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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 under different land-use and climate (soil moisture and temperature) we conducted a laboratory incubation experiment.

Emission measurements of carbon dioxide under controlled conditions were conducted using soil monoliths of nine sites from the ÉCLAIRE flux network. Sites are located ~~all over~~ Europe; from the UK in the west to the Ukraine in the east; Italy in the south to Finland in the north ~~and can be separated according to four land-uses~~ ~~(~~forests, grasslands, arable lands and one peatland~~)~~. Intact soil cores 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) % water filled pore space, WFPS), ~~before~~ analysed for CO_2 fluxes 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-uses ~~being~~ grassland > peatland > forest/arable land ($P < 0.001$). ~~CO_2~~ efflux responded strongly to varying temperature and moisture content with optimum moisture content~~s~~ for CO_2 emissions between 40–70 % 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 0.86–10.85 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. ~~We found at both~~ coniferous forest sites ~~a strong increase of the~~ temperature sensitivity ~~at~~ a moisture range between 20–40 % WFPS.

In our study moisture sensitivity (MS) of CO_2 efflux 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 for 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 of 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 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 therefor~~ 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) could 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 at 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).

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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.

Janssens and Pilegaard (2003) and Qi et al. (2002) expect 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) describe~~s~~ in a 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 of 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 describe 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 ÉCLAIRE flux network, Europe and incubated in the laboratory under 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. Sites are located all over Europe; from the UK in the west to the Ukraine in the east; 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 ~~respective~~ to sampling conditions. Soil cores were collected at 6 randomly distributed plots of approximately 10 m^2 within an overall area of approximately 50 m × 50 m at each site. Six soil samples were collected from each 10 m^2 plot at 6 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. ~~3~~ soil cores were used to determine gravimetric water content~~s~~. The gravimetric water content was determined for mineral soil by oven drying at 103 °C for three days to a constant weight. ~~These~~ water content~~s~~ ~~were~~ assumed to be representative for the rest of the soil samples from the same location, ~~so that~~ 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.

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 % water filled pore space, WFPS), ~~before~~ analysed for CO_2 fluxes. ~~To design the experiment realistically~~ moisture levels for the peatland site (UK-AMo) were set between 20–100 % WFPS. To reach the required moisture contents, distilled water was either added to ~~too dry samples~~, or ~~too moist~~ samples were dried at 4 °C until they reached the required moisture ~~content~~. 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 6 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 three remaining cores soil characteristics (Table 2) were analyzed. Ammonium and nitrate was quantified according to Hood-Nowotny et al. (2010) using the ~~ration~~ 2.5 g soil : 25 ml ~~KCL~~ solution. Photometric analyses were conducted with a photometer ~~from PerkinElmer® type 2300 EnSpire™~~. Conductivity was measured with a conducting meter ~~2F191 (WTW)~~ and pH was measured in 0.01 m $CaCl_2$, using the ratio 10 g soil : 25 m~~L~~ $CaCl_2$ 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 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 ~~of~~ each reference chamber 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 $R(T) = R_0 \cdot e^{aT+bT^2}$

(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 ~~has been~~ 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. 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) % water filled pore space, WFPS) before 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). 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 (±87.81) and 420.70 (±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 (±26.16) mg CO_2–C m^{-2} h^{-1} ~~for UK-AMo.~~ ~~Forests~~ and arable sites ranged between 27.60 (±1.69) and 126.00 (±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 $R(T) = R_0 \cdot e^{aT+bT^2}$ (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 of the five temperatures per moisture content and site were calculated to fit the equation. 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 to 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. Also IT-BFo at 26 % WFPS, NL-Spe at 18 % WFPS showed no relationship to temperature and CH-Po at 5 % WFPS and UK-AMo at 83 % WFPS showed a small increase of 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 ~~5~~ 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 of temperature sensitivity at lower temperatures ~~at~~ a moisture range between 20–40 % 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 0.445–0.984 for forest sites; 0.840–0.927 for grassland and peatland sites; and 0.337–0.980 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}) ~~were ranging~~ between 41–54 % WFPS for forest sites except for the coniferous site NL-Spe (38–74 % WFPS) which showed no significant moisture trend (Fig. 1); 53–59 % WFPS for the grassland site CH-Po; 44–54 % WFPS for the peatland site UK_AMo; and 43–54 % 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 ~~5~~ temperatures investigated for a grassland site (CH-Po) and one arable land investigated (UA-Pet). Results showed that moisture sensitivities were highest at very wet and dry conditions. ~~Addi-~~

~~tionally~~ 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 arable ~~lands~~, FR-Gri and UA-Pet.

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); 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 $R(T) = R_0 \cdot e^{aT+bT^2}$ (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 5–15 °C for each moisture content and site investigated and were ranging between 0.86–10.85 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, and also 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 to temperature which was true for most of the moisture contents and sites investigated ~~(except one arable land UA-Pet and IT-BFo at 26 % WFPS, NL-Spe at 18 % WFPS; CH-Po at 5 % WFPS and UK-AMo at 83 % WFPS)~~. ~~Additionally~~ temperature sensitivity converged towards 2 as temperature increased for all moisture contents at all sites investigated. We found that precipitation can influence temperature sensitivity of CO_2 efflux due to the decrease of 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. Additionally to the Gaussian model equation we applied the Arrhenius function ($R(T) = R_0 \cdot e^{aT^{-1}}$) to our results which showed similar trends but unrealistic Q_{10} values at temperatures below 8 °C (Q_{10} ranging between 20 and 2000).

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 a 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 at 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, and thus 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). Also 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 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, 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 of the temperature sensitivity ~~at~~ a moisture range between 20–40 % 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

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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 higher activation energy of recalcitrant substrate (Hartley and Ineson, 2008; Vanhala et al., 2008). We hypothesize that a moisture range between 20–40 % WFPS promotes decomposition of recalcitrant material in coniferous forests. Not the absolute amount of carbon dioxide increases at this moisture range as NL-Spe shows no significant CO_2 maximum at any moisture content and Hyytiälä has its maximum between 40–70 % WFPS. Results rather state that within this moisture range recalcitrant material is being favourably decomposed to ~~easy~~ degradable material. Initially discriminative differences in Q_{10} values between moisture contents ~~evened out~~ with increasing temperature as Q_{10} values converged towards 2 for all moisture contents.

We couldn't 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 of Q_{10} values among ecosystem types but did compare 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

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 ~~influence~~ 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 at very dry and wet conditions. Results by Moyano et al. (2012) indicate that moisture sensitivity is negatively correlated to 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~~ at dry conditions decreasing progressively with increasing moisture content until converging to a certain value. Our approach to calculate moisture sensitivities ~~indicates~~ that moisture sensitivities 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 of CO_2 emissions with increasing moisture content; positive values indicate an increase of CO_2 emissions with increasing moisture content). ~~Therefor~~ we can show that changing moisture content has a higher impact on CO_2 emissions at dry and wet conditions than at intermediate moisture conditions.

No relationship between moisture sensitivity and temperature could be found for forests, grasslands and peatlands. However, moisture sensitivity was 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. Also tillage can change physical protection of organic matter, diffusivity as well as improve 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).

5 Conclusions

Our experiments showed that ~~under cold~~ temperatures temperature sensitivit~~ies~~ of CO_2 emission ~~were~~ highest 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 temperature~~s~~ 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.

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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] annual soil temperature [°C]	Average annual air temperature [°C]	Average annual preciptiation [mm]	Average	Location type	Climate
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	Hyytiälä	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	Atlantic Northern
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	Solánum lycopérsicum	66	13	10.1	464	46°27′22.1″ N; 30°20′9.9″ E	Moderately continental

Table 2. Soil characteristics of the ~~9~~ sampling sites. Indicated soil textures are loamy sand (LS), sandy loam (SL), sandy clay (SC), Silt loam (SiL), and clay (C).

Landuse	Site	Ammonium [NH_4^+ – N µg g^{-1}]	Nitrate [NO_3^- – N µg g^{-1}]	Bulk densitiy [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

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 6 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 ($Q_{10\mathrm{Max}} - Q_{10\mathrm{Min}}$).

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		

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Table 3. Continued.

Site	MC [% WFPS]	n	R^2	P	Q_{10} (5 °C)	Q_{10} (15 °C)	Var(5 °C)	Var(15 °C)
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		

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 6 replicants; relative values). Calculated moisture content (MC_{Opt}), where CO_2 emissions show their optimum and calculated moisture sensitivity (MS) at 5 % WFPS.

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

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Table 4. Continued.

Site	T [°C]	n	R^2	P	MC_{Opt} [%WFPS]	MS (5 %WFPS)
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

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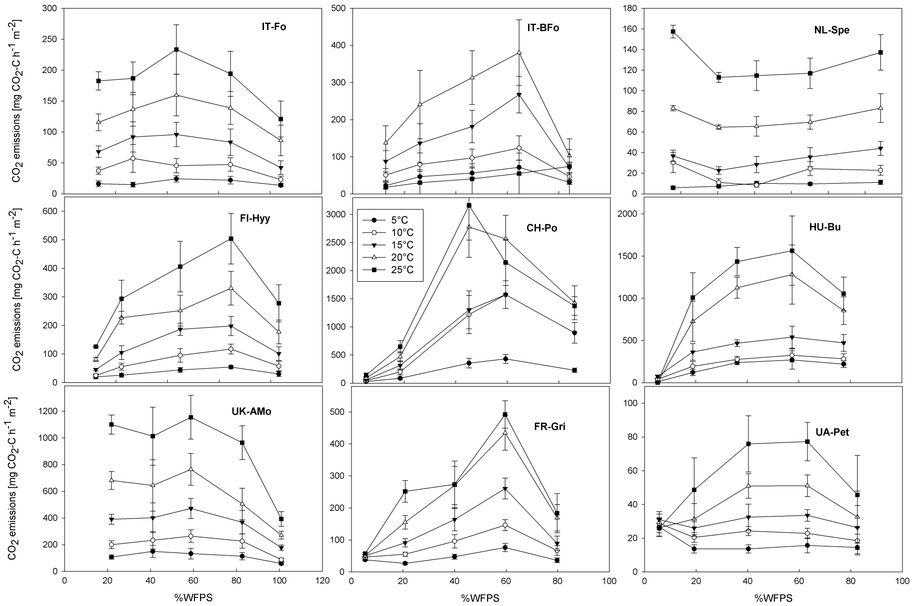

Figure 1. Mean CO_2 flux rates measured at ~~5~~ temperatures and ~~5~~ moistures contents (real values) from the ~~9~~ study sites, starting with the deciduous forests (IT-IFo, IT-BFo) followed by the coniferous forests (NL-Spe, FI-Hyy), grasslands (CH-Po, HU-Bu), the peatland site (UK-AMo) and the arable ~~lands~~ (FR-Gri, UA-Pet).

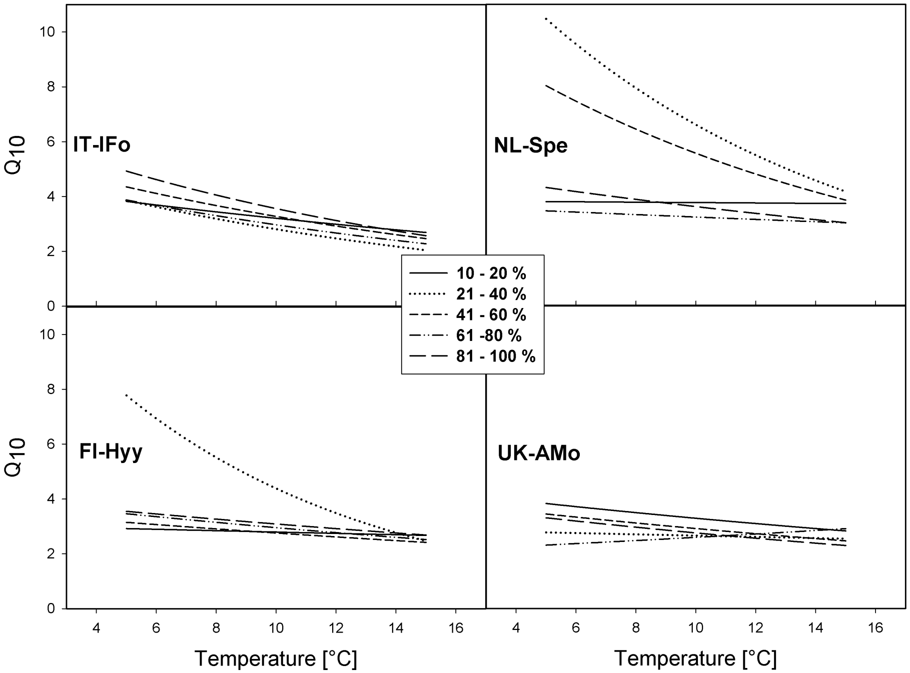

Figure 2. Calculated Q_{10} values of CO_2 efflux derived from the Gaussian model as a function of temperature for each of the investigated moisture contents here shown for the deciduous forest IT-IFo, the ~~2~~ coniferous forests NL-Spe and FI-Hyy and the peatland site UK-AMo.

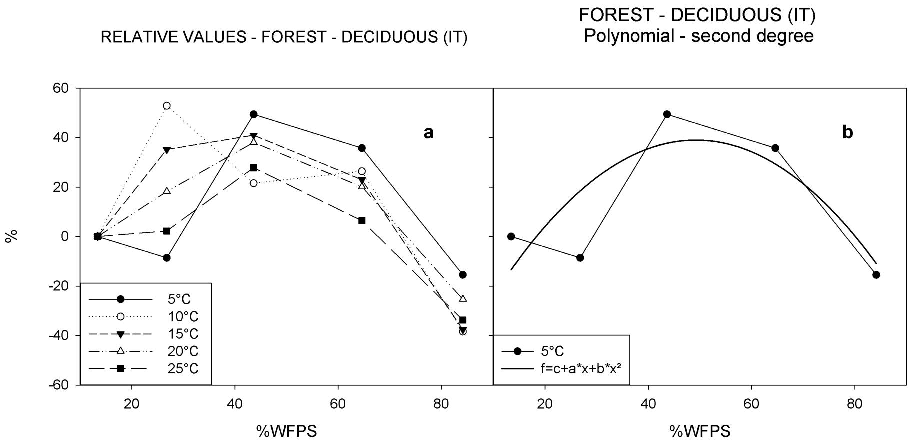

Figure 3. (a) Relative CO_2 flux rates measured at 5 temperatures and 5 moistures contents (real values) from the deciduous forest IT-IFo; **(b)** ~~Polynomial~~ function ~~of second degree~~ fitted ~~of~~ the moisture relationship of relative CO_2 values at 5 °C.

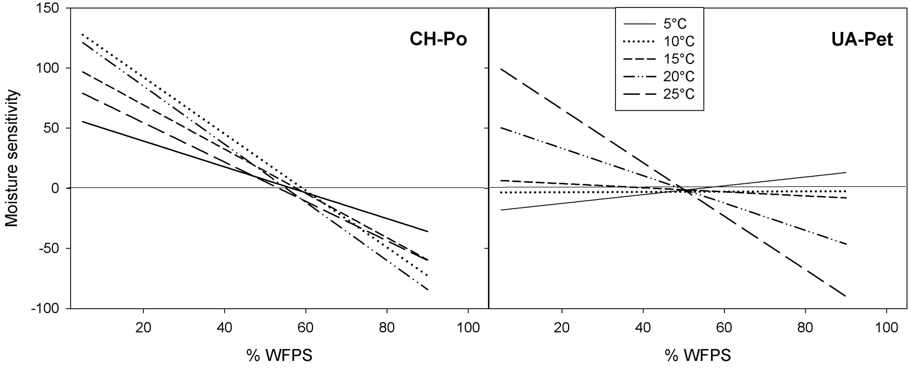

Figure 4. Illustrated moisture sensitivity (MS) of relative CO_2 efflux in relations to soil moisture content. MS was calculated as the slope of a ~~polynomial~~ function ~~of second degree~~ for each of the ~~5~~ temperatures investigated here shown for the grassland site CH-Po and the arable site UA-Pet. ~~Cutpoint on~~ *x* axis indicates optimum moisture content for CO_2 emissions at respective temperature. Negative values of moisture sensitivity after reaching the optimum moisture content (MC_{Opt}) indicate a decrease of CO_2 emissions with increasing moisture content; positive values indicate an increase of CO_2 emissions with increasing moisture content.