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Reference:

Vicca Sara, Fivez Lise, Kockelbergh Fred, van Pelt Dimitri, Segers Jan J.R., Meire Patrick, Ceulemans Reinhart, Janssens Ivan.- No signs of thermal acclimation of heterotrophic respiration from peat soils exposed to different water levels
Soil biology and biochemistry - ISSN 0038-0717 - 41:9(2009), p. 2014-2016
Full text (Publishers DOI): http://dx.doi.org/doi:10.1016/j.soilbio.2009.07.007
Handle: http://hdl.handle.net/10067/776580151162165141

Short communication:

No signs of thermal acclimation of heterotrophic respiration from peat soils exposed to different water levels

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Number of text pages: 13

Number of figures: 3

Number of tables: 2

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Abstract

In a mesocosm experiment, with bare peat soils exposed to different water levels (WL), we examined whether heterotrophic respiration (R_h) acclimated to a 3 °C temperature increase. Across all WLs, R_h at 15 °C was never lower in the heated treatment than in the unheated treatment, indicating that R_h did not acclimate to the warmer conditions. We hypothesize that this lack of thermal acclimation is due to the unlimited substrate availability in these organic soils. These results imply that peat soils may exhibit a sustained positive feedback to global warming.

Keywords: Heterotrophic respiration; Peat soil; Thermal acclimation; Warming; Substrate depletion

In mineral soils, warming-induced increases in soil respiration (R_{soil}) are often restricted to the early stages of heating experiments, after which R_{soil} frequently returns to its original level (Hyvönen et al., 2007). Possible mechanisms for such thermal acclimation are (i) physiological adaptations of soil microorganisms (e.g., shifts in temperature optima), (ii) shifts in microbial community structure towards species with higher temperature optima, and (iii) labile substrate depletion. Whereas the importance of the first two mechanisms is still under debate, modeling studies (Kirschbaum, 2004; Eliasson et al., 2005) demonstrated that depletion of labile substrates is very likely to play a key role.

Peat soils, on the other hand, store enormous amounts of carbon (Gorham et al., 1991) of which a large fraction is relatively labile. Hence, depletion of easily degradable organic matter is less likely in these soils. If substrate limitation is indeed the main causal mechanism for thermal acclimation, R_{soil} in organic soils may thus not acclimate to warming. To our knowledge, acclimation of R_{soil} to altered temperature regimes has not yet been demonstrated in peat soils, but was so far assessed only in one study (Hartley et al., 2008). Nonetheless, a sustained positive warming effect on R_{soil} could have important implications on climate change feedbacks, in particular because peat soils comprise up to 24% of global soil carbon stocks (Maltby and Immirzi, 1993). Moreover, if R_{soil} shows no thermal acclimation in organic soils, this could imply that in mineral soils substrate depletion is indeed the main driver for thermal acclimation of R_{soil}.

In a mesocosm experiment, we exposed peat soils to two temperature regimes and hypothesized that heterotrophic respiration (R_h; the component of R_{soil} that is potentially affected by depletion of labile carbon) did not acclimate to elevated temperatures.

Because hydrology plays a key role in determining CO_2 emissions from hydromorphic soils (e.g., Jungkunst et al., 2008), we examined whether water level (WL) influenced thermal acclimation of R_h.

In August 2006, an experimental platform was established at the University of Antwerp. Three mesocosms (58 cm x 48 cm, 31 cm high) in each of six greenhouses contained fen peat from nature reserve 'Het Wik' (Genk, Belgium; 50° 57' N, 5° 25' E; see Table 1 for soil characteristics) that was homogenized by hand to overcome variability among mesocosms.. The peat was excavated from the top 50 cm and aboveground plant parts (mainly *Erica cinerea*, *Pieris* sp. and *Sphagnum* sp.) were removed. One PVC collar (10 cm diameter) was inserted in the middle of each mesocosm. Before and in between measurements, mesocosms were darkened with aluminum foil to avoid plant growth. After a 20 month equilibration period - during which all mesocosms were exposed to ambient temperatures and a WL of 10 cm below the surface - WLs and air temperatures were altered. From April 2008 on, WLs were set at 5, 10, and 17 cm below the surface, with the three WLs randomly positioned in each greenhouse. Water levels were controlled via the principle of communicating vessels. One side of each mescosm was connected to a large vessel filled with rain water. At the other side of the mesocosm, an outlet tube was set at the desired height, such that excess water could drain from the mesocosm. Moreover, we controlled WLs three times per week and made slight adjustments whenever necessary. Air temperatures in the greenhouses were unaltered (unheated treatment) or increased by 3 °C relative to the unheated treatment (heated treatment; three greenhouses per temperature treatment). The experiment contained three replicates per treatment.

Between 29 September and 20 October 2008, we measured soil CO_2 emissions six times in each mesocosm by fitting a PVC headspace on the PVC collars. The headspace (height: 9.5 cm) was connected to a 1.1 l bottle and an air pump that circulated air between bottle and headspace. Via a septum in the headspace, six air samples were taken within 20 min after enclosure. Samples, collected in 20 ml vacuum vials, were analyzed for CO_2 concentrations with a gas chromatograph equipped with a ^{63}Ni electron capture detector (Trace GC Ultra, Thermo Electron S.p.A., Milan, Italy). A calibration gas (1612 ppm CO_2) was measured at regular intervals. We calculated R_h as the slope of the linear regression fitted to the data (concentration versus time). In the rare case where we observed an indication of saturation, only the first four data points were used (which never showed any sign of saturation).

Besides CO_2 fluxes, we also measured soil water content (SWC) and O_2 concentrations at different soil depths. We measured SWC with a PR2 soil probe (Delta-T Devices Ltd., UK) utilizing the profile probe tube (554 mm length) that installed in each mesocosm. Oxygen concentrations were measured using O_2 optrodes (PreSens GmbH, Regensburg, Germany). Small round pieces (4 mm diameter) of O_2 sensitive foil were fixed on the dead end of a glass pipe. These glass pipes were permanently installed at the desired depth (above and below the WL; see also Table 2). For O_2 determination, a polymer optical fiber, connected to an O_2 meter, was inserted in the glass pipe.

To obtain a sufficiently large temperature range, with overlaps between the treatments, air temperatures were altered several times during the measurement period (Fig. 1). This resulted in flux measurements covering soil temperatures (at 5 cm depth) between 9 and 22 °C. Subsequently, we fitted Eq. 1 to the data to compute basal respiration (BR) at one reference temperature (15 °C) for all mesocosms (regressions were fitted in Matlab; 7.2.0.232, The Mathworks, US).

$$R_h = BR * Q_{10}^{((Ts-15)/10)}, \quad (1)$$

with T_s the soil temperature at 5 cm depth and Q_{10} the temperature sensitivity. Thermal acclimation would result in a lower BR in the heated versus the unheated treatment.

We calculated the weighted mean BR for each treatment using the inverse of the standard error of BR as weight factor. A weighted ANCOVA (Analysis of Covariance), with WL as covariate and temperature (T) treatment as a fixed factor, was used to test for WL and T effects and for WL x T interactions. Statistical analyses were performed in SAS (SAS system 9.1, SAS Institute, Cary, NC, USA).

In agreement with other studies on organic soils (e.g., Moore and Dalva, 1997; Jungkunst et al., 2008), R_h increased with increasing depth of water level ($p = 0.10$; Fig. 2). We further observed that R_h showed similar BRs in heated and unheated mesocosms, for all WLs (T effect: $p = 0.84$; WL x T interaction: $p = 0.97$; Fig. 2). Hence, we did not detect any sign of thermal acclimation. Even relative to pretreatment measurements, no indication of thermal acclimation was apparent; in contrast, at the two higher WLs, increases in BR accompanied the heated treatment (Fig. 2). Neither SWC, nor O_2 concentration can be responsible for the lack of acclimation, as both parameters were similar in heated and unheated mesocosms (Fig. 3 and Table 2).

Our results confirm the only other study on organic soils (Hartley et al., 2008), which also found no thermal acclimation of R_h following temperature manipulation. This lack of thermal acclimation contrasts with observations in mineral soils, where temperature-induced reductions of R_h are frequently detected (Luo et al., 2001; Melillo et al., 2002;

Hyvönen et al 2007). As was demonstrated via modeling (Kirschbaum, 2004; Eliasson et al., 2005), and recently also experimentally (Bradford et al., 2008), substrate limitation could be an important mechanism underlying the thermal acclimation of R_h. The lack of any indication of a lower BR in heated versus unheated soils might thus be taken to suggest that warming did not induce substrate depletion in our experiment, not even at WL = -5 cm, where the aerobic zone of CO_2 production was smallest.

In agreement with our results, Weintraub and Schimel (2003) found that, despite considerable carbon losses, soil organic matter chemistry of different organic tundra soils remained largely unchanged after one year incubation at room temperature. This suggested that substrate availability did not limit microbial activity. Furthermore, an incubation study where organic soils were exposed to different temperature and moisture regimes also demonstrated that microbial respiration was not limited by carbon availability (Shaver et al., 2006).

We thus conclude that we were not able to detect thermal acclimation of heterotrophic respiration. If this would be a general response, global warming could generate a persistent positive climate feedback in peatland ecosystems.

Acknowledgements

We thank Marc Fourier, custodian of nature reserve ‘Het Wik’, for the peat soil of this nature reserve. We thank Wout Opdekamp, Bert Gielen, Stefanie De Rocker and Marilyn Roland for very useful help with the field experiments. We also thank two anonymous reviewers for their constructive review. Sara Vicca holds a grant from the Institute for

Promotion of Innovation through Science and Technology in Flanders (IWT-Vlaanderen). Lise Fivez holds a Ph.D. fellowship of the Research Foundation - Flanders (FWO).

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Tables

Table 1: Initial soil characteristics.

Bulk density ($g\ cm^{-3}$)	Organic matter (% loss of ignition at 105 °C)	C content (%)	N content (%)	C/N	pH
0.012	72.4	44.2	2.2	20	6.6

Table 2: Mean O_2 concentration (% of air saturation) measured at different soil depths and the standard deviation on the mean (SD) for the two temperature treatments at the three water levels (WL) (n = 3).

	WL = - 5 cm				WL = - 10 cm				WL = - 17 cm			
	unheated		heated		unheated		heated		unheated		heated	
Depth	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
- 4 cm	48.3	42.0	46.7	40.8	71.1	0.4	70.8	7.6	70.7	0.9	69.1	10.0
- 6 cm	0.0	0.0	0.0	0.0	\	\	\	\	\	\	\	\
- 10 cm	\	\	\	\	\	\	\	\	71.7	1.9	71.5	8.2
- 12 cm	\	\	\	\	0.0	0.0	0.0	0.0	\	\	\	\
- 18 cm	\	\	\	\	\	\	\	\	0.0	0.0	0.0	0.0

Figures

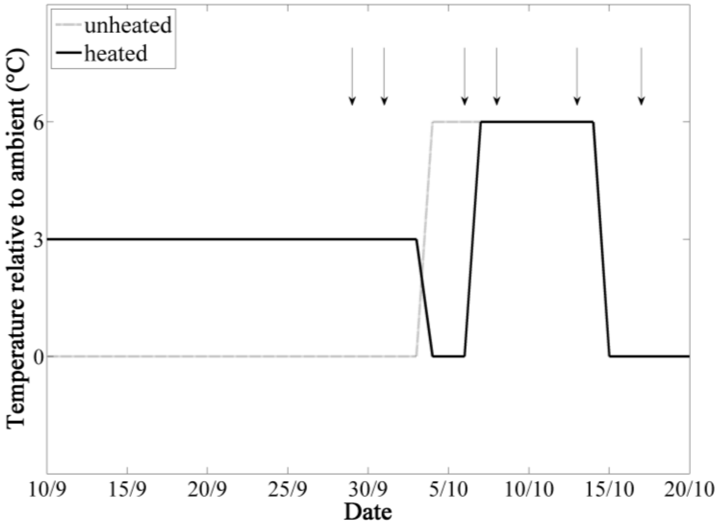

Figure 1: Adjustments of air temperatures in both temperature treatments just before and during the period of gas flux measurements. Arrows indicate the measurement dates.

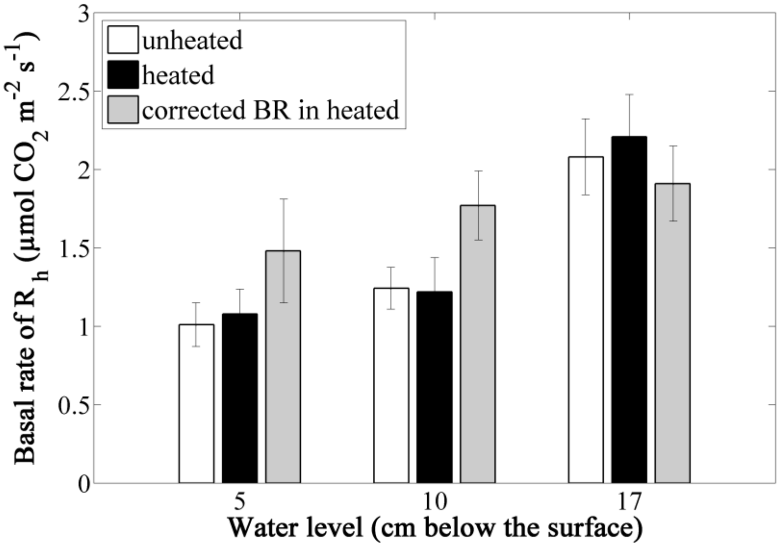

Figure 2: Weighted mean basal rate (BR; i.e., heterotrophic respiration (R_h) at 15 °C) for the two temperature treatments at the three water levels (n = 3). To ensure that the results were not affected by pretreatment differences, we corrected the basal rates as follows: corrected BR in heated = BR in heated * (BR pretreatment in unheated/BR pretreatment in heated). Error bars represent one standard error on the weighted mean.

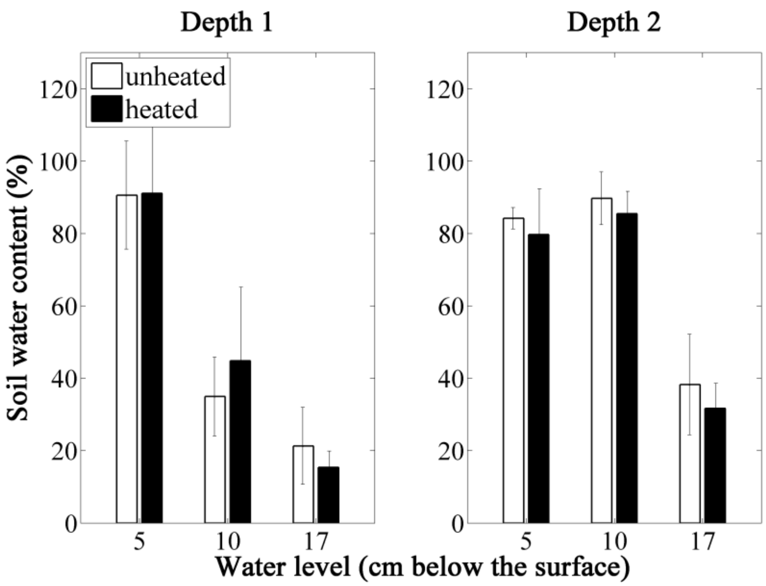

Figure 3: Mean soil water content for the two temperature treatments at the three water levels (n = 3). Soil water content was measured between 5 and 15 cm depth (depth 1) and between 10 and 20 cm depth (depth 2). Error bars present the standard deviation on the mean.