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Interdependencies between temperature and moisture sensitivities of CO_2 emissions in European land ecosystems

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Abstract. Soil respiration is one of the largest terrestrial fluxes of carbon dioxide (CO_2) to the atmosphere. Hence, small changes in soil respiration rates could have large effects on atmospheric CO_2. In order to assess CO_2 emissions from diverse European soils with different land-use types and climate (soil moisture and temperature), we conducted a laboratory incubation experiment.

Emission measurements of CO_2 under controlled conditions were conducted using soil monoliths of nine sites from a European flux network (ÉCLAIRE). The sites are located all over Europe – from the United Kingdom in the west to Ukraine in the east, and from Italy in the south to Finland in the north – and can be separated according to four land-use types (forests, grasslands, arable lands and one peatland). Intact soil cores were incubated in the laboratory in a two-way factorial design, with temperature (5, 10, 15, 20 and 25 °C) and water-filled pore space (WFPS; 5, 20, 40, 60 and 80 %) as the independent variables, while CO_2 flux was the response variable. The latter was measured with an automated laboratory incubation measurement system.

Land use generally had a substantial influence on carbon dioxide fluxes, with the order of CO_2 emission rates of the different land-use types being grassland > peatland > forest/arable land ($P < 0.001$). CO_2 efflux responded strongly to varying temperature and moisture content with optimum moisture contents for CO_2 emissions between 40 and 70 % WFPS and a positive relationship between CO_2 emissions and temperature. The relationship between temperature and CO_2 emissions could be well described by a Gaussian model. Q_{10} values ranged between 0.86 and 10.85 and were negatively related to temperature for most of the moisture contents and sites investigated. At

higher temperatures the effect of water and temperature on Q_{10} was very low. In addition, under cold temperatures Q_{10} varied with moisture contents, indicating a stronger prospective effect of rain events in cold areas on temperature sensitivity. At both coniferous forest sites we found a strong increase in the temperature sensitivity at a moisture range between 20 and 40 % WFPS.

We developed a new approach to calculate moisture sensitivity (MS) of CO_2 efflux. MS was calculated as the slope of a polynomial function of second degree. Moisture sensitivities were highest under dry and wet conditions. In addition we found a positive relationship between MS of CO_2 efflux and temperature for both arable lands.

1 Introduction

Most reported impacts of climate change are attributed to warming and/or to shifts in precipitation patterns (IPCC, 2014), which are known to be key drivers of ecosystem functioning and biochemical cycles (Larsen et al., 2011). The temperature sensitivity of organic matter decomposition is of considerable eco-physiological importance, especially in the context of possible climate-change feedback effects (Kirschbaum, 2006). Disagreement exists if carbon stored belowground is transferred via CO_2 emissions to the atmosphere by a warming-induced acceleration of its decomposition (positive feedback to climate change) or if increases in plant-derived carbon inputs to soils exceed increases in decomposition (negative feedback to climate change) (Davidson and Janssens, 2006).

The production of CO_2 in non-calcareous soils originates almost entirely from autotrophic (root respiration) and heterotrophic respiration (microbial decomposition of soil organic matter (SOM)). Like all chemical and biochemical reactions, these processes are temperature-dependent (Wu et al., 2010) and subject to water content (Davidson and Janssens, 2006; Suseela et al., 2012). Because root respiration has its own short-term temperature dependence (over periods of more than a few hours root respiration can become relatively insensitive to climate; Atkin et al., 2000), it is necessary to separate autotrophic and heterotrophic soil respiration when investigating the effect of temperature and moisture on ecosystem functioning (Baggs, 2006; Kirschbaum, 2006).

The effects of soil temperature on heterotrophic soil respiration are mostly direct and entail a positive correlation between temperature and CO_2 emissions as long as other factors are not limiting (Ferréa et al., 2012; Meixner, 2006). A widely used term to describe the temperature sensitivity of SOM decomposition is the Q_{10} value, which is calculated as the proportional increase in CO_2 efflux for a $10\,°C$ increase in temperature (Vanhala et al., 2008). In the context of this paper, we use the term "temperature sensitivity of SOM decomposition" to refer to the short-term temperature dependence of organic matter decomposition as described in Kirschbaum (2006). Other authors have reported that land use/cover types, soil moisture content, quality of SOM and temperature itself were found to affect the Q_{10} value of soil CO_2 efflux (Shrestha et al., 2004; Wang and Fang, 2009). Temperature sensitivity of SOM decomposition increases with decreasing SOM lability and therefore increasing recalcitrance of SOM (Conant et al., 2008; Lützow and Kögel-Knabner, 2009; Thornley and Cannell, 2001; Zimmermann and Bird, 2012) due to the higher activation energy associated with the breakdown of recalcitrant substrates that result in a greater temperature sensitivity of decomposition (Davidson and Janssens, 2006; Hartley and Ineson, 2008). The Arrhenius equation predicts that the Q_{10} of chemical reactions decreases with increasing temperature, as is also commonly observed in nature (Kirschbaum, 1995). The theoretical explanation for this negative correlation is that as temperature increases, there is a declining relative increase in the fraction of molecules with sufficient energy to react (Ågren and Wetterstedt, 2007; Davidson and Janssens, 2006). Tuomi et al. (2008) were able to show that the relationship between temperature and heterotrophic soil respiration can be described best using a Gaussian model.

The effect of soil moisture is more complex. Soil water influences the rate of O_2 supply and thereby determines whether aerobic or anaerobic processes prevail within the soil (Pilegaard et al., 2006; Schindlbacher, 2004). The water content is also important for the substrate supply for soil microorganisms (Meixner, 2006). Highest CO_2 emissions have been reported at intermediate moisture content, while under dry and wet conditions CO_2 emissions decline (Schaufler et al., 2010; Suseela et al., 2012). However, if soil moisture becomes limiting, CO_2 fluxes are suppressed irrespective of high soil temperatures (Davidson et al., 1998; Garten et al., 2008).

To describe the effect of moisture on soil microbial activity, quadratic functions are common (Moyano et al., 2013; Rodrigo et al., 1997). Moyano et al. (2012) calculated moisture sensitivity as the proportional response of soil microbial respiration to a 0.01 increase in soil moisture of a certain unit. Moisture sensitivity showed highest values at dry conditions decreasing progressively with increasing moisture content.

Conflicting results can be found in the literature about the interdependencies between the factors temperature and moisture and their sensitivities of heterotrophic soil respiration. Janssens and Pilegaard (2003) and Qi et al. (2002) expected a positive relationship between temperature sensitivity and moisture content due to the assumption that the effects of soil temperature and moisture are negatively correlated. Thus, soil moisture would be positively correlated with the temperature sensitivity of soil respiration. While Mäkiranta et al. (2009) and Gaumont-Guay et al. (2006) found an actual positive relationship between temperature sensitivity and soil moisture content in their field measurements, Peng et al. (2009) described, in their review of 52 papers (all field measurements), a negative correlation between Q_{10} values and mean annual precipitation. However, Curiel Yuste et al. (2004) presented a case study of how the seasonal Q_{10} of soil respiration calculated from field measurements can be decoupled from the temperature sensitivity of heterotrophic soil respiration, indicating that the large differences in seasonal Q_{10} do not represent differences in the temperature sensitivity of the soil microbial metabolism.

Land use influences the production and consumption of soil CO_2 emissions through vegetation type (Raich and Tufekciogul, 2000), root density, N input (Skiba et al., 1998) and management (Flechard et al., 2005). Peng et al. (2009) even found differences in Q_{10} values between ecosystem types by comparing field measurements.

In field studies the seasonal development of soil temperature and soil moisture usually is reflected in the seasonal course of soil gas emissions (Schaufler et al., 2010). Authors have described difficulties when investigating the influence of a single climate parameter from seasonal field measurements, because confounding factors like N deposition, litterfall and nitrogen availability (Davidson et al., 2000; Pilegaard et al., 2006) co-vary or interact. With these confounding factors, measurements under natural field conditions cannot provide an unbiased estimate of the temperature sensitivity of SOM decomposition (Kirschbaum, 1995). For field soil CO_2 fluxes, further complications arise from the contribution of autotrophic soil respiration (Schaufler et al., 2010). Laboratory incubations provide the best and least biased basis for estimating the temperature dependence of SOM decomposition (Kirschbaum, 2006). This assumption can be extended to the assessment of soil moisture dependence of

heterotrophic soil respiration (Schaufler et al., 2010). The combined effects of temperature and moisture changes are not necessarily additive (Beierkuhnlein et al., 2011; Larsen et al., 2011; Leuzinger et al., 2011). A two-factorial incubation design provides the opportunity to assess temperature and moisture effects independently and to investigate how the two climatic factors affect each other (Schaufler et al., 2010).

To investigate the combined effects of soil temperature and moisture on heterotrophic soil respiration from different land-use types, intact soil cores were taken from four representative land-use types from the European ÉCLAIRE flux network and incubated in the laboratory with varying soil temperature and moisture levels. The main objectives of this study were (1) to determine the influence of soil temperature and moisture on CO_2 efflux, (2) to calculate temperature and moisture sensitivities of CO_2 efflux coming from different land-use types, (3) to investigate the influence of moisture and land use on temperature sensitivity of CO_2 efflux, and (4) to investigate the influence of temperature and land use on moisture sensitivity of CO_2 efflux.

2 Material and methods

2.1 Study sites

Emission measurements of carbon dioxide under controlled conditions were conducted using soil monoliths from nine sites from the ÉCLAIRE flux network. The sites are located all over Europe: from the United Kingdom in the west to Ukraine in the east, and from Italy in the south to Finland in the north. A list of all sites including relevant site information can be found in Table 1. The sites can be separated according to four land-use types (forests, grasslands, arable lands and one peatland). Relevant soil characteristics are given in Table 2.

2.2 Sampling and experimental layout

Thirty-three undisturbed soil cores were collected at each of the investigation sites in spring 2012 after weekly-averaged soil temperatures reached 8 °C. This was done to provide comparable conditions across sites with respect to sampling conditions. Soil cores were collected at six randomly distributed plots of approximately 10 m^2 within an overall area of approximately 50×50 m at each site. Six soil samples were collected from each 10 m^2 plot at six spots. The upper 6 cm of the soil was collected in stainless steel cylinders (diameter, 7.2 cm; height, 7 cm). Soil cores were capped and sealed in plastic bags to ensure original conditions and shipped in insulated coolers equipped with ice cartridges to our laboratory in Austria, where they were stored at 4 °C before being used for CO_2 flux measurements. Three soil cores were used to determine gravimetric water contents. The gravimetric water content was determined for mineral soil by oven drying at 103 °C for 3 days to a constant weight.

These water contents were assumed to be representative of the rest of the soil samples from the same location, and thus different water contents for the gas measurements could be established. The real gravimetric water content for each core was determined after gas flux measurements were completed. WFPS was determined by dividing volume percent water by porosity. Porosity was calculated with soil density and particle density.

Intact soil cores were incubated in the laboratory for 22 h at the temperatures 5, 10, 15, 20, and 25 °C in a two-factorial design of five soil moisture levels (5, 20, 40, 60, 80 % WFPS) before being analysed for CO_2 fluxes. To design the experiment, realistically moisture levels for the peatland site (UK-AMo) were set between 20 and 100 % WFPS. To reach the required moisture contents, either distilled water was added to too-dry samples or too-moist samples were dried at 4 °C until they reached the required moisture content. Respiration may show hysteresis during dry-down or wet-up and therefore might differ on the dry-down and wet-up phases of the moisture cycle. However, due to the inclusion of peatland soil samples to the experiment the common technique to avoid hysteresis effects (dry all soils down to a common moisture content and then re-wet them to desired levels) was not possible due to a very different structure of Peatland soils compared to the other soils analysed. In order to handle all soils equally, this method (either add water or dry down samples) was used. The lowest possible moisture content was 5 to 15 % WFPS for soil samples when drying at 4 °C. The second variable, soil temperature, was set by controlling the incubator to the desired temperature. Starting with 5 °C, the temperature was increased every day in 5 °C steps up to an end temperature of 25 °C. We used six replicates for each moisture content in a complete factorial design in which each of the moisture contents was matched with each of the temperatures for all soil cores investigated.

From the three remaining cores, soil characteristics (Table 2) were analysed. Ammonium and nitrate were quantified according to Hood-Nowotny et al. (2010) using the ratio 2.5 g soil : 25 mL KCL solution. Photometric analyses were conducted with a type 2300 EnSpire™ photometer from PerkinElmer®. Conductivity was measured with a WTW 2F191 conductivity meter and pH was measured in 0.01 m $CaCl_2$, using the ratio 10 g soil : 25 mL $CaCl_2$ solution. The contents of total soil carbon (C_t) and nitrogen (N_t) were determined with elemental analysis (NA-1500 Carlo Erba, Italy; ÖN1998).

2.3 Gas flux measurements

A fully automatic laboratory incubation system was used (Schindlbacher, 2004) to measure CO_2 flux rates. The system analysed CO_2 fluxes with an open flow system using a PP SYSTEMS WMA-2 (Amesbury, MA, USA) infrared CO_2 analyser. Twenty-four modified Kilner jars were placed in a temperature-controlled incubator and connected to the

Table 1. Sampling sites with information on ecosystem, geographical location, climate type, long-term mean annual temperature and rainfall.

Country/ site code	Site	Ecosystem	Vegetation	Elevation (m)	Average annual soil temperature (°C)	Average annual air temperature (°C)	Average annual precipitation (mm)	Location	Climate type
Italy IT-IFo	Ispra	Forest	*Quercus robur* (dominant), *Robinia pseudoacacia*, *Alnus glutinosa*, *Pinus rigida*	210	11.2	11.6	1140	45°48′47.9″ N; 8°38′21.0″ E	Continental climate with warm, humid summers and dryer winters
Italy IT-BFo	Bosco Fontana	Forest	*Quercus robur*, hornbeam	36	13	12.6	1154	45°41′18.4″ N; 9°36′40.5″ E	Continental climate with warm, humid summers and dryer winters
Netherlands NL-Spe	Speulderbos	Forest	*Pseudotsuga menziesii*	52	9.4	9.7	925	52°15′8.1″ N; 5°41′25.8″ E	Temperate atlantic
Finland FI-Hyy	Hyytiäla	Forest	*Pinus sylvestris*	181	3.5	3	700	61°51′0″ N; 24°16′60″ E	Boreal
Switzerland CH-Po	Posieux	Grassland	*Lolium perenne*, *Trifolium repens*, *Taraxacum officinalis*	641	10.7	8.9	1075	46°46′4.1″ N; 7°6′28.1″ E	Temperate mixed
Hungary HU-Bu	Bugac	Grassland	*Cynodonti-Festucetum pseudovinae*	111	11	10.4	562	46.7° N, 19.6° E	Pannonian
United Kingdom UK-AMo	Auchencorth Moss	Peatland	*Calluna vulgaris*, *Juncus effusus*	270	7.6	7.7	1000	55°47′36″ N; 3°14′41′′ E	Northern Atlantic
France FR-Gri	Grignon	Arable	rotation: maize – wheat – rapeseed – wheat	125	11.3	11.5	600	48°51′0″ N; 1°57′5.4″ E	Oceanic climate with moderate continental influence
Ukraine UA-Pet	Petrodolinskoye	Arable	*Solanum lycopersicum*	66	13	10.1	464	46°27′22.1″ N; 30°20′9.9″ E	Moderately continental

Table 2. Soil characteristics of the nine sampling sites. Indicated soil textures are loamy sand (LS), sandy loam (SL), sandy clay (SC), silt loam (SiL), and clay (C).

Land use	Site	Ammonium (NH_4^+–N $\mu g\,g^{-1}$)	Nitrate (NO_3^-–N $\mu g\,g^{-1}$)	Bulk density ($g\,cm^{-3}$)	Conductivity (μS)	pH	Texture	C / N
Forest	IT-IFo	38.0	21.0	0.46	37.0	3.4	LS	19.6
Forest	IT-BFo	32.5	26.0	0.68	53.4	4.0	SL	17.8
Forest	NL-Spe	13.9	17.5	0.89	34.8	2.9	LS	32.7
Forest	FI-Hyy	23.0	17.5	0.61	20.9	3.1	LS	42.1
Grassland	CH-Po	5.7	28.2	0.77	100.4	6.7	SC	12.9
Grassland	HU-Bu	79.3	155.3	0.70	91.1	6.9	LS	13.0
Peatland	UK-AMo	42.9	29.1	0.12	38.9	3.2	organic	23.7
Arable	FR-Gri	1.9	21.5	1.11	65.5	6.8	SiL	13.3
Arable	UA-Pet	1.7	20.0	0.99	29.3	6.5	C	16.4

instruments by Teflon tubes. Two of the chambers in the incubator were empty and served as control chambers for the gas measurements. The incubation chamber was flushed constantly with compressed ambient air ($1.0\,L\,min^{-1}$). The air sampling period in each test chamber was 6 min, and that of each reference chamber was 4 min. A steady state was achieved after approximately 4 min in the test chambers and 2.5 min in the reference chambers (Schindlbacher, 2004). Gas flux rates were calculated based on gas concentration changes over time according to Schindlbacher (2004) and mean values are shown with standard errors (SE).
To examine the temperature and moisture sensitivity of heterotrophic soil respiration, regression analyses were conducted using the equations $R(T) = R_0 \times e^{aT+bT^2}$ (Tuomi et al., 2008) for temperature–CO_2 efflux relations and $R(M) = R_0 + aM + bM^2$ for moisture–CO_2 efflux relations.

To investigate how moisture content, temperature and land use influence moisture sensitivity, relative CO_2 values (relative to the CO_2 efflux of the lowest moisture content) were calculated to exclude the temperature contribution from the absolute CO_2 values. Moisture sensitivity was calculated as the slope of a polynomial function of second degree which was fitted over the relative CO_2 values. This was done for each temperature and site investigated.

2.4 Statistical analysis

Statistical analyses were performed with R (version 3.0.2) and SigmaPlot (version 11.0). Data were tested for normal distribution with the Shapiro–Wilk normality test and for variance homogeneity with the constant variance test. Data with non-normal distributions and/or unequal variances were transformed (log, square root) for parametric analysis. For multiple comparisons, the ANOVA test was performed to analyse significant differences. Significance of all tests was accepted at P levels < 0.05.

3 Results

Intact soil cores from nine sites of the ÉCLAIRE flux network were incubated in the laboratory at the temperatures 5, 10, 15, 20, and 25 °C in a two-factorial design of five soil moisture levels (5, 20, 40, 60, 80, (100) % WFPS) before being analysed for CO_2 fluxes. Data were normally distributed (Shapiro–Wilk test) and showed homogeneity of variances (constant variance test). CO_2 emissions differed significantly among sites, temperatures and moisture contents (ANOVA). Analysis of covariance was performed among soil characteristic data and mean CO_2 values over all temperatures and moisture contents but did not reveal any significant correlations (data not shown). Comparison of CO_2 fluxes calculated as mean values over all temperature and moisture contents indicate that grassland sites showed the highest CO_2 emissions with 848.39 ($\pm$87.81) and 420.70 ($\pm$40.68) mg CO_2-C m^{-2} h^{-1} for CH-Po and HU-BU, respectively, followed by the peatland site with 303.25 ($\pm$26.16) mg CO_2-C m^{-2} h^{-1} for UK-AMo. Forests and arable sites ranged between 27.60 ($\pm$1.69) and 126.00 ($\pm$12.43) mg CO_2-C m^{-2} h^{-1}.

Figure 1 shows absolute mean values of CO_2 emissions at each temperature and moisture content for all nine sites investigated. Highest CO_2 emissions occurred with intermediate moisture content (40–70 % WFPS) over all sites investigated except NL-Spe, where no significant moisture optimum could be detected. Additionally, a positive relation between CO_2 emissions and temperature is clearly visible.

3.1 Temperature sensitivity

The relationship between CO_2 emissions and temperature could be well described by a Gaussian model with the equation $R(T) = R_0 \times e^{aT+bT^2}$ (Tuomi et al., 2008) for all sites investigated. Table 3 summarizes the fit of the Gaussian model for all sites investigated, with all forest sites and the peatland site ranging between an R^2 of 0.990 and 1, grasslands between an R^2 of 0.871 and 1, and arable lands between an R^2 of 0.639 and 1. The temperature course of individual soil cores exhibited a good fit to the Gaussian model. As a result, mean values of CO_2 fluxes for each temperature and site were calculated to fit the equation and to exclude variations between soil cores when investigating temperature sensitivities. When taking all samples R^2 ranged between 0.019 (UA-Pet; 6 % WFPS) and 0.958 (NL-Spe; 30 % WFPS) due to the variability between soil cores.

Based on the Gaussian model temperature sensitivities were calculated as Q_{10} values from 5–15 °C for each moisture content and site investigated. Table 3 shows Q_{10} at the lowest and highest temperatures investigated: 5 and 15 °C. Q_{10} values of almost every moisture content and site showed that temperature sensitivity was negatively correlated with temperature (Q_{10} values were decreasing from 5 to 15 °C) for all sites investigated except one arable land (UA-Pet), which showed no distinct relationship between temperature

sensitivity and temperature. IT-BFo at 26 % WFPS and NL-Spe at 18 % WFPS also showed no relationship to temperature, and CH-Po at 5 % WFPS and UK-AMo at 83 % WFPS showed a small increase in Q_{10} values with temperature. Additionally, Q_{10} at 15 °C showed that temperature sensitivity converged towards 2 as temperature was increasing. There was no positive or negative relationship of temperature sensitivities to increasing moisture content. However, the variability between Q_{10} values of different moisture contents (highest Q_{10} value minus lowest Q_{10} value illustrated in Table 3 for 5 and 15 °C) at a certain temperature decreases with increasing temperature. Figure 2 shows Q_{10} values calculated from 5–15 °C for each of the five moisture contents investigated at the sites IT-IFo, NL-Spe, FI-Hyy, and UK-AMo. At both the coniferous forest sites (NL-Spe, FI-Hyy) results show a strong increase in temperature sensitivity at lower temperatures at a moisture range between 20 and 40 % WFPS (Q_{10}(5 °C) = 10.85 at NL-Spe, Q_{10}(5 °C) = 7.78 at FI-Hyy), which can also be seen in Table 3.

3.2 Moisture sensitivity

Moisture sensitivity (MS) was calculated as the slope of a quadratic function fitted over relative CO_2 values (to exclude the temperature contribution). Figure 3a shows relative values calculated for a deciduous forest in Italy (IT-IFo) and Fig. 3b shows the quadratic function fitted over relative CO_2 emissions for the same forest at 5 °C. Table 4 shows the fit of the regression analysis (polynomial function of second degree) to relative CO_2 values, with R^2 ranging between 0.445 and 0.984 for forest sites, 0.840–0.927 for grassland and peatland sites, and 0.337 to 0.980 for arable sites. Using the quadratic function, optimum moisture contents were calculated when moisture sensitivities reached zero, which equals highest CO_2 values. Optimum moisture contents (MC$_{Opt}$) ranged between 41 and 54 % WFPS for forest sites except for the coniferous site NL-Spe (38–74 % WFPS), which showed no significant moisture trend (Fig. 1); 53 and 59 % WFPS for the grassland site CH-Po; 44 and 54 % WFPS for the peatland site UK_AMo; and 43 and 54 % WFPS for the arable sites (Table 4). Relative values could not be calculated for HU-Bu because CO_2 values at lowest moisture contents were missing due to technical problems. Figure 4 shows calculated moisture sensitivities at all five temperatures investigated for a grassland site (CH-Po) and one arable land (UA-Pet). Results showed that moisture sensitivities were highest under very wet and dry conditions. Additionally, moisture sensitivities of CO_2 fluxes coming from arable lands showed a positive relationship to temperature, which can be also seen in Table 4, namely that moisture sensitivities at 5 % WFPS increased with temperature for both of the arable lands: FR-Gri and UA-Pet.

Table 3. Regression analysis of temperature relationship of heterotrophic soil respiration at all moisture contents (MC; shown in real values) investigated (Gaussian model equation); determination coefficient R^2, standard error of estimate, significance level P, and number of observations n (mean values over six replicants); Q_{10} values at 5 and 15 °C for all moisture contents and all sites investigated; and variability (Var) at 5 and 15 °C. Variability was calculated as the highest Q_{10} value at a certain temperature minus the lowest Q_{10} value at a certain temperature ($Q_{10,max} - Q_{10,min}$). na: not available.

Site	MC (% WFPS)	n	R^2	P	Q_{10} (5 °C)	Q_{10} (15 °C)	Var (5 °C)	Var (15 °C)
IT-IFo	13	5	1.00	< 0.001	3.8	2.7	1.1	0.6
IT-IFo	27	5	0.99	0.008	3.9	2.0		
IT-IFo	44	5	1.00	0.001	4.4	2.5		
IT-IFo	65	5	1.00	< 0.001	3.9	2.3		
IT-IFo	84	5	0.99	0.007	4.9	2.6		
IT-BFo	13	4	1.00	0.026	3.8	2.8	2.1	0.9
IT-BFo	26	4	1.00	0.004	2.9	3.0		
IT-BFo	46	4	1.00	0.021	3.3	3.1		
IT-BFo	65	4	0.99	0.089	4.3	2.7		
IT-BFo	84	4	1.00	0.005	2.3	2.2		
NL-Spe	18	5	0.99	0.010	3.7	3.8	7.5	1.3
NL-Spe	30	5	0.99	0.006	10.9	4.3		
NL-Spe	42	5	0.99	0.007	8.6	3.9		
NL-Spe	55	5	1.00	0.003	3.4	3.0		
NL-Spe	74	5	1.00	< 0.001	4.3	3.0		
FI-Hyy	15	5	1.00	0.005	2.9	2.7	4.9	0.3
FI-Hyy	22	5	0.99	0.009	7.8	2.5		
FI-Hyy	45	5	0.99	0.009	3.1	2.4		
FI-Hyy	65	5	1.00	< 0.001	3.5	2.5		
FI-Hyy	83	5	1.00	< 0.001	3.5	2.7		
CH-Po	5	5	1.00	0.001	2.1	2.3	1.3	1.2
CH-Po	18	5	1.00	0.002	3.1	2.1		
CH-Po	45	5	0.95	0.046	3.1	1.7		
CH-Po	59	5	0.89	0.105	2.9	1.2		
CH-Po	86	5	0.87	0.129	3.4	1.1		
HU-Bu	5	3	na	na	na	na	2.1	0.5
HU-Bu	19	5	0.99	0.007	4.9	2.5		
HU-Bu	36	5	0.96	0.037	5.2	2.5		
HU-Bu	57	5	0.96	0.041	5.3	2.3		
HU-Bu	77	5	0.98	0.020	3.2	2.0		
UK-AMo	22	5	1.00	< 0.001	3.8	2.8	1.5	0.6
UK-AMo	41	5	1.00	< 0.001	2.8	2.5		
UK-AMo	59	5	1.00	< 0.001	3.4	2.5		
UK-AMo	83	5	0.99	0.010	2.3	2.9		
UK-AMo	101	5	1.00	0.003	3.3	2.3		
FR-Gri	5	5	0.94	0.062	1.3	1.1	3.5	1.6
FR-Gri	21	5	1.00	< 0.001	3.2	2.7		
FR-Gri	40	5	0.99	0.013	4.8	1.6		
FR-Gri	60	5	0.99	0.007	4.5	1.8		
FR-Gri	80	5	0.96	0.036	3.5	1.8		
UA-Pet	6	5	0.64	0.361	1.1	0.9	1.1	1.5
UA-Pet	19	5	0.98	0.017	1.6	1.9		
UA-Pet	40	5	0.99	0.006	2.0	2.4		
UA-Pet	63	5	1.00	< 0.001	2.2	2.3		
UA-Pet	83	5	1.00	0.005	1.7	1.8		

4 Discussion

Land use generally had a substantial influence on carbon dioxide fluxes, with the order of CO_2 emission rates of the different land use being grassland > peatland > forest/arable land ($P < 0.001$), which is in line with observations by Schaufler et al. (2010), Raich and Tufekciogul (2000) and Ambus and Robertson (2006). Heterotrophic soil respiration responded strongly to varying temperature and moisture content (Ferréa et al., 2012; Gasche and Papen, 1999; Papen and Butterbach-Bahl, 1999; Schindlbacher, 2004; Suseela et al., 2012; Wu et al., 2010). Optimum moisture contents for CO_2 emissions occurred with intermediate moisture content (Bowden et al., 1998; Schaufler et al., 2010; Suseela et al., 2012) over all sites investigated (except for the coniferous forest site NL-Spe, where no significant moisture optimum could be detected). Possible explanations for a decline of CO_2 emissions at dry and wet conditions according to literature are (1) limiting diffusivity of air at wet conditions and (2) osmotic stress of soil microbial communities at dry conditions (Smith et al., 2003), which means a thinner film of water coats the soil particles, slowing the diffusion of labile substrates and reducing the activity of exo-enzymes needed for the decomposition of organic matter (Stark and Firestone, 1995). Additionally, results showed a positive correlation between CO_2 emissions and temperature (Davidson et al., 1998; Luo et al., 2012; Wang et al., 2006; Wu et al., 2010). In agreement with other studies, the relationship between CO_2 emissions and temperature could be well described by a Gaussian model with the equation $R(T) = R_0 \times e^{aT+bT^2}$ (Tuomi et al., 2008; Vanhala et al., 2008).

4.1 Temperature sensitivity

Q_{10} values were calculated based on the Gaussian model equation for the whole temperature range between 5 and 15 °C for each moisture content and site investigated and ranged between 0.86 and 10.85, which is in agreement with the estimation (2.0–6.3) of European and North American forest ecosystems (Davidson et al., 1998; Peng et al., 2009) and Janssens and Pilegaard (2003), who found Q_{10} values up to 16, as well as with results for temperate grasslands by Wu et al. (2010). Our findings confirm results from previous studies (Kirschbaum, 1995; Lloyd and Taylor, 1994; Luo et al., 2001) that temperature sensitivity is negatively correlated with temperature, which was true for most of the moisture contents and sites investigated (except one arable land site, UA-Pet, as well as IT-BFo at 26 % WFPS, NL-Spe at 18 % WFPS, CH-Po at 5 % WFPS and UK-AMo at 83 % WFPS). In addition to the Gaussian model equation we applied the Arrhenius function ($R(T) = R_0 \times e^{aT^{-1}}$) to our results, which showed similar trends but unrealistic Q_{10} values at temperatures below 8 °C (Q_{10} ranging between 20 and 2000).

A lot of conflicting literature exists on how temperature sensitivity relates to other factors like moisture content or land use. Conflicting results are often due to differing initial starting points, assumptions or interfering factors in field measurements (seasonality, autotrophic respiration, etc.). Kirschbaum (2006) and Lützow and Kögel-Knabner (2009) considered laboratory incubations to provide the best and least biased basis for estimating the temperature sensitivity of organic matter decomposition. In our laboratory incubation study we attempted to find an answer to this problem. We found that temperature sensitivity converged towards 2 as temperature increased for all moisture contents at all sites investigated. We also found that precipitation can influence temperature sensitivity of CO_2 efflux due to the decrease in the variability between Q_{10} values of different moisture contents (highest Q_{10} value minus lowest Q_{10} value) at each moisture point with increasing temperature. At low temperatures Q_{10} values vary more between dry and wet conditions. At higher temperatures the effect of water and temperature on Q_{10} is very low as Q_{10} converges towards 2.

Our results showed that no distinct relationship (neither positive nor negative) could be found between temperature sensitivity and moisture content at any of the investigated sites. Janssens and Pilegaard (2003) and Qi et al. (2002) expected a positive relationship between temperature sensitivity and moisture content due to the assumption that the effects of soil temperature and moisture are negatively correlated. Thus, soil moisture would be positively correlated with the temperature sensitivity of soil respiration. While Mäkiranta et al. (2009) and Gaumont-Guay et al. (2006) found an actual positive relationship between temperature sensitivity and soil moisture content in their field measurements, Peng et al. (2009) described, in their review of 52 papers, a negative correlation between Q_{10} values and mean annual precipitation. However, all these conclusions were achieved through seasonal field measurements, for which derivation of the influence of a single climate parameter is difficult because of incorporated seasonal changes in root biomass, litter inputs, microbial population, nitrogen availability and other seasonally fluctuating processes and conditions; thus these conclusions reflect community responses, which may differ from temperature and moisture responses of the respiratory processes (Davidson et al., 2000; Janssens and Pilegaard, 2003; Pilegaard et al., 2006) and can even be partly decoupled from actual soil temperature and moisture (Curiel Yuste et al., 2004; Schaufler et al., 2010). Moreover, most of the studies did not separate autotrophic from heterotrophic soil respiration. Curiel Yuste et al. (2004) presented a case study of how the seasonal Q_{10} of soil respiration can be decoupled from the temperature sensitivity of soil respiration, indicating that the large differences in seasonal Q_{10} do not represent differences in the temperature sensitivity of the soil metabolism. Kirschbaum (2006) and Lützow and Kögel-Knabner (2009) considered that laboratory incubations provide the best and

Table 4. Regression analysis of moisture relationship of heterotrophic soil respiration at all temperatures investigated (polynomial second degree); determination coefficient R^2, standard error of estimate, significance level P, and number of observations n (mean values over six replicants; relative values); optimum moisture content (MC_{Opt}), calculated as the MC where moisture sensitivities cut the x axis and CO_2 emissions show their optimum; and calculated moisture sensitivity (MS) at 5 % WFPS to show the temperature dependence of MS.

Site	T (°C)	n	R^2	P	MC_{Opt} (% WFPS)	MS (5 % WFPS)
IT-IFo	5	5	0.66	0.338	49	3.6
IT-IFo	10	5	0.80	0.202	41	3.1
IT-IFo	15	5	0.99	0.007	43	3.7
IT-IFo	20	5	0.98	0.016	45	3.0
IT-IFo	25	5	0.90	0.102	42	2.3
IT-BFo	5	5	0.87	0.132	52	12.4
IT-BFo	10	5	0.80	0.199	50	8.6
IT-BFo	15	5	0.70	0.304	50	11.5
IT-BFo	20	5	0.85	0.148	49	11.8
IT-BFo	25	5	–	–	–	–
NL-Spe	5	5	0.89	0.106	74	0.2
NL-Spe	10	5	0.89	0.106	75	3.7
NL-Spe	15	5	0.45	0.555	46	−4.5
NL-Spe	20	5	0.76	0.241	38	−2.5
NL-Spe	25	5	0.90	0.101	45	−2.2
FI-Hyy	5	5	0.87	0.134	54	9.3
FI-Hyy	10	5	0.93	0.069	53	20.3
FI-Hyy	15	5	0.98	0.018	52	20.6
FI-Hyy	20	5	0.83	0.174	53	15.2
FI-Hyy	25	5	0.92	0.080	54	15.6
CH-Po	5	5	0.91	0.091	57	55.4
CH-Po	10	5	0.89	0.106	59	127.7
CH-Po	15	5	0.93	0.074	58	96.9
CH-Po	20	5	0.90	0.096	55	121.2
CH-Po	25	5	0.84	0.160	53	79.0
HU-Bu	5	–	–	–	–	–
HU-Bu	10	–	–	–	–	–
HU-Bu	15	–	–	–	–	–
HU-Bu	20	–	–	–	–	–
HU-Bu	25	–	–	–	–	–
UK-AMo	5	5	0.95	0.046	52	3.2
UK-AMo	10	5	0.93	0.066	54	3.7
UK-AMo	15	5	0.93	0.073	51	2.5
UK-AMo	20	5	0.92	0.080	44	1.6
UK-AMo	25	5	0.88	0.119	46	1.7
FR-Gri	5	5	0.34	0.663	52	3.2
FR-Gri	10	5	0.64	0.362	51	7.8
FR-Gri	15	5	0.70	0.302	49	16.2
FR-Gri	20	5	0.78	0.224	51	28.3
FR-Gri	25	5	0.74	0.265	49	27.7
UA-Pet	5	5	0.66	0.338	54	−1.8
UA-Pet	10	5	0.48	0.523	292	−0.3
UA-Pet	15	5	0.25	0.751	43	0.6
UA-Pet	20	5	0.88	0.118	49	5.0
UA-Pet	25	5	0.98	0.020	50	9.9

least biased basis for estimating the temperature sensitivity of organic matter decomposition. This assumption can be extended to the assessment of soil moisture sensitivity of organic matter decomposition (Schaufler et al., 2010). Another

laboratory incubation study by Schindlbacher et al. (2007) showed that different soil moisture contents of trenched and control plots affected rates of heterotrophic soil respiration
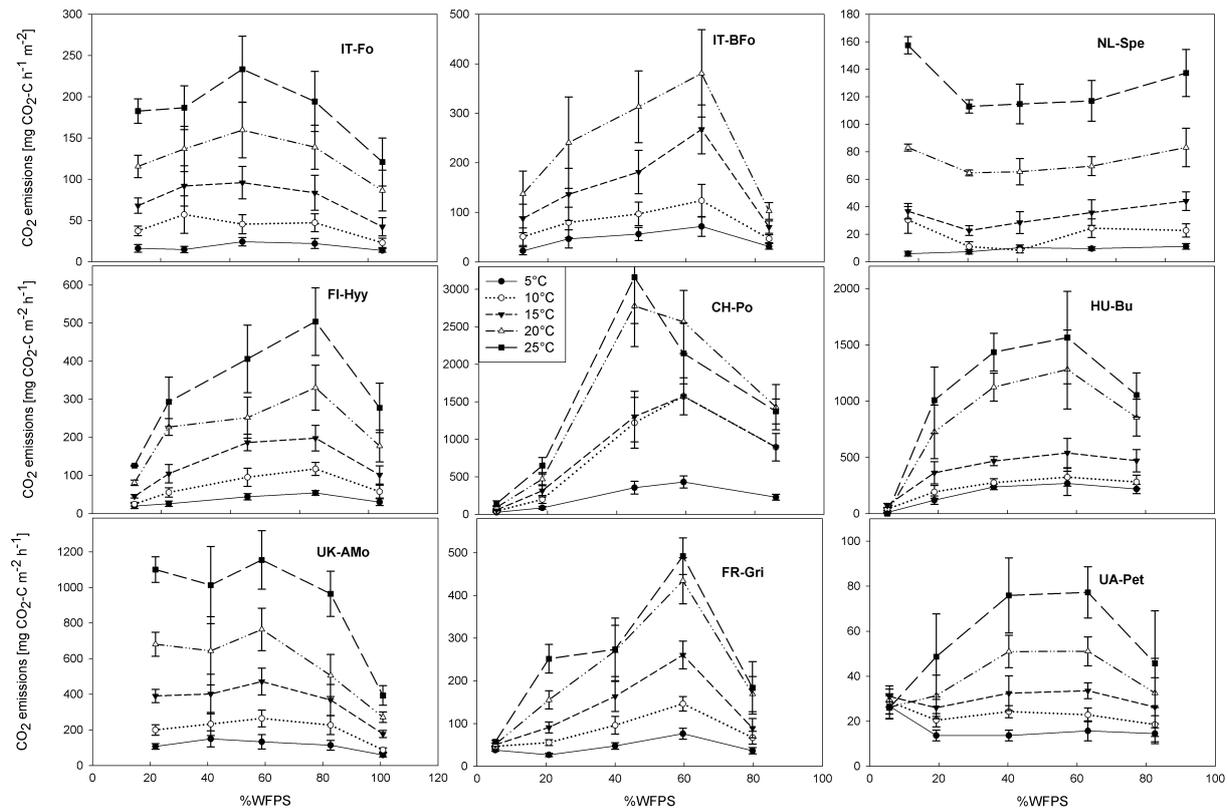
Figure 1. Mean CO_2 flux rates measured for five temperatures and five moisture contents (real values) from the nine study sites, starting with the deciduous forests (IT-IFo, IT-BFo) and followed by the coniferous forests (NL-Spe, FI-Hyy), grasslands (CH-Po, HU-Bu), the peatland site (UK-AMo) and the arable lands (FR-Gri, UA-Pet).

but did not affect the temperature sensitivity of heterotrophic respiration, which is in agreement with our results.

We found at both the coniferous forest sites a strong increase in the temperature sensitivity at a moisture range between 20 and 40 % WFPS. At coniferous sites the amount of recalcitrant material is higher (Landsberg and Gower, 1997; Wang et al., 2006) than at all other sites investigated. Temperature sensitivity of soil respiration increases with substrate recalcitrance as long as environmental constraints are not limiting decomposition (Conant et al., 2008; Hartley and Ineson, 2008; Karhu et al., 2010; Lützow and Kögel-Knabner, 2009; Zimmermann and Bird, 2012) because of the higher number of steps needed for decomposition of more complex substrates. Also, according to kinetic theory, the temperature sensitivity of decomposition increases with increasing molecular complexity of the substrate due to the higher activation energy of recalcitrant substrates (Hartley and Ineson, 2008; Vanhala et al., 2008). We hypothesize that a moisture range between 20 and 40 % WFPS promotes decomposition of recalcitrant material in coniferous forests. Results state that recalcitrant material is being favourably decomposed to easily degradable material within this moisture range. Initially, discriminative differences in Q_{10} values between moisture contents evened out with increasing tempera-

ture as Q_{10} values converged towards 2 for all moisture contents.

We could not see any obvious trends of Q_{10} values among land uses, which is in agreement with Wu et al. (2010). Peng et al. (2009) found differences in Q_{10} values among ecosystem types; however, they compared field measurements and different temperatures, which both result in different Q_{10} values (Curiel Yuste et al., 2004; Janssens and Pilegaard, 2003; Kirschbaum, 1995; Lloyd and Taylor, 1994; Luo et al., 2001; Schindlbacher et al., 2009).

4.2 Moisture sensitivity

We found a new approach to calculate moisture sensitivities. In our study, moisture sensitivity was calculated as the slope of a polynomial function of second degree. The use of quadratic functions for the description of the relationship between heterotrophic soil respiration and moisture content is widely common (Moyano et al., 2013; Rodrigo et al., 1997). Our results show that significant moisture effects ($P < 0.05$) occurred only at higher temperatures, which is in agreement with other studies (Teepe et al., 2004; Wu et al., 2010). To calculate the moisture sensitivity without temperature influ-
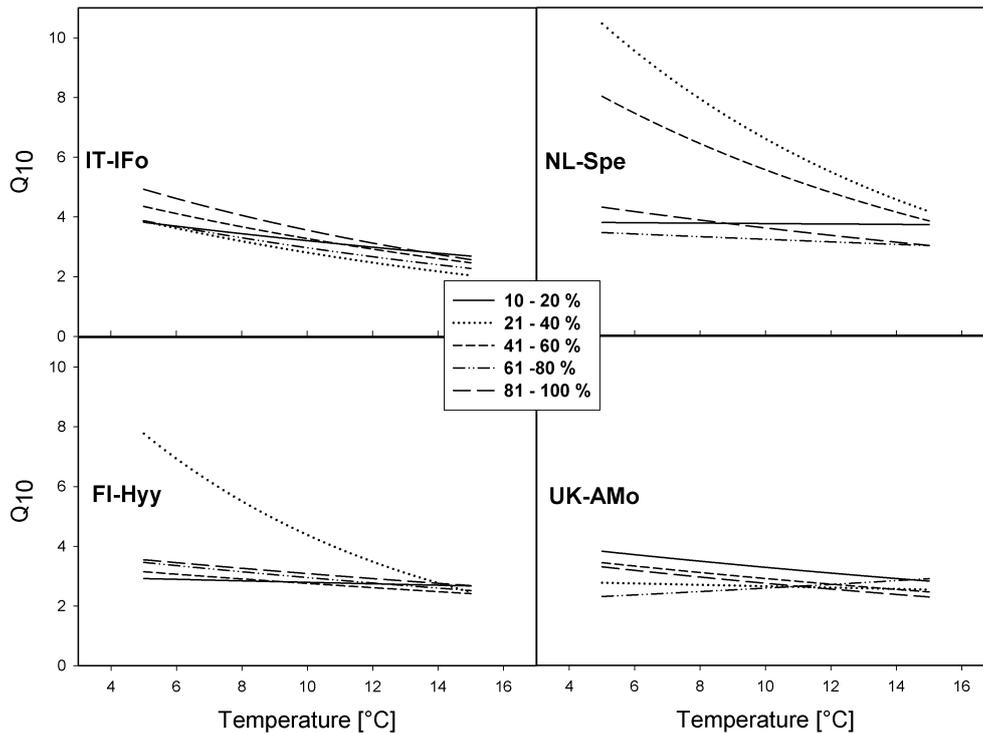
Figure 2. Calculated Q_{10} values of CO_2 efflux derived from the Gaussian model as a function of temperature for each of the investigated moisture contents shown here for the deciduous forest IT-IFo, the two coniferous forests NL-Spe and FI-Hyy, and the peatland site UK-AMo.
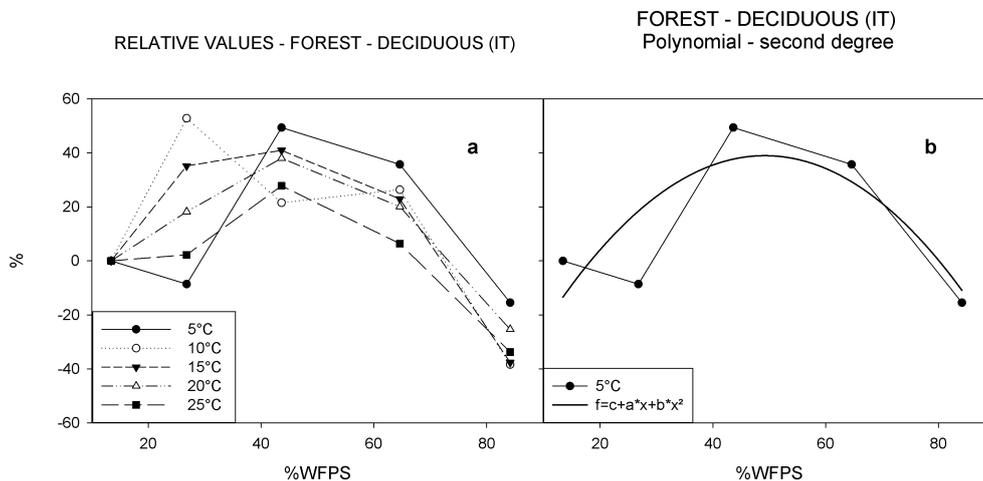
Figure 3. (a) Relative CO_2 flux rates measured for five temperatures and five moisture contents (real values) from the deciduous forest IT-IFo. **(b)** Polynomial function of second degree fitted of the moisture relationship of relative CO_2 values at 5 °C.

ence, we took relative CO_2 values for regression analysis to exclude the temperature contribution.

Many articles can be found on the topic of temperature sensitivity. However, much fewer articles calculate moisture sensitivities. Our results indicate that moisture sensitivity is highest under very dry and wet conditions. Results by Moyano et al. (2012) indicate that moisture sensitivity is negatively correlated with soil moisture. However, Moyano et

al. (2012) calculated moisture sensitivity as the proportional response of soil microbial respiration to a 0.01 increase in soil moisture of a certain unit. As CO_2 values decline after a moisture optimum, this mathematical approach results in moisture sensitivities showing highest values under dry conditions decreasing progressively with increasing moisture content until converging to a certain value. Our approach to calculating moisture sensitivities indicates that moisture sen-
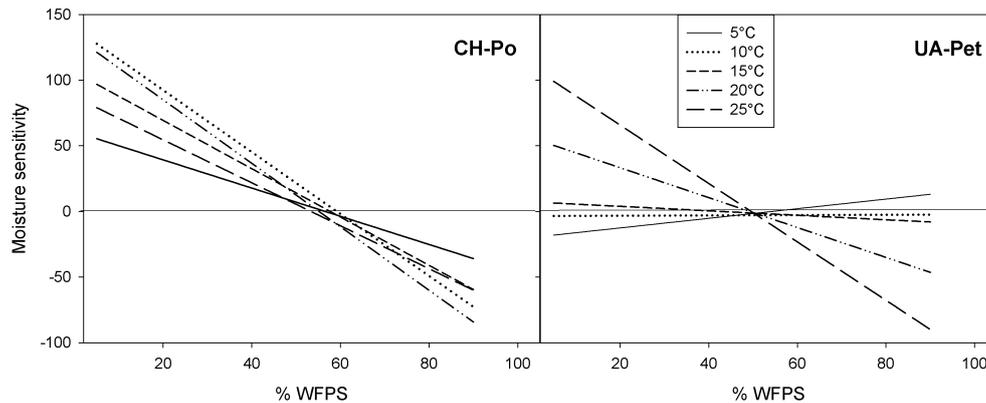
Figure 4. Illustrated moisture sensitivity (MS) of relative CO_2 efflux from the grassland site CH-Po and the arable site UA-Pet in relation to soil moisture content for all temperatures investigated. MS was calculated as the slope of a polynomial function of second degree. The cutpoint on the x axis indicates optimum moisture content for CO_2 emissions at their respective temperature. Negative values of moisture sensitivity after reaching the optimum moisture content (MC_{Opt}) indicate a decrease in CO_2 emissions with increasing moisture content; positive values indicate an increase in CO_2 emissions with increasing moisture content.

sitivities decrease until reaching the moisture optimum and increase again after that (negative values after reaching the optimum moisture content (MC_{opt}) only indicate a decrease in CO_2 emissions with increasing moisture content; positive values indicate an increase in CO_2 emissions with increasing moisture content). Therefore we can show that changing moisture content has a higher impact on CO_2 emissions under dry and wet conditions than under intermediate moisture conditions.

No relationship between moisture sensitivity and temperature could be found for forests, grasslands and peatlands. However, we found moisture sensitivity to be positively correlated with temperature for both arable lands, which both showed the highest bulk densities of all sites ($> 1.00\,\mathrm{g\,m^{-3}}$; Table 2). Moyano et al. (2012) found that bulk density influences moisture sensitivity but did not investigate the influence of temperature. Tillage can also change physical protection of organic matter and diffusivity, as well as improving the exchange with deeper soil layers (Davidson and Janssens, 2006). There are several characteristics in which arable lands differ from other ecosystems with respect to carbon-cycle responses to climate change. Cropland systems are entirely managed and the soil–vegetation system can be reset regularly through harvest and agricultural management such as tillage, manure/residue management and irrigation. Consequently, the response to climate is highly modulated by human intervention both immediately and over longer periods (Reichstein et al., 2013). This might be a reason for the positive relationship between moisture sensitivity and temperature we found for arable lands.

5 Conclusions

Our experiments showed that temperature sensitivities of CO_2 emission were highest under cold temperatures, which means that, in cold areas (e.g. northern latitudes or mountain areas), warming will have a larger impact on CO_2 emissions. In addition, Q_{10} values varied strongly under cold temperatures, with moisture content indicating an effect of rain events in cold areas on temperature sensitivity.

Moisture sensitivity was prominent under dry or wet conditions, which indicates that increased moisture in dry areas or drying of wet areas will largely promote CO_2 emissions. Moisture sensitivities of CO_2 emissions from cropland soils were positively related to temperature; hence irrigation of arable lands might have a higher impact on CO_2 emissions in warmer regions in the south of Europe than in the north.

The responses observed in this study hold true for both short-term changes (like those manipulations performed here) and longer-term shifts. However, investigations on acclimation or adaptation of ecosystem processes to climate change in the longer term might lead to different responses, leaving room for future research.

References

Ågren, G. I. and Wetterstedt, J. Å. M.: What determines the temperature response of soil organic matter decomposition?, Soil Biol. Biochem., 39, 1794–1798, 2007.

Ambus, P. and Robertson, G. P.: The Effect of Increased N Deposition on Nitrous oxide, Methane and Carbon dioxide Fluxes from Unmanaged Forest and Grassland Communities in Michigan, Biogeochemistry, 79, 315–337, 2006.

Atkin, O. K., Edwards, E. J., and Loveys, B. R.: Response of root respiration to changes in temperature and its relevance to global warming, New Phytol., 147, 141–154, 2000.

Baggs, E. M.: Partitioning the components of soil respiration: a research challenge, Plant Soil, 284, 1–5, 2006.

Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E., and Kreyling, J.: Ecotypes of European grass species respond differently to warming and extreme drought, J. Ecol., 99, 703–713, 2011.

Bowden, R. D., Newkirk, K. M., and Rullo, G. M.: Carbon dioxide and methane fluxes by a forest soil under laboratory-controlled moisture and temperature conditions, Soil Biol. Biochem., 30, 1591–1597, 1998.

Conant, R. T., Drijber, R. A., Haddix, M. L., Parton, W. J., Paul, E. A., Plante, A. F., Six, J., and Steinweg, J. M.: Sensitivity of organic matter decomposition to warming varies with its quality, Glob. Change Biol., 14, 868–877, 2008.

Curiel Yuste, J., Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity, Glob. Change Biol., 10, 161–169, 2004.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, 2006.

Davidson, E. A., Belk, E., and Boone, R. D.: Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, Glob. Change Biol., 4, 217–227, 1998.

Davidson, E. A., Keller, M., Erickson, H. E., Verchot, L. V., and Veldkamp, E.: Testing a Conceptual Model of Soil Emissions of Nitrous and Nitric Oxides: Using two functions based on soil nitrogen availability and soil water content, the hole-in-the-pipe model characterizes a large fraction of the observed variation of nitric oxide and nitrous oxide emissions from soils, BioScience, 50, 667–680, 2000.

Ferréa, C., Zenone, T., Comolli, R., and Seufert, G.: Estimating heterotrophic and autotrophic soil respiration in a semi-natural forest of Lombardy, Italy, Pedobiologia, 55, 285–294, 2012.

Flechard, C. R., Neftel, A., Jocher, M., Ammann, C., and Fuhrer, J.: Bi-directional soil/atmosphere N2O exchange over two mown grassland systems with contrasting management practices, Glob. Change Biol., 11, 2114–2127, 2005.

Garten, C. T., Classen, A. T., and Norby, R. J.: Soil moisture surpasses elevated CO2 and temperature as a control on soil carbon dynamics in a multi-factor climate change experiment, Plant Soil, 319, 85–94, 2008.

Gasche, R. and Papen, H.: A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany: 2. NO and NO_2 fluxes, Journal of Geophysical Research: Atmospheres (1984–2012), 104, 18505–18520, 1999.

Gaumont-Guay, D., Black, T. A., Griffis, T. J., Barr, A. G., Jassal, R. S., and Nesic, Z.: Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand, Agricul. Forest Meteorol., 140, 220–235, 2006.

Hartley, I. P. and Ineson, P.: Substrate quality and the temperature sensitivity of soil organic matter decomposition, Soil Biol. Biochem., 40, 1567–1574, 2008.

Hood-Nowotny, R., Umana, N. H.-N., Inselbacher, E., Oswald-Lachouani, P., and Wanek, W.: Alternative methods for measuring inorganic, organic, and total dissolved nitrogen in soil, Soil Sci. Soc. Am. J., 74, 1018–1027, 2010.

IPCC: Summary for Policymakers, in: Climate Change 2014: Impacts, Adaptation, and Vulnerability – Part A: Global and Sectoral Aspects, Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change edited by: Field, C. B., Barros, V. R., Dokken, D. J., Mach, K. J., Mastrandrea, M. D., Bilir, T. E., Chatterjee, M., Ebi, K. L., Estrada, Y. O., Genova, R. C., Girma, B., Kissel, E. S., Levy, A. N., MacCracken, S., Mastrandrea, P. R., and White, L. L., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1–32, 2014.

Janssens, I. A. and Pilegaard, K. I. M.: Large seasonal changes in Q_{10} of soil respiration in a beech forest, Glob. Change Biol., 9, 911–918, 2003.

Karhu, K., Fritze, H., Tuomi, M., Vanhala, P., Spetz, P., Kitunen, V., and Liski, J.: Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles, Soil Biol. Biochem., 42, 72–82, 2010.

Kirschbaum, M.: The temperature dependence of organic-matter decomposition – still a topic of debate, Soil Biol. Biochem., 38, 2510–2518, 2006.

Kirschbaum, M. U. F.: The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage, Soil Biol. Biochem., 27, 753–760, 1995.

Landsberg, J. J. and Gower, S. T.: Applications of physiological ecology to forest management, Physiol. Ecol., ISBN-9780080527383, 161–184, 1997.

Larsen, K. S., Andresen, L. C., Beier, C., Jonasson, S., Albert, K. R., Ambus, P. E. R., Arndal, M. F., Carter, M. S., Christensen, S., Holmstrup, M., Ibrom, A., Kongstad, J., Van Der Linden, L., Maraldo, K., Michelsen, A., Mikkelsen, T. N., Pilegaard, K. I. M., PriemÉ, A., Ro-Poulsen, H., Schmidt, I. K., Selsted, M. B., and Stevnbak, K.: Reduced N cycling in response to elevated CO_2, warming, and drought in a Danish heathland: Synthesizing results of the CLIMAITE project after two years of treatments, Glob. Change Biol., 17, 1884–1899, 2011.

Leuzinger, S., Luo, Y., Beier, C., Dieleman, W., Vicca, S., and Korner, C.: Do global change experiments overestimate impacts on terrestrial ecosystems?, Trends. Ecol. Evol., 26, 236–241, 2011.

Lloyd, J. and Taylor, J.: On the temperature dependence of soil respiration, Funct. Ecol., 8, 315–323, 1994.

Luo, G. J., Brüggemann, N., Wolf, B., Gasche, R., Grote, R., and Butterbach-Bahl, K.: Decadal variability of soil CO_2, NO, N_2O, and CH_4 fluxes at the Höglwald Forest, Germany, Biogeosciences, 9, 1741–1763, doi:10.5194/bg-9-1741-2012, 2012.

Luo, Y., Wan, S., Hui, D., and Wallace, L. L.: Acclimatization of soil respiration to warming in a tall grass prairie, Nature, 413, 622–625, 2001.

Lützow, M. and Kögel-Knabner, I.: Temperature sensitivity of soil organic matter decomposition – what do we know?, Biol. Fert. Soils, 46, 1–15, 2009.

Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., and Minkkinen, K.: Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity, Soil Biol. Biochem., 41, 695–703, 2009.

Meixner, F. X.: Biogenic emissions of nitric oxide and nitrous oxide from arid and semi-arid land, in: Dryland Ecohydrology, Springer, Netherlands, 233–255, 2006.

Moyano, F. E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Curiel Yuste, J., Don, A., Epron, D., Formanek, P., Franzluebbers, A., Ilstedt, U., Kätterer, T., Orchard, V., Reichstein, M., Rey, A., Ruamps, L., Subke, J.-A., Thomsen, I. K., and Chenu, C.: The moisture response of soil heterotrophic respiration: interaction with soil properties, Biogeosciences, 9, 1173–1182, doi:10.5194/bg-9-1173-2012, 2012.

Moyano, F. E., Manzoni, S., and Chenu, C.: Responses of soil heterotrophic respiration to moisture availability: An exploration of processes and models, Soil Biol. Biochem., 59, 72–85, 2013.

Papen, H. and Butterbach-Bahl, K.: A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany: 1. N_2O emissions, J. Geophys. Res., 104, 18487, doi:10.1029/1999JD900293, 1999.

Peng, S., Piao, S., Wang, T., Sun, J., and Shen, Z.: Temperature sensitivity of soil respiration in different ecosystems in China, Soil Biol. Biochem., 41, 1008–1014, 2009.

Pilegaard, K., Skiba, U., Ambus, P., Beier, C., Brüggemann, N., Butterbach-Bahl, K., Dick, J., Dorsey, J., Duyzer, J., Gallagher, M., Gasche, R., Horvath, L., Kitzler, B., Leip, A., Pihlatie, M. K., Rosenkranz, P., Seufert, G., Vesala, T., Westrate, H., and Zechmeister-Boltenstern, S.: Factors controlling regional differences in forest soil emission of nitrogen oxides (NO and N_2O), Biogeosciences, 3, 651–661, doi:10.5194/bg-3-651-2006, 2006.

Qi, Y., Xu, M., and Wu, J.: Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: nonlinearity begets surprises, Ecol. Modell., 153, 131–142, 2002.

Raich, J. and Tufekciogul, A.: Vegetation and soil respiration: Correlations and controls, Biogeochemistry, 48, 71–90, 2000.

Reichstein, M., Bahn, M., Ciais, P., Frank, D., Mahecha, M. D., Seneviratne, S. I., Zscheischler, J., Beer, C., Buchmann, N., Frank, D. C., Papale, D., Rammig, A., Smith, P., Thonicke, K., van der Velde, M., Vicca, S., Walz, A., and Wattenbach, M.: Climate extremes and the carbon cycle, Nature, 500, 287–295, 2013.

Rodrigo, A., Recous, S., Neel, C., and Mary, B.: Modelling temperature and moisture effects on C–N transformations in soils: comparison of nine models, Ecol. Modell., 102, 325–339, 1997.

Schaufler, G., Kitzler, B., Schindlbacher, A., Skiba, U., Sutton, M. A., and Zechmeister-Boltenstern, S.: Greenhouse gas emissions from European soils under different land use: effects of soil moisture and temperature, European J. Soil Sci., 61, 683–696, 2010.

Schindlbacher, A.: Effects of soil moisture and temperature on NO, NO_2, and N_2O emissions from European forest soils, J. Geophys. Res., 109, D17302, doi:10.1029/2004JD004590, 2004.

Schindlbacher, A., Zechmeister-Boltenstern, S., Kitzler, B., and Jandl, R.: Experimental forest soil warming: response of autotrophic and heterotrophic soil respiration to a short-term 10 °C temperature rise, Plant Soil, 303, 323–330, 2007.

Schindlbacher, A., Zechmeister-Boltenstern, S., and Jandl, R.: Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally?, Glob. Change Biol., 15, 901–913, 2009.

Shrestha, B. M., Sitaula, B. K., Singh, B. R., and Bajracharya, R. M.: Fluxes of CO_2 and CH_4 in soil profiles of a mountainous watershed of Nepal as influenced by land use, temperature, moisture and substrate addition, Nutr. Cycl. Agroecosys., 68, 155–164, 2004.

Skiba, U. M., Sheppard, L. J., Macdonald, J., and Fowler, D.: Some key environmental variables controlling nitrous oxide emissions from agricultural and semi-natural soils in Scotland, Atmos. Environ., 32, 3311–3320, 1998.

Smith, K. A., Ball, T., Conen, F., Dobbie, K. E., Massheder, J., and Rey, A.: Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes, Eur. J. Soil Sci., 54, 779–791, 2003.

Stark, J. M. and Firestone, M. K.: Mechanisms for soil moisture effects on activity of nitrifying bacteria, Appl. Environ. Microbiol., 61, 218–221, 1995.

Suseela, V., Conant, R. T., Wallenstein, M. D., and Dukes, J. S.: Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment, Glob. Change Biol., 18, 336–348, 2012.

Teepe, R., Vor, A., Beese, F., and Ludwig, B.: Emissions of N_2O from soils during cycles of freezing and thawing and the effects of soil water, texture and duration of freezing, Eur. J. Soil Sci., 55, 357–365, 2004.

Thornley, J. H. M. and Cannell, M. G. R.: Soil Carbon Storage Response to Temperature: an Hypothesis, Ann. Botany, 87, 591–598, 2001.

Tuomi, M., Vanhala, P., Karhu, K., Fritze, H., and Liski, J.: Heterotrophic soil respiration – Comparison of different models describing its temperature dependence, Ecol. Modell., 211, 182–190, 2008.

Vanhala, P., Karhu, K., Tuomi, M., Björklöf, K., Fritze, H., and Liski, J.: Temperature sensitivity of soil organic matter decomposition in southern and northern areas of the boreal forest zone, Soil Biol. Biochem., 40, 1758–1764, 2008.

Wang, C., Yang, J., and Zhang, Q.: Soil respiration in six temperate forests in China, Glob. Change Biol., 12, 2103–2114, 2006.

Wang, W. and Fang, J.: Soil respiration and human effects on global grasslands, Glob. Planet. Change, 67, 20–28, 2009.

Wu, X., Yao, Z., Brüggemann, N., Shen, Z. Y., Wolf, B., Dannenmann, M., Zheng, X., and Butterbach-Bahl, K.: Effects of soil moisture and temperature on CO_2 and CH_4 soil–atmosphere exchange of various land use/cover types in a semi-arid grassland in Inner Mongolia, China, Soil Biol. Biochem., 42, 773–787, 2010.

Zimmermann, M. and Bird, M. I.: Temperature sensitivity of tropical forest soil respiration increase along an altitudinal gradient with ongoing decomposition, Geoderma, 187/188, 8–15, 2012.