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Enzyme inactivation and microbial energy limitation explain negative temperature response of recalcitrant soil carbon decomposition

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SOM decomposition & temperature: contradictory conclusions

➤ Arrhenius theory:

$$k = a \cdot \exp(-E_a / RT)$$

E_a = activation energy

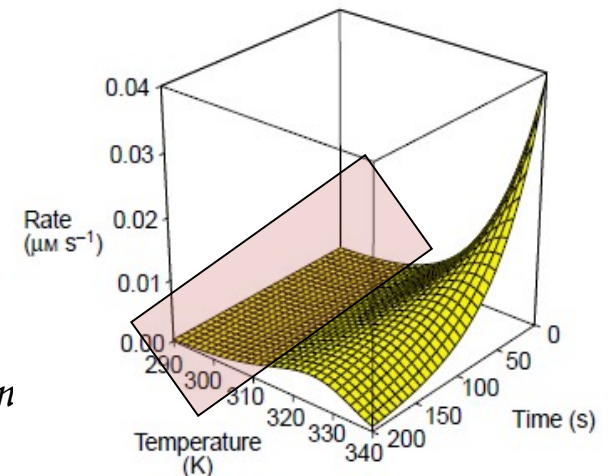
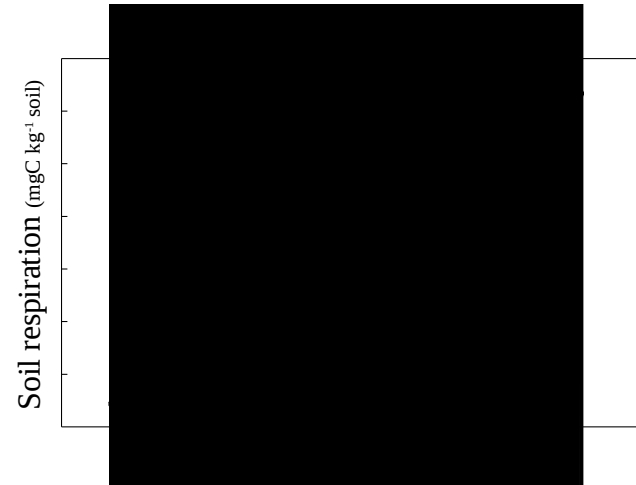
Increasing temperature response with increasing recalcitrance of OM (higher E_a)

➤ Short-term lab incubations:

-Support Arrhenius theory

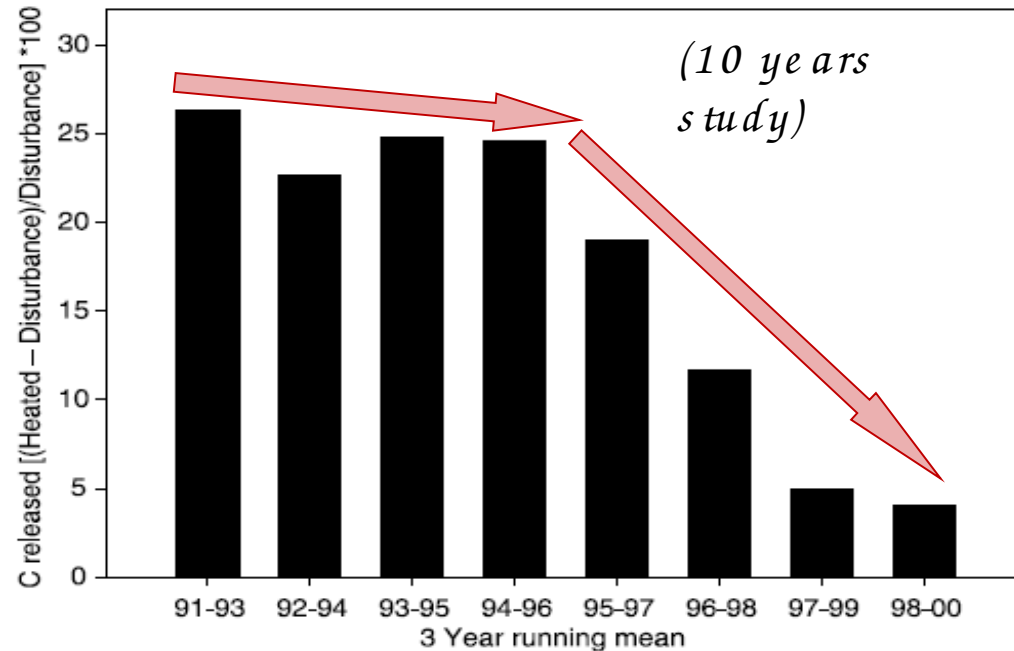
'Increased SOM decomposition & enzyme activity with temperature un-temperature'

(Kirschbaum 1995; Kätterer et al. 1998; Bol et al. 2003; Fierrer et al. 2003; Waldrop & Firestone 2004; Koch et al. 2007; Yuste et al. 2007; Conant et al. 2008).



SOM decomposition & temperature: contradictory conclusions

➤ Long-term soil warming field experiments:



(Mellilo et al. 1998)

- Luo et al 2001 (1 yr); Eliasson et al 2005 (10 yrs); Bradford et al 2008 (15 yrs).

**➤ no effect of temperature in long run, no negative effect of temperature on C stocks;
even positive effect! (Phillips et al 1998; Sanderman et al 03)**

Objective of study:

➤ ***To reconcile these contradictory conclusions***

➤ ***Possible missing points in literature***

1) Energy limitation of microbes

2) Temperature dependent enzyme inactivation

Inactivation = Enzyme is unable to catalyse a particular reaction, irreversible

➤ ***We developed a simple model and then tested it with an experiment.***

Model:

1) **SOM decomposition:**
$$\frac{dSOM}{dt} = -k_{act} \times E$$

Temperature-dependent specific enzyme activity

$$k_{act} = A_{act} \cdot \exp^{-EA_{act} / RT}$$

2) Dynamics of enzymes :

$$\frac{dE}{dt} = -k_{inact} \times E + k_f \times C_f$$

Temperature-dependent enzyme inactivation

$$k_{inact} = A_{inact} \cdot \exp^{-EA_{inact} / RT}$$

Production rate of enzymes

$$k_f = A_f \cdot \exp^{-EA_f / RT}$$

Model:

3) Dynamics of energy-rich fresh C:

$$\frac{dC_f}{dt} = \Phi C_f(t) - k_f \times C_f$$

➤ At steady state for FOM pool (Cf) and Enzymes (E):

$$\frac{dC_f}{dt} = 0$$

$$\frac{dE}{dt} = 0$$



$$C_f^* = \frac{\Phi C_f(t)}{k_f}$$

$$E^* = \frac{\Phi C_f(t)}{k_{inact}}$$

At equilibrium the rate of SOM decomposition can be written as:

$$\left(\frac{dSOM}{dt} \right)^* = -k_{act} \times E^*$$

$$E^* = \frac{\Phi C_f(t)}{k_{inact}}$$

$$k_{act} = A_{act} \cdot \exp^{-EA_{act} / RT}$$

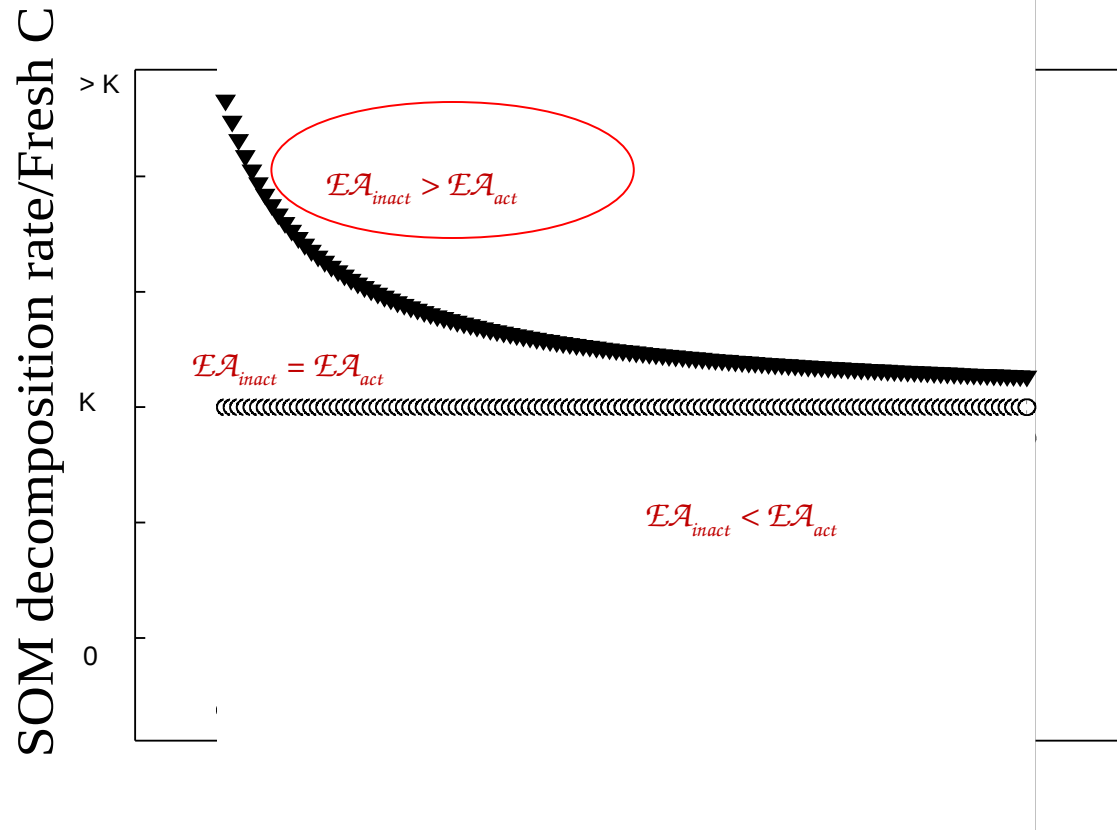
$$\left(\frac{dSOM}{dt} \right)^* = -\Phi C_f(t) \cdot K \cdot \exp^{\frac{EA_{inact} - EA_{act}}{RT}}$$

$$A_{act}/A_{inact} = K$$

➤ **Thus temperature response of SOM decomposition depends on difference of activation energies of enzyme activity and inactivation.**

Model Results:

$$\left(\frac{dSOM}{dt} \right)^* / \Phi C_f(t) = -K \cdot \exp \left(\frac{EA_{inact} - EA_{act}}{RT} \right)$$



➤ In enzymology, $EA_{inact} > EA_{act}$ has been shown for large number of enzymes

. See Daniel et al; 2010

➤ Thus we assume negative relationship between SOM decomposition and temperature.

Experimental test of theory

- ***The need to distinguish the plant derived (fresh energy) C from soil derived (SOM) C.***

$$\left(\frac{dSOM}{dt} \right)^* = -\Phi C_f(t) \cdot \frac{A_{act}}{A_{inact}} \cdot \exp \frac{EA_{inact} - EA_{act}}{RT}$$

- ***If soil derived C is lumped with fresh C, may confound the temperature response.***

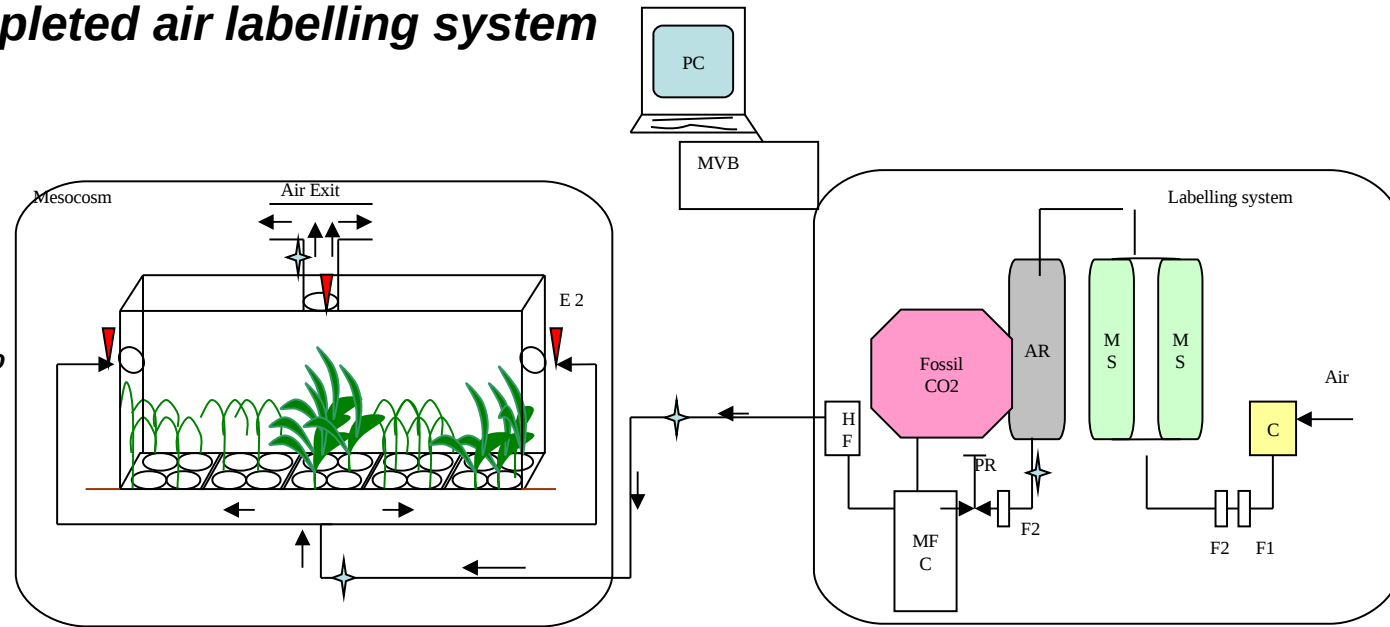
Labelling system & mesocosm

➤ Continuous ^{13}C depleted air labelling system

Air $\delta^{13}\text{C} = -38.55 \text{ ‰}$

Biomass $\delta^{13}\text{C} = -57.68 \text{ ‰}$

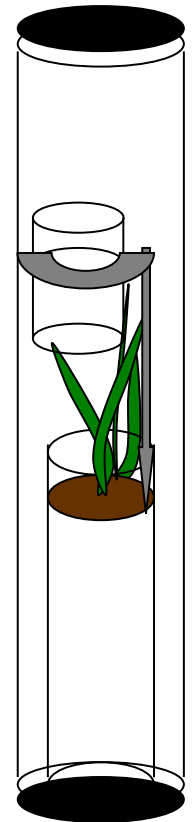
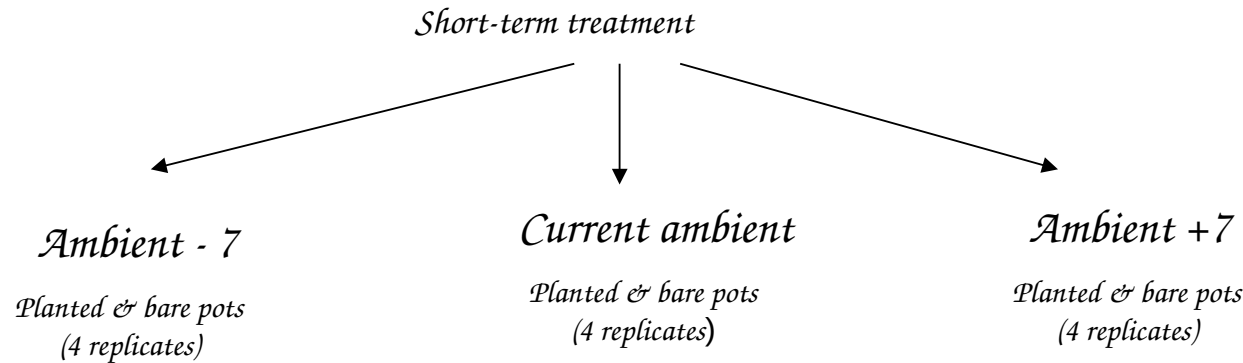
Duration = 479 days



Soil, plant & temperature treatments

- *A Cambisol from upland prairie*
- *10-40 horizon sampled & sieved (5mm)*
- *Put into PVC pots*
- *12 pots sown with *Lolium perenne* & 12 left bare*
- **2 types of temperature treatments for respiration measures**

1) Short-term (24 hrs) treatment under controlled chambers

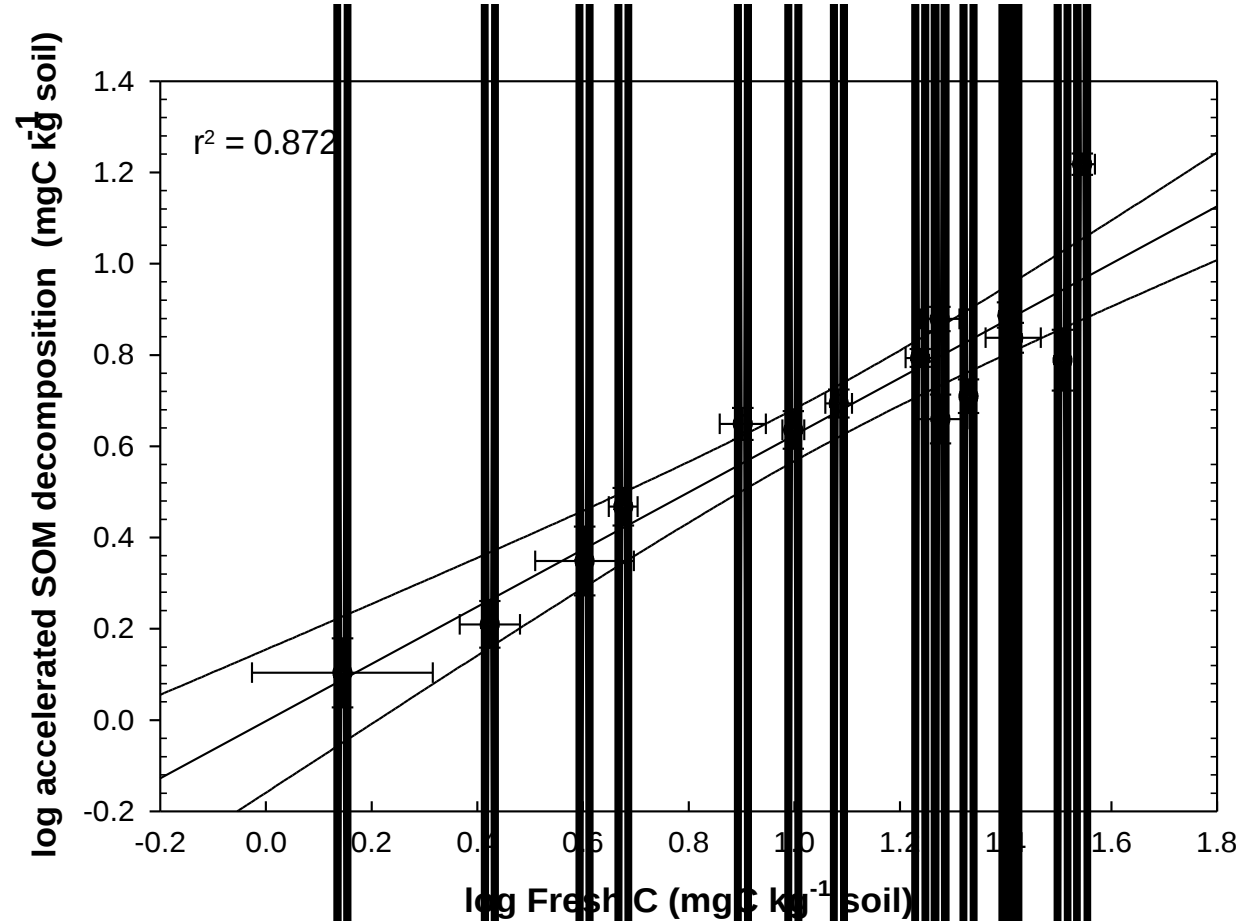


Placed for 24 hrs under controlled temperature

2) Seasonal temperature variation: Spring 2009 – Summer 2010

Results & Discussion:

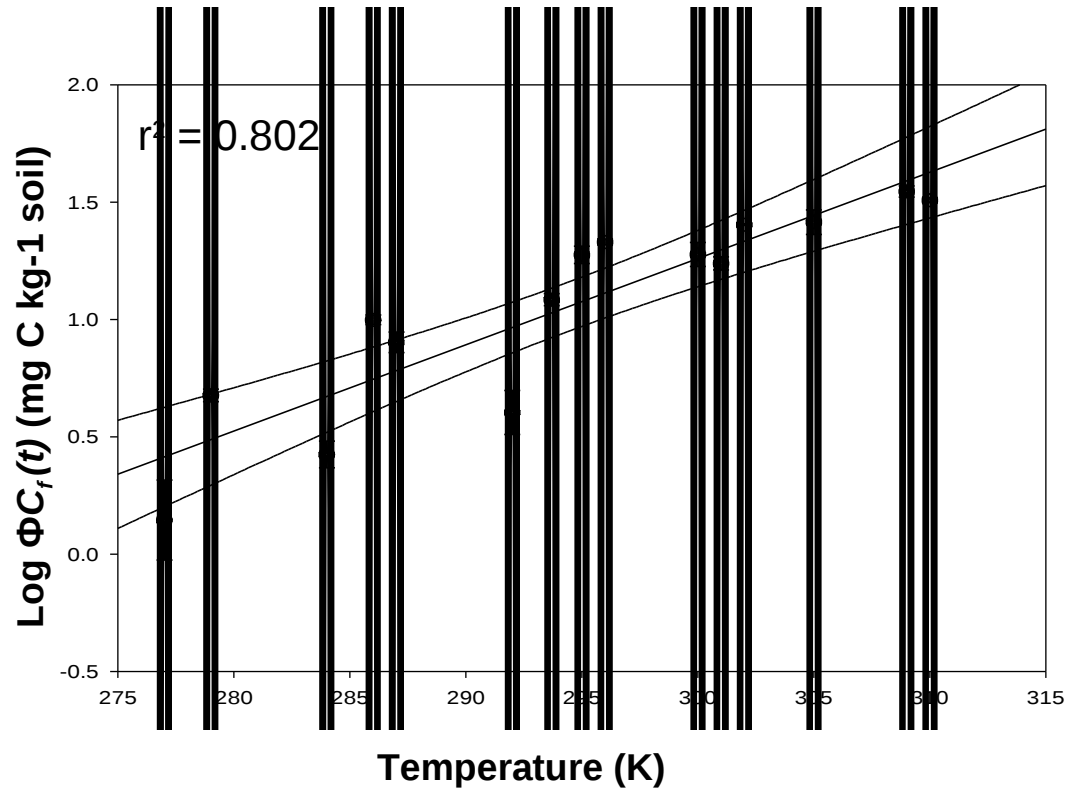
➤ *SOM decomposition of fresh C controlled by fresh energy supply*



The decomposition of SOM is limited by energy available to SOM decomposers as suggested by « Priming Effect » theory

Results & Discussion:

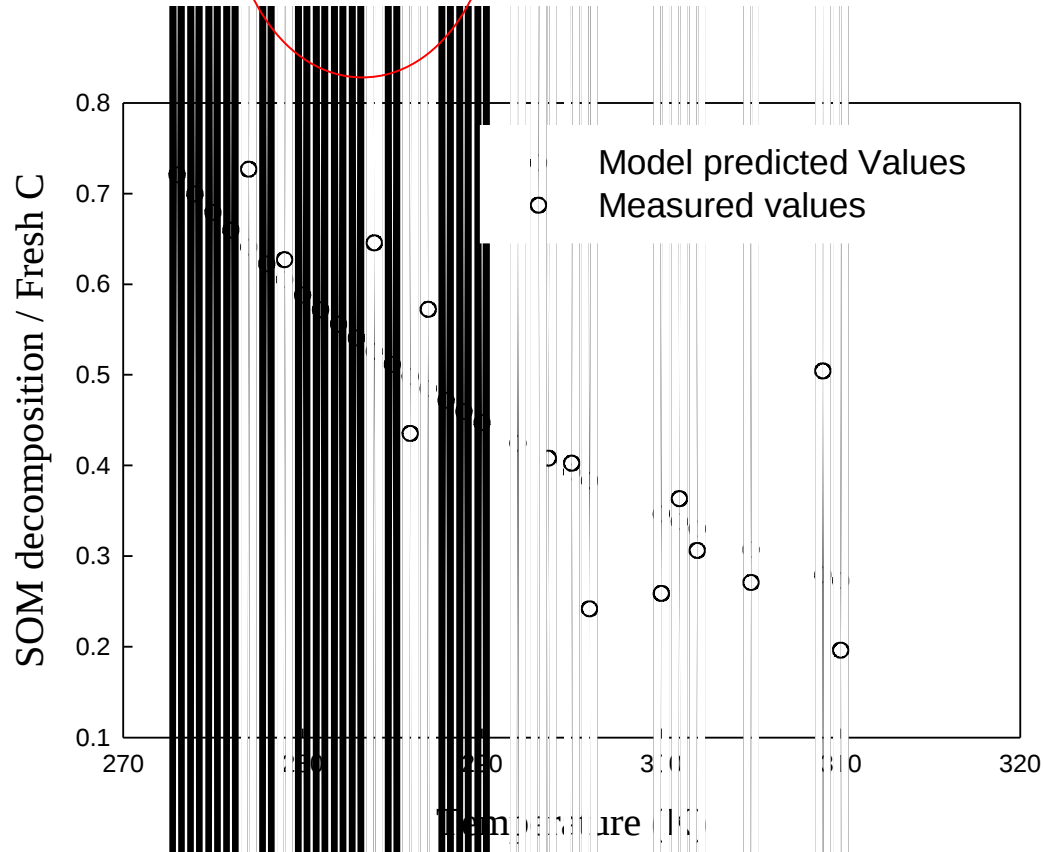
Temperature increases microbial consumption of fresh energy



Model Fit:

Equation:

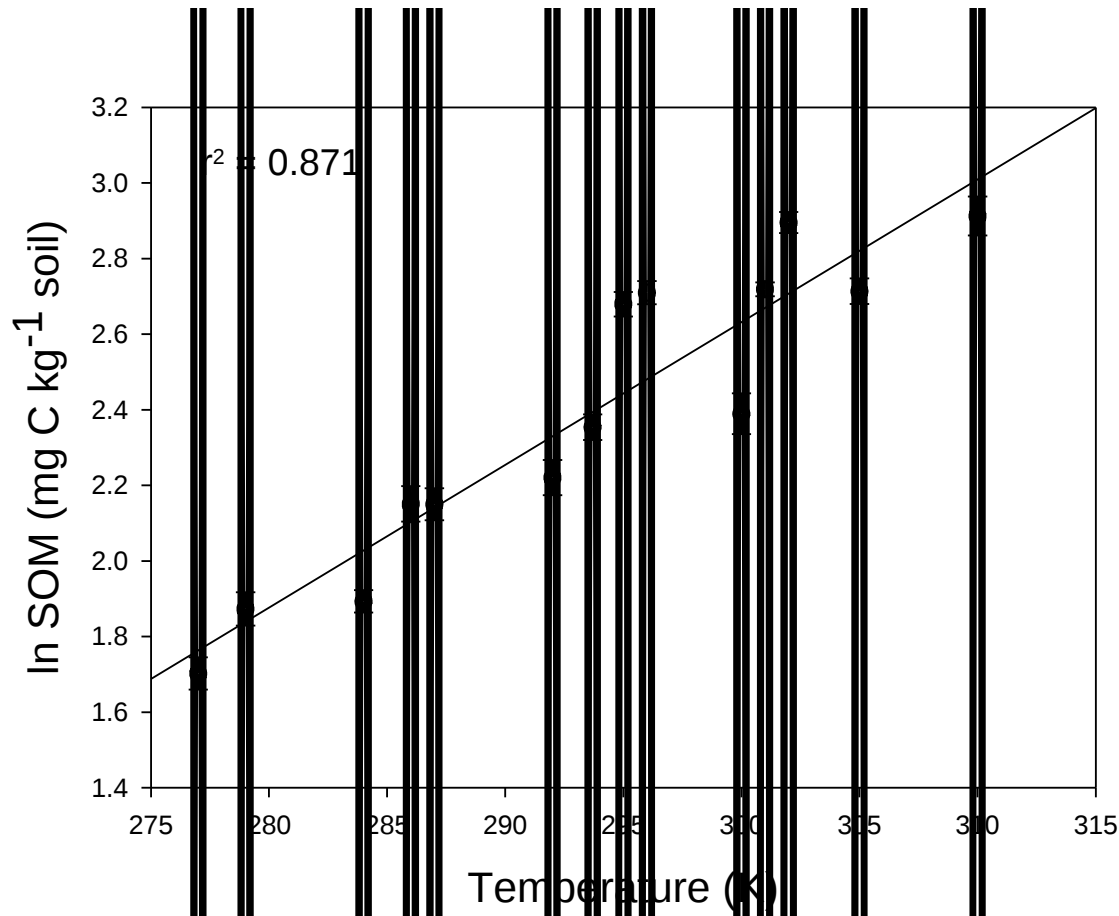
$$\frac{\left(\frac{dSOM}{dt}\right)^*}{\Phi C_f(t)} = -K \cdot \exp \frac{EA_{inact} - EA_{act}}{RT}$$



Experiment supports our theory: temperature has negative relationship with SOM decomposition

Results & Discussion:

If effect of fresh energy supply isn't separated from that of temperature, we observe an apparent +ve response to temperature!



Thus positive temperature response of SOM decomposition: An artefact !

Conclusions & Synthesis:

Linking theory with long term experiments

- ***Our results, theory & experiment, reveal negative relationship between SOM decomposition and temperature if enzyme inactivation and energy limitation of microbes is taken into account.***
- ***This explains the results of long-term ecosystem experiments which show no or weak positive effect of temperature on SOM storage.***
- ***This could explain other empirical results like SOM storage in tropical ecosystems under high temperatures.***

Linking theory with results of lab incubations & enzyme assay:

$$\frac{dSOM}{dt} = -k_{act} \times E_0$$

For enzyme assays & soil incubations, there is no fresh C supply

$$\frac{dE}{dt} = -k_{inact} \times E + \cancel{k_f \times C_f}$$

$$\frac{dC_f}{dt} = \cancel{\Phi C_f(t)} - \cancel{k_f \times C_f}$$

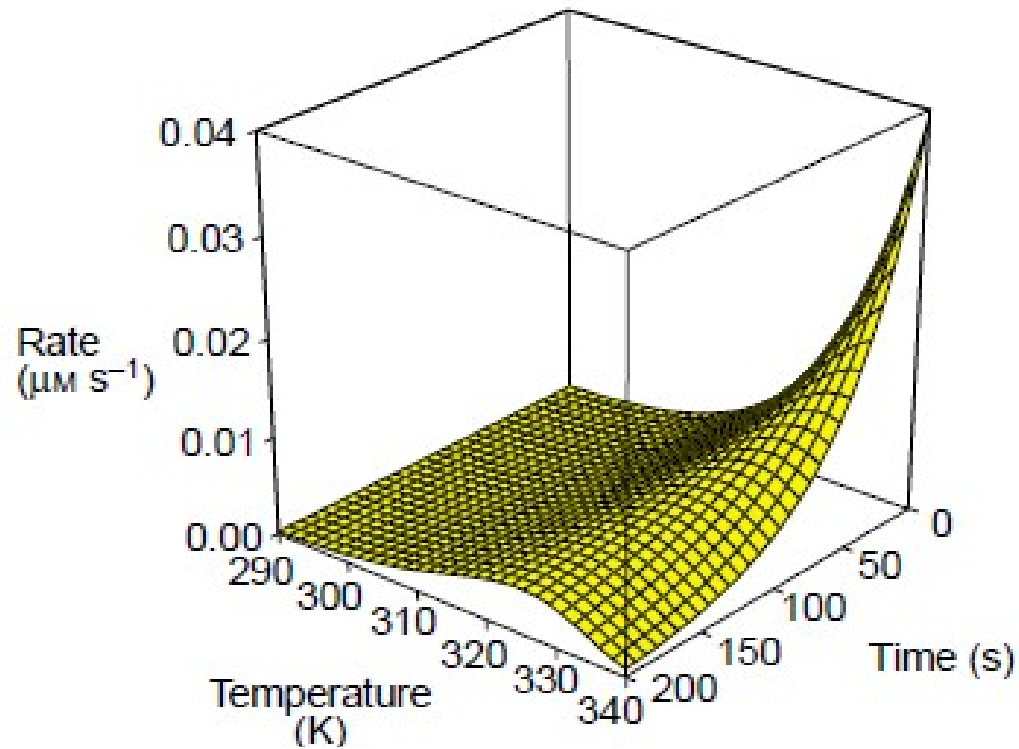
After simplifying, SOM decomposition & enzyme activity can be calculated as

$$A(t, T) = k_{act} \cdot E_0 \cdot \exp^{-k_{inact} \cdot (t)}$$

A (t, T) = Soil respiration & Enzymatic activity as function of time and temperature

E₀ = Initial enzyme pool.

Optimum temperature



This is observed in enzyme assays and short-term soil incubations

Conclusions & Synthesis:

- 1) Our model explains effect of temperature in soil-incubations and long term experiments
- 2) These results aren't contradictory but we can not simply compare the results of lab incubations with long-term soil warming experiments.
- 3) We suggest that global warming will not have important direct effect on SOM storage however we should focus indirect effects like drought that can result in de-synchronisation of microbial and plant functioning.

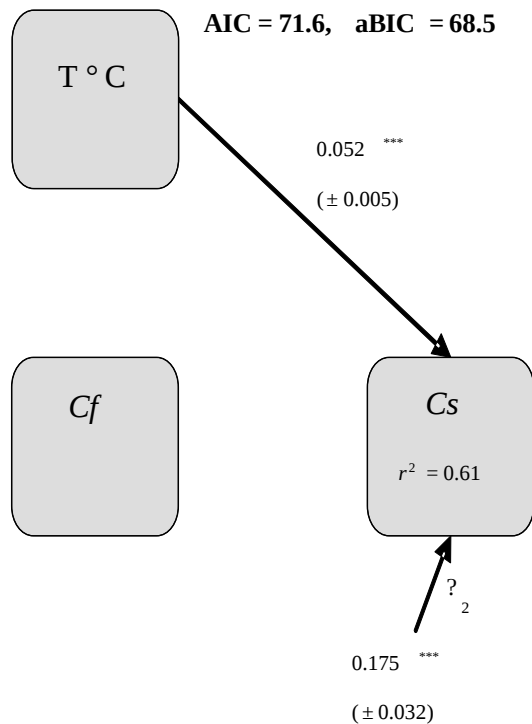
limitations:

- not valid for frozen soils
- Neither for extreme temperatures

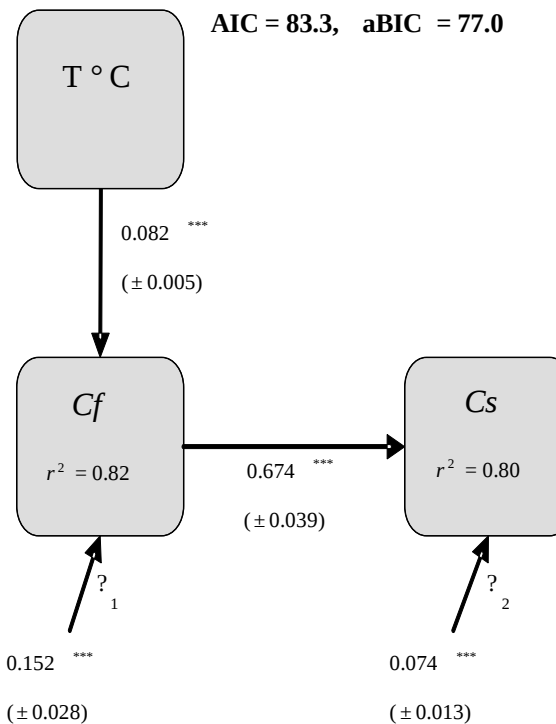
Merci bien

Plant cover & temperature effects on SOM decomposition:

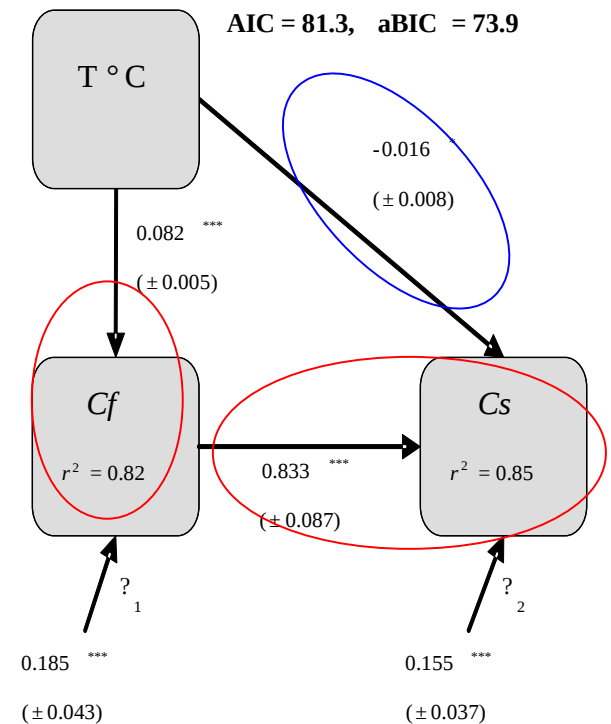
Net temperature effect



Indirect temperature effect

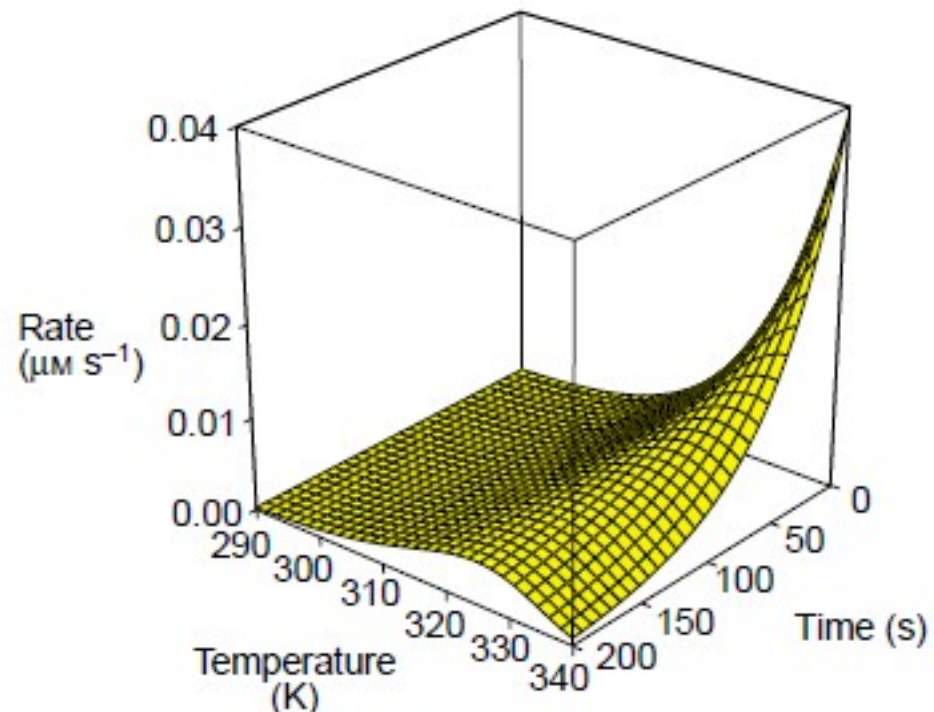


Direct and indirect temperature effects



Enzyme assay:

$$V_{\max} = k_{cat} \cdot [E_0] \exp^{-k_{inact} \cdot t}$$



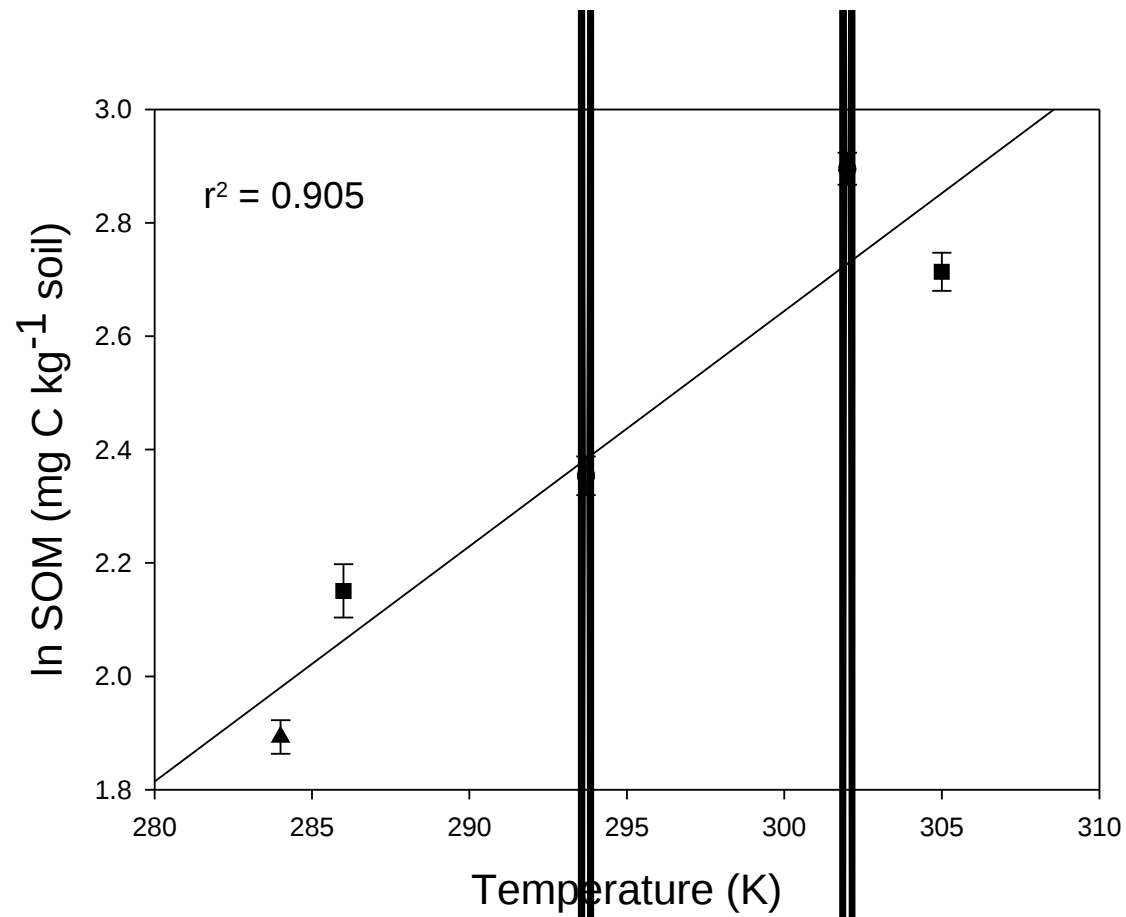
Results & Discussion:

➤ Effect of plant cover, temperature & plant cover X temperature

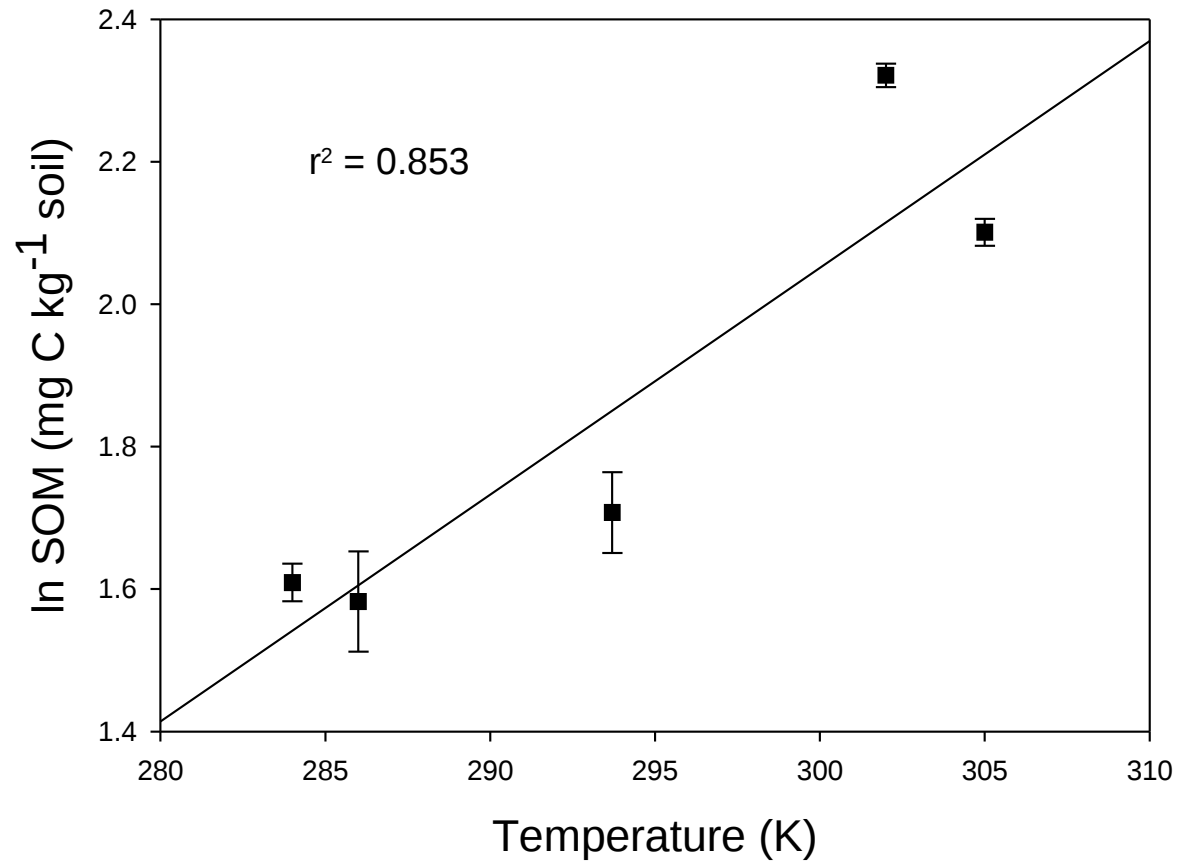
Factors	Df	Variance explained (%)	F-ratio	P-value
Date (Plant)	4	5.7		
Plant	1	8.7	61.8	< 0.001
Temperature	1	85.3	607.4	< 0.001
Plant x Temperature	1	0.28	2.01	ns
Overall	117	$r^2 = 0.94$		

Repeated measures ANOVA

Seasonal temperature variations: Planted soils



Seasonal temperature variations: bare soils soils



Long term C storage :

Meta-analysis: eddy covariance, 21 sites, +ve sign represents net ecosystem gain

