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The moisture response of soil heterotrophic respiration: interaction with soil properties

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Abstract

Soil moisture is of primary importance for predicting the evolution of soil carbon stocks and fluxes, both because it strongly controls organic matter decomposition and because it is predicted to change at global scales in the following decades. However, the soil functions used to model the heterotrophic respiration response to moisture have limited empirical support and introduce an uncertainty of at least 4 % in global soil carbon stock predictions by 2100. The necessity of improving the representation of this relationship in models has been highlighted in recent studies. Here we present a data-driven analysis of soil moisture-respiration relations based on 90 soils. With the use of linear models we show how the relationship between soil heterotrophic respiration and different measures of soil moisture is consistently affected by soil properties. The empirical models derived include main and moisture interaction effects of soil texture, organic carbon content and bulk density. When compared to other functions currently used in different soil biogeochemical models, we observe that our results can correct biases and reconcile differences within and between such functions. Ultimately, accurate predictions of the response of soil carbon to future climate scenarios will require the integration of soil-dependent moisture-respiration functions coupled with realistic representations of soil water dynamics.

1 Introduction

Soil moisture is one of the most important environmental factors driving productivity and carbon cycling in terrestrial ecosystems. Next to temperature, it is a primary determinant of the rate at which soil carbon is mineralized by microbes into carbon dioxide (Greaves and Carter, 1922; Davidson et al., 2000; Davidson and Janssens, 2006; Cook and Orchard, 2008) and the main driver of soil microbial activity in many ecosystems (Davidson et al., 2000; Jassal et al., 2008; Liu et al., 2009). It is also expected to change significantly at global scales as a result of climate change in the

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coming decades (IPCC, 2007; Burke and Brown, 2010), potentially leading to large scale changes in soil carbon stocks in different regions, such as the amazon basin (Jones et al., 2005; Falloon et al., 2011).

The relationship between soil moisture and soil respiration is known to be variable. It depends not only on the soil type (Franzluebbers, 1999; Vincent et al., 2006) but also on the diversity of measures used to express water conditions in soils, each having a unique relationship with soil microbial activity (Ilstedt et al., 2000; Paul et al., 2003). Soil factors including total pore space, bulk density and texture have been shown to influence this relationship (Franzluebbers, 1999; Thomsen et al., 1999). However, such studies have been few with most concentrating on finding the measure of moisture that best predicts respiration rates (e.g. water potential, water-filled pore space, etc.) or the single function that best describes this relationship (e.g. linear, polynomial, etc.). A systematic analysis of variations in response to a wide range of soil types has been lacking.

Soil carbon models use soil moisture-respiration functions that, in theory, represent an average response of microbial respiration to soil moisture content; i.e. they do not account for any natural variation in this relationship (Rodrigo et al., 1997). These functions are generally developed and validated using soils from specific sites and, as a consequence, do not well represent a wider range of soil types. Accordingly, the few studies comparing different moisture-respiration functions have indicated that the related differences in soil carbon budget predictions can be important (Rodrigo et al., 1997; Bauer et al., 2008; Falloon et al., 2011). Fallon et al. (2011) showed that the divergence in simulations related to the moisture function alone is nearly 4 % of global carbon stocks by 2100. However, since all these functions represent an "average" response, the real uncertainty is probably larger. A better understanding of how this relationship actually depends on soil properties will help to quantify and reduce such uncertainties (Franzluebbers, 1999; Schjonning et al., 1999; Thomsen et al., 1999).

Here we present results from a meta-analysis of multiple soil incubation datasets that describe how soil properties regulate the relationship between soil microbial respiration

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and moisture. We use the terms “soil respiration” or simply “respiration” referring to soil CO_2 emissions from heterotrophic microbial activity. The soil respiration response to moisture is the result of several processes – including osmotic stress, diffusion and oxygen limitations – that combined produce a net effect on the rate of carbon decomposition. Consequently, we did not look for a function that acts as the best single average predictor, as it would invariably underperform in most soil types. Instead, we treated the respiration response as a variable that changes freely at different levels of moisture and is explained by moisture itself and other soil properties.

The main outcome of this analysis are statistical models that predict the proportional response of soil respiration to moisture as a soil-type dependent variable. This can then be used to derive relative soil respiration curves for a given soil type. We illustrate the results by comparing the model we derive, using data from soils of England and Wales (Bellamy et al., 2005), with other currently used functions.

2 Materials and methods

Data were assembled from studies where soil carbon dioxide emissions were measured together with variations in soil moisture under controlled laboratory conditions. Treatments varied across studies (e.g. intact vs. homogenized soils) but only homogenous samples with respect to soil properties were used. Incubations with temperatures outside the 10 to 35 °C range were excluded. We converted the measures of soil CO_2 emissions, moisture and soil properties to the same units and normalized soil respiration to a 0–1 scale. Respiration data from incubations with moisture changing over time were corrected for substrate depletion using data from control samples. Pore space, if not available, was calculated assuming a mineral density of 2.65 and organic matter density of 1.4.

The resulting database consisted of 90 different soils originating from 42 sites and characterized by a broad range of soil properties (Tables 1 and 2). We defined a dataset as soil respiration data related to one or more out of four ways of expressing

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soil moisture. These measures are: mass related or gravimetric moisture (θ_m), volumetric moisture (θ_v), fraction of water saturation (θ_s), and the logarithm of water potential (ψ_{log}). θ_m is a laboratory standard while θ_v is the most widely used field measure, often associated with high frequency carbon flux data. θ_s and ψ_{log} are often considered optimal predictors of microbial respiration as they are related to air space and water energy status, respectively (Orchard and Cook, 1983; Skopp et al., 1990). For convenience, the measure of ψ_{log} used was $(-\log_{10}|\psi|_{kPa})/5+1$, thus obtaining an approximate range of 0 to 1. For other measures we used: $gH_2O \cdot g^{-1}$ dry soil (θ_m), cm^3 $H_2O\,cm^{-3}$ total (θ_v), cm^3 $H_2O\,cm^{-3}$ pore-space (θ_s). When possible, missing moisture measures were derived, e.g. using bulk density or pore space for converting θ_v to θ_m or θ_s, respectively, and vice versa. The following analysis was performed in parallel for each moisture measure using the R statistical software (Supplement: R Code and data files MRD.txt, DD.txt and funs.txt).

We started by assuming that a response to a change in soil moisture is proportional to the value of respiration itself, as normally done in soil carbon models. By using the proportional response we make our results generalizable, avoiding the problem of comparing absolute respiration values which vary largely across soils. Since the respiration response varies along the moisture axis, we defined the Proportional Response of Soil Respiration (PR_{SR}) related to a 0.01 increase in soil moisture as the central unit for analysis. We then tested how PR_{SR} is affected by diverse soil properties.

To obtain PR_{SR} values we used general additive models (GAMs) to fit smooth curves to each of 310 datasets (Supplement: Fig. S1). Linear or polynomial fits were used instead if the number of moisture points in a dataset was less than 4. Respiration values at each 0.01 moisture interval were then derived from the curves between the minimum and maximum of each dataset. The PR_{SR} of each 0.01 increase in moisture was calculated, at moisture M, as the average of $SR(M)/SR(M-0.01)$ and $SR(M+0.01)/SR(M)$.

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To analyze relationships of soil properties with PR_{SR} we used soil pore space, bulk density, soil organic carbon, and sand, silt and clay content. We also tested soil pH and the interaction between organic carbon and clay but found no significant effects. Preliminary results revealed important differences between soils with high and low organic carbon content, so soils with over $50\,\mathrm{mg\,C\,g^{-1}}$ soil, hereafter referred to as organic soils, were analyzed separately from mineral soils. To isolate the effect of each soil property we used linear regression models of the form:

$$PR_{SR} = \beta_1 M + \beta_2 M^2 + \beta_3 M^3 + \beta_i SP_i + \beta_i M \cdot SP_i + \varepsilon \,, \qquad (1)$$

where M is soil moisture (either θ_m, θ_v, θ_s or ψ_{log}) and SP are soil properties which can interact with M. Stepwise model selection was applied. Since the proportional increase in respiration tended to be very large at values near 0, producing a strong bias in the models, we excluded outliers defined as any PR_{SR} value further than 3 standard deviations from the mean.

Model simplification led to excluding pore space (strongly correlated with BD), sand, silt and the SOC-M interaction. As bulk density is often not available for use in large scale soil simulations, we fitted a second model for mineral soils including only clay and organic carbon. The final linear models predicting PR_{SR} were:

$$PR_{SR} = \beta_1 M + \beta_2 M^2 + \beta_3 M^3 + \beta 4 BD + \beta_5 M \cdot BD + \beta_6 Clay + \beta_7 M \cdot Clay + \beta_8 SOC \,, \qquad (2)$$

$$PR_{SR} = \beta_1 M + \beta_2 M^2 + \beta_3 M^3 + \beta_6 Clay + \beta_7 M \cdot Clay + \beta_8 SOC \,, \qquad (3)$$

$$PR_{SR} = \beta_1 M + \beta_2 M^2 + \beta_3 M^3 \,, \qquad (4)$$

where M is soil moisture, BD is bulk density, SOC is soil organic carbon and β are model coefficients. Model 1 (Eq. 2) and Model 2 (Eq. 3) are mineral soil models, with the latter excluding bulk density (Table 3). Model 3 (Eq. 4) is for organic soils and has only moisture as a predictor. Few datasets were available for these soils and significant correlations with soil properties were not found (Table 3).

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With the PR_{SR} values obtained from the above models, respiration was predicted using the equation:

$$SR(M) = \left(\prod_{k=M_0}^{M} PR_{SR_k} \right) \cdot SR_0 \, , \tag{5}$$

where soil respiration (SR) as a function of soil moisture (M) is equal to an initial respiration value (SR_0) multiplied by the product of all PR_{SR} values at each k 0.01 moisture interval from the initial moisture (M_0) to M (for $M_0 < M$; otherwise the product term divides SR_0). PR_{SR} values at each k interval are predicted with a PR_{SR} model.

Relative respiration curves, which scale respiration from 0 to 1, were obtained in a two-step calculation: 1. Using Eq. (2) to predict PR_{SR} values for each 0.01 moisture interval and 2. Using Eq. (5) to calculate respiration values along the moisture axis (with an arbitrary SR_0 of 1) and dividing all values by the maximum obtained. As data at low moistures extremes was generally missing, regression models did not well reproduce the high PR_{SR} related to respiration values approaching 0. As a result, depending on the soil type, curve intercepts were variably higher than 0. To obtain curves with a 0 intercept we applied a rescaling of respiration from 0 to 1 in the range of 0 to optimum moisture (Supplement: R Code lines 392–396).

In order to compare our results with existing functions, we applied Eq. (3) using θ_s or ψ_{log} to predict respiration curves for 106 soil series from England and Wales covering an area of ca. 50 000 km^2. Soil organic carbon and clay content in these soils ranged between 0.01–0.05 $g\,g^{-1}$ and 80–610 g clay kg^{-1} soil. We compared these results with functions from six other models using the same moisture measures, plotting the resulting range of respiration values next to θ_s functions belonging to the RothC (Coleman and Jenkinson, 1999; Bauer et al., 2008), CANDY (Franko et al., 1995; Powlson et al., 1996), Bethy (Knorr, 2000) and SimCycle (Ito and Oikawa, 2002) models and ψ_{log} functions from the Daisy (Abrahamsen and Hansen, 2000; Bauer et al., 2008) and SOILCO2 (Šimunek and Suarez, 1993; Bauer et al., 2008) models. To use θ_s with

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the RothC function we followed the same assumption as Bauer and colleagues (Bauer et al., 2008).

3 Results

For each dataset, PR_{SR} values are highest at dry conditions and decrease progressively with increasing moisture (Fig. 1), with values below 1 corresponding to a negative trend in respiration rates. Mean PR_{SR} values for θ_s and ψ_{log} decreased monotonically with increasing moisture (Fig. 1c and 1d) while those for θ_m and θ_v showed more discontinuities related to sharp variations in soil types (Fig. 1a,b). All moisture measures had a wide range of soil moisture associated to an optimum for respiration, defined as the point where PR_{SR} crosses 1. Taking θ_s as an example, the PR_{SR} mean value reaches 1 at 0.63 θ_s, consistent with the commonly reported range of 0.6–0.7, but different datasets had values of optimum moisture as low as 0.4 and as high as 0.9 water saturation.

For mineral soils, significant correlations were found between PR_{SR} and all soil properties, with the correlation strength and significance being strongly dependent on the moisture range and type of moisture measure (Fig. 2). With θ_m and θ_v, correlation coefficients of PR_{SR} versus bulk density were negative and tended to increase with increasing moisture. Correlations with pore space, not shown in Fig. 2, were identical but of opposite sign, i.e. positive. Fewer or no significant correlations of these properties were seen for θ_s and ψ_{log}.

Significant PR_{SR} correlations with texture and organic carbon were found for all moisture measures but most importantly for θ_m and θ_v. Correlations were generally negative for sand and positive for clay, silt and organic carbon. Correlations with clay and silt followed a similar pattern that mirrored the behavior of sand. Correlations with organic carbon content were similar to those of clay and silt. In contrast, organic soils showed no significant correlations between PR_{SR} and carbon content (data not shown).

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The range of values used for fitting the multiple linear regression models is given in Table 2. Models using θ_m and θ_v showed the largest improvement in their root mean square deviation after adding soil properties to the basic moisture polynomial. However, models using θ_s and ψ_{log} remained the best predictors, with ψ_{log} having a slightly better performance. An analysis of model residuals resulted in no trend or significant correlation with soil incubation temperature and incubation duration.

Relative respiration curves are shown in Fig. 3. The effect of clay content on respiration was mainly at low (aerobic) moisture ranges and strongly affected the spread in the curve. Less clay resulted in a wider range of soil moisture values associated to optimal respiration and a respiration peak at lower water contents. Soil organic carbon produced a shift in the curve under all moisture measures with the exception of water potential. More carbon content did not affect the spread of the curve but drove the point of maximum respiration towards higher values of moisture. With changes in bulk density, respiration changed relatively little for a constant volumetric moisture (θ_v curve) or water potential (ψ_{log} curve) but changed strongly under a constant gravimetric moisture (θ_m curve) or water saturation fraction (θ_s curve).

When compared to currently used models (Fig. 4), results from our model covered much of the range of variability between other functions based on θ_s, which either under- or overestimate average respiration, with a strong tendency towards the latter. Functions using ψ_{log} were comparable to our predictions, where we observed a limited influence of soil properties, but they showed a general overestimation of respiration values in most of the range of suboptimal moisture conditions.

4 Discussion

This comparison of multiple datasets revealed a strong soil-dependent variation of the moisture-respiration relationship, in clear contrast to the simple functions found in all current models. The large range of variability observed (e.g. respiration maximums ranging from 40–100 % water saturation) reflects differences between ecosystems that

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are largely ignored in the more common and simplified representations of this relationship. A major difference observed was in the response of organic vs. mineral soils. In the case of organic soils we found little or no effects of soil properties on the PR_{SR}. The models derived for organic soils use moisture as the only predictor and serve as a best approximation. However, they remain rough averages given the limited available data and the often incomplete characterization of soil properties. More data will be needed to better characterize moisture effects in these soils.

For mineral soils (with less than 50 mg C g soil^{-1}) the soil factors having an influence on the moisture-respiration relationship involved aeration and structure (bulk density), texture (clay) and composition (carbon content). The models we derived from the data include clay but not silt or sand. This was a result of the large effect of clay and the relatively small influence of silt when including one or the other in the linear regression. This is probably caused by the much larger specific surface of clay particles which affects water retention and availability. The observed increase in the optimum water content for respiration with increasing clay fraction has also been observed in field conditions (Balogh et al., 2011). Water potential is the only measure of soil moisture for which this pattern was not observed.

In accordance with theory (Orchard and Cook, 1983; Orchard et al., 1992), the relation between soil respiration and soil water potential (ψ_{log}) was the least affected by soil properties, making this measure the best predictor of respiration rates. However, since large changes in water potential are often associated to small changes in water content, predicting water potential in soils could itself be associated with large errors. Among the models based on measures of water content (θ_s, θ_m or θ_v), those using θ_s resulted in the lowest root mean square deviation and were thus the best predictor of respiration rates. Ultimately, finding the measure that performs best in large scale simulations will require a validation of model performance against actual field data.

The data from England and Wales soils used for model comparison represents a large range of properties characteristic of soils in temperate regions. The range of respiration curves we predicted (Fig. 4), related to variations in the properties of

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these soils, covered most of the differences between strongly differing functions such as those used in the RothC, CANDY and Bethy models. Thus, the variability in model predictions, associated with different moisture functions, can be largely reduced or eliminated by using a common, but generally valid, soil-dependent moisture-respiration function. Depending on the model, soil and climate, significantly different predictions of soil carbon decomposition are expected after including these soil-dependent functions. In most cases this will tend towards lower rates of respiration and, consequently, to an increased sequestration of carbon in soils.

5 Conclusions

Our empirical analysis has shown that the microbial soil respiration response to moisture depends on soil properties in a consistent and largely predictable way. Future studies should concentrate on reducing uncertainties in these relationships and on better representing specific field conditions, such as the depth-dependence of oxygen availability and the dynamics of soil water. It remains unclear if soils will cause a positive or negative feedback to global warming as global changes in climatic patterns affect soil temperature and moisture (IPCC, 2007; Kendon et al., 2009; Burke and Brown, 2010), but the moisture response of soil carbon decomposition will likely have an important role in determining any future evolution.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/8/11577/2011/bgd-8-11577-2011-supplement.zip.

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Table 1. Description of the data used in the analysis. Each line represents a specific site or location. DS is number of data sets, representing different soil types related to each site. Site averages of soil properties used in the analysis are shown. BD = bulk density, SOC = soil organic carbon, N = soil nitrogen.

Reference	DS	Country	Ecosystem	BD ($g\,cm^{-3}$)	SO ($mg\,g^{-1}$)	N ($mg\,g^{-1}$)	Clay (%)	Silt (%)	Sand (%)	pH
Bouckaert, not published	3	Belgium	Forest	1.6	44	3.5	18	49	33	5.4
Bowden et al. (1998)	1	USA	Forest	0.3	NA	NA	NA	NA	NA	3.3
Cook, not published	1	New Zealand	Grassland	1.3	64	4.7	16	6	79	5.4
Cook, not published	1	New Zealand	Grassland	0.9	55	5.5	17	33	50	5.7
Cook, not published	1	New Zealand	Grassland	0.8	71	6.2	52	34	14	6.1
Cook et al. (1985)	1	New Zealand	Grassland	NA	NA	NA	NA	NA	NA	NA
Craine and Gelderman (2010)	8	USA	Grassland	NA	46	3.3	33	60	8	6.7
Curiel Yuste et al. (2007)	2	USA	Forest	0.9	102	3.5	11	29	60	5.5
Curiel Yuste et al. (2007)	2	USA	Grassland	1.5	28	2.5	14	44	43	6.4
Don, not published	1	Germany	Grassland	1.5	11	1.1	9	10	81	4.5
Doran (1990)	1	USA	Forest	1.1	31	NA	14	16	70	6.8
Doran (1990)	1	USA	Cultivated	1.2	14	NA	18	29	53	6.8
Doran (1990)	1	USA	Cultivated	1.1	21	NA	22	75	3	6.8
Doran (1990)	1	USA	Grassland	1.2	8	NA	26	19	55	6.8
Doran (1990)	1	USA	Grassland	1.1	22	NA	17	64	19	6.8
Doran (1990)	1	USA	Grassland	1.0	16	NA	46	42	12	6.8
Doran (1990)	1	USA	NA	1.1	35	NA	14	37	49	6.8
Doran (1990)	1	USA	Cultivated	1.2	13	NA	20	51	29	6.8
Doran (1990)	1	USA	Grassland	1.2	7	NA	22	24	54	6.8
Doran (1990)	1	USA	Cultivated	1.1	13	NA	58	35	7	6.8
Doran (1990)	1	USA	Cultivated	1.1	11	NA	16	68	16	6.8
Skopp et al. (1990)	1	USA	Grassland	1.2	13	NA	24	54	22	6.8
Epron, not published	1	France	Forest	0.8	27	2.5	20	66	14	4.6
Formanek, not published	3	Czech Republic	Forest	NA	318	11.2	NA	NA	NA	4.8
Franzluebbers (1999)	15	USA	Grassland	1.2	16	1.1	19	16	65	6.2
Gulledge and Schimel (1998)	2	USA	Grassland	NA	61	NA	NA	NA	NA	NA
Ilstedt et al. (2000)	3	Malaysia	Forest	0.6	52	4.1	27	32	42	4.7
Ilstedt et al. (2000)	1	Sweden	Forest	0.5	556	NA	NA	NA	NA	4.1
Linn and Doran(1984)	1	USA	Cultivated	NA	21	1.6	34	54	12	5.8
Liu et al. (2009)	1	China	Grassland	NA	16	1.5	17	20	63	6.8
Lomander et al. (1998)	2	Sweden	Cultivated	NA	18	1.9	57	38	5	8.2
Nyhan (1976)	1	USA	NA	1.4	9	NA	NA	NA	NA	6.8
Orchard and Cook (1983)	1	New Zealand	Grassland	NA	NA	NA	NA	NA	NA	NA
Orchard et al. (1992)	1	New Zealand	Grassland	NA	56	3.5	24	NA	NA	5.2
Orchard et al. (1992)	1	New Zealand	Grassland	NA	NA	NA	NA	NA	NA	NA
Reichstein et al. (2005)	1	Germany	Forest	0.9	45	2.0	10	38	52	2.9
Rey et al. (2005)	2	Italy	Forest	1.0	49	6.0	NA	NA	NA	5.7
Ruamps, not published	1	France	Cultivated	1.5	14	1.2	17	53	30	6.8
Thomsen et al. (1999)	15	Denmark	Cultivated	1.3	15	1.5	23	14	64	6.9
Skopp et al. (1990)	1	USA	Cultivated	1.4	9	NA	3	7	90	6.8
Stott et al. (1986)	1	USA	Cultivated	NA	4	0.6	NA	NA	NA	7.0
Wickland and Neff (2008)	3	USA	Forest	NA	318	14.5	NA	NA	NA	NA

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Table 2. Range of values for soil moisture (SM), soil organic carbon (SOC), clay, and bulk density (BD) used to fit linear regression models. Soil moisture units depend on the measure used, as described in methods.

Model and moisture measure	SM		SOC ($g\,g^{-1}$ soil)		Clay (fraction)		BD ($g\,cm^{-3}$)	
	min	max	min	max	min	max	min	max
Model 1 (mineral soils)								
θ_m	0.04	0.65	0.01	0.05	0.09	0.45	0.8	1.5
θ_v	0.05	0.60	0.01	0.05	0.03	0.58	0.8	1.5
θ_s	0.07	1.00	0.01	0.05	0.03	0.58	0.8	1.5
ψ_{log}	0.22	1.02	0.01	0.03	0.09	0.45	0.6	1.5
Model 2 (mineral soils)								
θ_m	0.04	0.66	0.01	0.05	0.09	0.57	NA	NA
θ_v	0.05	0.60	0.01	0.05	0.03	0.58	NA	NA
θ_s	0.07	1.00	0.01	0.05	0.03	0.58	NA	NA
ψ_{log}	0.22	1.02	0.01	0.03	0.09	0.45	NA	NA
Model 3 (organic soils)								
θ_m	0.05	1.1	0.05	0.40	NA	NA	NA	NA
θ_v	0.05	0.85	0.06	0.35	NA	NA	0.24	0.9
θ_s	0.07	0.99	0.06	0.35	NA	NA	0.24	0.9
ψ_{log}	0.27	0.97	0.06	0.56	NA	NA	NA	NA

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Table 3. Variables and coefficients for linear models predicting the proportional response of soil respiration (PR_{SR}) at 0.01 moisture intervals. SM = soil moisture, BD = bulk density, SOC = soil organic carbon. Coefficient values and standard errors are given under the corresponding moisture measure. All terms are significant at $p < 0.001$. Values are also shown for the number of datasets used and the model root mean square deviation (RMSD).

Variables	Gravimetric moisture (θ_m)	Volumetric moisture (θ_v)	Fraction of saturation (θ_s)	Log water potential (ψ_{log})
Model 1 (mineral soils)				
n-datasets	50	52	52	42
RMSD	0.023	0.024	0.014	0.012
Intercept	1.00 ± 0.02	0.98 ± 0.01	1.02 ± 0.00	1.26 ± 0.02
SM	−0.80 ± 0.09	−0.48 ± 0.08	−0.29 ± 0.02	−1.36 ± 0.05
$(SM)^2$	3.5 ± 0.2	1.8 ± 0.3	0.37 ± 0.04	2.26 ± 0.08
$(SM)^3$	−3.1 ± 0.2	−1.6 ± 0.3	−0.19 ± 0.03	−1.12 ± 0.04
BD (g cm^{-3})	0.10 ± 0.01	0.1 ± 0.01	0.03 ± 0.00	0.05 ± 0.01
BD (g cm^{-3}) H_2O	−0.44 ± 0.05	−0.3 ± 0.04	–	−0.09 ± 0.01
Clay (fraction)	0.33 ± 0.03	0.18 ± 0.02	0.09 ± 0.01	0.17 ± 0.02
Clay (fraction) H_2O	−0.7 ± 0.1	−0.31 ± 0.06	−0.08 ± 0.01	−0.25 ± 0.02
SOC (g $gSoil^{-1}$)	1.5 ± 0.1	1.4 ± 0.09	0.8 ± 0.04	–
Model 2 (mineral soils)				
n-datasets	59	65	66	43
RMSD	0.025	0.025	0.015	0.013
Intercept	1.13 ± 0.01	1.11 ± 0.01	1.059 ± 0.003	1.31 ± 0.01
SM	−1.31 ± 0.05	−0.83 ± 0.07	−0.26 ± 0.02	−1.45 ± 0.05
$(SM)^2$	3.0 ± 0.2	1.5 ± 0.3	0.32 ± 0.04	2.18 ± 0.08
$(SM)^3$	−2.23 ± 0.2	−1.0 ± 0.3	−0.15 ± 0.03	−1.07 ± 0.04
Clay (fraction)	0.26 ± 0.02	0.08 ± 0.01	0.08 ± 0.01	0.12 ± 0.01
Clay (fraction) H_2O	−0.39 ± 0.05	–	−0.09 ± 0.01	−0.16 ± 0.02
SOC (g g $Soil^{-1}$)	1.07 ± 0.07	1.28 ± 0.08	0.57 ± 0.04	0.19 ± 0.06
Model 3 (organic soils)				
n-datasets	16	6	6	3
RMSD	0.020	0.10	0.008	0.014
Intercept	**1.146** ± 0.005	**1.178** ± 0.004	**1.134 ± 0.003**	**1.42 ± 0.04**
SM	**-0.57** ± 0.03	**−1.12** ± 0.03	**−0.67 ± 0.02**	**−1.9 ± 0.2**
$(SM)^2$	0.79 ± 0.07	2.22 ± 0.09	**1.08 ± 0.05**	**2.9 ± 0.4**
$(SM)^3$	−0.37 ± 0.04	−1.40 ± 0.06	**−0.57 ± 0.03**	**−1.4 ± 0.2**

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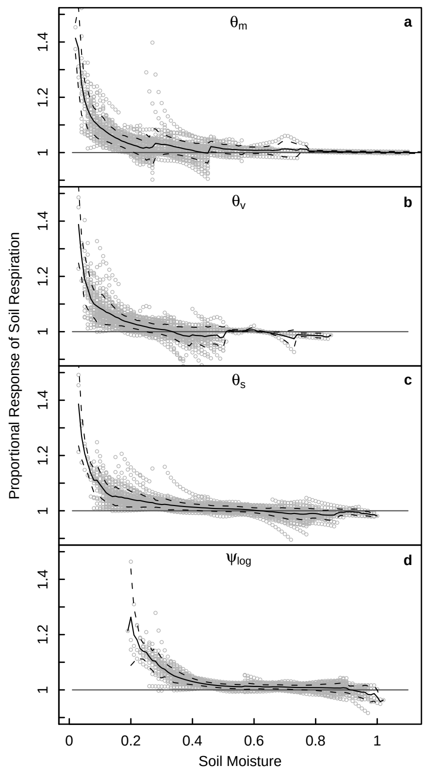

Fig. 1. Proportional response of soil microbial respiration (PR_{SR}) to moisture. PR_{SR} values correspond to a 0.01 increase in soil moisture. Values are shown for all datasets and for θ_m (gravimetric moisture, **a**), θ_v (volumetric moisture, **b**), θ_s (fraction of saturation, **c**), and ψ_{log} (log water potential, **d**). Units of soil moisture in the *x*-axis are: $g\,H_2O\,g^{-1}$ dry soil **(a)**, $cm^3\,H_2O\,cm^{-3}$ total **(b)**, $cm^3\,H_2O\,cm^{-3}$ pore-space **(c)** and $(-\log_{10}|\psi|_{kPa})/5+1$ **(d)**. Grey circles represent the PR_{SR} of each 0.01 moisture increase. The black and dashed lines are mean and standard deviations, respectively.

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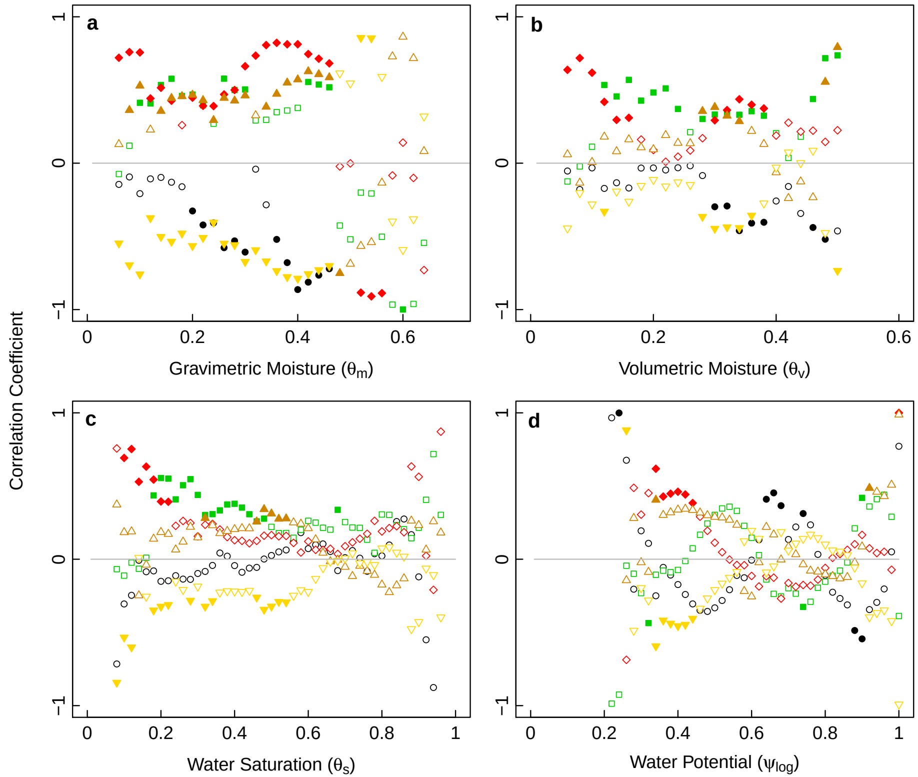

Fig. 2. The respiration response to moisture (PR_{SR}) correlated with soil properties of mineral soils. Correlation coefficients of PR_{SR} vs. bulk density (black circles), organic carbon (green squares), sand (yellow inverted triangles), silt (brown triangles) and clay (red diamonds) on the y-axis are shown for different levels of soil moisture (SM) on the x-axis. Full symbols denote correlations significant at $p < 0.05$. Units of soil moisture in the x-axis are: $g\,H_2O\,g^{-1}$ dry soil **(a)**, $cm^3\,H_2O\,cm^{-3}$ total **(b)**, $cm^3\,H_2O\,cm^{-3}$ pore-space **(c)** and $[-\log_{10}|\psi|_{kPa}]/5+1$ **(d)**.

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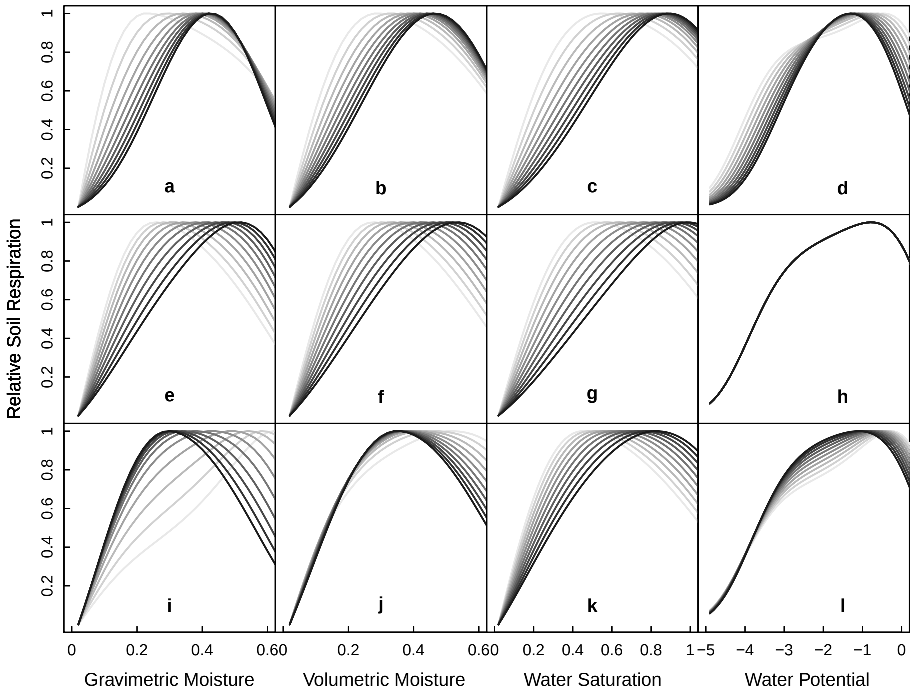

Fig. 3. The response of predicted soil moisture-respiration curves to variations in soil properties. Darker lines represent higher values of a given property. Variations are shown for clay content from 100 to 1000 g kg^{-1} **(a–d)**, organic carbon from 5 to 50 mg g^{-1} soil **(e–h)**, and bulk density from 0.6 to 1.6 g cm^{-3} **(i–l)**. Units are: g H_2O g^{-1} dry soil **(a,e,i)**, cm^3 H_2O cm^{-3} total **(b, f, j)**, cm^3 H_2O cm^{-3} pore-space **(c, g, k)**, and $-\log_{10}|\psi|_{kPa}$ **(d, f, l)**.

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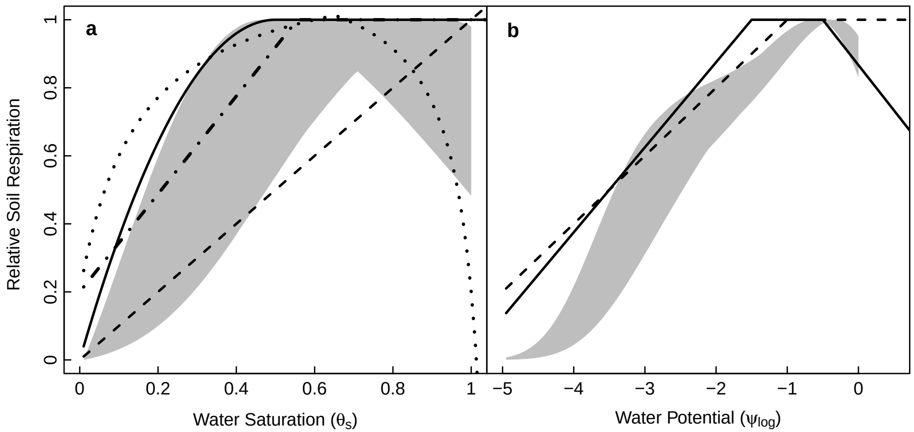

Fig. 4. Comparison of predicted relative soil heterotrophic respiration as a function of soil moisture. The grey area marks the full range of values obtained with Eqs. (3) and (5) using θ_s **(a)** or ψ_{log} **(b)** for 106 soil series from England and Wales ranging from 8 to 50 mg g^{-1} SOC and 0.08 to 0.61 clay fraction. Other lines are moisture-respiration functions from existing models using either θ_s **(a)** or ψ_{log} **(b)** as a predictor. In **(a)** CANDY model (full line), Bethy model (dashed line), SimCycle model (dotted line), RothC model (dot-dash line). In **(b)** Daisy model (full line), SOILCO2 model (dashed line).

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