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EDITED BY
Evan S Kane,
Michigan Technological University,
United States

REVIEWED BY
Antti Juhani Rissanen,
Tampere University, Finland
Xiangjin Shen,
Chinese Academy of Sciences (CAS),
China
Zichun GUO,
Chinese Academy of Sciences (CAS),
China

*CORRESPONDENCE
Tracy Rankin,
✉ tracy.rankin@mail.mcgill.ca

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Partitioning autotrophic and heterotrophic respiration in an ombrotrophic bog

Tracy Rankin[1]*, Nigel Roulet[1], Elyn Humphreys[2], Matthias Peichl[3] and Järvi Järveoja[3]

[1]Geography Department, McGill University, Montreal, QC, Canada, [2]Department of Geography and Environmental Sciences, Carleton University, Ottawa, ON, Canada, [3]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

Northern peatlands are globally significant carbon stores, but the sink strength varies from year to year due to changes in environmental conditions. Ecosystem respiration (ER) is composed of both autotrophic respiration (AR) that consists of respiration by plant parts, and heterotrophic respiration (HR) that consists of respiration by microbial bacteria in the soil, fungi, etc. Manual measurements only crudely partition AR and HR, which may lead to erroneous estimates if a change favours one form of respiration over another and may influence our interpretation in the magnitude of respiration. HR has also been thought to be more linked to vegetation dynamics, particularly in wetter, sedge-dominated ecosystems like fens. It is unknown whether such plant-soil-root interactions influence HR in peatlands dominated by woody shrubs whose water table is located further below the surface. The objectives of this study were to 1) determine the contributions of AR and HR at Mer Bleue, an ombrotrophic bog, 2) explore how environmental conditions influence ER and its components, 3) determine how different methodological approaches (e.g. directly measured respiration using automatic chambers vs. extrapolated calculations) can influence our interpretation in the magnitude of respiration, and 4) compare the respiration dynamics with those found in the literature for other peatland types. Our results revealed differences in AR and HR contributions to ER compared to other peatland types reported in the literature. The AR/HR ratio was 3.0 and AR contributions to ER were ~75% at our study bog, which is generally higher than AR contributions from fens, but also decreased substantially during extended drier periods. HR contributions increased with rising temperature and water table depth. Directly measured ER was smaller than when ER was estimated using night-time relationships with temperature. The magnitude of ER changed depending on the plant biomass, which we believe to be a result of vegetation dynamics influencing HR. The results of this study improved our understanding of peatland carbon cycling as well as the conceptualization of HR.

KEYWORDS

peatlands, carbon exchange, autotrophic respiration, heterotrophic respiration, plant-root-peat interactions

1 Introduction

Northern peatlands play a significant role in the global carbon (C) cycle as long-term sinks of C since primary production exceeds decomposition. Peatlands cover 12% of Canada's terrestrial surface (Tarnocai et al., 2011) yet contain up to 56% of the organic C stored in Canadian soils (Tarnocai, 2006). Following the last glaciation, peatlands have accumulated C at an average rate of 23–26 g m^{-2} yr^{-1} (Charman et al., 2013; Loisel et al., 2014). However, on shorter time scales, a peatland may become a source or a sink of C depending on the environmental conditions of a given year (Roulet et al., 2007; Dorrepaal et al., 2009). Ecosystem respiration (ER) has both an autotrophic component that consists of respiration by plant parts, and a heterotrophic component that consists of respiration by microbial bacteria in the soil, fungi, etc. Most peatland C studies only crudely partition respiration into its autotrophic and heterotrophic components, which may influence our interpretation in the magnitude of respiration (Janskaate et al., 1997; Phillips et al., 2017). For example, heterotrophic respiration (HR) of old soil C may control the response to climate change, because the system could lose C from belowground sources to the atmosphere that had been stored for hundreds of years. In contrast, if autotrophic respiration (AR) controls the response to climate change, the system may fix more C (Hicks Pries et al., 2013).

Most of the variability in CO_2 exchange comes from changes in gross primary production and AR (Blodau, 2002; Heimann and Reichstein, 2008), variables that respond predictably and which we understand more fully. The dynamics of HR, on the other hand, is more complicated. HR is predominantly defined in the literature as respiration by microbial bacteria communities that is correlated with environmental and substrate variables, such as litter quality and moisture, and is often synonymously referred to as belowground respiration (Chapin et al., 2006; Minkkinen et al., 2007; St-Hilaire et al., 2010). More recently, however, HR has also been linked to vegetation dynamics and aboveground production. Bond-Lamberty et al. (2004) suggest, for example, that there is no standard practice on whether to include rhizosphere respiration (peat respiration in the vicinity of plant roots) with AR or HR, which may be due to the difficulty in separating root functions from total soil CO2 fluxes, which contains all belowground C sources (Chapin et al., 2006). Similarly, Basiliko et al. (2012) highlight the difficulties in separating root respiration from HR. Furthermore, *Sphagnum* mosses are capable of fixing the respired CO_2 from the vegetation that surrounds them rather than only using the CO_2 directly from the atmosphere in the process of photosynthesis (Turetsky and Wieder, 1999; Kuiper et al., 2014). Here, the rate of litter supply is related to plant production through root-soil interactions and belowground processes rather than through plant biomass (Shao et al., 2022). As *Spha*gnum mosses are sensitive to changes in CO_2 concentrations (Serk and Schleucher, 2020), vascular plant coverage (i.e., shrub biomass) may also influence ER, and possibly the magnitude of HR, if the presence of shrubs that provide C to be fixed by the mosses is altered (Shao, 2022). Thus, partitioning AR and HR assuming HR only consists of microbial community respiration when there may also be a possible contribution of a plant-associated component to HR would result in a biased interpretation of the C response.

Consequently, belowground processes are more connected to aboveground production than just the slow decomposition of dead organic matter (Ryan and Law, 2005; Van Hees et al., 2005), which has been seen in sedge-dominated (Kurbatova et al., 2013; Wang et al., 2014; Järveoja et al., 2018) and in permafrost ecosystems (Crow and Wieder, 2005; Hicks Pries et al., 2015). It is unknown whether this same level of vegetation influence on HR exists in shrub-dominated bogs. Where fens make up a greater proportion of peatlands in European countries (Janska et al., 2017; Jimenez-Alfaro, 2018), bogs make up about 70% of peatlands in Canada (Tarnocai et al., 2011). This distinction is very important when considering respiration dynamics of peatlands as future changes in climate could have an impact on Canada's overall greenhouse gas emissions.

The contributions of AR and HR to total respiration can differ among peatland types (Schuur and Trumbore, 2006) as the respiration components depend on environmental and biogeochemical conditions (Griffis et al., 2000; Ojanen et al., 2012). Moore et al. (2002) estimated that HR contributed about 46% to total annual ER at the Mer Bleue bog. Hicks Pries et al. (2013), on the other hand, found that HR contributed only 6%–18% to total ER at a tundra site in Alaska underlain by permafrost using direct methods. Hicks Pries et al. (2013) also state that the C losses were compensated by an increase in net productivity as the permafrost thaw deepened with increased warming, but that HR may increase substantially if the respiration of older soil eventually outpaces productivity. This statement contradicted the authors' later study, where long-term warming experiments did not lead to an increase in HR, but rather to an increase in both plants' AR/HR ratios and the contribution of AR to total ER (Hicks Pries et al., 2015). It would be reasonable to assume that sites not underlain with permafrost, and perhaps not as sensitive to changes in temperature, would show greater AR contributions.

A plant's response to a change in environmental conditions or following a disturbance can also be explained by the various mechanisms by which the plants utilise water resources (Cernusak, 2020; Zia et al., 2021). Malhotra et al. (2020) suggest that environmental changes (e.g., warming) can alter fine root production, affecting water and nutrient uptake and hence ER and C storage. Oke and Hager (2020) suggest that physiological tolerances and ecological strategies influence a plant's distribution. Where bogs receive their water source from precipitation, fens receive water inputs from precipitation, surface runoff from adjacent land, and from the groundwater below, which causes environmental constraints on the growth of mosses through enhanced free movement of water through a fen leading to increased oxygenation of the organic substrate and enhanced decomposition (Baldwin and Batzer, 2012). A 50/50 split in AR and HR contributions to ER was found at Degerö Stormyr, a fen in northern Sweden (Järveoja et al., 2018). However, fens have a high water table for most of a growing season, whereas in bogs, the water tables are mainly below the surface, leading to more aerobic conditions (Mitsch and Gosselink, 2007; Moore, 2008). Bogs, as a result, may show a greater contribution of HR than fens.

Finally, one's interpretation of ER measurements may be influenced by the methods used. Typically, respiration during the day is estimated using relationships between respiration measured at night with eddy covariance towers, and temperature (Peichl et al., 2014; Humphreys et al., 2015). But this method can lead to an overestimation of daytime respiration. For example, at a treed fen in Alberta (Cai et al., 2010), they found that direct measurements made with dark chambers during the day resulted in smaller ER fluxes than when the ER during the day was estimated by night-time relationships with temperature. Different diel temperature responses may explain the mismatch between dark daytime and extrapolated nighttime to daytime respiration (Järveoja et al., 2020). Photorespiration though, may also explain part of this discrepancy, as photorespiration tends to be reduced in dark respiration measurements (Pirk et al., 2016). Environmental variables will also play a role since photorespiration has been shown to be stimulated in high temperature and water stress conditions (Lloyd, 2006; Dusenge et al., 2019). Hence, using a standardised definition of HR and measuring dark respiration directly will be key to a better understanding of peatland C cycling.

The objectives of this study are to partition autotrophic and heterotrophic respiration at Mer Bleue, an ombrotrophic bog, using continuous automatic chamber plot measurements. Specifically, this project aims to 1) determine the contributions of autotrophic and heterotrophic respiration, 2) explore the environmental conditions' influence on respiration and its components, 3) determine how different methodological approaches can influence our interpretation in the magnitude of respiration, and 4) compare the respiration dynamics with those found in the literature for other peatland types.

2 Materials and methods

2.1 Study site

Mer Bleue is a relatively large (28 km^2) ombrotrophic raised bog located near Ottawa, Ontario (45.41°N, 75.52°W). The region has a cool continental climate, with a mean annual temperature of 6.4°C ranging from -10.3°C in January to 21.0°C in July. Mean annual precipitation is 943 mm, 350 mm of which falls from May to August, with a mean annual snowfall of 223 cm (Environment Canada, 2023). Peat depth reaches about 5–6 m near the centre of the bog and is <0.3 m near the edge of the peatland. Bog development began 7100–6800 years ago, and now consists of a hummock-lawn microtopography (Roulet et al., 2007). While the surface of the bog is covered by *Sphagnum* mosses (*Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum fallax, Sphagnum magellanicum*), Mer Bleue is primarily dominated by low growing ericaceous evergreen shrubs that make up about 80% of the areal coverage (mainly *Chamaedaphne calyculata*, with some *Ledum groenlandicum, Rhododendron groenlandicum,* and *Kalmia angustifolia*). There is also an occasional mix of sedges (*Eriophorum vaginatum*) that make up about 3%–5% of the areal coverage (Lai, 2012; Humphreys et al., 2015).

2.2 Automatic chamber setup and CO_2 flux calculations

CO_2 fluxes were determined using an automatic chamber set up, and separated into two clusters based on the CO_2 exchange from baseline measurements conducted in 2017 (not shown), where the plots in a given cluster all responded similarly to one another but the clusters behaved differently with regards to their C response.

In June 2018, we manipulated some of the plots; A breakdown of the manipulations conducted in the two clusters is provided in Table 1. One chamber from each cluster was darkened with aluminum foil to mimic dark respiration. All the aboveground vegetation was removed in the darkened plot from each cluster (i.e., only peat remained), with a layer of green mesh placed on top to account for temperature differences. These plots were also trenched and root exclosures installed. We assumed these plots gave an approximation of HR but realise that the roots may not have been completely decomposed. One chamber in Cluster one was only darkened with no vegetation manipulation, which we assume represents a direct measurement of ER during the day. Finally, one chamber in each cluster was left clear (transparent), which we assume to approximate ER where respiration during the day was derived from a relationship of night-time respiration and temperature. Autotrophic respiration was then derived as the difference between ER and HR in the respective cluster. In Cluster 1, two separate measures of AR were determined: one was the difference between ER in the clear plot and HR from the clipped plot, and the other was the difference between ER from the darkened plot and HR from the clipped plot.

The calculation of CO_2 fluxes from the automatic chambers has been previously described in Lai (2012). The collars were covered at set intervals by plastic domes with a height of 20 cm, a diameter of 52 cm and a thickness of 1 cm. The automatic chambers were programmed to close sequentially by a datalogger (CR23X, Campbell Scientific, UT, USA) to measure gas concentrations for 2 min during the day and 15 min at night. Concentrations of CO_2 were measured with a closed-path infrared gas analyser (LI-6262, LI-COR, NE, USA). Using linear regression equations of concentrations over time, one measured flux was obtained for each chamber every 30 min, providing CO_2 fluxes on an hourly timescale. Unfortunately, the measurements of 2018 were not usable due to an issue with the pressure in the pumps that circulate the air through the chambers (Model CPFAC2600P, Porter Cable, TN, USA), which resulted in air escaping to the atmosphere. Thus, we only show the 2019 growing season results from the automatic chambers, expressed as hourly averages of CO_2 fluxes. Only regressions where the regression coefficients (R^2) were greater than 0.95 were kept and all other measurements were discarded, about 5% of the raw data.

Others have performed manipulations to their chamber set ups to determine contributions of AR and HR by trenching the phloem in the aboveground stem, eliminating belowground allocation, a process known as girdling (Hahn et al., 2006; Hardie et al., 2009). However, this was done mainly in forested systems; In a bog, the surrounding vegetation like the mosses surrounding the vascular plants would have been highly disturbed with this approach. Hence, we opted to remove only the aboveground vegetation (leaving the phloem intact), while keeping in mind that residuals of the roots left behind may contribute to the fluxes we measure. Root exclosures (plastic corrugated sheets) were installed though to minimise the need for re-clipping of the plots, as suggested by Marinier et al. (2004).

TABLE 1 Automatic chamber set up with descriptions of manipulations and reported measurements.

Cluster #	Plot manipulation	Measurement method
1	Full vegetation, Darkened chamber	ER, direct daytime measurement
	Darkened chamber, all aboveground vegetation removed	HR, direct daytime measurement
	Full vegetation, clear reference chamber	Daytime ER assumed from night-time relationship with temperature
2	Full vegetation, clear reference chamber	Daytime ER assumed from night-time relationship with temperature
	Darkened chamber, all aboveground vegetation removed	HR, direct daytime measurement

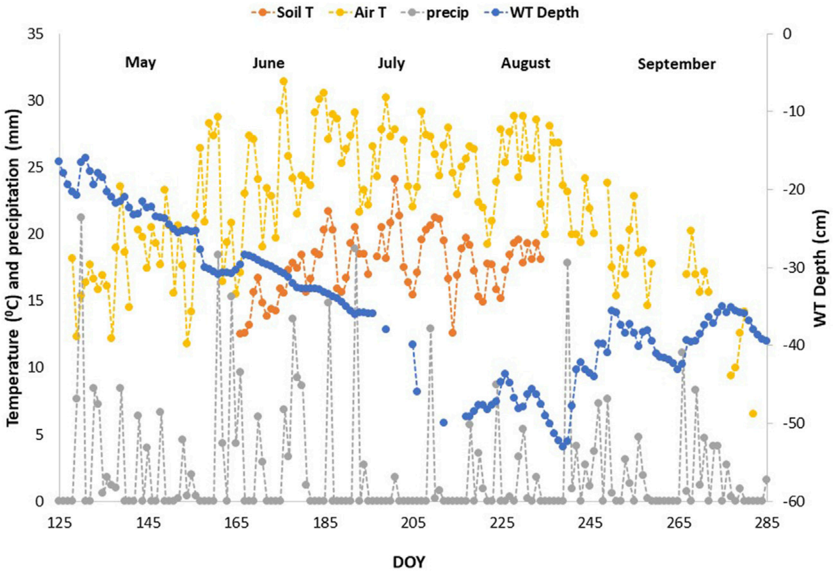

FIGURE 1
Environmental Variables across the growing season of 2019, derived from the eddy covariance tower near the automatic chamber set up. Soil T is soil temperature at 10 cm depth, WT is water table, T is temperature, and precip is the precipitation amounts obtained from Environment Canada's weather station nearby.

2.3 Environmental variables

Water table (WT) depth and soil temperature were continuously monitored throughout the same sampling period as the automatic chambers. Thermocouples were previously installed next to the automatic chambers that were hooked up to a datalogger (CR1000X, Campbell Scientific, UT, United States) which measured continuous soil temperatures at 10 and 40 cm depths. Continuous 30-min records of water table position were also obtained with capacitance water level probes (Odyssey, Dataflow Systems PTY Limited, Christchurch, New Zealand) that were placed inside PVC tubes previously inserted in the peat beside each of the automatic chambers (Lai et al., 2014). Manual measurements of WT depth were taken periodically beside each automatic chamber to match against the values obtained by the capacitance probes and the continuous measurements of WT depth were constructed from these interpolations. Air temperature and photosynthetically active radiation (PAR) were measured at the meteorological station attached to the eddy covariance tower at the site, approximately 30 m away from the automatic chamber set up (Lafleur et al., 2005). Finally, precipitation amounts (reported in mm) were obtained from a weather station nearby (Environment Canada; Historical Weather).

2.4 Biomass estimates

Even though the plots in the autochamber setup all contained a mixture of *Sphagnum* mosses and the dominant shrub species at the site, *Chamaedaphne calyculata*, the automatic chambers in Cluster two had a greater contribution of *Ledum* and roughly 27% lower overall shrub biomass than Cluster 1, partly explaining the difference in C response between the clusters in 2017 (as mentioned above).

The non-destructive point intercept method (Bonham, 2013) was used to estimate biomass in the automatic chamber plots. Square grids were constructed using PVC pipes for the frame and string for the grid. The grid was about 55 cm wide, with grid intersections every 5 cm. The grid was placed above the plots. The placement of the grid

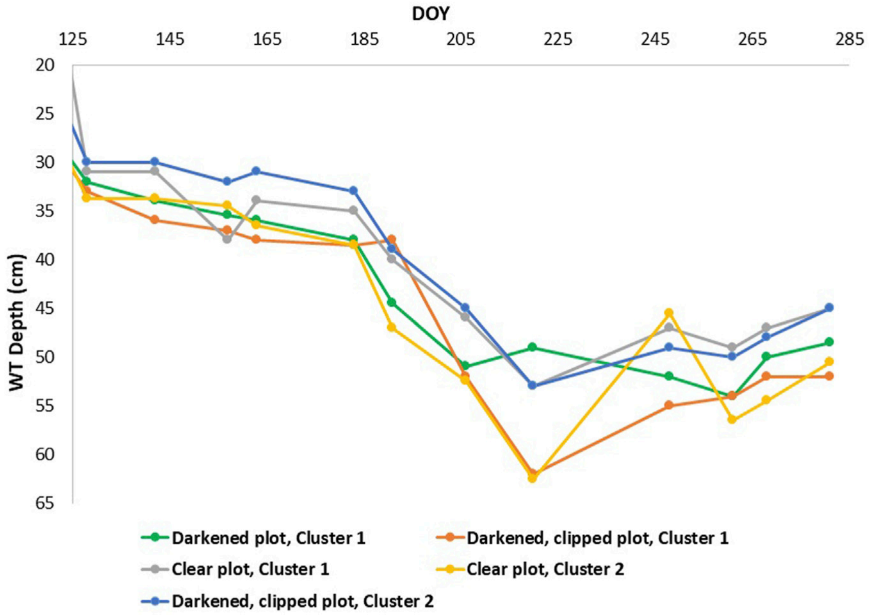

FIGURE 2
Water table (WT) depth taken from manual measurements in 2019.

was random for each sampling day, but the grid covered the whole collar. A plastic rod with a diameter of about 1 cm was stuck down vertically at a grid intersection point until it touched the peat surface. The number of leaves, shoots and flowers of each plant species touching the rod was recorded, where every other grid point in each column was sampled. Measurements were taken either six or seven times, depending on the plot, between June 27th and 27 August 2018.

Destructive sampling was carried out about 30 m away from the automatic chamber set up. A 25 cm diameter collar was randomly placed on a hummock similarly to the placement of the autochambers. The biomass was sampled non-destructively using the same point intercept method, as outlined above. The above ground vascular biomass in the plot was then clipped and bagged. In the lab, the samples were sorted by organ and species, dried at 70°C for 30 h, and then weighted. Ten measurements were made between July 13th and July 30th in 2018. The number of hits of plant organs was normalised using the number of grid points in that sample. Linear regressions were generated to relate the number of hits per grid point of a plant organ to biomass. R^2 values were also generated and were all above 0.97 with a p-value <0.001. These equations were then used to estimate the biomass in each of the four automatic chambers before manipulations to the plots were conducted.

The automatic chambers in Cluster one had an average estimated shrub biomass of 372 ± 10 $g\,m^{-2}$ and the automatic chambers in Cluster two had an average estimated shrub biomass of 272 ± 42 $g\,m^{-2}$, with ~13% contribution from *Ledum* to overall shrub biomass in Cluster 1, and ~23% contribution from *Ledum* to overall shrub biomass in Cluster 2. Biomass measurements were similar to those found previously from the site using similar sampling techniques (Humphreys et al., 1997; Moore et al., 2002).

2.5 Statistical analyses

Statistical analyses were performed using the R statistical software (R Core team, 2020). First, simple linear and multiple regressions were conducted among the respiration fluxes (ER, HR, and AR) and the various environmental variables using the “stats” package in R. Second, coefficients of variation (standard deviation/mean of population) were conducted to determine the degree of variability in AR contributions to ER, as described in Abdi (2010). Third, repeated measures Analysis of Variance (ANOVA) tests were conducted using the “car” package in R (a tool for modelling irregularly sampled time series data) to determine if the fluxes from the different treatments were significantly different (Belcher et al., 1994). Finally, two sample t-tests were conducted using the “stats” package to determine whether the fluxes of ER as measured by the darkened chamber were significantly different from the ER estimated by a temperature relationship with night-time respiration in the clear plots. An additional comparison (two sample t-test) was made between ER measured during the day in the darkened plot of cluster one and ER estimated by a temperature relationship with night-time respiration in the same plot. We consider individual p-values less than or equal to 0.10 as significant.

3 Results

3.1 Environmental variables

The growing season of 2019 was wetter in May and June compared to the normal averages, then consistently became warmer and drier as the growing season progressed (Figure 1), with WT depth similar to normal averages in July and August (Teklemariam et al., 2010), albeit a bit drier than those measured in previous years (He et al., 2023). Mean daily air temperatures from the eddy covariance tower nearby ranged

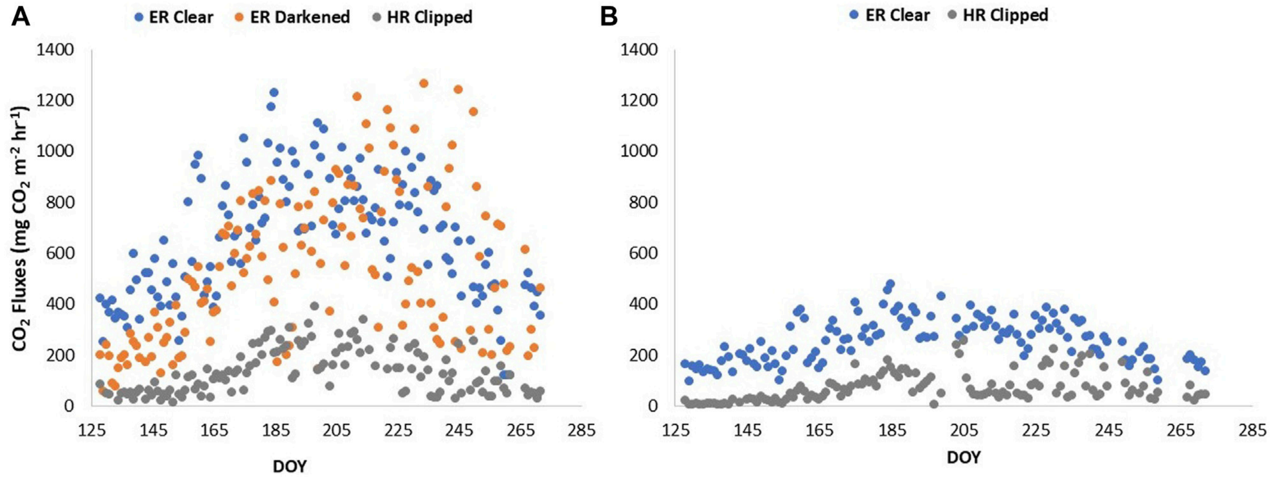

FIGURE 3
ER fluxes estimated in the clear plot based on temperature relationship with night-time respiration values, ER fluxes measured in the darkened plot, and HR fluxes measured in the clipped plot, across the growing season of 2019 in **(A)** cluster 1, and **(B)** cluster 2. ER is ecosystem respiration, and HR is heterotrophic respiration.

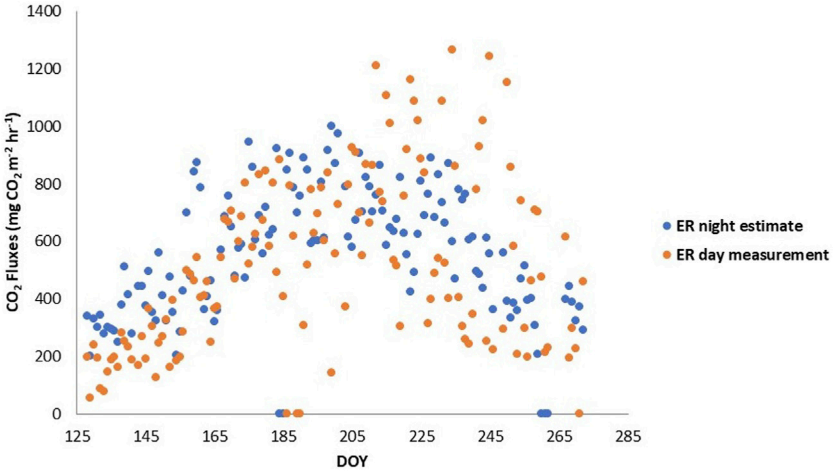

FIGURE 4
Ecosystem respiration (ER) flux comparison between daytime measurements and estimates conducted with nighttime measurements in the darkened plot of cluster 1.

between 23°C and 31°C (May - August), soil temperatures at 10 cm depth ranged between 12°C and 22°C, and precipitation amounts ranged from 0 mm to a few rain events that reached between 15 and 20 mm. The average WT depth ranged between 10 cm and 53 cm (May–August mean WT = 36.5 cm depth), although, the local WT depth varied slightly depending on the location of the automatic chamber (Figure 2).

3.2 CO$_2$ fluxes

Estimated ER based on the temperature relationship with night-time respiration from the clear chamber in cluster one ranged between 100 and 1220 mg CO$_2$ m^{-2} hr^{-1}, and HR in Cluster one ranged between 0 and 390 mg CO$_2$ m^{-2} hr^{-1} (Figure 3A). In contrast, ER estimated from the clear chamber in Cluster 2, based on the temperature relationship with night-time respiration, ranged between 100 and 475 mg CO$_2$ m^{-2} hr^{-1}, and HR ranged between 0 and 250 mg CO$_2$ m^{-2} hr^{-1} (Figure 3B). ER measured during the day from the darkened chamber in Cluster one ranged between 50 and 1250 mg CO$_2$ m^{-2} hr^{-1}, and between 250 and 1000 mg CO$_2$ m^{-2} hr^{-1} when daytime ER was estimated from night-time measurements (Figure 4).

3.3 Derived AR fluxes

Derived AR fluxes ranged from 200 to 1000 mg CO$_2$ m^{-2} hr^{-1}, 300–1100 mg CO$_2$ m^{-2} hr^{-1}, and 100–400 mg

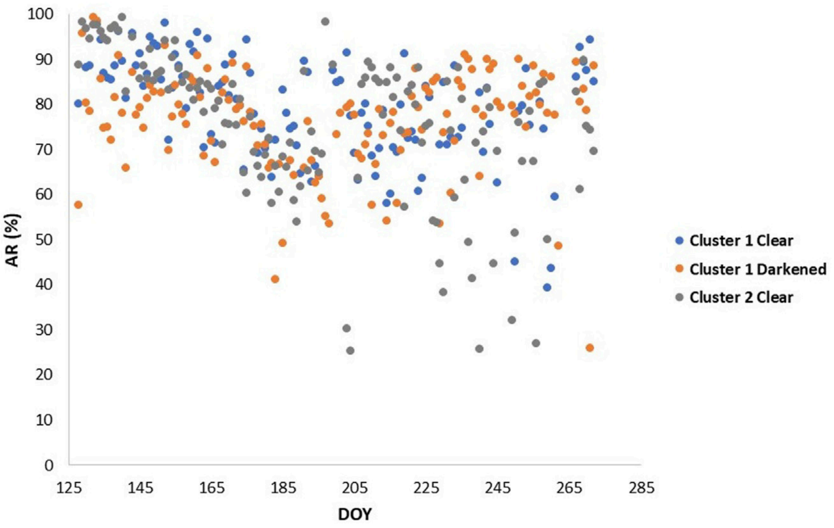

FIGURE 5
Autotrophic respiration (AR) contributions (%) derived for the darkened plot and clear plot in cluster 1, and clear plot in cluster 2.

CO_2 m^{-2} hr^{-1} for the darkened and reference plot in Cluster one and reference plot in Cluster 2, respectively (Figure A1). Consequently, the AR contributions to ER were 76.5 ± 11.2%, 79.0 ± 11.4% and 75.1 ± 21.4%. The coefficients of variation in AR contributions were 15%, 14% and 22% for the darkened and clear plot in Cluster one and clear plot in Cluster 2, respectively (Figure 5).

3.4 Statistical analyses

Repeated measures ANOVA show that the fluxes from the different manipulation treatments (ER vs. HR) were significantly different between the reference and clipped plots in Cluster 1 ($F = 245.4$, $p < 0.00001$) and cluster 2 ($F = 451.3$, $p < 0.00001$). ER measured from the darkened plot during the day was significantly different than ER estimated using night-time relationships with temperature in the clear plot from Cluster 1 ($T = -3.7$, $p = 0.0001$), but not significantly different when compared with the estimated ER from night-time measurements in the darkened plot ($T = -1.3$, $p > 0.2$). Additionally, the difference in ER fluxes between the two clusters was significant ($T = -18.0$, $p < 0.00001$), as well as the difference in HR fluxes between the two clusters ($T = -6.7$, $p < 0.00001$).

Linear regression analyses support these findings. ER, AR and HR all generally increased as WT depths increased (became drier) and soil and air temperature increased. Although, there were instances where we saw the opposite effect, which caused a difference in the amount of variance explained by the environmental variables. In the reference plot of Cluster 1, when environmental variables were considered individually, ER and AR correlated with air temperature and somewhat with WT depth above 35 cm and soil temperature, whereas HR correlated with WT depth and somewhat with air temperature. More variance was explained by the interaction of environmental variables for AR only when multiple regression was used. It was a similar case in Cluster 2, where ER and AR were associated more with air temperature and somewhat with WT depth above 35 cm and soil temperature, whereas HR was correlated more with WT depth and somewhat with air temperature. However, the interaction of multiple variables increased the variance explained for all three fluxes (Table 2).

In contrast, for the darkened plot in Cluster 1, ER, AR and HR were all mostly correlated with WT depth above 35 cm, where more than 50% of the variance was explained, and air temperature explained less than 15% of the variance for all three fluxes when linear regression was used. There were no significant relationships with soil temperature for the darkened plot, and the interaction of multiple variables did not increase the variance explained for any of the fluxes when multiple regression was used (Table 2). There were no significant relationships found with WT depth when the WT dropped below 35 cm depth for any of the automatic chambers.

4 Discussion

4.1 AR and HR contributions to ER

Although ER fluxes were lower in the plots with less vascular biomass (Figure 3), the magnitude of the ER fluxes was consistent with those found in other studies (Bubier et al., 2007; Sulman et al., 2010; Flanagan and Syed, 2011; Lai et al., 2014). One would assume HR from the clipped plots to be the same between the two clusters though, which was not the case in our study (Figure 3). With a greater abundance of vascular plants, a greater contribution of residual decomposing roots would have been expected (Zeh et al., 2020). However, the difference in HR could also be due to the species composition of the plots prior to clipping, where the automatic chambers that had a slightly greater contribution of *Ledum* would have led to a difference in decomposition rates (Murphy et al., 2009b; Murphy and Moore, 2010). Thus, this may be explained by inherent spatial variability.

An additional explanation is that the vascular plants were inhibiting the respiration of the microbes below, with the mosses providing a priming effect to heterotrophic respiration. Gavazov et al.

TABLE 2 Coefficient of determination (R^2) for linear and multiple regressions between the respiration fluxes (ER, AR, and HR) in the automatic chamber plots and the environmental variables in 2019. ER is ecosystem respiration, AR is autotrophic respiration and HR is heterotrophic respiration. WT is water table depth above 35 cm depth, Soil T is soil temperature at 10 cm depth, and Air T is air temperature measured at the flux tower. All relationships are significant at $p < 0.001$; All blank entries are not significant.

Automatic chamber	Respiration flux	WT	Air T	Soil T	WT + air T	WT + air T + soil T
Cluster 1, darkened plot	**ER**	0.64	0.09		0.68	
	AR	0.52			0.55	
	HR	0.50	0.15		0.51	
Cluster 1, reference plot	**ER**	0.52	0.93	0.26	0.93	0.91
	AR	0.32	0.79	0.17	0.87	0.84
	HR	0.53	0.23		0.53	
Cluster 2	**ER**	0.53	0.93	0.21	0.93	0.89
	AR	0.28	0.50	0.14	0.85	0.82
	HR	0.63	0.36		0.76	

(2018) found enhanced heterotrophic decomposition of peat C due to rhizosphere priming. At the Mer Bleue bog, the mosses assimilate C released from the roots of the shrubs back to the atmosphere as an additional source of respiration to be used in the process of photosynthesis. Turetsky and Wieder (1999) saw this similar phenomenon in their study. Considering that mosses are sensitive to changes in CO_2 concentration (Serk and Schleucher, 2020), it is possible that where there were less shrubs present, there was a lower contribution of plant-associated HR, and more peat decomposition. For example, Shao (2022) showed in his modelling study that when the ericoid mycorrhiza fungi around the shrub roots were removed from the model, the autotrophic respiration of the mosses increased from ~75 $gCm^{-2}yr^{-1}$ to ~125 $gCm^{-2}yr^{-1}$, highlighting the importance of shrub-moss-mycorrhizae associations to C cycling in peatlands. In contrast, the results of the study by Defrenne et al. (2023) suggest that host plant abundance might not be tightly associated with a change in the dominant type of mycorrhizal association. They do note though, that experimental manipulations of plant community composition along with water table variability would be necessary to directly establish causality.

AR fluxes were inherently low when ER fluxes were low (Figure A1). Although overall AR contributions (%) were slightly lower in the automatic chambers with less biomass, the AR contributions to ER at Mer Bleue was around 75%, which is considerably higher than the contribution of AR reported in other studies of bogs. Moore et al. (2002) for example, estimated that AR contributed about 54% to total ER at Mer Bleue by using a peatland decomposition model, and Hardie et al. (2009) report AR contributions from a blanket bog in the United Kingdom uplands to range between 41% and 54% of the total ecosystem CO_2 flux using direct static chamber measurements. It is possible that the greater AR contributions we found at Mer Bleue are due to the specific environmental conditions the plants were subjected to in 2019, and it would have been interesting to see the comparison with results from 2018 to confirm this. McPartland et al. (2019) for example, found a change in vascular plant community with warming. It may also be that the plant biomass was lower though at the blanket bog than at the Mer Bleue bog, but the authors don't provide biomass estimates to confirm.

4.2 Variability in ER, AR, and HR fluxes

While its seems that vegetation dynamics may have explained the magnitude of the respiration fluxes, environmental variables seemed to have influenced the short-term variations in respiration and its components. Temporal and spatial variability in ER arose because AR and HR differ in their response and sensitivity to changes in temperature and/or water table position. For example, Asemaninejad et al. (2018) found that warming induced a change in the mycorrhizal root-associated fungi which would alter HR. Similarly, Tian et al. (2020) found a shift in aboveground to belowground allocation of C with increasing temperatures, altering both AR and HR so that the C sink in their study was maintained, but they note that this is assuming the hydrological conditions are not altered. Wang et al. (2014) found that both HR and AR are affected by changes in air temperature, but HR more slowly than AR. Similarly, Grogan and Jonasson (2005) found that newly photosynthesized C by plants was more sensitive to changes in temperature than the C derived from older stores of soil organic matter deeper in the peat, so we often see a shift towards lower AR contributions in warming experiments. Since in our study AR was derived from the difference between ER and HR, and ER was estimated using nighttime relationships with temperature in the clear plots, AR fluxes may have been skewed towards a temperature influence on the response. This would explain why ER measured during the day in the darkened plot of cluster two was more related to WT depth.

Cai et al. (2010) discovered, though, that both photosynthesis and respiration rates were higher in drier *and* warmer conditions in a treed fen. Indeed, AR contributions to ER were highest in cooler and wetter conditions and lowest in hotter and drier conditions in our study (Figure 5). 2019 had less variable weather conditions than normal, with much wetter conditions in May and June, and we saw higher AR towards the start of the growing season that slowly decreased into the hotter and drier parts of the summer. DOY 191–217 in 2019 was one of the hotter and drier parts of the growing season with less sporadic rain events, and is consequently where we see the lowest AR.

Similarly, Mäkiranta et al. (2018) determined that warming on its own was not enough and found that only when a drawdown of water was included in their experiment did they notice a decrease in aboveground production and an increase in belowground biomass. While AR was related mostly to air temperature, HR was related mostly to WT depth in our study (Table 2). Bubier et al. (1998) also found that lower water tables corresponded with higher CO_2 emissions. This could be due to local WT changes between the automatic chambers influencing the HR dynamics. For example, in Cluster 1, when the WT started to drop and air temperatures were still rising, we saw a decrease in HR until a certain threshold was met (~40 cm), and when the WT continually dropped below 55 cm, we saw HR start to jump up. However, in Cluster 2, where the WT never dropped below 55 cm depth (Figure 2), we did not see this same rise in HR.

It is also likely that the inherent nature of the vegetation present influenced the respiration dynamics at Mer Bleue as a species' ability to sequester C is largely based on how they respond to water stress and changes in hydrology (Zhong et al., 2020). The *Chamaedaphne* shrubs in this study allocate most of their biomass to belowground roots that spread out laterally and remain relatively close to the surface. Thus, if the WT drops below a certain threshold, the hydrological dynamics may become disconnected from surface processes, and the shrubs rely more on the water retained in the mosses (Murphy et al., 2009a; Murphy et al., 2009b). Even with a slight decrease in temperature and a small jump in rain events towards the beginning of August, the WT at Mer Bleue did not rebound quickly; it wasn't until the end of August that the WT crept back up toward the surface (Figure 1). In our study, warmer temperatures led to drier conditions, which allowed for more aeration of the peat with a drop in WT depth, and hence a greater HR contribution with more decomposition. In contrast, In the Degerö wet fen in northern Sweden, soil temperature was the main influencing factor to respiration than WT depth (Järveoja et al., 2018), highlighting the need to distinguish between short term physiological responses and a slower response to a change in soil conditions when exploring respiration responses in peatlands.

4.3 Effects of measurement method on the interpretation of ER fluxes

ER was lower in magnitude for most of the growing season when measured with a darkened chamber during the day versus when ER was interpolated from night-time relationships with temperature (Figures 3, 4). The noticeable differences in the magnitudes of, and short-term variations in, ER may partially be due to different diel temperature responses of AR and HR (He et al., 2023). Similarly, a discrepancy between the same two measurement methods was found at the Degerö Stormyr fen near Umeå, northern Sweden, where the darkened chambers revealed a bimodal diel pattern that contrasted the unimodal pattern implied by extrapolation of the nighttime temperature response for estimating daytime ER fluxes. They attribute this to divergent temperature dependencies of daytime and night-time ER by varying contributions from HR and AR (Järveoja et al., 2020). In our study, the darkened plot revealed a similar overestimation of ER when estimated with night-time measurements, but only for the wetter months of May and June (Figure 4). The latter part of the growing season (DOY >215) showed estimated ER from night-time measurements to be in the middle of the measured ER during the day with considerably more variability. This would explain why the two-sample *t*-test resulted in a non-significant difference between the two measurements (i.e., the means were in the end, similar despite the bigger range in the daytime measured fluxes of ER). When we separate the time series to ranges before and after DOY 215, the latter part of the season's two sample *t*-test resulted in a *p*-value of 0.405, whereas when the statistical *t*-test was performed on the time series before DOY 215, the two responses in ER fluxes were statistically different ($p = 0.018$). The period after DOY 215 also coincides with where AR contributions drastically dropped and is the part of the season where the plants have just passed peak biomass. Consequently, the difference in ER fluxes may be because the relationship with temperature is not capturing all that determines ER. We found that WT depth (when the WT was above 35 cm depth) seemed to explain most of the variability in ER and its components rather than temperature when ER was measured directly during the day. In contrast, where ER fluxes were estimated by night-time relationships with temperature, air and soil temperature explained most of the variability in ER. This may be due to an assumed temperature response where it was not the most important factor related to ER fluxes.

The discrepancy in ER fluxes is more likely to have been influenced by photorespiratory effects, whereby plants take up oxygen in the light and release carbon dioxide, contrary to the general pattern of photosynthesis (Wingler et al., 2000). Consequently, photorespiration is reduced in dark measurements during the day (Pirk et al., 2016). Similarly, Cai et al. (2010) found that ER measured during the day with darkened chambers was lower than ER determined by night-time relationships with temperature in a treed fen in Alberta, which they also associated with photorespiratory effects. However, it has been shown that photorespiration is stimulated in high temperature and water stress conditions (Lloyd, 2006; Dusenge et al., 2019). According to Voss et al. (2013), the photorespiration pathway protects plants from stress-induced damage. Similarly, Poczta et al. (2012) suggest that high temperatures and high vapour pressure deficit (due to the closure of stomata by the plants in drier conditions) leads to enhanced photorespiration. This would explain why the difference in ER fluxes between the measurement methods was more pronounced when conditions became drier and warmer later in the growing season. The greater short-term variability in measured ER at Mer Bleue during the hotter and drier part of the season may be due to the added water stress the plants are subjected to, which is supported by the statistically significant variance explained by WT depth. In contrast, Serk et al. (2021) found that photorespiration was suppressed under low WT conditions, which they attribute to the *Sphagnum* mosses' photosynthetic capacity. However, this was found where WT depths ranged between 10 and 40 cm; when the WT was below 40 cm, they did not see the same photorespiration suppression. This is reminiscent of the trend we saw at Mer Bleue; where WT depths were greater than 40 cm for the majority of August is where we suspect to have had a greater photorespiratory effect. It is likely a combination of the method used and environmental conditions then, that explains the variability in ER fluxes throughout the growing season.

4.4 Respiration comparison between bogs and other peatland types

The diel pattern found at Degerö Stormyr by Järveoja et al. (2020) was most pronounced during the middle of the growing season as compared to the green up and senescence periods. We did not observe the same double peak in ER fluxes at Mer Bleue though (Figure A2). This could be because AR dominates ER at the Mer Bleue bog, at least for most of the season, hence the diel pattern follows mostly that of AR, whereas at the Degerö fen, there is a 50/50 contribution of AR and HR, so the contrasting diel dynamics might be more pronounced. However, this phenomenon may also have to do with differences in environmental conditions and in geographical location. The Degerö fen is wetter and cooler than the Mer Bleue bog (Peichl et al., 2014). Annual average air temperatures are around 1.2°C, with July and January average temperatures of 14.7°C, and -12.4°C, respectively, and WT depths are much closer to the surface (never dropping below 25 cm) despite a lower average annual rainfall than Mer Bleue of 523 mm (Nilsson et al., 2008). Due to its higher latitude, the amount of solar radiation also allows for longer days and evening periods at Degerö Stormyr.

One of the keys to understanding how the vegetation adapts to their surrounding environment is to determine how they deal with water stress (Belyea and Malmer, 2004). Sedges have root structures that extend vertically downwards, sometimes up to 50 cm depth, and can consequently tap into the water table at deeper depths even during the drier parts of the season as well as support a greater aboveground biomass than shrubs, especially when WT depths fluctuate a lot (Buttler et al., 2015; Pouliot et al., 2023). In contrast, the shrubs allocate more of their biomass to belowground roots, which tend to spread out laterally rather than vertically with root lengths limited to within the first 20–30 cm of the surface (Murphy et al., 2009a; Iversen et al., 2018), hence supporting a greater belowground/aboveground biomass than sedges. Shrubs also allocate energy to needle-like stems (small in diameter but great in height) so they can make use of whatever water is available to the plants in the soil, while minimising the loss of water through transpiration (Bonan, 2008). These shrub stems are also buried annually by the mosses, contributing significantly to the greater belowground biomass (Murphy et al., 2009b). Considering that shrubs are more disconnected from the water table for large parts of the growing season, they tend to rely on the water retained by the mosses closer to the surface, and hence show a greater magnitude in AR as compared to other peatland types like fens, which are comprised of more sedge-like plants (Mccarter and Price, 2014). The Degerö fen, for example, has only dwarf shrub species which are probably even more shallow rooted than the shrub species at the Mer Bleue bog (Wu et al., 2013).

There could also be a vegetation effect and more plant stress with a greater abundance of sedges at Degerö Stormyr. The average AR/HR ratio at Mer Bleue was ~3.0, but varied considerably, decreasing in drier and warmer conditions. In comparison, the average AR/HR ratio at the Degerö fen was ~1.5 (Järveoja et al., 2018). Manual chamber methods measuring CO_2 fluxes were conducted at Mer Bleue on both the dominant shrub species and on the less abundant sedge species, *Eriophorum* (Rankin et al., 2022). Average AR/HR ratios for the shrubs was also ~3.0 as was found with the automatic chambers, but the average AR/HR ratio for the sedges was ~1.2, closer to that found in the sedge-dominated fen. Based on our results though, the lower temperatures and wetter conditions at the Degerö fen should have led to a greater AR. Also, the total absolute amount of biomass is higher at the Mer Bleue bog (Laine et al., 2012), so there is more potential for AR overall. It is more likely then, that the lower contribution of AR to HR at Degerö is due to the interactive effect of different environmental conditions and Mer Bleue having a greater biomass of shrubs than Degerö has of sedges.

The partitioning of AR and HR has not, to the best of our knowledge, been studied often in other bogs. However, dynamics of AR and HR have been studied more extensively in permafrost sites, and the higher contributions of AR at Mer Bleue seem more similar to those found in cooler regions. For example, Hicks Pries et al. (2015) found AR/HR ratios to average about 1.0 at a subarctic bog in Sweden that is underlain with permafrost, but this ratio substantially increased to almost 2.0 after subjected to warming experiments, which translates to an AR contribution of about 60%. And, in a tundra site in Alaska, Hicks Pries et al. (2013) found AR contributions to be closer to 70% at the peak of the growing season. Perhaps the wetter conditions at Mer Bleue mimic the moisture conditions in a site with thawing permafrost, which is generally associated with greater production and respiration by plant parts.

5 Conclusion

ER fluxes were lower when measured directly with a darkened chamber than when interpolated from night-time relationships with temperature, which we attributed to photorespiratory effects. The magnitude of ER, AR and HR fluxes changed drastically depending on the plant biomass present in the plots, whereas the differing short-term variations in respiration fluxes were related more to environmental conditions than vegetation dynamics. AR contributions to ER were generally high at Mer Bleue, with an average of 75%, but decreased substantially in extended periods of drought, mainly due to a shift in plant functioning with warmer and drier conditions. The resulting average AR/HR ratio of 3.0 at the Mer Bleue bog is consequently higher than the average AR/HR ratio found at the Degerö fen (~1.5), where temperatures are lower, water tables are much less variable, and plant biomass is lower.

Future studies should obtain an inter-annual comparison of respiration and its components across the various plant types found in peatlands to get a better grasp on the complex dynamics of HR. A closer look at changes in microbial community response to environmental changes and their link with aboveground production and the plants that surround them would be beneficial to our understanding of peatland C exchange as well.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

TR: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Writing–original draft, Writing–review and editing. NR: Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing–review and editing. EH: Software, Supervision, Writing–review and editing, Conceptualization, Methodology, Resources. MP: Conceptualization, Methodology, Writing–review and editing. JJ: Conceptualization, Methodology, Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix

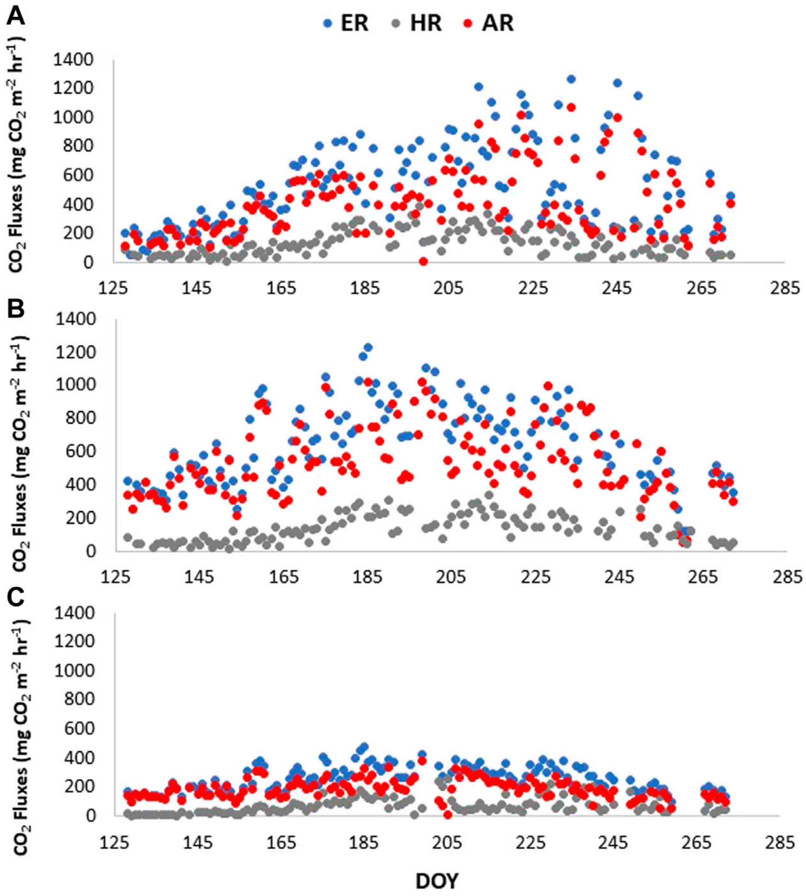

FIGURE A1
ER, HR, and AR fluxes in 2019 for the a) darkened plot, where ER was measured during the day and HR was pulled from the clipped plot in cluster 1, for the b) clear plot in cluster 1, where ER was estimated from nighttime and HR was pulled from the clipped plot in cluster 1, and for the c) clear plot in cluster 2, where ER was estimated from nighttime and HR was pulled from the clipped plot in cluster 2. ER is ecosystem respiration, AR is autotrophic respiration and HR is heterotrophic respiration.

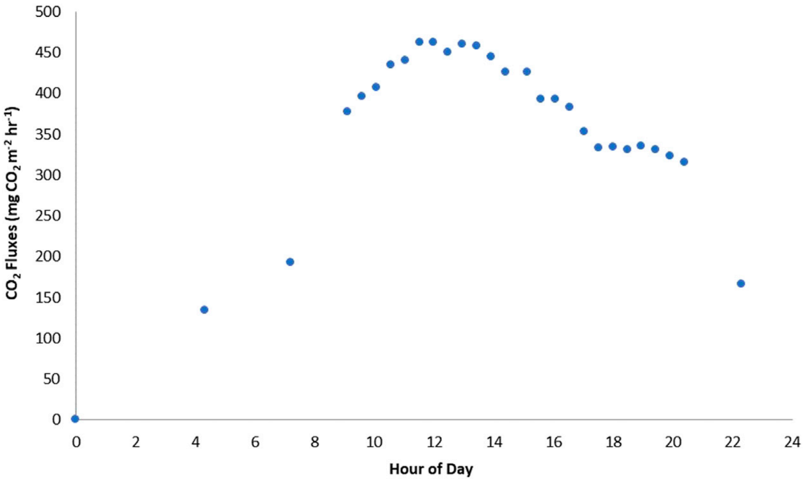

FIGURE A2
Average Ecosystem respiration (ER) fluxes across a 24-h period in the darkened plot of cluster 1.