Linking temperature sensitivities of soil enzymes to temperature responses of different organic matter pools in the DAISY model

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Abstract

Soil organic carbon (SOC) losses under a changing climate are driven by the temperature sensitivity of SOC mineralization (usually expressed as Q_{10}, the multiplier of activity with 10 °C temperature increase). The activation energy theory (AET) suggests that, due to higher activation energies, the more complex the carbon, the higher is mineralization Q_{10}. However, studies on Q_{10} have been inconsistent with regard to AET. Measurements of potential soil enzymes activity Q_{10} even contradicted AET: Phenoloxidase (representing complex carbon) had consistently lower Q_{10} than the more labile xylanase and glucosidase. This study used two approaches of examining Q_{10} in SOC modeling: 1) Bayesian calibration (BC) and 2) using different measured enzyme Q_{10} as proxies for mineralization Q_{10} of different SOC pools. The SOC model was DAISY (S. Hansen et al., 2012). BC informed Q_{10} by field measured data, while the second approach tested if directly using enzyme Q_{10} (of phenoloxidase, glucosidase and xylanase) for DAISY pools improved simulation results. Both approaches used the temperature sensitive measurements of CO_2 evolution and soil microbial biomass. The measured enzyme Q_{10} were from field manipulation experiments with bare fallow and vegetated plots in the two regions of Kraichgau and Swabian Jura in Southwest Germany. The enzyme-derived Q_{10} were used for modelling those fields and furthermore for in-situ litterbag decomposition experiments at 20 sites in the same region. Two further laboratory experiments with temperature manipulation were included: an incubation of the field residues into soil and an incubation of bare soil from the start and year 50 of a long duration bare fallow (from Ultuna). The BC made use of CO_2 and microbial data to inform about the range of Q_{10} of different carbon pools for the individual experiments and combined data.

The BC of the residue incubation experiment constrained Q_{10} for metabolic (~3) and structural litter (~2). Estimated 95% credibility intervals did not overlap. The BC for Ultuna could constrain the slow and fast SOC pool with Q_{10} ~2.8 and ~3, respectively, but credibility intervals of both pools overlapped. The Q_{10} of field experiments, which had most abundant data, could not be constrained by BC, probably because their annual temparature variability was too low. However, the model errors of the field experiment could be reduced by the second approach, when the Q_{10} of phenoloxidase was used for to the structural litter pool as well as for the fast and slow SOC pools. Thus regional enzyme Q_{10} improved the model fit but only for regional simulations. Therefore, they

could be useful proxies when natural temperature range is too small to inform temperature sensitivity by BC. Any trends found in this study contradicted AET, both from measured enzymes and BC of the incubation experiments. This calls for alternative Q_{10} hypotheses and the need for individual Q_{10} values for different SOC pool rather than a general one. BC approaches would benefit from a wider temperature range of field experiments and understanding what causes variable enzyme Q_{10} could help to improve future SOC models.

Experiment overview:

A number of field and laboratory incubation experiments were combined to test the hypotheses, a) whether pool specific Q_{10} in models should be used and b) whether measured enzyme Q_{10} would represent a proxy for pool specific Q_{10}.

Table 1 Soil characteristics of the manipulation experiments used in this study, according to IUSS Working Group WRB 2007.

Study Site or origin of soil material/ Experiment no.	UTM Degrees Latitude	UTM Degrees Longitude	Mean annual temperature (°C)/ precipitation (mm)	Study type	Soil type	Clay (%)	Silt (%)	Initial SOC (%)	Types of available measurements
Kraichgau 1 **/1+2**	48.928517	8.702794		Field manipulation (fallow/ vegatated)	Stagnic Luvisol	18	77	0.90	SOC, SMB-C, soil CO_2
Kraichgau 2 **/1+2**	48.927748	8.708884	9.4/890	Field manipulation (fallow/ vegatated)	Stagnic Luvisol	18	80	1.04	SOC, SMB-C, soil CO_2
Kraichgau 3 **/1+2**	48.927197	8.715891		Field manipulation (fallow/ vegatated)	Stagnic Luvisol	17	81	0.89	SOC, SMB-C, soil CO_2
Swabian Jura 4 **/1+2**	48.527510	9.769429		Field manipulation (fallow/ vegatated)	Calcic Luvisol	38	56	1.78	SOC, SMB-C, soil CO_2
Swabian Jura 5 **/1+2**	48.529857	9.773253	7.5/1040	Field manipulation (fallow/ vegatated)	Anthrosol	29	68	1.95	SOC, SMB-C, soil CO_2
Swabian Jura 6 **/1+2**	48.547035	9.773176		Field manipulation (fallow/ vegatated)	Rendzic Leptosol	45	51	1.91	SOC, SMB-C, soil CO_2
Kraichgau and Swabian Jura **/3**	Experiment 3 adjacent to experiment 1 and 2 fields			Field litterbag incubation					litter C
Crop-litter lab incubation **/4**	48.739626	8.931971	NA	Lab incubation of crop residues in bulk soil	Haplic Luvisol	23	75	2.25	Soil CO_2
Ultuna **/5**	59.821879	17.656348	NA	Lab incubation of bulk soil	Eutric Cambisol	37	41	1.50	soil C

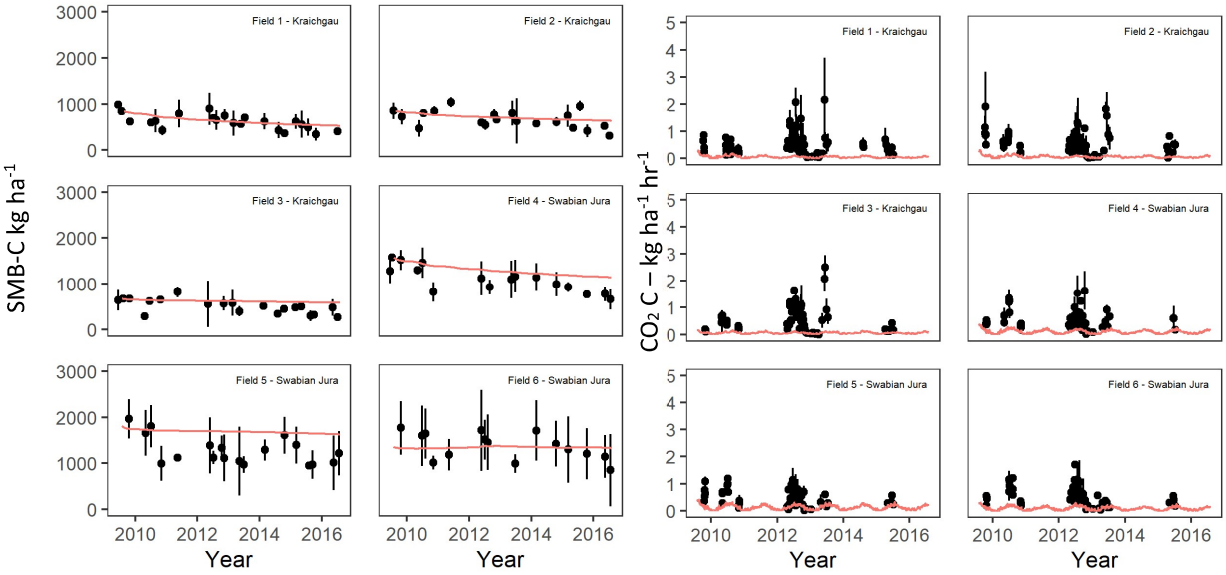
UTM = Universal Transverse Mercator reference system; [A] (Eshonkulov et al., 2019); [B] (Menichetti et al., 2013)

Initial simulations with the standard Q_{10} of 2 from Daisy:

Experiment 1- bare soil

1.1 SMB-C

1.2 CO_2 C



Experiment 2 - vegetation plots

2.1 SMB-C

2.2 CO_2 C

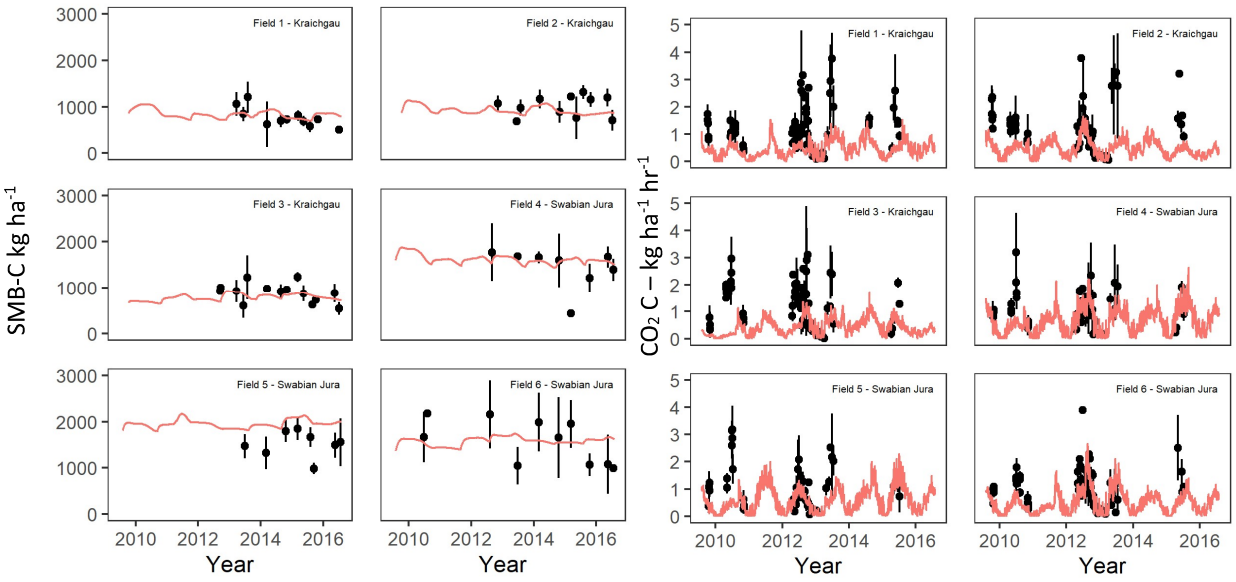


Figure 1 Simulations of SMB-C (left) and CO_2 (right) for experiment 1 (top) and experiment 2 (bottom) with the 0 hypothesis (all Q_{10} equal 2).

Experiment 3 - regional litterbag incubation:

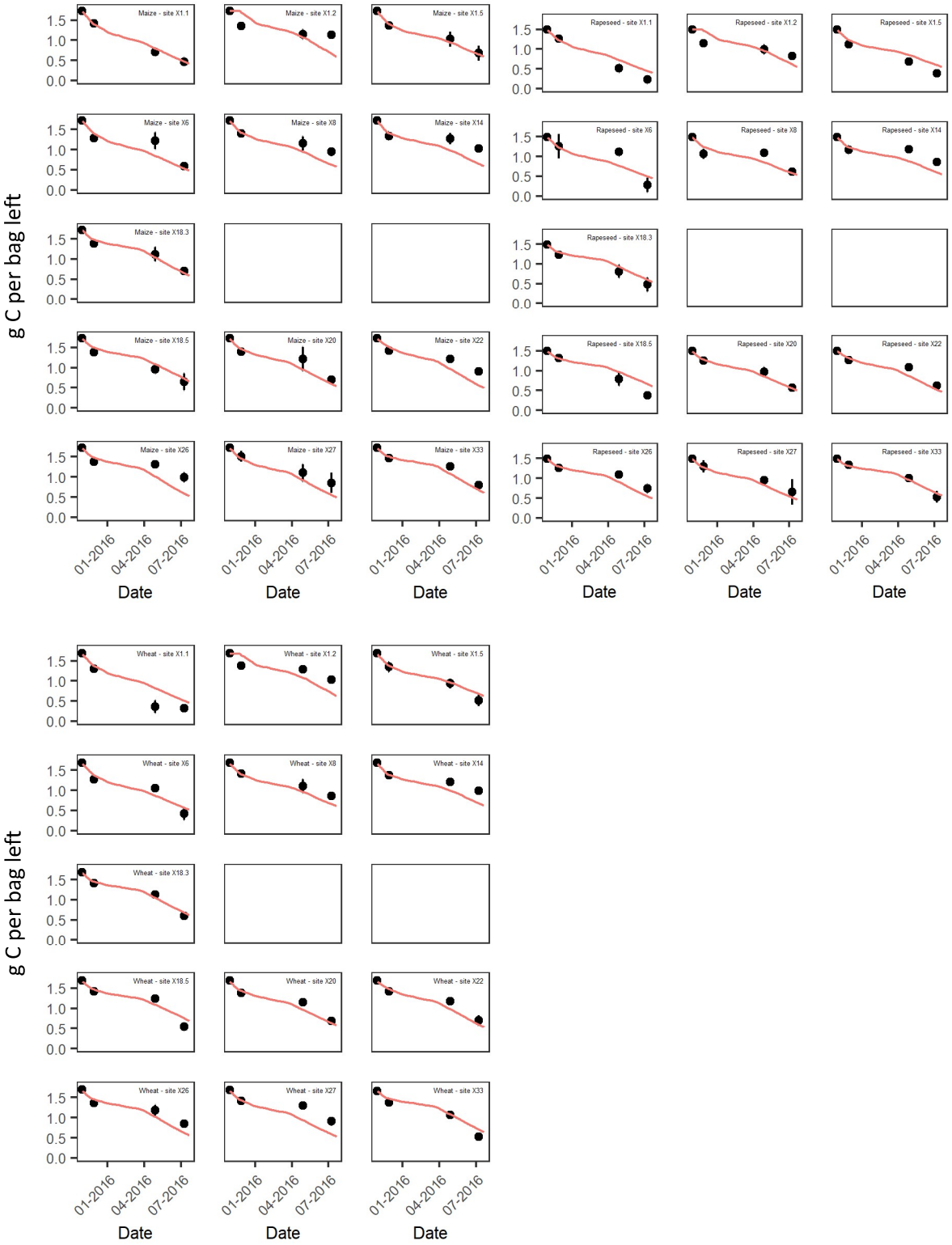


Figure 2 Simulations of remaining C in litterbags of experiment 3 with the 0 hypothesis (all Q_{10} equal 2).

Experiment 4 - crop-litter incubation

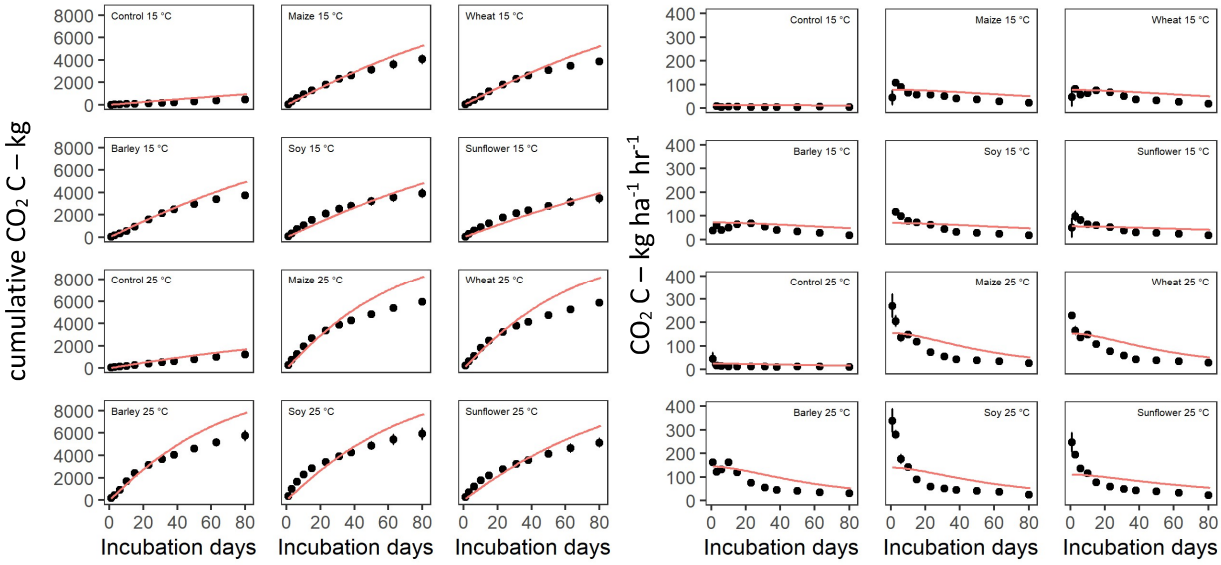


Figure 3 Simulations of experiment 4. Displayed are cumulative CO_2 evolution (top-left), rate of CO_2 evolution (top-right), with the 0 hypothesis (all Q_{10} equal 2).

Experiment 5 - Ultuna fallow soil incubation

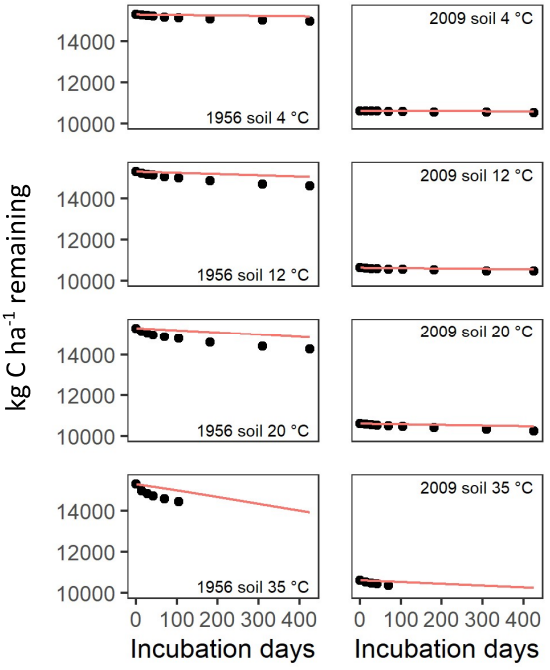


Figure 4 Simulations of remaining C of experiment 5 with the 0 hypothesis (all Q_{10} equal 2).

Bayesian calibration inferred Q_{10}:

In order to test pool specific Q_{10}, a clear definition of pools in the Daisy model was necessary. Division of pools was done as follows: litter by the lignin to nitrogen (L/N) ratio (Parton et al., 1987), and SOM by the ratio of aliphatic/aromatic-carboxylate carbon (Laub et al., 2020).

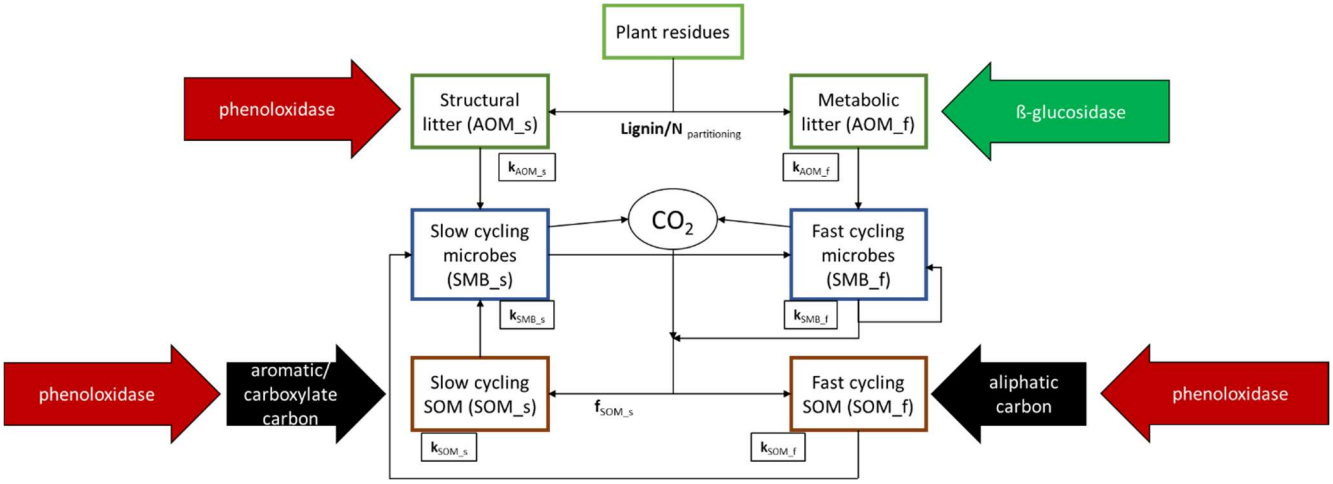


Figure 5 Structure of the adapted Daisy soil organic matter model, as used in this study. The partitioning of litter into structural and metabolic is controlled by the lignin to nitrogen (L/N) ratio, kSOM, kSMB and kAOM are turnover rates of the pools and fSOM_slow is the amount of recalcitrant materials from soil microorganisms Measured enzyme Q_{10} of phenoloxidase and ß-glucosidase were applied as pool specific Q_{10}, compared to a standard Q_{10} of 2 for all pools.

Next to Bayesian calibration, field measured enzyme Q_{10} were applied as pools specific Q_{10}. They were measured in experiment 1 (Ali et al., 2015).

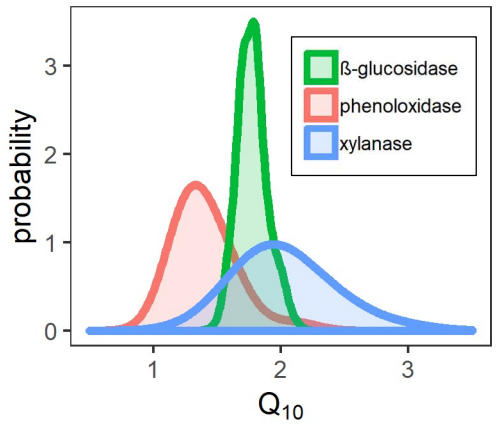


Figure 6 Distribution densities of measured ß-glucosidase, xylanase and phenol/peroxidase Q_{10}, from experiment 1 and 2, that matched the quality criteria of a modelling efficiency >0.7 and were used in this study. The Median values were applied as pool specific Q_{10}. Those were a Q_{10} of 1.35 for phenoloxidase and 1.82 for ß-glucosidase. Xylanase, with a Q_{10} of 1.98 was to close to the standard of 2 and not tested separately.

Table 2 Performance statistics of the hypothesis 0 model, using a standard Q_{10} for all pools. The performance of simulated compared to measured values within the different experiments were assessed. Used were measurements of soil microbial biomass C (SMB-C), CO_2 evolution from the soil remaining C in litterbags and remaining C of incubated soil Squared bias (SB), nonunity slope (NU) and lack of correlation (LC) are displayed as their percentage of the mean squared deviation. The properties of each experiment are explained in detail in Table 1.

Experiment	Property	Unit	RMSD	R^2	SB (%)	NU (%)	LC (%)
1	SMB-C	kg C ha^{-1}	282.9	0.67	22.6	10.5	67
1	CO_2 evolution	kg CO_2 C ha^{-1} hr^{-1}	2.48	0.10	70.4	27.3	2.3
2	SMB-C	kg C ha^{-1}	363.4	0.45	1.8	19.3	78.9
2	CO_2 evolution	kg CO_2 C ha^{-1} hr^{-1}	18.57	0.07	74.5	25.3	0.2
3	C in litterbag	g C per bag	0.186	0.72	2.9	11.8	85.3
4	CO_2 evolution	kg CO_2 C ha^{-1} hr^{-1}	39.9	0.61	6.8	3.6	89.6
5	C remaining	kg C ha^{-1}	213.9	0.99	51	16.8	32.1

Performance statistics indicated that some simulations were biased with standard parameters, therefore, Bayesian calibration let the parameters vary at the same time as Q_{10} values, to account for potential experiment bias due to unsuitable parameter values. Experiment 1 to 3 were combined in Bayesian calibration, as they were in the same region.

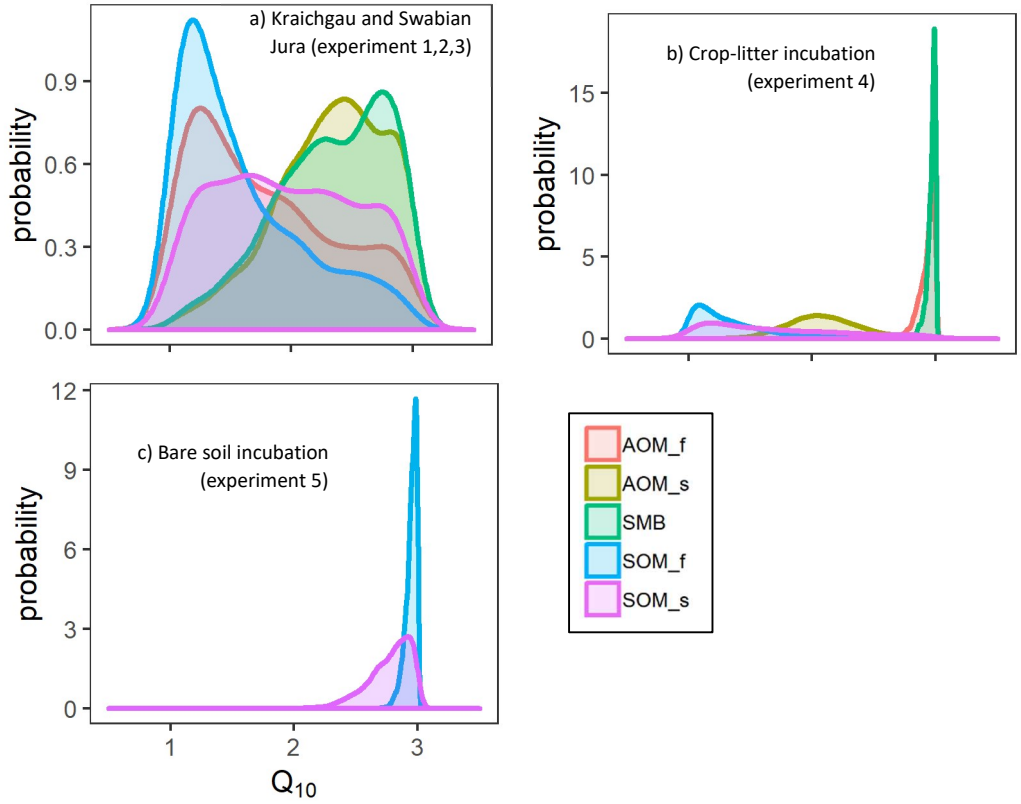


Figure 7 The Q_{10} values of different SOM pools which were assigned by the three individual Bayesian calibrations when all other Daisy parameters were allowed to vary at the same time (a = combining agricultural bare fallow plots, vegetation plots and a litterbag experiment , all in the field, Exp. 1,2 and 3; b = incubating crop-litter at different temperatures in the laboratory, Exp. 4; c = incubation of long term fallow soil from Ultuna using soil of year 0 and 54, Exp. 5).

Bayesian calibration could only constrain laboratory incubation experiments, but not the field experiment. Some of the inferred Q_{10} values were significantly higher than the Daisy standard of 2.

Table 3 Improvement of simulations by using enzyme Q_{10} as pool specific Q_{10}. Displayed are the root mean squared deviations (RMSD) as percentage of the RMSD of the 0 hypotheses (all Q_{10} being 2) for measurements of soil microbial biomass C (SMB-C), CO_2 evolution from the soil, remaining C in litterbags and remaining C of incubated fallow soil. Additionally, the numbers in parentheses represent the Akaike information criterion (AIC).

Experiment	Hypothesis / Property	**Standard 0 hypothesis, all Q_{10} = 2**	**Using enzyme Q_{10} as pool specific Q_{10}**
1	SMB-C	100 (1485)	90 (1466)
1	CO_2 evolution	100 (1784)	91 (1715)
2	SMB-C	100 (909)	96 (908)
2	CO_2 evolution	100 (3196)	93 (3139)
3	C in litterbag	100 (-60)	97 (-63)
4	CO_2 evolution	100 (1329)	109 (1357)
5	C remaining	100 (518)	111 (530)

Applying measured enzyme Q_{10} as pool specific Q_{10} reduced RMSD and AIC for the field experiments, but not for the laboratory incubation experiments. The results suggest, that Q_{10} are not fix, and should be represented as pool specific Q_{10}. Varying optimal Q_{10} between experiments for the same defined pool, as inferred by Bayesian calibration, suggested that Q_{10} is not mainly an intrinsic substrate property. Instead, it seems to strongly depend on experimental conditions. In this context, measured enzyme Q_{10} could serve as a proxy for regionally different pool specific Q_{10} values. However, as enzyme Q_{10} is expensive to measure, the driving factors behind differences in pool specific Q_{10} need to be better understood.

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