluctuation of CO₂ concentration at the beginning of measuring time (most likely CO₂ probe did not reach the ambient CO₂ concentration before the start of the measurement), and it was solved by discarding 10 s from the beginning.

Soil respiration in peat soils is influenced by soil temperature, water-table level, and site type (Silvola et al. 1996a), which together determine the volume of aerated peat and the availability of water in the surface peat layers. In well-drained peatlands, temperature and water-table level are typically the key variables explaining temporal variation in momentary soil respiration (Silvola et al. 1996a; Mäkiranta et al. 2008). Therefore, to calculate seasonal CO₂ effluxes for each site, we developed site-specific models predicting heterotrophic soil respiration (HR) using an Arrhenius-type exponential approach instead of a linear regression model. Half-hourly soil temperature (T_s , °C) at a 5 cm depth was used as the primary independent variable. The model took the following exponential form:

$$HR = a \times e^{(b \times T_s)} \quad (2)$$

Where HR is the heterotrophic respiration rate (g CO₂ m⁻² h⁻¹), a represents the base respiration rate at low

temperature, b describes the temperature sensitivity of heterotrophic soil respiration (Table 3). In some cases, we also explored the effect of water-table level (WL, cm) using a power-type fit to assess its influence on HR. The goodness of fit to the measured flux data was evaluated using the coefficient of determination (R^2), which is commonly applied in soil respiration modeling (Lloyd and Taylor 1994; Fang and Moncrieff 2001). In addition, the risk of overfitting and underfitting of the models was assessed using the Akaike Information Criterion (AIC) (Akaike 1973) (Table 3).

Results

Soil temperature and water table level

Soil temperature at 5 cm depth showed a clear seasonal pattern, rising steadily from the beginning of June, reaching its maximum at the end of June, and then declining till the end of September in 2021 (Figure 2). In 2021, the average soil temperatures were 15.9 ± 3.4 °C for the DB-50 stand, 15.7 ± 3.5 °C for the DB-10 stand, and 15.4 ± 3.9 °C for the DB-80 stand. In 2022, the corresponding averages were 14.6 ± 1.8 °C, 15.5 ± 2.0 °C, and 13.8 ± 1.9 °C, as detailed in Table 2. Soil temperature in 2022 rose from the beginning of June, reached its maximum in the first week of July, fluctuated during August, and then declined until the end of September (Figure 2). A similar trend in soil temperature at 30 cm depth was observed at all the study sites (Table 2).

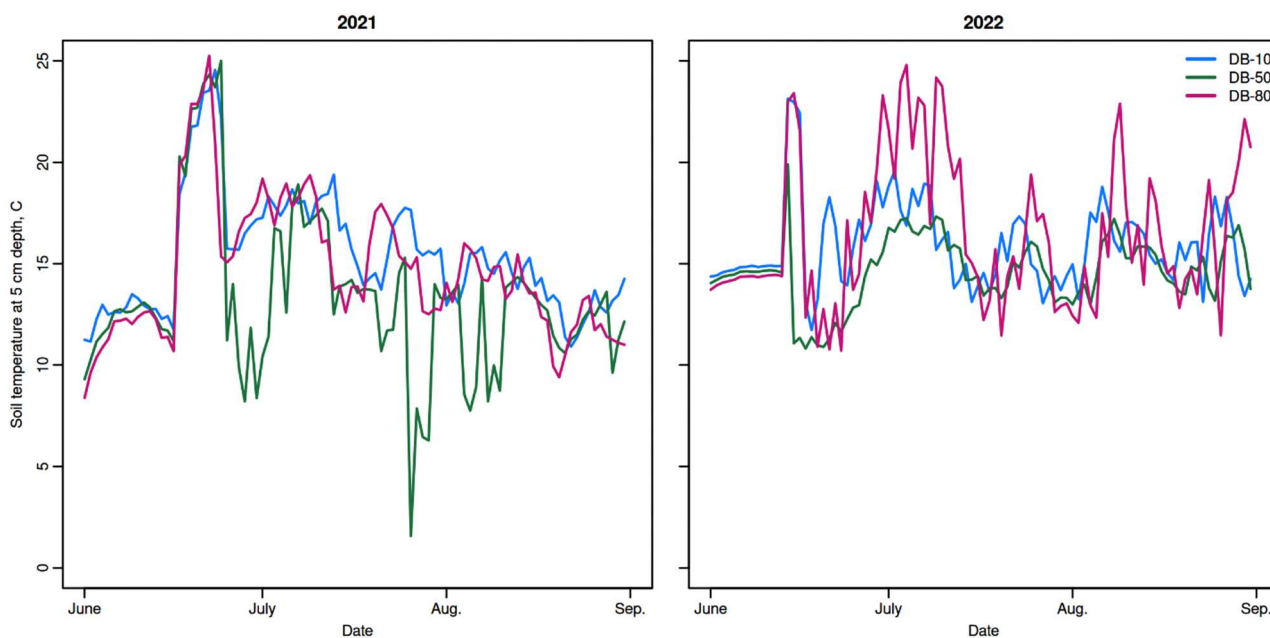


Figure 2. Daily mean soil temperature (°C) at 5 cm depth in DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites (June–September in 2021 and 2022). Data were recorded using iButton loggers (model 1921G) at 3-hour intervals.

Table 2. Seasonal (June–September) soil temperature (5 and 30 cm, °C), soil ground water table level (WL, cm), and heterotrophic soil respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) (mean \pm standard deviation) across the sites and year.

| Variables Year | DB-10 (Young stand) | | DB-50 (Middle-aged stand) | | DB-80 (Mature stand) | |
|--|---------------------|-------------------|---------------------------|-------------------|----------------------|-------------------|
| | 2021 | 2022 | 2021 | 2022 | 2021 | 2022 |
| Soil temperature at 5 cm (°C) | 15.69 \pm 3.48 | 15.54 \pm 1.97 | 15.89 \pm 3.43 | 14.64 \pm 1.81 | 15.39 \pm 3.88 | 13.78 \pm 1.93 |
| Soil temperature at 30 cm (°C) | 14.46 \pm 3.75 | 11.72 \pm 1.50 | 14.48 \pm 3.75 | 12.29 \pm 1.49 | 13.26 \pm 4.10 | 11.54 \pm 1.79 |
| Soil water level (cm) | 53.08 \pm 9.15 | 56.92 \pm 11.83 | 48.65 \pm 15.76 | 47.69 \pm 10.45 | 65.02 \pm 10.27 | 77.29 \pm 10.09 |
| Heterotrophic soil respiration ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) | 0.74 \pm 0.24 | 0.65 \pm 0.20 | 0.46 \pm 0.30 | 0.50 \pm 0.36 | 0.93 \pm 0.25 | 0.56 \pm 0.24 |

Soil water table level showed a less clear seasonal pattern than soil temperature (Figure 3) for all sites. WL in the year 2021 increased from the beginning of June, reaching its maximum in the first week of August, and then declining till the end of August (Figure 3). The arithmetic means of WL during the summer period varied from 49 cm to 65 cm between the study sites (Table 2). In 2022, the seasonal pattern of WL for the DB-10 and DB-50 was similar to each other, but for the DB-80 stand the water level loggers could not measure the water level exceeding 80 cm depth from the soil surface (Figure 3). Consequently, the recorded water levels for July appear uniform because the actual water depths surpass the loggers' measurement capabilities. The average WL during the summer period varied from 48 cm to 77 cm between the study sites in 2022 (Table 2).

The effect of soil temperature and water level on heterotrophic soil respiration

Soil heterotrophic respiration showed a strong and consistent relationship with soil temperature at 5 cm depth, explaining 88–96% of the temporal variation in measured CO_2 fluxes across the three birch-dominated forestry-drained peatland stands ($R^2 = 0.88$ for DB-10, 0.96 for DB-50, and 0.94 for DB-80; $p < 0.001$; Table 3, Figure 4a). Among the sites, the middle-aged stand (DB-50) exhibited the strongest temperature sensitivity, followed by the mature (DB-80) and young (DB-10) stands. In addition to temperature, water level (WL) also demonstrated a strong and nonlinear influence on heterotrophic respiration (Figure 4b), independently explaining 96–97% of the variation in measured fluxes ($R^2 = 0.96$ for DB-10, 0.97 for DB-50, and 0.96 for DB-80). The highest fluxes were associated with moderately deep-water tables (50–70 cm), suggesting a threshold-like response likely

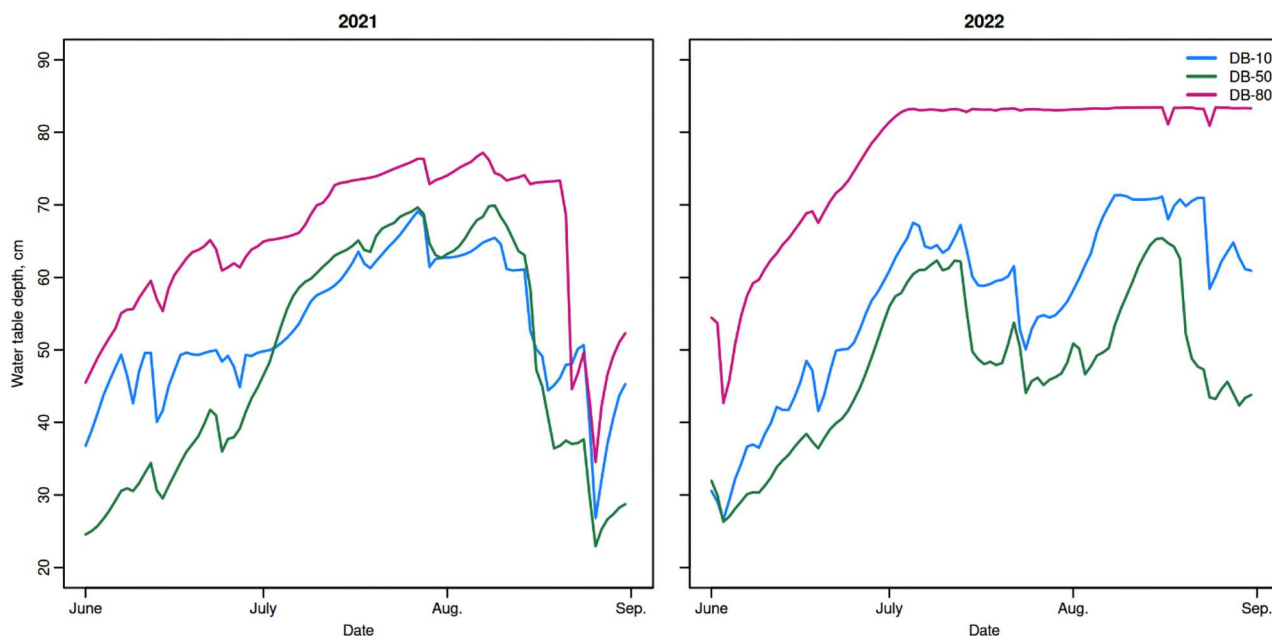


Figure 3. Daily mean water level (cm) at DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites (June–September in 2021 and 2022). Data were recorded using Odyssey[®] capacitance water loggers (Dataflow Systems Ltd, 2022) at 30-minute intervals. The DB-80 water table data for 2022 show unusually stable values with minimal fluctuation, which may indicate a sensor malfunction, logger drift, or other site-specific issue affecting measurement accuracy. These data should therefore be interpreted with caution.

Table 3. Regression models for heterotrophic soil respiration ($HR = a \times e^{(b \times T_s)}$, $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) fitted separately for each stand based on flux measurements during the 2021–2022 growing seasons.

| Stand | a | b | SE_a | SE_b | R ² | Adj. R ² | AIC |
|---------------------|--------|-------|--------|--------|----------------|---------------------|--------|
| DB-10 (Young) | 0.1045 | 0.127 | 0.0121 | 0.0067 | 0.88 | 0.87 | −92.4 |
| DB-50 (Middle-aged) | 0.0953 | 0.140 | 0.0102 | 0.0052 | 0.96 | 0.95 | −108.6 |
| DB-80 (Mature) | 0.0831 | 0.132 | 0.0115 | 0.0064 | 0.94 | 0.93 | −100.1 |

Parameter estimates (a , b), their standard errors (SE_a , SE_b), coefficient of determination (R^2 and adjusted R^2), and Akaike Information Criterion (AIC) are shown. The model describes the exponential relationship between soil temperature at 5 cm depth (T_s) and heterotrophic CO_2 flux for young (DB-10), middle-aged (DB-50), and mature (DB-80) birch-dominated forestry-drained peatland sites.

related to optimal aeration conditions for microbial activity (Figure 5). These results indicate that while soil temperature is the dominant control of seasonal respiration dynamics, water level plays an important complementary role that should not be overlooked.

The modeling of heterotrophic soil respiration revealed a strong temperature dependence across all sites, with statistically significant fits ($p < 0.001$) and high coefficients of determination ($R^2 = 0.88$ for DB-10, 0.96 for DB-50, and 0.94 for DB-80; Table 3). The middle-aged stand (DB-50) exhibited the strongest temperature sensitivity and best model fit, as also illustrated in Figure 4a. Parameter estimates further support this, with DB-50 showing a high value for the temperature sensitivity parameter b . In contrast, the relationship between WL and measured CO_2 flux, shown in Figure 4b, was nonlinear and site-dependent, yet still exhibited high explanatory power ($R^2 = 0.96$ – 0.97), with fluxes peaking at moderately deep-water tables (50–70 cm). These results indicate that while soil temperature is the dominant control of seasonal respiration dynamics, water level also plays an important

nonlinear role, especially under optimal aeration conditions. Additionally, closer inspection of the scatterplot in Figure 4b reveals the emergence of seasonally distinct groupings within the WL– CO_2 flux relationship. These clusters likely reflect differing hydrological and thermal contexts – such as spring (cooler soils drying out) versus late summer or early autumn (warmer soils with receding water tables). While we did not separately model these seasonal groupings due to limited within-season data, their presence suggests the possibility of hysteresis-type behavior, where similar water levels correspond to differing flux rates depending on the seasonal phase. This observation further underscores the complex, seasonally modulated nature of the water table's influence on soil respiration.

Measured and modeled heterotrophic soil respiration

There was a large temporal variation in soil heterotrophic respiration at all sites (Figure 6). In 2021, measured momentary CO_2 fluxes ranged from 0.09 to 1.16 g m^{-2}

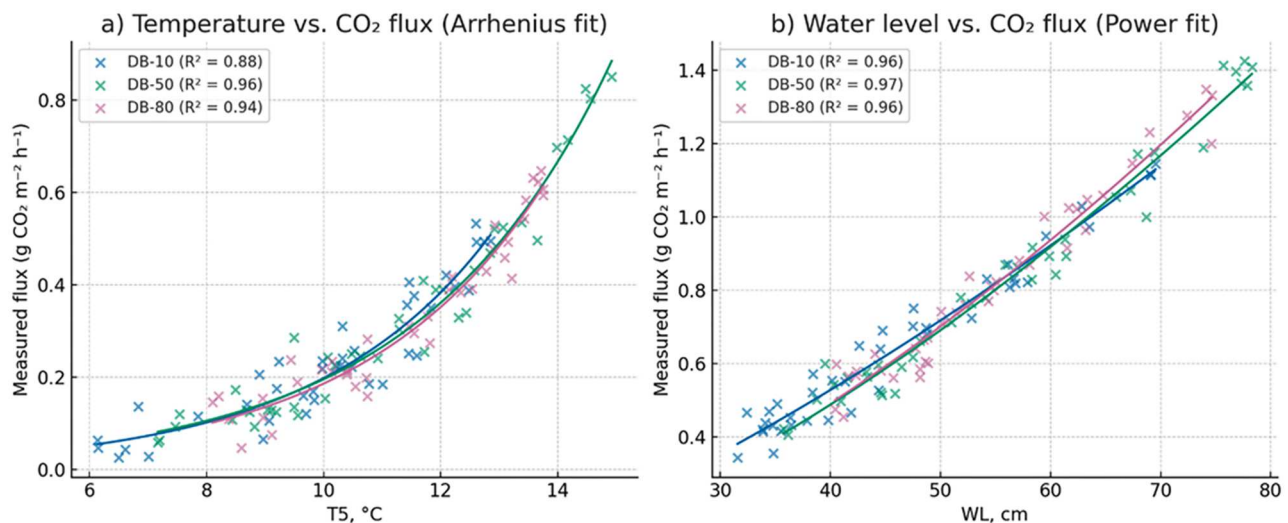


Figure 4. Relationships between measured heterotrophic CO_2 flux ($\text{g m}^{-2} \text{ h}^{-1}$) and (a) soil temperature at 5 cm depth (T_5 , $^\circ\text{C}$) and (b) water table depth (WL, cm from surface) for three forestry-drained peatland stands: DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand). Flux measurements and corresponding environmental data were recorded simultaneously during chamber campaigns in the growing seasons of 2021 and 2022 (six times per season per site). In panel (a), an Arrhenius-type exponential function ($HR = a \times e^{(b \times T_s)}$) was fitted to describe the temperature–flux relationship. In panel (b), a power function ($HR = c \times WL^d$) was used to represent the relationship between water level and flux. Coefficients of determination (R^2) are provided for each regression.

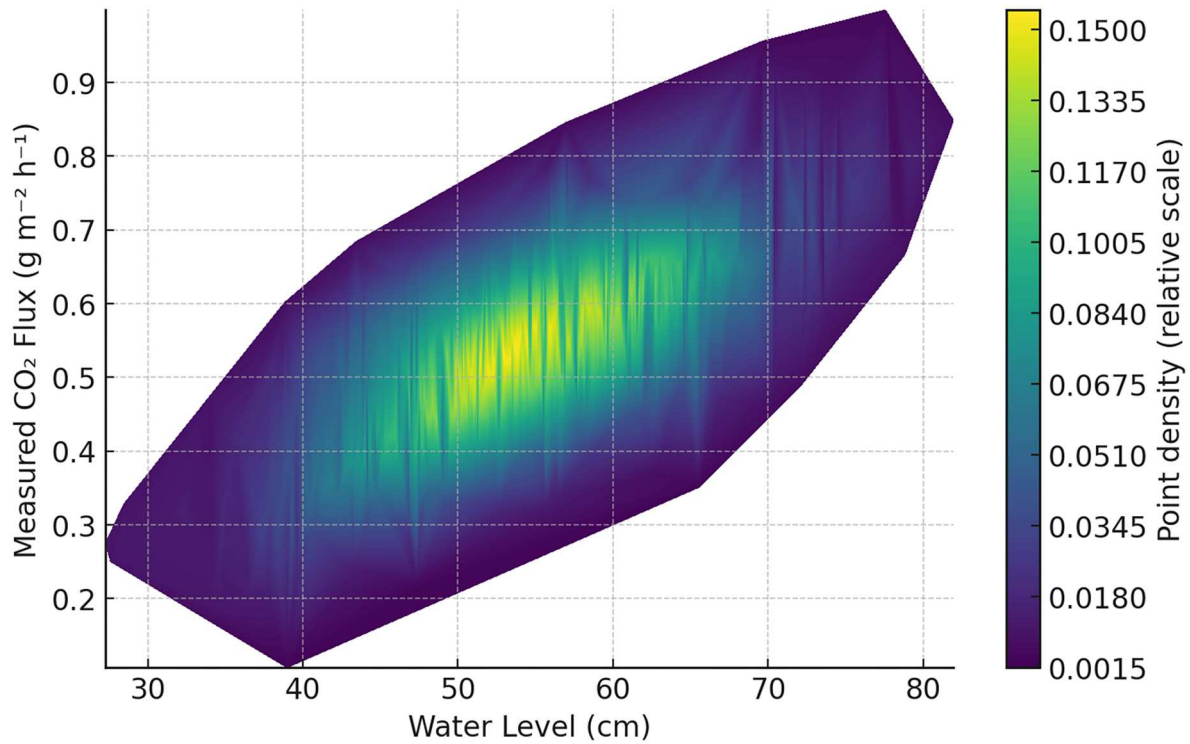


Figure 5. Kernel density contour plot showing the relationship between water level (cm) and measured soil CO₂ flux (g CO₂ m⁻² h⁻¹) across all sites. Higher density regions (yellow green) represent areas with more frequent observations. The color scale indicates relative data point density, with warmer colors corresponding to higher concentrations of observations.

h⁻¹, with average values of $0.74 \pm \text{SD } 0.24 \text{ g m}^{-2} \text{ h}^{-1}$, $0.46 \pm \text{SD } 0.30 \text{ g m}^{-2} \text{ h}^{-1}$, and $0.93 \pm 0.25 \text{ g m}^{-2} \text{ h}^{-1}$ for young, middle-aged, and mature stands, respectively (Figure 6,

Table 2). Fluxes decreased from young to middle-aged stand and slightly increased from middle-aged to mature age stand in 2022; average summertime fluxes

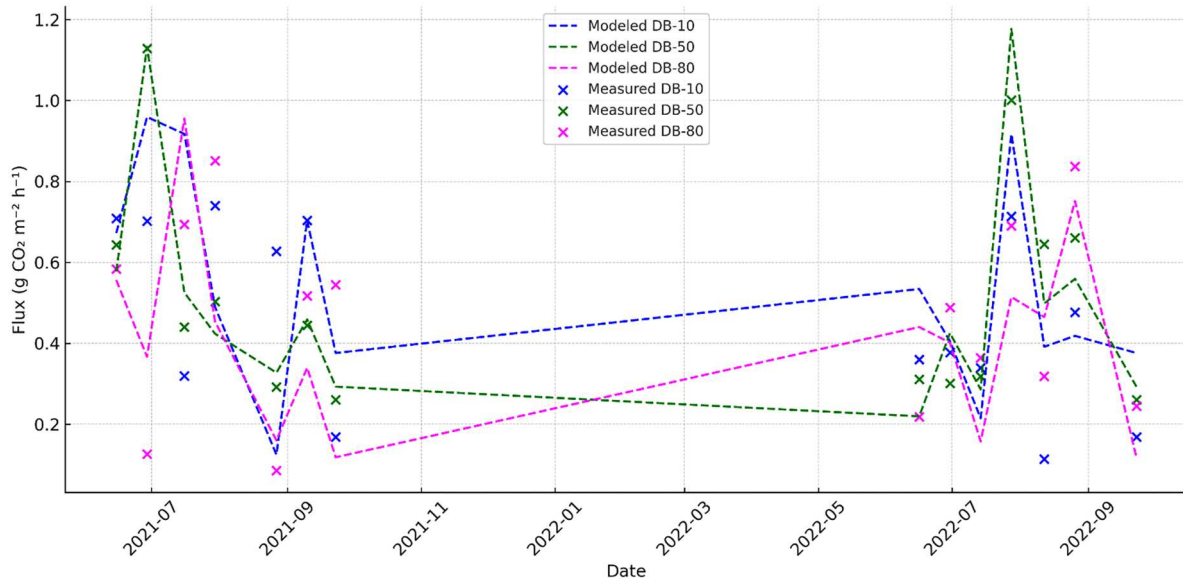


Figure 6. Measured (points) and modeled (dashed lines) CO₂ fluxes (g CO₂ m⁻² h⁻¹) for the DB-10, DB-50, and DB-80 stands during the 2021 and 2022 growing seasons. The model, driven solely by soil temperature at 5 cm depth, captures seasonal trends well during the active growing period (June–September), when temperature strongly regulates soil respiration. During cooler months, however, modeled fluxes increasingly deviate from observations, likely due to the absence of other key controls such as water level, snow cover, and suppressed microbial activity.

were 0.65, 0.50 and 0.56 g m⁻² h⁻¹ in young, middle-aged, and matured stands, respectively (Table 2). The highest instantaneous fluxes (up to 1.37 g m⁻² h⁻¹) were measured at 50-year-old stand at the end of July 2022 (Figure 6). Correlations of heterotrophic soil respiration with summertime weekly mean air temperature (°C) showed a weak correlation (Pearson correlation coefficient, $r = 0.20$, $p = 0.60$, 95% CI [-0.42, 0.66]) while with weekly precipitation sum(mm) showed negative correlation (Pearson correlation coefficient, $r = -0.45$, $p = 0.12$, 95% CI [-0.80, 0.14], results not shown).

Modeled daily CO₂ efflux showed substantial between-site variation and closely followed the changes in measured momentary fluxes (Figure 6). In 2021, cumulative mean CO₂ fluxes for stands aged 10, 50, and 80 years were estimated at 30.0 ± 2.5 g m⁻² day⁻¹, 22.4 ± 1.9 g m⁻² day⁻¹, and 26.4 ± 2.1 g m⁻² day⁻¹, respectively. During the summer months (June–August), the highest cumulative fluxes were recorded at the 10-year-old stand (2895 g m⁻²), followed by the 80-year-old stand (2540 g m⁻²), and the lowest at the 50-year-old stand (2152 g m⁻²). The R-squared values for predicted versus observed fluxes ranged between 0.88 and 0.94 ($p < 0.001$, Table 3). In 2022, the cumulative mean daily CO₂ fluxes were slightly higher at the 10-year-old stand (30.3 ± 2.6 g m⁻² day⁻¹) and the 50-year-old stand (23.0 ± 2.0 g m⁻² day⁻¹), while the 80-year-old stand showed a markedly lower flux (11.6 ± 2.0 g m⁻² day⁻¹). Summer totals in 2022 also reflected this trend, with the highest flux again observed at the 10-year-old stand (2927 g m⁻²), followed by the 50-year-old stand (2221 g m⁻²), and the lowest at the 80-year-old stand (1113 g m⁻²).

Discussion

Soil temperature and water table level

In this study, our objective was to estimate heterotrophic soil respiration in downy birch-dominated, forestry-drained peatlands and to identify the main controlling factors, particularly soil temperature and water level, as they relate to peat decomposition. Our findings demonstrate that soil temperature at 5 cm depth is the dominant driver of heterotrophic respiration, explaining a substantial portion of the temporal variation in CO₂ fluxes across all study sites, in line with previous studies (Laine et al. 2019; Lafleur et al. 2005; Mäkiranta et al. 2007, 2008). Although water level also explained a considerable share of the variation, its effect was nonlinear and site dependent. The kernel density contour plot (Figure 5) further illustrates that elevated CO₂ fluxes occurred most frequently at

moderately deep-water tables (50–70 cm), indicating threshold behavior rather than a simple linear response.

The temperature recorded at the peat surface depth in our measurement plots likely exhibited higher variability and extreme fluctuations compared to natural conditions due to the removal of moss and litter layers, which undoubtedly influenced the thermal conductivity of the soil. Consequently, it is probable that the manipulation of moss and litter layers also altered the moisture and oxygen conditions within the measurement plots. The decomposing litter layer in undisturbed conditions consumes oxygen and restricts its diffusion into the peat, probably maintaining lower oxygen levels compared to the treated plots. Additionally, in the absence of transpiring vegetation, the peat surface may remain moister during the summer months. Previous research has shown that drying of the peat surface during warm summer months can decrease decomposition rates of needle and root litter in forestry-drained peatlands compared to undrained ones (Laiho et al. 2004). Consequently, our method probably overestimated the heterotrophic respiration of peat soil because of the combined disturbance impacts of these treatments.

The high-temperature sensitivity of peat decomposition in peat soils may be related to a correlation between the amount of decomposable material available in the active decomposition process and temperature (Davidson and Janssens 2006). During the summer season, an increase in soil temperature commonly coincides with a drawdown of the water table, leading to a thicker aerated peat layer and enhanced microbial activity. As a result, both warming and drying can synergistically increase soil heterotrophic respiration, particularly in drained peatlands where the oxic layer extends deeper into the peat profile (Ojanen and Minkkinen 2019). However, in our study, we found only a weak correlation between measured soil temperature and water level during the measurement period, and the correlation coefficients between temperature and water level were similar across sites with both higher and lower average water tables (Pearson correlation coefficient, $r = 0.23$ – 0.25 , $p < 0.001$, 95% CI [0.09, 0.27]). This suggests that in well-drained sites with relatively stable hydrology, temperature and water table may act more independently in regulating heterotrophic respiration.

The effect of soil temperature and water level on heterotrophic soil respiration

Our measured CO₂ efflux of 0.09 to 1.37 g m⁻² h⁻¹ aligned with previous studies from forestry-drained peatlands. For instance, Minkkinen et al. (2007) reported measured CO₂ fluxes from 0 to 1.29 g m⁻² h⁻¹ at three

forestry-drained Norway spruce-dominated peatland sites in Finland. Similarly, Mäkiranta et al. (2010) found a range from 0 to $1.7 \text{ g m}^{-2} \text{ h}^{-1}$ at three forestry-drained Norway spruce-dominated peatland sites in Finland, while Ojanen et al. (2010) reported measured momentary fluxes of CO_2 between -0.01 and $2.14 \text{ g m}^{-2} \text{ h}^{-1}$ at 68 forestry-drained peatland sites in Finland.

The temporal dynamics of CO_2 fluxes were influenced by both soil temperature at 5 cm depth and water table depth, with water level showing a slightly stronger explanatory power in our study. This suggests that moisture conditions – regulated by the position of the water table – play a crucial role in controlling heterotrophic respiration in forestry-drained peatlands. This observation contrasts slightly with some earlier studies, such as Mäkiranta et al. (2008), which emphasized temperature as the dominant driver. However, our results align with the understanding that in drained peatlands, recent organic inputs (e.g. fine root litter with high decomposition potential) accumulate in the upper peat layers (~ 10 cm), where their decomposition is highly sensitive to changes in moisture availability. While water tables typically remain below 30 cm in such systems, even moderate variations in depth can influence oxygen availability and thus microbial activity (Ojanen et al. 2010). Therefore, the slightly stronger correlation between water table and CO_2 fluxes in our data highlights the site-specific role of hydrological conditions in regulating peat decomposition. Moreover, the scatter in Figure 4b indicates seasonally distinct groupings, which may reflect hysteresis effects – i.e. differing CO_2 flux responses to similar water table depths depending on whether the soil is wetting or drying – highlighting the seasonally dynamic nature of water table control on respiration. Recent studies have further examined these dynamics. For instance, Mäkiranta et al. (2018) investigated the responses of phenology and biomass production of boreal fens to climate warming under different water-table level regimes, highlighting the complex interplay between temperature, water table depth, and carbon fluxes. Additionally, Laine et al. 2019 explored warming impacts on boreal fen CO_2 exchange under wet and dry conditions, emphasizing the significance of moisture conditions in regulating CO_2 gas exchange in peatlands. These studies underscore the importance of considering both temperature and hydrological conditions when assessing carbon dynamics in boreal peatlands.

The thickness of the aerobic peat layer, which is difficult to measure directly but can be inferred from WL measurements, is a key factor regulating heterotrophic respiration in peat soils. Recent studies have shown that lower WL generally increases the volume

of oxygenated peat, thereby enhancing microbial decomposition and CO_2 emissions (Laine et al. 2019; Ojanen and Minkkinen 2019). Our findings revealed a comparable relationship between WL and heterotrophic respiration, with a slightly stronger correlation than with soil temperature. This suggests that hydrological control plays a meaningful role in regulating peat decomposition in our sites. However, the overall strength of the relationship was somewhat weaker than reported in studies covering a wider range of site types and WL fluctuations. This is likely due to the relatively narrow WL range across our well-drained study sites. These results highlight the importance of considering site-specific drainage status and WL variability when assessing decomposition rates and soil carbon dynamics in managed peatlands.

Our study provides further evidence for the strong influence of both soil temperature and water table depth on heterotrophic respiration in drained peatlands, particularly at sites dominated by deciduous trees. This relationship is clearly reflected in our results, where both variables emerged as key controls on soil CO_2 fluxes. These findings offer new insights into peat decomposition dynamics in well-drained, forestry-drained peatlands – conditions that remain underrepresented in earlier research. Notably, water table depth in our study showed a slightly stronger explanatory power than soil temperature, emphasizing the importance of hydrological conditions in regulating microbial activity and CO_2 emissions. Given this, we suggest that context-specific measurements of water table depth – especially in representative peatland types – could complement temperature-based models and enhance the accuracy of CO_2 flux estimates in land-use inventories. The ecological relevance of water table fluctuations further supports its inclusion in future monitoring and modeling strategies. Previous studies have suggested that climate warming may increase the efflux of carbon from soils to the atmosphere through enhanced heterotrophic respiration (Bellamy et al. 2005; Knorr et al. 2005), potentially triggering a positive feedback loop. More recent findings further suggest that this feedback could be particularly pronounced in northern regions, despite longer growing seasons in the south (Domisch et al. 2006; Comyn-Platt et al. 2018). However, our dataset does not allow for regional comparisons of this trend. Our results across the study sites underscore the importance of incorporating both soil temperature and water table depth into carbon balance assessments for improved projections of peatland emissions under changing climate conditions. In addition to the point-based analyses, we also applied a gap-filling approach to simulate seasonal CO_2 efflux based on measured soil temperature and water

table depth. While this approach allows for visualization of temporal patterns and relative differences between stands, we acknowledge that the cumulative heterotrophic respiration estimates derived from the model should be interpreted with caution. The limited number of flux measurement dates and potential uncertainties in extrapolating environmental drivers across unmeasured periods introduce a degree of uncertainty in the absolute flux totals. Therefore, the main value of the cumulative estimates lies in their ability to reveal differences in seasonal dynamics and relative site-level fluxes, rather than to provide definitive carbon loss values.

Acknowledgments

We would like to express gratitude to all laboratory staff at Hyytiälä forestry station in central Finland.

Author contributions

Conceptualization, Formal analysis: M.R.K and J.A; investigation: M.R.K and S.S; data curation, writing – review and editing: M.R.K, J.A, K.R.G, and S.S; writing – original draft preparation: M.R.K and J.A.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was funded by the “Finish Cultural Foundation” (decision number: 00230553). Katja Rinne-Garmston acknowledges funding from the European Research Council (755865) and the Academy of Finland (343059).

Generative Artificial Intelligence (AI)

The ChatGpt 4 (basic version) was utilized for language improvement, according to the Taylor & Francis AI Policy.

References

- Akaike H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*. 60(2):255–265. <https://doi.org/10.1093/biomet/60.2.255>
- Alm J et al. 2007. Methods for determining emission factors for the use of peat and peatlands flux measurements and modelling.
- Bellamy PH, Loveland PJ, Bradley RI, Lark RM, Kirk GJ. 2005. Carbon losses from all soils across England and Wales 1978–200.
- Bergman I, Lundberg P, Nilsson M. 1999. Microbial carbon mineralisation in an acid surface peat: effects of environmental factors in laboratory incubations. *Soil Biol Biochem*. 31(13):1867–1877. [https://doi.org/10.1016/S0038-0717\(99\)00117-0](https://doi.org/10.1016/S0038-0717(99)00117-0)
- Blake GR, Hartge KH. 1986. Bulk density. *Method Soil Anal: Part 1 Phys Miner Meth*. 5:363–375.
- Blodau C, Basiliko N, Moore TR. 2004. Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*. 67:331–351. <https://doi.org/10.1023/B:BIOG.0000015788.30164.e2>
- Comyn-Platt E et al. 2018. Carbon budgets for 1.5 and 2 C targets lowered by natural wetland and permafrost feedbacks. *Nat Geosci*. 11(8):568–573. <https://doi.org/10.1038/s41561-018-0174-9>
- Davidson EA, Janssens IA. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*. 440(7081):165–173. <https://doi.org/10.1038/nature04514>
- Domisch T, Finér L, Laine J, Laiho R. 2006. Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. *Eur J Soil Biol*. 42(2):74–81. <https://doi.org/10.1016/j.ejsobi.2005.09.017>
- Fang C, Moncrieff JB. 2001. The dependence of soil CO₂ efflux on temperature. *Soil Biol Biochem*. 33(2):155–165. [https://doi.org/10.1016/S0038-0717\(00\)00125-5](https://doi.org/10.1016/S0038-0717(00)00125-5)
- Hynynen J et al. 2010. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. *Forestry*. 83(1):103–119. <https://doi.org/10.1093/forestry/cpp035>
- Knorr W, Prentice IC, House JI, Holland EA. 2005. Long-term sensitivity of soil carbon turnover to warming. *Nature*. 433(7023):298–301. <https://doi.org/10.1038/nature03226>
- Lafleur PM, Moore TR, Roulet NT, Frohking S. 2005. Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table. *Ecosystems*. 8:619–629. <https://doi.org/10.1007/s10021-003-0131-2>
- Laiho R. 2006. Decomposition in peatlands: reconciling seemingly contrasting results on the impacts of lowered water levels. *Soil Biol Biochem*. 38(8):2011–2024. <https://doi.org/10.1016/j.soilbio.2006.02.017>
- Laiho R, Finér L. 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland. *Scand J Forest Res*. 11(1-4):251–260. <https://doi.org/10.1080/02827589609382934>
- Laiho R, Laine J, Trettin CC, Finér L. 2004. Scots pine litter decomposition along drainage succession and soil nutrient gradients in peatland forests, and the effects of inter-annual weather variation. *Soil Biol Biochem*. 36(7):1095–1109. <https://doi.org/10.1016/j.soilbio.2004.02.020>
- Laine AM et al. 2019. Warming impacts on boreal fen CO₂ exchange under wet and dry conditions. *Glb Chg Bio*. 25(6):1995–2008. <https://doi.org/10.1111/gcb.14617>
- Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Funct Ecol*. 8:315–323. <https://doi.org/10.2307/2389824>
- 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 Biol Biochem*. 40(7):1592–1600. <https://doi.org/10.1016/j.soilbio.2008.01.009>
- Mäkiranta P, Riutta T, Penttilä T, Minkkinen K. 2010. Dynamics of net ecosystem CO₂ exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest. *Agric For Meteorol*. 150(12):1585–1596. <https://doi.org/10.1016/j.agrformet.2010.08.010>

- Mäkiranta P et al. 2007. Soil greenhouse gas emissions from afforested organic soil croplands and cutaway peatlands. *Boreal Environ Res.* 12:159–175.
- Mäkiranta P et al. 2018. Responses of phenology and biomass production of boreal fens to climate warming under different water-table level regimes. *Glb Chg Bio.* 24(3):944–956. <https://doi.org/10.1111/gcb.13934>
- Minkkinen K et al. 2007. Heterotrophic soil respiration in forestry-drained peatlands. *Boreal Environ Res.* 12:115–126.
- Minkkinen K et al. 2023. The impacts of forestry on peatland carbon stocks, greenhouse gas dynamics, and climate. In: Strack M, editor. *Peatlands and climate change—scientific facts and figures for decision-makers*. 2nd ed. International Peatland Society; p 192–265.
- Moore TR, Dalva M. 1993. The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. *J Soil Sci.* 44(4):651–664. <https://doi.org/10.1111/j.1365-2389.1993.tb02330.x>
- Moore TR, Dalva M. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. *Soil Biol Biochem.* 29(8):1157–1164. [https://doi.org/10.1016/S0038-0717\(97\)00037-0](https://doi.org/10.1016/S0038-0717(97)00037-0)
- Nichols JE, Peteet DM. 2019. Rapid expansion of northern peatlands and doubled estimate of carbon storage. *Nat Geosci.* 12(11):917–921. <https://doi.org/10.1038/s41561-019-0454-z>
- Niemistö P, Korhonen KT. 2008. Koivuvarat ja kasvu. In: Niemistö P, Viherä-Aarnio A, Velling P, Heräjärvi H, Verkasalo E, editors. *Koivun kasvatusta ja käyttöä*. Metla and Metsäkustannus Oy; p. 175–181. [In Finnish].
- Obradović N et al. 2023. Reoxidation of reduced peat organic matter by dissolved oxygen: combined laboratory column-breakthrough experiments and in-field push-pull tests. *J Geophys Res Biogeosci.* 128(11):e2023JG007640. <https://doi.org/10.1029/2023JG007640>
- Ojanen P, Minkkinen K. 2019. The dependence of net soil CO₂ emissions on water table depth in boreal peatlands drained for forestry. *Mires and Peat.* 24(Article 27):27.
- Ojanen P, Minkkinen K, Alm J, Penttilä T. 2010. Soil–atmosphere CO₂, CH₄ and N₂O fluxes in boreal forestry-drained peatlands. *For Ecol Manag.* 260(3):411–421. <https://doi.org/10.1016/j.foreco.2010.04.036>
- Šantrůčková H et al. 2005. Heterotrophic fixation of CO₂ in soil. *Microb Ecol.* 49:218–225. <https://doi.org/10.1007/s00248-004-0164-x>
- Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ. 1996a. CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *J Ecol.* 84:219–228. <https://doi.org/10.2307/2261357>
- Straková P, Penttilä T, Laine J, Laiho R. 2012. Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. *Glb Chg Bio.* 18(1):322–335. <https://doi.org/10.1111/j.1365-2486.2011.02503.x>
- Updegraff K, Bridgman SD, Pastor J, Weishampel P, Harth C. 2001. Response of CO₂ and CH₄ emissions from peatlands to warming and water table manipulation. *Ecol Appl.* 11(2):311–326.
- Vasander H, Laine J. 2008. Site type classification on drained peatlands. In: Korhonen R, Korpela L, Sarkkola S, editors. *Finland-Fenland: research and sustainable utilisation of mires and peat*. Finnish Peatland Society Maahenki; p 146–151.
- von Arnold K, Nilsson M, Hånell B, Weslien P, Klemedtsson L. 2005a. Fluxes of CO₂, CH₄ and N₂O from drained organic soils in deciduous forests. *Soil Biol Biochem.* 37(6):1059–1071. <https://doi.org/10.1016/j.soilbio.2004.11.004>
- von Arnold K, Weslien P, Nilsson M, Svensson BH, Klemedtsson L. 2005b. Fluxes of CO₂, CH₄ and N₂O from drained coniferous forests on organic soils. *For Ecol Manag.* 210(1-3):239–254. <https://doi.org/10.1016/j.foreco.2005.02.031>
- Waddington JM et al. 2015. Hydrological feedbacks in northern peatlands. *Ecology.* 8(1):113–127. <https://doi.org/10.1002/eco.1493>