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Interactions among temperature, moisture, and oxygen concentrations in controlling decomposition rates

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Abstract. Determining environmental controls on soil organic matter decomposition is of importance for developing models that predict the effects of environmental change on global soil carbon stocks. There is uncertainty about the environmental controls on decomposition rates at temperature and moisture extremes, particularly at high water content levels and high temperatures. It is uncertain whether observed declines of decomposition rates at high temperatures are due to declines in the heat capacity of extracellular enzymes as predicted by thermodynamic theory, or due to simultaneous declines in soil moisture. It is also uncertain whether oxygen limits decomposition rates at high water contents. Here we present results from a full factorial experiment using organic arctic soils incubated at high temperatures (25 and 35 degrees C), a wide range of water-filled pore space WFPS (15, 30, 60, 90%), and contrasting oxygen concentrations (1 and 20%). We found support for the hypothesis that decomposition rates increase at high temperatures provided enough moisture and oxygen is available for decomposition. Furthermore, we found that decomposition rate is mostly limited by oxygen concentrations at high moisture levels; even at 90% WFPS, decomposition proceeded at high rates in the presence of oxygen. Our results suggest an important degree of interactions among temperature, moisture, and oxygen in determining decomposition rates at the soil-core scale.

1 Introduction

The physical environment has a strong control on soil organic matter dynamics by modulating the rates of biological activity and therefore the rates at which organic matter decomposes. Hence, environmental change produced by global warming or changes in land use, can significicaly affect organic matter decomposition rates and the capacity of soils to store carbon (Trumbore, 1997; Schlesinger and Andrews, 2000; Davidson and Janssens, 2006; Luo et al., 2016).

Among different environmental factors, temperature, moisture, and oxygen levels in soils have a strong control on the rate of soil organic matter (SOM) decomposition (Greenwood, 1961; Bunnell et al., 1977; Swift et al., 1979; Skopp et al., 1990; Davidson et al., 2012; Moyano et al., 2013). Yet, there are still large uncertainties in our understanding on how to model environmental controls on decomposition rates. For instance, many different functions have been previously proposed to represent environmental controls on decomposition rates, most functions disagree at the extremes of the temperature and moisture ranges, and it is difficult to select appropriate functions due to large uncertainties in available data (Sierra et al., 2015b).

In particular, there is uncertainty about the shape of decomposition functions at high temperature levels. Traditional Arrhenius kinetics predict that rates of decomposition increase monotonically as temperature increases (Sierra, 2012), a behavior well supported by thermodynamic theory, and in particular by its second law (Reif, 2009). However, an important number of biochemical studies shows that at a certain temperature threshold, generally above 45°C, enzymes denature and lose their capacity to catalyze reactions, slowing down rates of substrate consumption (Fields, 2001). Hobbs et al. (2013) and Schipper et al. (2014) suggest that this temperature limit for enzyme denaturation may be too high to be relevant in soils, and propose an alternative thermodynamic theory that predicts a lower temperature threshold when decomposition rates reach a maximum. Their macromolecular rate theory (MMRT) is based on the idea that the activation energy in the Arrhenius equation is temperature dependent and related to negative changes in the heat capacity of enzyme-catalyzed reactions.

Both enzyme denaturalization and MMRT operate at the enzyme-substrate level where single reactions occur, and assume that other environmental factors such as moisture remain constant as temperature increases. At larger spatial and temporal scales though, multiple reactions occur simultaneously at different rates, and different environmental factors interact with temperature. For instance, there is large empirical and theoretical evidence showing that interactions with soil moisture lead to strong changes in decomposition rates not predicted by changes in temperature alone (Bunnell et al., 1977; Davidson and Janssens, 2006; Sierra et al., 2015b; Tucker and Reed, 2016; Zhou et al., 2016).

Soil moisture plays two contrasting roles as a modulator of decomposition rates. On the one hand, soil water solubilizes substrates and increase their availability in active microbial sites through diffusion. On the other hand, as moisture increases it fills up available pore spaces and reduces oxygen levels necessary for aerobic microbial activity (Skopp et al., 1990; Moyano et al., 2013; Manzoni et al., 2014). Oxygen exerts an important control on the speed of aerobic decomposition for its role as an electron acceptor in the mineralization of SOM (Greenwood, 1961; Keiluweit et al., 2016). As moisture increases in soils, aeration and oxygen levels inevitably decrease.

Progress in understanding multiple-factor effects on SOM decomposition has been hindered by a paucity of experimental research (Dieleman et al., 2012; Leuzinger et al., 2011; Zhou et al., 2016). Full factorial experiments with multiple factors and levels are rare, even though they provide basic understanding on the independent and combined effects of environmental factors on decomposition.

Here, we use a full-factorial incubation experiment in combination with model-data integration to address the questions: i) do decomposition rates remain high at high temperatures provided moisture and oxygen are not limiting?, ii) do decomposition rates remain high at high moisture levels provided oxygen and temperature are not limiting? These questions are important because they provide insights about the best possible model structures required to represent SOM decomposition at extreme environmental conditions, and in light of global environmental change.

2 Methods

2.1 Soils and incubation experiment

We developed a full factorial incubation experiment with the manipulated treatments being temperature (25, 35 °C), soil water content (15, 30, 60 90% water-filled pore space), and oxygen concentration in the pore space (1 and 20%) of soil cylinders containing 450 g of homogenized soil. Organic soil was collected from the A horizon of a boreal forest dominated by black spruce at the Caribou Poker watershed in central Alaska, USA (65° 9' 21.365" N, 147°, 29', 28.74" W). The soil is classified as a *Histic Pergelic Cryaquept* in a Gilmore silt loam series from the United States Department of Agriculture Natural Resource Conservation Service system. It has a depth of 1 m fallowed by permafrost, and a water table depth of 20 cm. The carbon (C) content of a subsample of the soil used for incubations was 46.9 ± 0.1 mg C g^{-1} soil. We chose an arctic soil for this experiment because its high organic matter content avoids potential substrate limitations during incubations, and the low temperatures at which its microbial community is constantly exposed facilitates the possibility of observing strong responses at the extreme of the temperature range. This soil is identical as the one used in a companion paper (Sierra et al., 2015a), with the exception that in that publication we used only one single treatment to illustrate results from an identifiability analysis, while here we report data from the complete full factorial experiment.

Prior to the incubations, the soil was homogenized, passed through a 2 mm sieve, and large roots ($>$ 2 mm diameter) were removed. Four replicates per treatment were placed in two climate chambers at a constant temperature each. The bottom of each column was connected to an air inlet system that continuously flushed soil columns from the bottom at a rate of 30 ± 3 ml min^{-1} with air of known oxygen concentration (1 or 20 %). The headspace exiting each column (after passing through the soil) was connected to an automated multiport stream selection valve, and then analyzed for CO_2 using an infrared gas analyzer (LI-6262 LI-COR Inc., Lincoln, USA). Moisture loss ($\sim$1 g per day per cylinder) due to continuous flushing of dry air was compensated by adding water to replace lost of mass once every week. Additional details about the system can be found in Malghani et al. (2013).

2.2 Statistics and model optimization

Treatment means of total respired CO_2 from the 35-day incubation period (total sum for each cylinder) were compared using analysis of variance F-statistic. We used a linear fixed effects model using as independent variables the three independent treatments as well as their combination.

To evaluate the effect of the different treatments on decomposition rates, we used a simple two-pool model. In a previous analysis, we found that for incubation data no more than 3 or 4 parameters can be optimized simultaneously without encountering identifiability problems (Sierra et al., 2015a). When the number of parameters to identify is larger and the number of observations low, the identifiability problem results in collinearity of the parameters. This means that changes in the value of one parameter can be compensated by changes in the value of another parameter without any effect in predicting the observed data. In these cases, multiple parameter sets predict equally well the data, and it is not possible to uniquely identify the best underlying mechanisms that explain the observations (Soetaert and Petzoldt, 2010; Sierra et al., 2015a). For this reason, we chose a simple model that has three main parameters and is expressed as

$$\frac{d\boldsymbol{C}}{dt} = \xi \cdot \begin{pmatrix} -k_1 & 0 \\ 0 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} C_1 \\ C_2 \end{pmatrix}; \quad \boldsymbol{C_0} = C_0 \cdot \begin{pmatrix} \gamma \\ 1-\gamma \end{pmatrix}, \tag{1}$$

where the amount of C in the system is stored in pools C_1 and C_2 with corresponding decomposition rates k_1 and k_2. The initial amount of carbon in the system C_0 is partitioned according to a proportion γ, and the environmental term ξ is a product of three functions that depend on the environment $f(T)$, $f(W)$, and $f(O)$ such that

$$\xi = f(T) \cdot f(W) \cdot f(O) = Q_{10}^{\frac{T-10}{10}} \cdot \frac{W}{K_W + W} \cdot \frac{O}{K_O + O}. \tag{2}$$

Notice that equation (2) is a simplified version of the DAMM model of Davidson et al. (2012).

We optimized two versions of the model of equation (1) to the observed data from the experiment using a Bayesian approach (Soetaert and Petzoldt, 2010). First, we optimized parameters of each treatment independently and setting $\xi = 1$. In this way we can observe possible trends in the parameters as a function of the environmental variables. Second, we pooled data from all treatments together and fitted the full model with ξ expressed as in equation (2).

All analyses were performed in R (The R Foundation for Statistical Computing, Vienna), and all code and data to reproduce our results are available as supplementary material.

3 Results

Total respired CO_2 after 35 days of incubation showed a strong treatment effect for the three main variables (F-statistic p-value < 0.001 for the main treatment effects). Interactions among all treatment levels showed statistically significant effects (F-statistic p-value $= 0.0505$) suggesting that CO_2 efflux for this soil responded to different combinations of the treatment levels (Figure 1). A statistically significant interaction (F-statistic p-value < 0.001) was also found between the soil moisture and oxygen treatments. The largest amount of respired CO_2 was observed at the treatment with the highest temperature, moisture and oxygen levels (35, 90, 20), while the lowest amount was observed at the treatment with the lowest values for these variables (25, 15, 1), confirming that these three environmental variables collectively exert a strong and significant control on CO_2 production. Total respired CO_2 during the experiment did not decrease at high temperature levels.

The results of the first optimization showed that temperature consistently increased decomposition rates of both fast and slow pools at similar moisture and oxygen levels (Figure 2). Under higher temperatures, we also observed a larger proportion of carbon being mineralized faster and contributing to the initial respiration pulse (parameter γ). At lower oxygen levels, decomposition rates were slower than in similar treatments with higher oxygen levels.

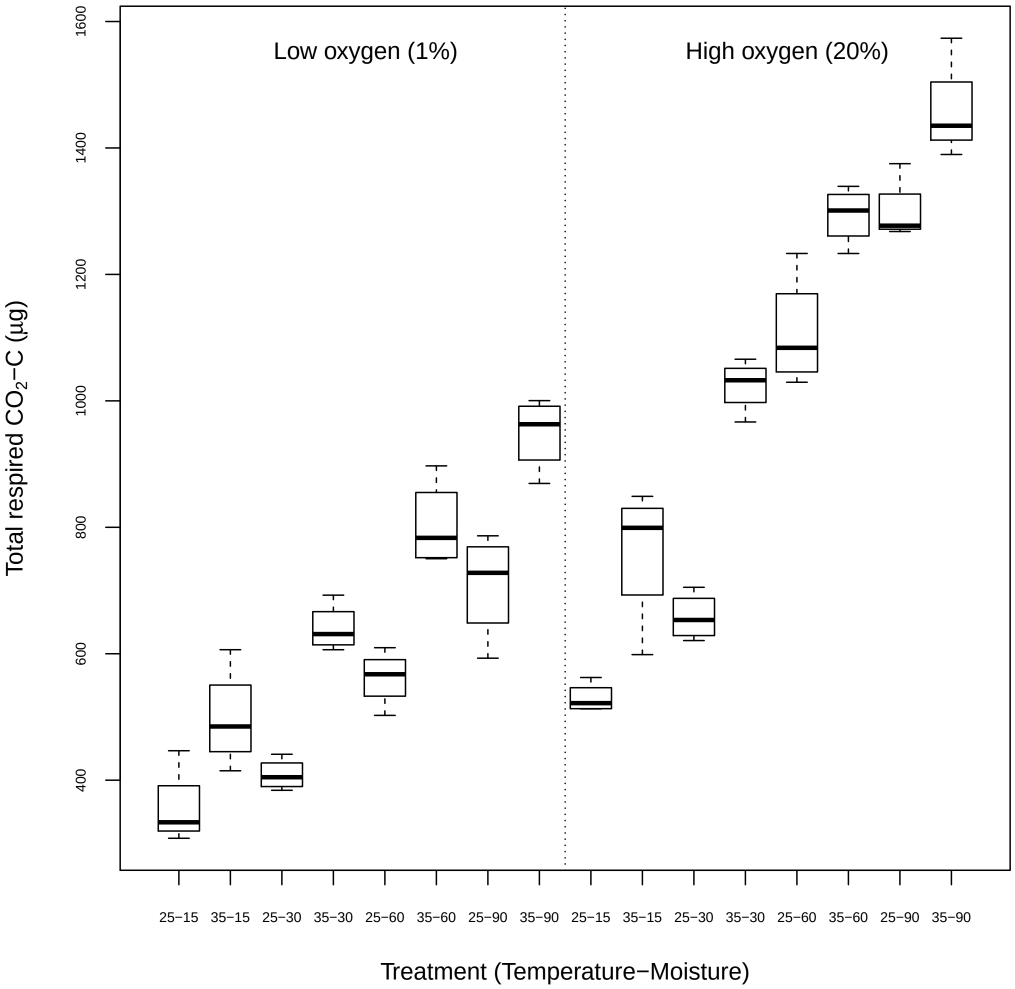

Figure 1. Total respired CO_2 integrated over the length of the experiment by treatment. Numbers in the treatment level represent the level of temperature (degrees Celsius) and soil water content (%).

Although we estimated only three parameters, there were already identifiability issues in this optimization (cf. Sierra et al., 2015a), which means that the obtained values of some parameters can be compensated by proportional changes in the values of other parameters. The second optimization with the full dataset reduced this collinearity problem.

The optimization of the full dataset did not provide evidence of strong collinearity as indicated by the low correlations among posterior values (Figure 3). The obtained posterior values indicate a strong sensitivity of ξ to temperature, and sensitivity with respect to moisture and oxygen at lower levels of these values.

Using the obtained mean values of the posteriors with their respective 25-75% uncertainty ranges, we calculated and plotted the response functions $f(X)$ with their intrinsic sensitivities $\partial f(X)/\partial X$ (Figure 4). The optimized functions showed larger

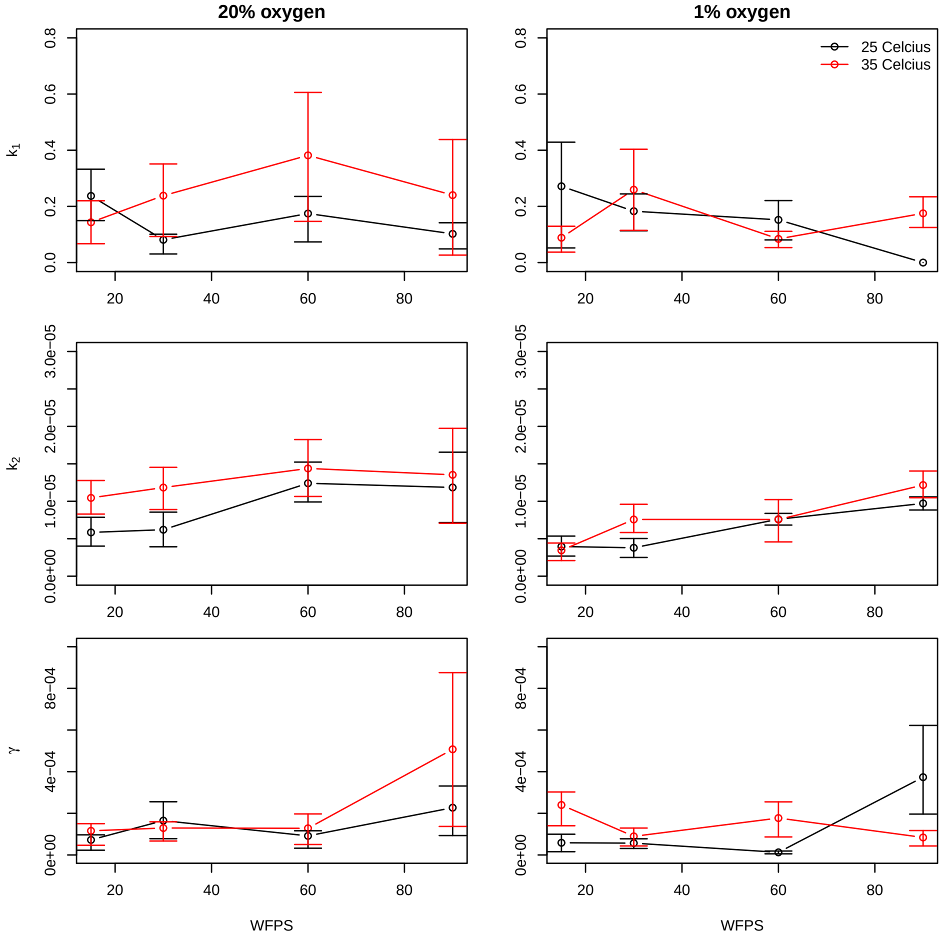

Figure 2. Results from the first optimization procedure for the two pool model applied to each experimental treatment independently. Parameters optimized were k_1: decomposition rate of fast pool, k_2: decomposition rate of slow pool, γ: fraction of the total initial carbon in the fast pool. The experimental treatments were water-filled pore space WFPS (15, 30, 60, 90 %), oxygen concentration (1, 20%), and temperature (25, 35° Celcius).

sensitivities with respect to temperature than with respect to moisture or oxygen. At the upper part of the temperature range, decomposition rates were predicted to increase as well as the intrinsic temperature sensitivity. Moisture and oxygen have both strong intrinsic sensitivities at the lower part of their ranges. Decomposition rates were highly sensitive at a narrow part of the oxygen range, while for moisture this range was wider (Figure 4).

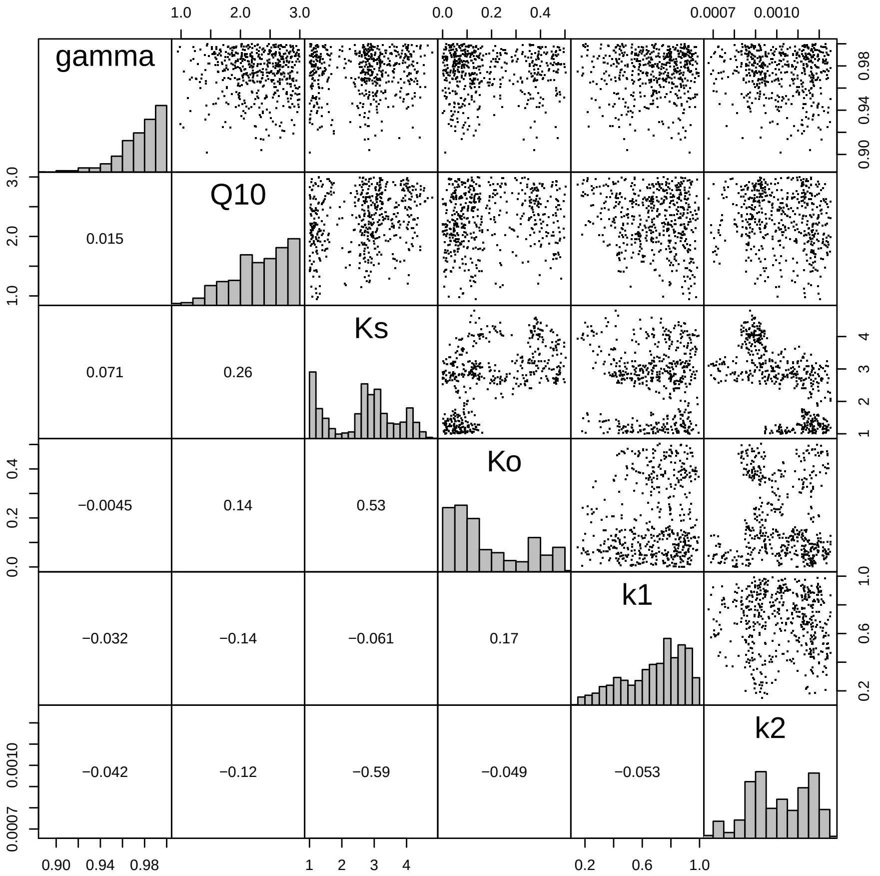

Figure 3. Posterior parameter values from the Bayesian optimization using the full model of equation (2). To avoid cluttering of the figure, only 1000 randomly samples values per posterior parameter set are plotted.

4 Discussion

The statistical comparison of the respiration data as well as the results from these two modeling exercises demonstrated strong interactions among three main environmental factors that control decomposition. The factorial nature of our experiment allowed us to calculate intrinsic sensitivities for these three environmental factors. Moreover, without controlled conditions, the effects of one variable would have been confounded by others. For example, increases in temperature almost always are accompanied by decreases in soil moisture, and increases in moisture are generally accompanied by decreases in soil oxygen concentrations. Our experimental design, with a continuous flow of oxygen through the soil column, helped us to control oxygen concentrations independent on moisture, which avoided possible confounding effects.

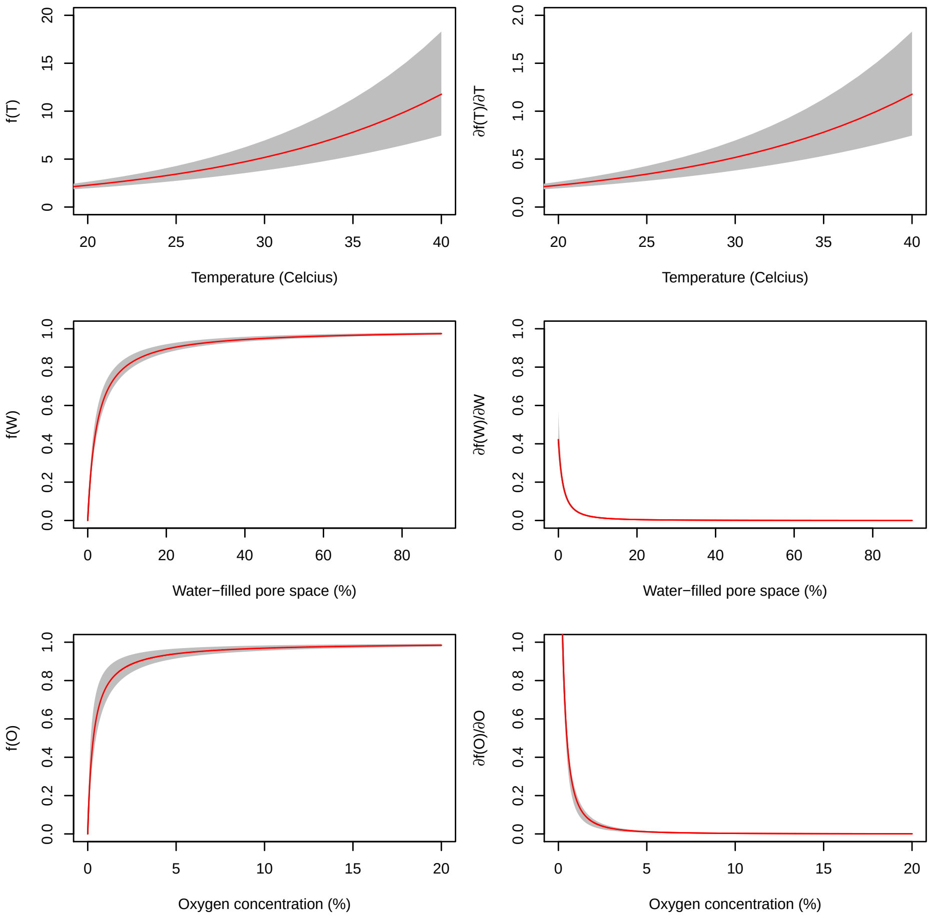

Figure 4. Shape of the response functions $f(T)$, $f(W)$, and $f(O)$ calculated with the values of the optimized parameters with their uncertainty, and their respective sensitivities $\partial f(T)/\partial T$, $\partial f(W)/\partial W$, and $\partial f(O)/\partial O$.

Our results support previous work on the control of these three environmental variables on decomposition (Bunnell et al., 1977; Davidson et al., 2012, 2014). In particular, decomposition rates at the soil-core scale are controlled by an interaction among three main environmental variables that generally change in concert with one another in the natural soil environment.

Tucker and Reed (2016) showed that the interaction between temperature and moisture play an important role for predicting soil respiration rates in dry soils. Similarly to our study, these authors did not find a decline in soil respiration rates at high temperatures. But rather, they found a strong interaction between an exponential function for temperature effects and a moisture function that reached a maximum at high moisture levels. This lack of decline of the moisture function is expected for dry soils that do not reach water saturation levels. The higher moisture range covered in our study shows more clearly that there is a decline at high moisture levels and it is mostly driven by oxygen availability.

Although our model has a parsimonious representation motivated partly by the available data, additional details may be included for its use with field observations. For instance, the additional functions in the DAMM model used to represent pore space from bulk density and temperature controls on the K_X terms (Davidson et al., 2012) can help to capture additional complexity under field conditions that are not necessarily relevant under laboratory conditions. The DAMM model, or a variant of it, can be used to represent the term $\xi(t)$ in a more complex model represented as a set of differential equations (e.g. equation 1) dynamically modifying a set of state variables (Sierra and Müller, 2015).

5 Conclusions

Based on the experimental data for this arctic soil and the model used, we conclude that decomposition rates can be high i) at high temperatures provided moisture and oxygen levels are not limiting, and ii) at high moisture levels provided oxygen concentrations are not limiting. We found no declines in decomposition rates at high temperatures as predicted by the MMRT. We interpret the mismatch of our results with the mentioned theoretical predictions as most likely due to differences in scale. We believe that at the scale of single enzyme-substrate pairs under controlled conditions (no changes in moisture levels) the predictions of the MMRT should still hold true (Hobbs et al., 2013; Schipper et al., 2014). At the level of a soil core or soil pit with simultaneous changes in moisture levels, strong interactions among temperature, moisture and oxygen levels override predictions at the scale of individual enzymes. These interactions exert a strong control on decomposition, and simultaneous changes of these variables under field conditions should determine the overall rate of decomposition in soils.

6 Code and data availability

Code and data necessary to reproduce all results from this manuscript are provided in the supplementary material. Furthermore, the soil incubation dataset used here is part of the soil incubation database (sidb) available as repository in GitHub (https://github.com/SoilBGC-Datashare/sidb).

Competing interests. The authors declare that they have no conflict of interest.

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