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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:

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

$Ea$  = activation energy

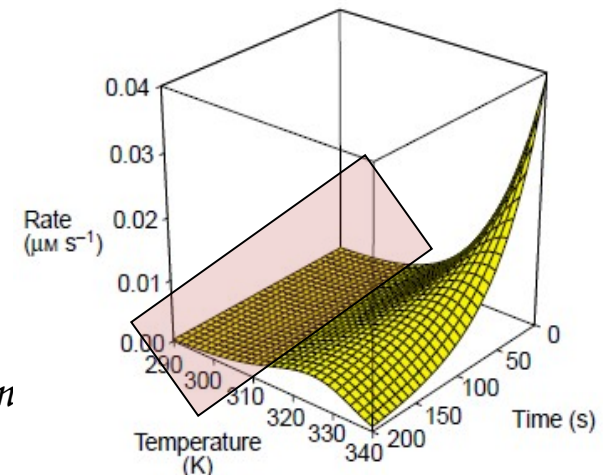
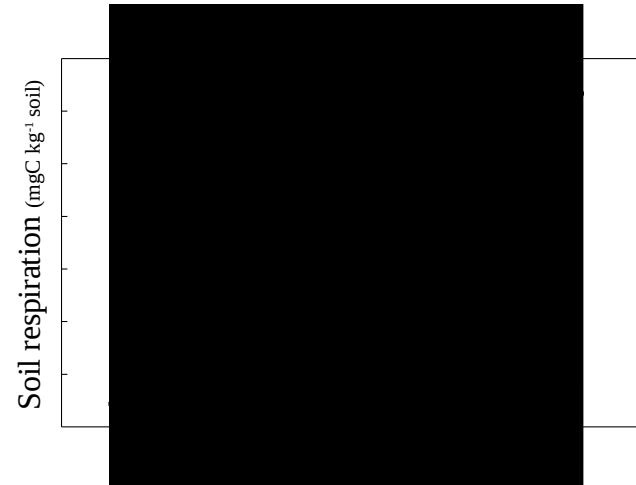
*Increasing temperature response with increasing recalcitrance of OM (higher  $Ea$ )*

## ➤ Short-term lab incubations:

*-Support Arrhenius theory*

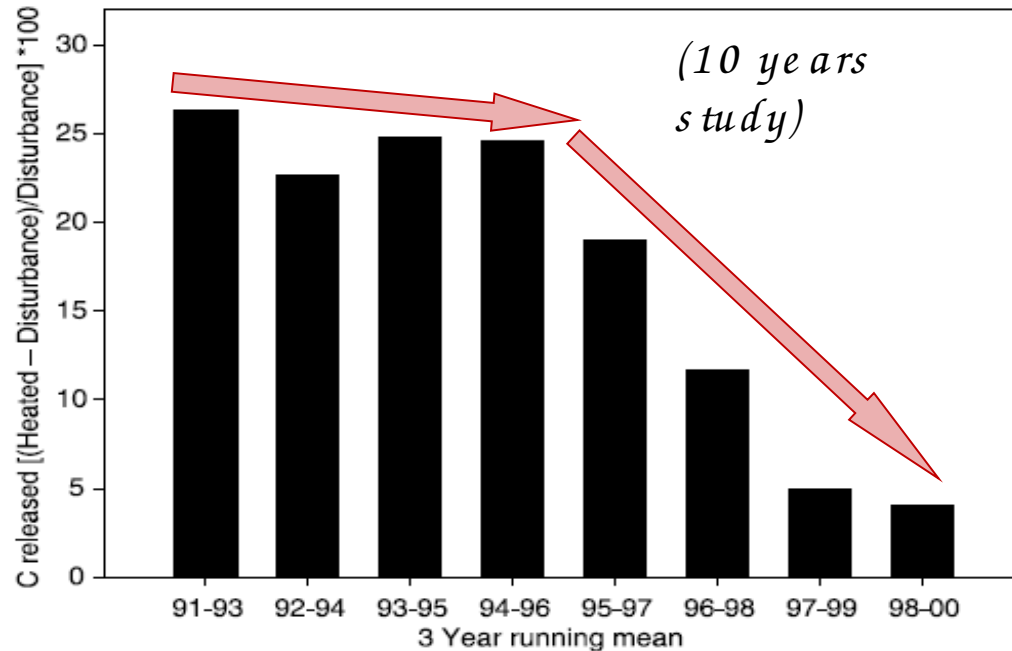
*Increased SOM decomposition & enzyme activity with temperature un-  
temperature'*

*(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:**



- 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:**

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

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

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

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

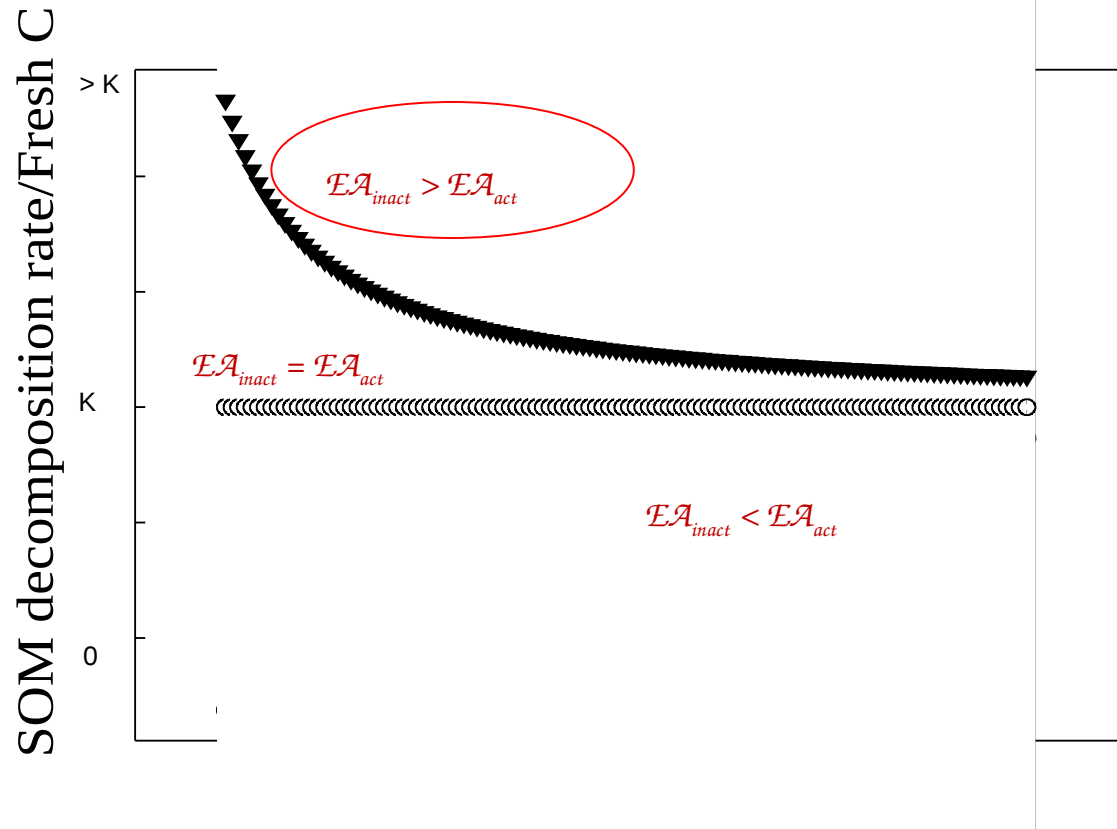
$$A_{act} / A_{inact} = K$$

➤ **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.*

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

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

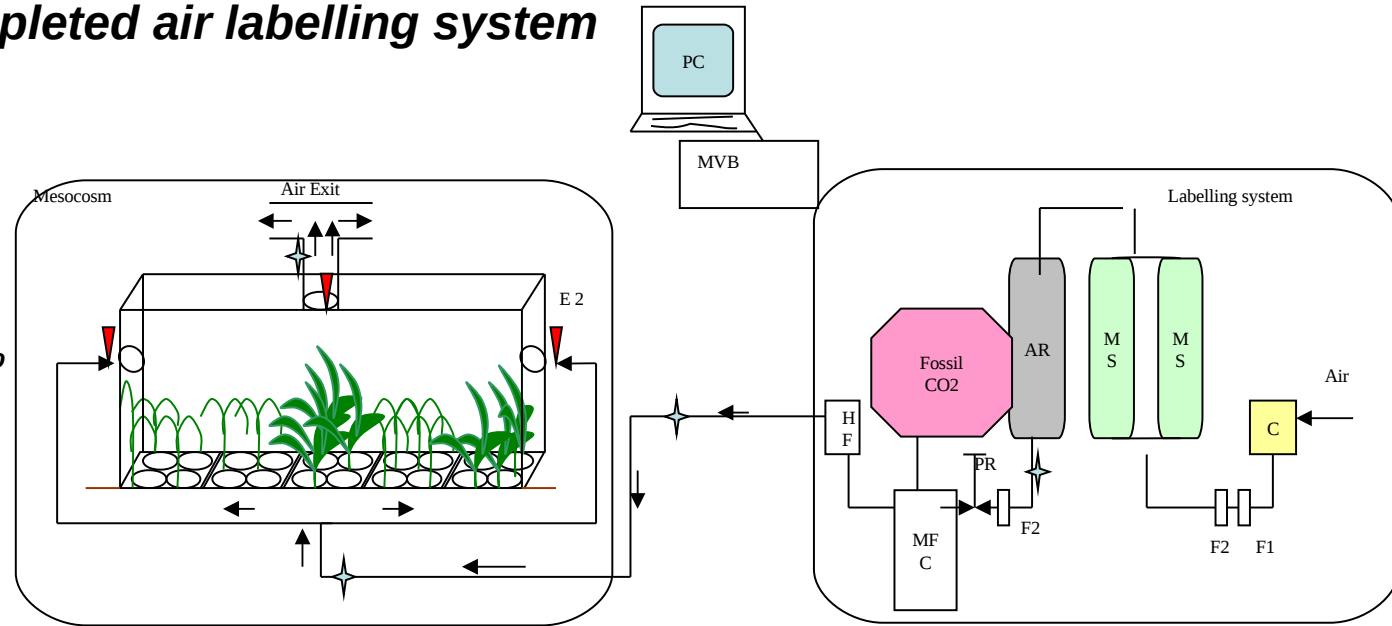
# Labelling system & mesocosm

## ➤ Continuous $^{13}\text{C}$ depleted air labelling system

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

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

Duration = 479 days

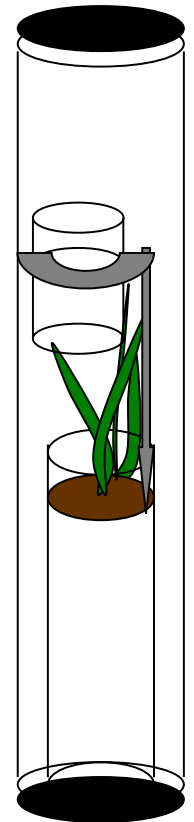
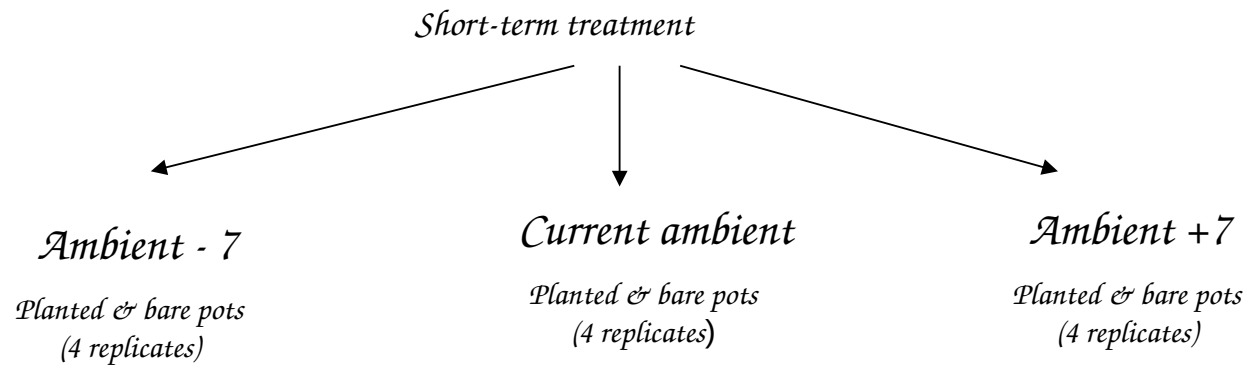


# Soil, plant & temperature treatments

- *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*

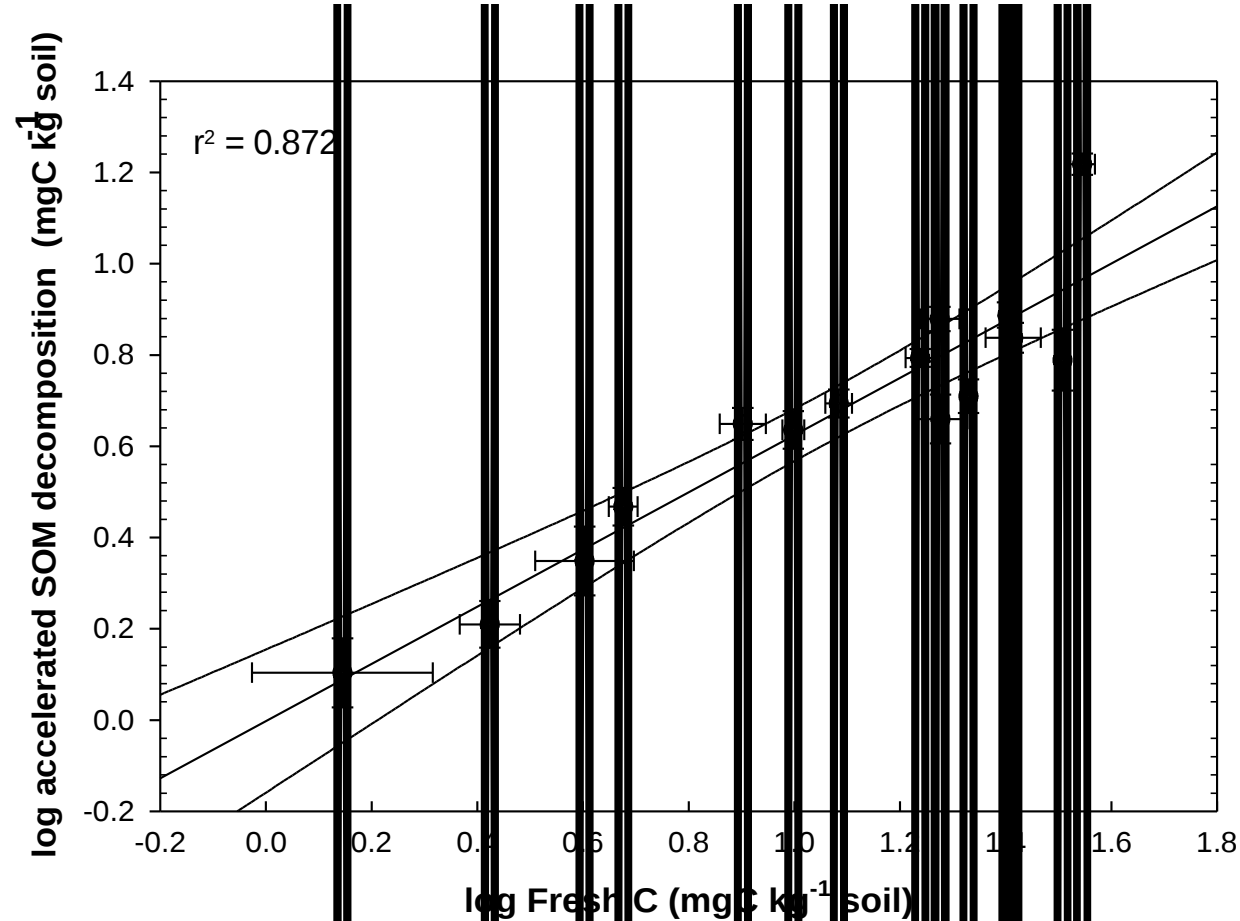


*Placed for 24 hrs under controlled temperature*

2) *Seasonal temperature variation: Spring 2009 – Summer 2010*

# Results & Discussion:

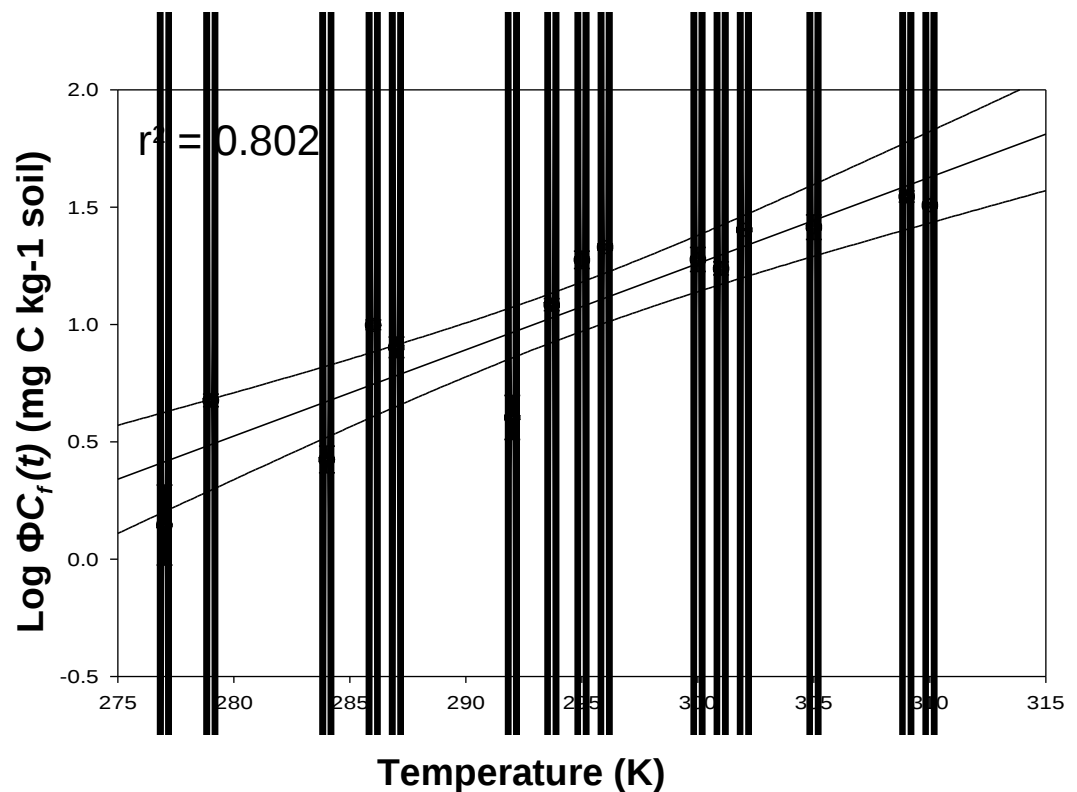
➤ *SOM decomposition of fresh C controlled by fresh energy supply*



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*

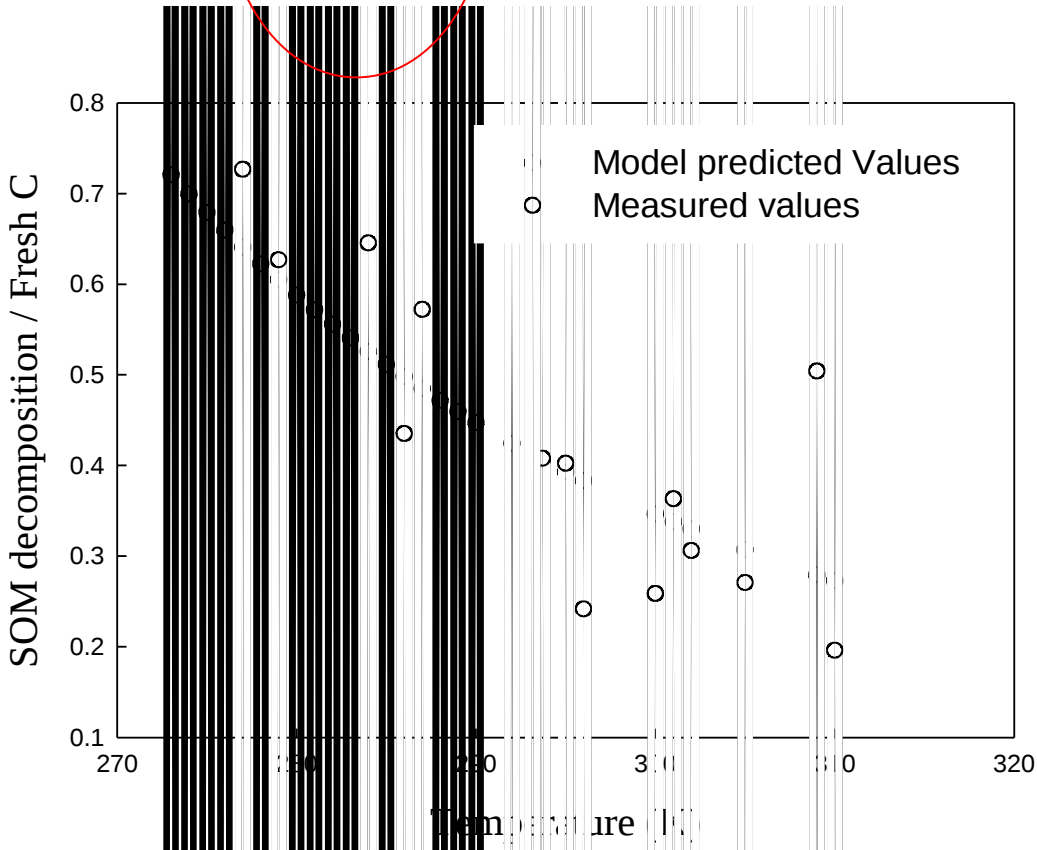


Seasonal variation in temperature causes changes in photosynthesis & fresh C input

# Model Fit:

Equation:

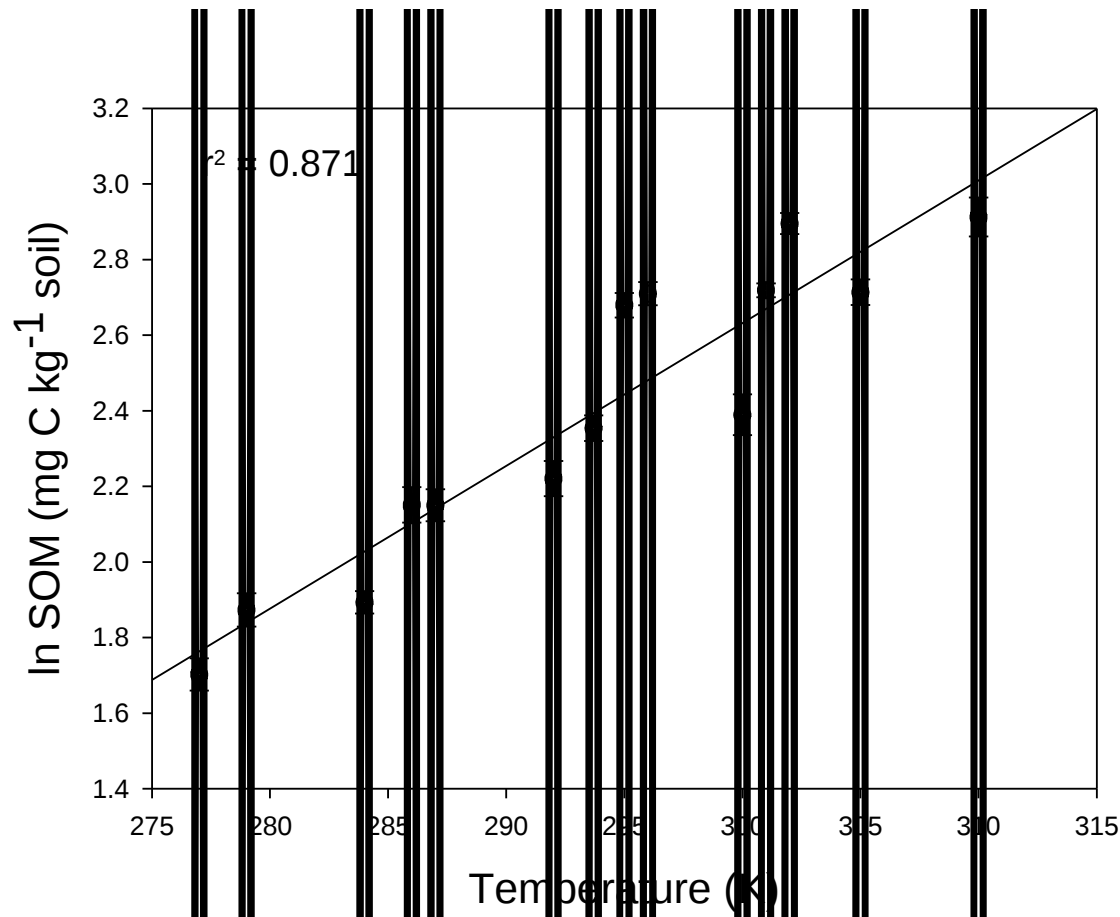
$$\left( \frac{dSOM}{dt} \right)^* = -K \cdot \exp \frac{EA_{inact} - EA_{act}}{RT}$$



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

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

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

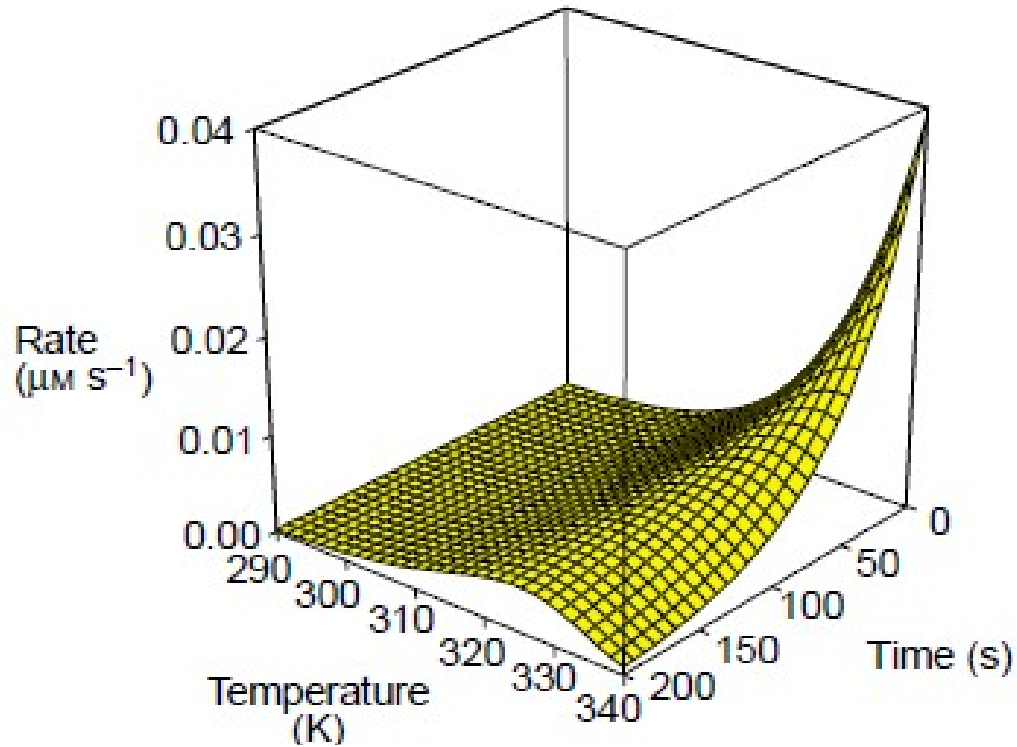
After simplifying, SOM decomposition & enzyme activity can be calculated as

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

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

**E<sub>0</sub>** = 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.

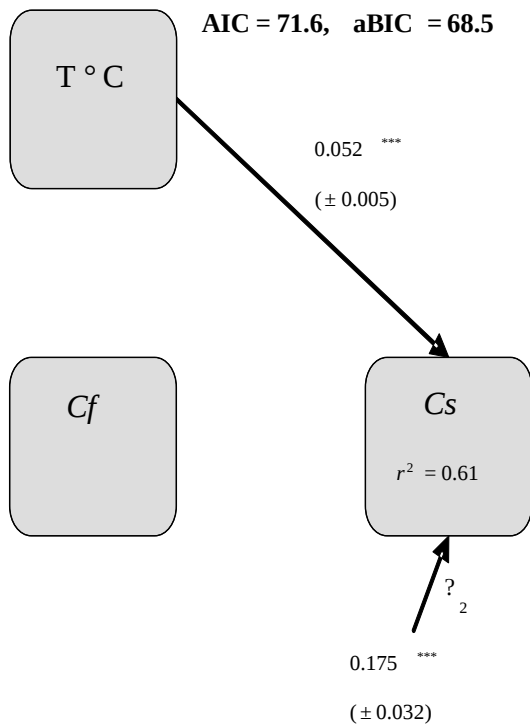
# ***limitations:***

- not valid for frozen soils
  
- Neither for extreme temperatures

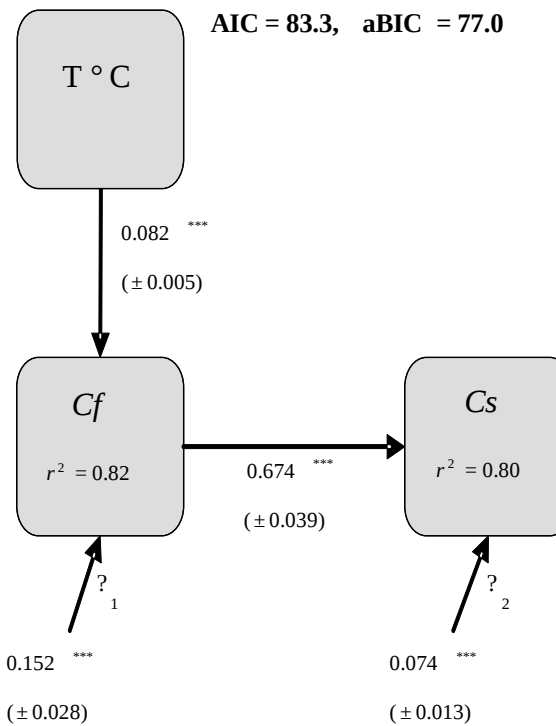
***Merci bien***

# Plant cover & temperature effects on SOM decomposition:

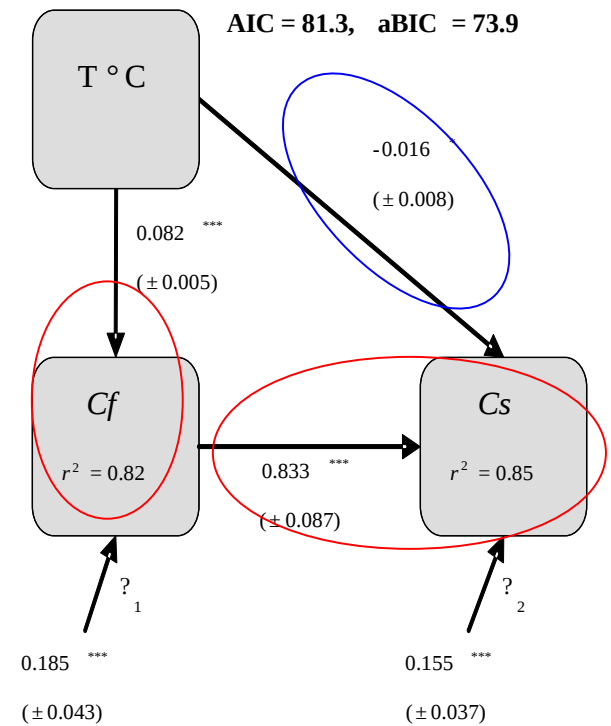
Net temperature effect



Indirect temperature effect

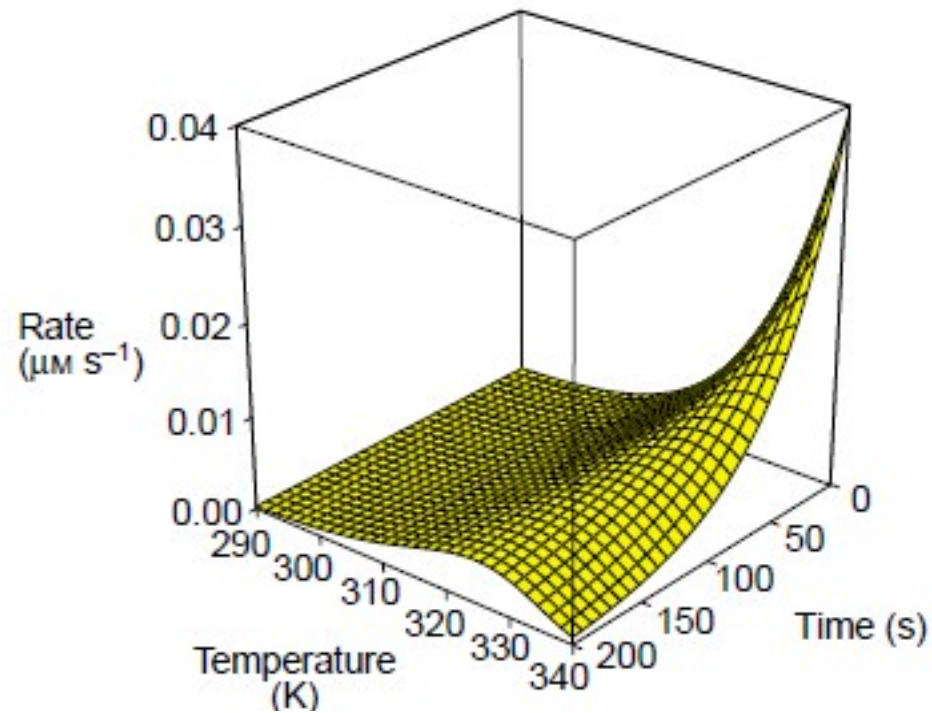


Direct and indirect  
temperature effects



# Enzyme assay:

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





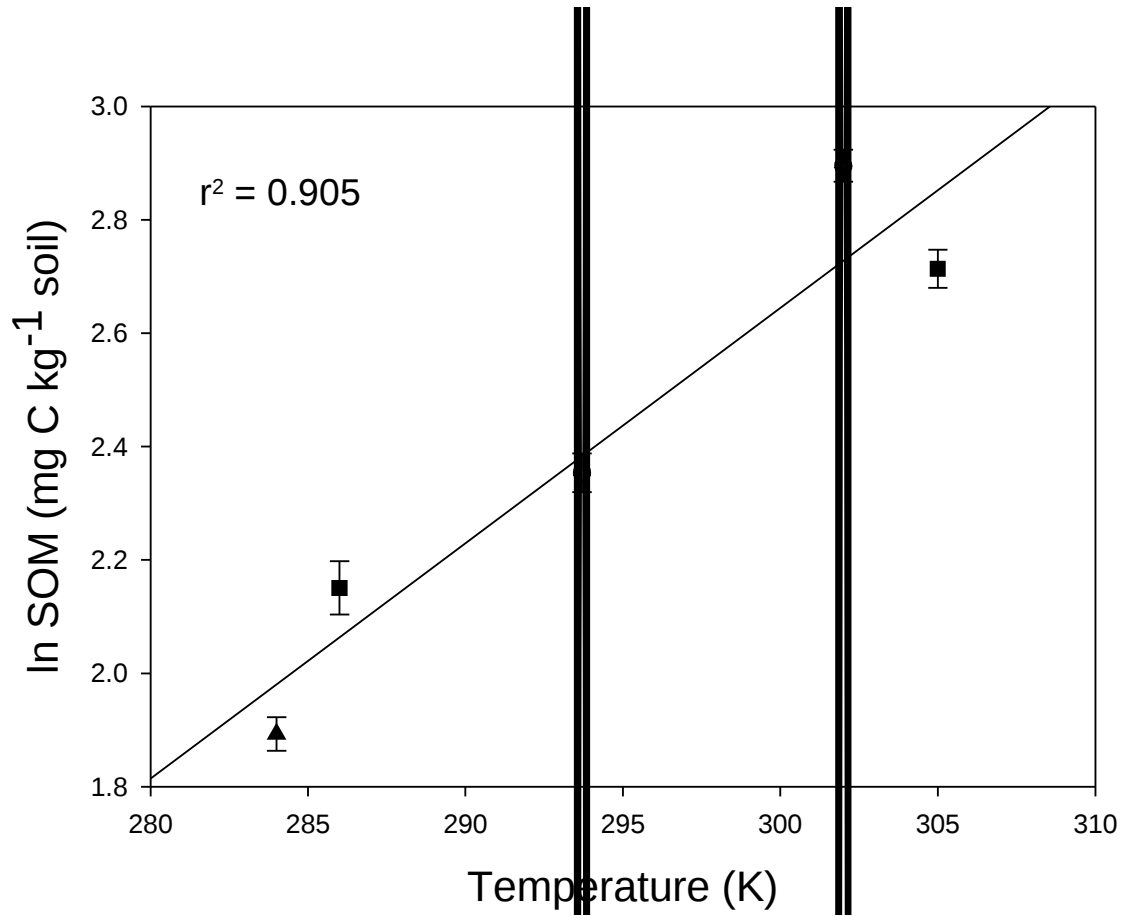
# Results & Discussion:

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

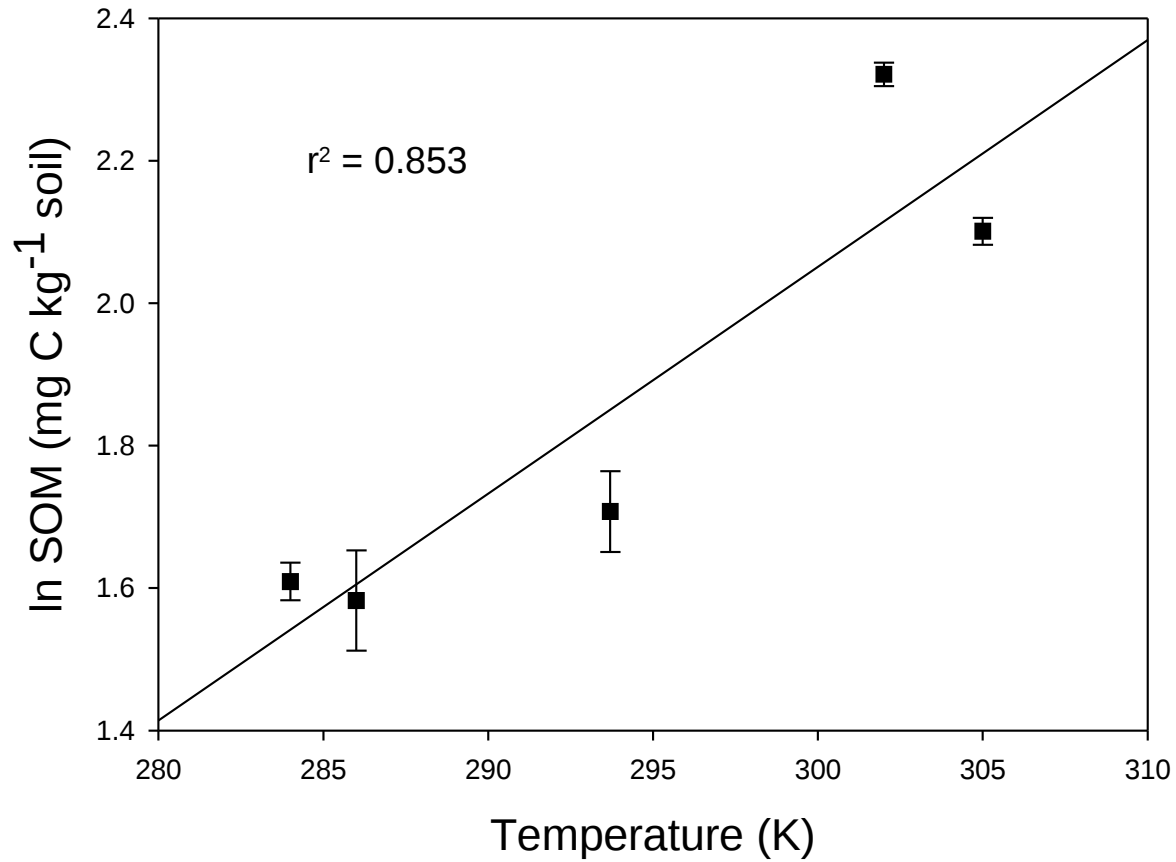
Factors	Df	Variance explained (%)	F-ratio	P-value
Date (Plant)	4	5.7		
Plant	1	8.7	61.8	< 0.001
Temperature	1	85.3	607.4	< 0.001
Plant x Temperature	1	0.28	2.01	ns
Overall	117	$r^2 = 0.94$		

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

