Biogeochemistry **54:** 147–170, 2001.

Decomposition of ^{13}C-labelled standard plant material in a latitudinal transect of European coniferous forests: Differential impact of climate on the decomposition of soil organic matter compartments

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Key words: ^{13}C labelling, climatic response functions, decomposition, first-order two-compartment models, global change, soil organic matter compartments

Abstract. ^{13}C labelled plant material was incubated *in situ* over 2 to 3 years in 8 conifer forest soils located on acid and limestone parent material along a north-south climatic transect from boreal to dry Mediterranean regions in western Europe. The objectives of the experiment were to evaluate the effects of climate and the soil environment on decomposition and soil organic matter dynamics. Changes in climate were simulated using a north-to-south cascade procedure involving the relocation of labelled soil columns to the next warmer site along the transect.

Double exponential, decay-rate functions (for labile and recalcitrant SOM compartments) *vs* time showed that the thermosensitivity of microbial processes depended on the latitude from which the soil was translocated. Cumulative response functions for air temperature, and for combined temperature and moisture were used as independent variables in first order kinetic models fitted to the decomposition data. In the situations where climatic response functions explained most of the variations in decomposition rates when the soils were translocated, the climate optimised decomposition rates for the local and the translocated soil should be similar. Differences between these two rates indicated that there was either no single climatic response function for one or both compartments, and/or other edaphic factors influenced the translocation effect. The most northern boreal soil showed a high thermosensitivity for recalcitrant organic matter compartment, whereas the labile fraction was less sensitive to climate changes for soils from more southern locations. Hence there was no single climatic function which describe the decay rates for all compartments. At the end of the incubation period it was found that the heat sum to achieve the same carbon losses was lower for soils in the north of the transect than in the south. In the long term, therefore, for a given heat input, decomposition rates would show larger increases in boreal northern sites than in warm temperate regions.

The changes in climate produced by soil translocation were more clearly reflected by decomposition rates in the acid soils than for calcareous soils. This indicates that the physico-chemical environment can have important differential effects on microbial decomposition of the labile and recalcitrant components of SOM.

Introduction

Climate warming due to anthropogenic gas emission is expected to increase the mean surface air temperature of the earth by 2 to 5 °C during the next 50–100 yrs and will consequently modify the hydrologic cycle (Houghton et al. 1990). As soil organic matter (SOM) is a major reservoir of organic carbon in the biosphere, any change in the rate of SOM decomposition due to climate change will lead to either a positive or a negative feedback to atmospheric CO_2 concentrations.

Various parameters have been used to represent temperature effects in models of SOM. For example, the sum of the daily temperature above 0 °C has been used as an approximation of the heat required to drive biological soil processes (Andrén & Paustian 1987; Honeycutt et al. 1988; Van Cleve et al. 1990; Sparrow et al. 1992) and the van't Hoff function was used to model the responses of decomposition to changing temperature (Jansson & Berg 1985; Andrén & Paustian 1987; Lloyd & Taylor 1994). In addition, several functions, including the Q_{10} relationship, have been used to describe decomposition response to temperature (Rodrigo et al. 1997; Lomander et al. 1998; Kätterer et al. 1998).

Responses to changes in soil moisture have been generally assessed in short-term, laboratory experiments at constant temperature (Bunnel & Tait 1974; Stott et al. 1986; Rodrigo et al. 1997) so that their relevance to field conditions is questionable. Furthermore, models of soil organic matter dynamics have related these response to soil moisture values predicted from water and heat transfer models derived from regional climatic data and response functions are based on soil moisture content or water potential (Jansson & Berg 1985; Andrén et al. 1992) or derived from potential evapotranspiration and precipitation (Parton et al. 1987). It is important that these critical parameters for predicting effects of climate change on soil processes are validated by measurements carried out over extended periods of time under realistic environmental conditions. Recently, soil-warming experiments have been carried out in the field in an attempt to simulate the expected effects of increases in soil temperature under conditions closer to those in the real world (Peterjohn et al. 1993; Harte et al. 1995, 1996; Ineson et al. 1998). A few attempts have been made to examine the climate controls on decomposition rates using natural climate gradients (Jansson & Berg 1985; Berg et al. 1993; Trumbore et al. 1996; Giardina & Ryan 2000). Ineson et al. (1998) used altitudinal translocation of soil cores as an analogue to climate change to minimise artefacts due to experimental warming.

In this present study, soils were translocated along a 40–64° north latitudinal transect to investigate the effects of climate changes on C mineralisation in sites with mean annual temperatures ranging from 0.2 to 15.2 °C, and annual precipitation from 396 to 1096 mm, monitoring the variation in ^{13}C mineralisation over a period of 2 to 3 yrs in a West-European, north-south transect of coniferous forest soils (Bottner et al. 2000). The present paper presents results of the modelling synthesis of data of this experiment. The objectives were to determine whether (1) a single climatic response function can be used to model decomposition of different fractions of the SOM, (2) these functions are the same for soils in different climatic areas, and (3) response functions vary for soil types within regions. This analysis was performed using a two-compartment model with first-order kinetics.

Materials and methods

Experimental design

The data used in the models came from a study conducted at 8 sites located in western Europe along two north-south climatic sequences of coniferous forests from northern Sweden (64°N, boreal climate) to Spain (40°N, dry Mediterranean climate). Major characteristics of the sites and soils are given in Table 1. The 2 sequences were chosen on the basis of parent materials: acid and calcareous soils. A comprehensive description of the sites and the soil translocation (cascade) procedure is given by Bottner et al. (2000). Briefly, columns (diameter: 12 cm, height: 25–30 cm) containing reconstituted soil were incubated for 2–3 years at their site of origin (donor site; local soil). In addition, columns from each site were translocated and incubated in the site immediately to the south of the donor site in each sequence (host site; translocated soil). The southward translocation was considered to be analogous to global temperature increases. A total of 704 columns were incubated in the field. Soil columns were reconstituted using sieved soil (4-mm mesh) from the different soil horizons according to the organic matter distribution in the profile. In the reconstituted columns, the layers were compacted to the initial volume, bulk density and thickness (from 2 to 4 cm) of the natural horizons. Discs of a 1 mm mesh polyester netting separated them. The major

Table 1. Characteristics of the study sites

Sites	Latitude Longitude	Forest type Stand age (years)	Soil types (FAO)	Human types of the studied	$pH_{(H_2O)}$	C (%)	N (%)	Climate type	Temperature* (°C)	Precipitation* (mm)	Water deficit* (mm)
Acid soils sequence											
VINDELN	64° 00′ N	*Picea abies*	ferric podzol	mor (Oh)	3.4	44.8	1.40	boreal	0.2	604	19
(Sweden)	21° 05′ E	100									
JÄDRAÅS	60° 49′ N	*Pinus sylvestris*	humo-ferric	mor (Oh)	3.5	35.7	0.83	boreal	3.9	763	30
(Sweden)	16° 01′ E	140	podzol								
HALDON	50° 37′ N	*Picea abies*	dystic cambisol	acid mull (A1)	5.1	5.8	0.39	Atlantic	10.1	1353	15
(UK)	03° 04′ W	52									
THEZAN	43° 07′ N	*Pinus pinaster*	chromic luvisol	acid xeromoder (Oh)	4.3	40.2	1.03	wet	14.4	579	187
(France)	02° 45′ E	>100		acid mull (A1)	5.2	5.3	0.13	Mediterranean			
DESERT	40° 06′ N	*Pinus pinaster*	chromic luvisol	acid mull (A1)	5.6	4.4	0.13	dry	14.9	538	232
(Spain)	00° 00′ E	>100						Mediterranean			
Calcareous soils sequence											
FRISTON	50° 37′ N	*Pinus sylvestris*	humic cambisol	neutral mull (A1)	4.1	5.2	0.36	Atlantic	11.1	801	59
(UK)	00° 12′ W	>55									
LA CLAPE	43° 09′ N	*Pinus halepensis*	chromic cambisol	neutral xeromoder (Oh)	5.2	40.2	1.64	wet	14.8	587	192
(France)	03° 08′ E	>100		calcic mull (A1)	7.3	2.6	0.14	Mediterranean			
MAIALS	41° 22′ N	*Pinus halepensis*	calcic regosol	neutral xeromoder (Oh)	7.3	36.5	1.20	dry	15.2	396	414
(Spain)	00° 22′ E	30		calcareous mull (A1)	7.3	4.82	0.30	Mediterranean			

*Long-term annual means.

organic horizon(s), Oh and/or A1 horizons depending on the soil types, were labelled by addition of ^{13}C (10% enrichment) standard plant material (mature uniformly labelled wheat) with low N content. In order to avoid modifying the physical and chemical characters of the SOM, the C in the labelled plant material added to the soil never exceeded 3.5% of the initial native soil C. Finally, the columns were covered with litter according to the species and litter depth of the donor site. The decomposition of this plant material reflected the activity of the total decomposer community in each type of soil and layer, giving comparative figures of the biological activity throughout the climatic transect. Four columns were destructively sampled on each sampling occasion (7 for Vindeln, 8 for Jädraås and 9 for the other sites). Total C and ^{13}C isotopic ratios were measured (1) in the initially labelled horizon and (2) in the horizons directly located above and below it, by the 'Service Central d'Analyses' of the CNRS, Vernaison (France), using a CN elemental analyser coupled with a mass spectrometer (Finnigan delta S or MAT 252).

Climate data

Daily air temperature and precipitation, both long-term and for the period of the experiment, were provided by national meteorological stations located at less than 10 km from the sites (Table 1). For the 2 French sites (Thézan and La Clape), the soil moisture was measured gravimetrically in columns reconstituted in the same way as the labelled ones. Moisture determinations were made every 2 or 3 days over 16 months for Thézan, and 6 months for La Clape. The water balance variables were calculated using the WATERBUD computer program (Sharpe & Prowse 1983). The maximum soil-water storage was fixed at 300 mm (e.g. Meentemeyer 1984; Dyer et al. 1990; Kurz et al. 1998) to allow comparisons with previous works. The water deficit (Table 1) is the difference between the potential evapotranspiration (PET) according to the procedures of Thornthwaite and Mather (1957) and the actual evapotranspiration (AET).

Non-linear regression models

All the basic data used for calculations were published earlier by Bottner et al. (2000). Non-linear regression was used to fit the amount of remaining ^{13}C to a variety of independent variables using the least-squares technique in PRISM (Graphpad Software, Inc., San Diego, USA). Amounts of ^{13}C found in the horizon located above the initially labelled horizon were negligible and the ^{13}C recovered in the horizon located directly below represented less than 2–3% of the initial label. Thus the upward migration and the downward leaching were low. Hence the total ^{13}C remaining in the soil was calculated as the sum of the 3 horizons, assuming that the initial ^{13}C = remaining ^{13}C +

evolved CO_2-^{13}C. The following two-compartment, first-order decay model was used (Eq. 1)

$$RC = Ae^{-k_a x} + Be^{k_b x} \tag{1}$$

where RC is the amount of ^{13}C remaining expressed as a percentage of the initial ^{13}C; A and B are the initial proportions of ^{13}C (as percent) in the fast and the slow decomposing compartments, respectively ($A+B = 100$); k_a and k_b are the decay rate constants for the A and B fractions, respectively, and x is the independent variable. The ^{13}C at time = 0 was measured on an aliquot of the initial mixture of ^{13}C-labelled straw and soil that was used to fill up the cylinders, and the total remaining ^{13}C during the time course of decomposition was calculated as a percent of this value. Since the same standard ^{13}C labelled plant material was used in all treatments, the initial proportions of the compartments A and B were assumed to be identical in all soils and fixed to 42% for A, the mean value obtained from free adjustments in the acid soil sequence (data not shown). This value is close to the value obtained using the CENTURY model (Parton et al. 1987) for partition between metabolic and structural compartments. Fixing the size of the compartments reduced the number of fitted parameters, therefore reduced the k_a and k_b fitting errors.

Time is generally used as the independent variable (x) in kinetic models. Since the 'time' parameter effectively stops when the temperature and moisture conditions prevent any microbial activity, we have used additional independent variables to model these processes. Here, we used two climate related variables: (1) τ_{sum}, the sum of τ (the daily van't Hoff's temperature response function calculated with Eqs. 2 and 3), and (2) $\tau\mu_{sum}$, the sum of the products of τ and μ (the moisture response function calculated on the basis of water deficit with Eqs. 4 and 5). The aim of this exercise was to define the optimised decomposition rates based on temperature and temperature × moisture, k_a and k_b because if climatic response functions completely explain the variations when the soils are translocated, the decomposition rates, k_a and k_b, of the local and the translocated soil should be similar. If this is not the case, the response function of one or both compartments is more complex and/or factors other than climate contribute to the effect of translocation.

The van't Hoff function (τ, Eq. 2) has frequently been used to describe temperature related decomposition kinetics (e.g. Jansson & Berg 1985; Andrén & Paustian 1987; Berg et al. 1990; Kätterer et al. 1998; Lomander et al. 1998):

$$\tau = Q_{10}^{(T_d - T_{max})/10} \tag{2}$$

where τ is a daily temperature response function normalised from 0 to 1, if $T_d \leq T_{max}$. Q_{10} is the rate multiplication factor when temperature increases by 10 °C, T_d is the mean daily air temperature and T_{max} was fixed at 30 °C, the highest mean daily temperature that was recorded during the experiment was calculated for $Q_{10} = 2.2$ according to the model fit and literature data (e.g. Jenny 1980 *in* Kirschbaum 2000).

The sum of the daily τ values (τ_{sum}) was used as an independent variable. This variable can be considered as a temperature corrected time factor and represents the time required to reach any given level of decomposition when the daily temperature is constantly at optimum for microbial processes

$$\tau_{sum} = \sum \tau \tag{3}$$

The moisture response function was calculated as

$$\mu = \frac{DEF_{\mathrm{lim}} - DEF}{DEF_{\mathrm{lim}}} \tag{4}$$

with $\mu = 0$ when $DEF > DEF_{\mathrm{lim}}$, where μ is a moisture response function ranging in value from 0 to 1, DEF is the actual water deficit computed with the WATERBUD model on a monthly basis. DEF_{lim} is the threshold over which the response function is zero. It was fixed at 90 mm based on the fit to the model.

The sum of the product ($\tau\mu_{sum}$) of the temperature and moisture response functions was also used as an independent variable.

$$\tau\mu_{sum} = \sum \tau \times \mu \tag{5}$$

$\tau\mu_{sum}$ is considered as a temperature x moisture corrected time and represents the time needed to reach the decomposition level when both temperature and moisture remain at their optimum.

Statistical treatments

Significance of the differences between the fitted parameters were based on the confidence interval of the fitting error ($p < 0.05$). By using successively time, τ_{sum}, and $\tau\mu_{sum}$ as the independent variable, we hypothesise that, if the introduction of a climatic component into the explanatory variable reduces the distances between the decomposition curves of the local and translocated soil, the difference between these decomposition kinetics is related to climate. To test the modification of this distance by the independent variable, for each soil, we fitted a common non-linear regression curve to the combined data of the local and translocated soils for the 3 independent variables. Then we used a Student t-test to compare the residuals of the local and the translocated data with respect to this common curve. If the climatic parameters have an

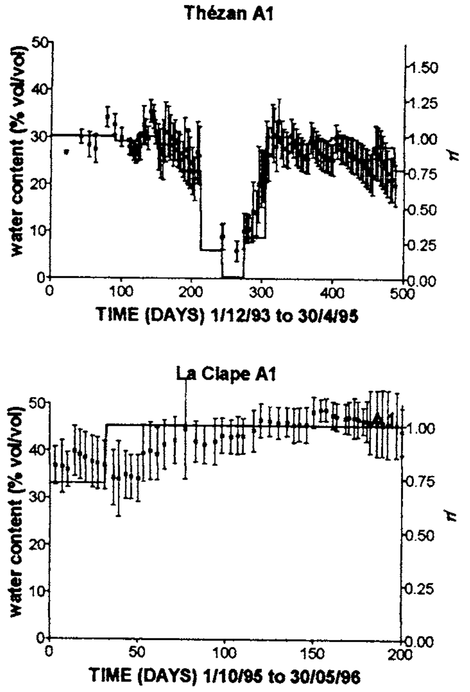

Figure 1. Gravimetric water content (vol/vol) (solid symbols) and moisture response functions, μ, (solid line) for Thézan A1 and La Clape A1. Error bars are standard deviations.

explanatory value, the difference should become non-significant. At least, the mean difference between the residuals should decrease with the introduction of temperature and moisture compared to that with time as the independent variable.

Results

Response functions

The mean annual τ_{sum}, the temperature response function, increased with decreasing latitude from 49 days at Vindeln to 144 days at Maials (Table 2). In the case of constant optimum temperature conditions (30 °C, $\tau = 1$), annual τ_{sum} would be 365 days.

The moisture response function (μ) was compared to the moisture contents in the A1 horizon for a period of 500 and 200 days at Thézan and La Clape, respectively (Figure 1). There was a good agreement between the two values for an optimal moisture content ($DEF = 1$) of 30 and 45% (vol/vol) at Thézan and La Clape respectively. The moisture response function was close

Table 2. Parameter values and coefficients of determination (R^2) for the two compartment first order model with time, τ_{sum} and $\tau\mu_{sum}$ as independent variable. A was fixed at 42%

Soil	Horizon	Host site*	Independent variable														
			x = time (days)					$x = \tau_{sum}$ (days)					$x = \tau\mu_{sum}$ (days)				
			k_a		k_b		R^2	k_a		k_b		R^2	k_a		k_b		R^2
Acid sequence																	
Vindeln	Oh	Vindeln	0.0088	bc**	0.00035	a	0.93	0.045	cd	0.0035	de	0.95	0.044	c	0.0044	bcd	0.95
	Oh	Jädraås	0.0093	c	0.00076	cd	0.97	0.042	c	0.0061	f	0.97	0.049	c	0.0066	e	0.96
Jädraås	Oh	Jädraås	0.0132	cd	0.00051	b	0.95	0.049	cd	0.0042	e	0.98	0.057	c	0.0046	cd	0.98
	Oh	Haldon	0.0082	bc	0.00085	d	0.97	0.050	cd	0.0038	e	0.97	0.056	c	0.0041	c	0.97
Haldon	A1	Haldon	0.0167	d	0.00069	c	0.96	0.104	d	0.0032	d	0.97	0.118	d	0.0034	b	0.97
	A1	Thézan	0.0059	b	0.00077	cd	0.95	0.030	bc	0.0020	b	0.93	0.025	b	0.0038	bc	0.94
Thézan	Oh	Thézan	0.0228	cd	0.00054	b	0.92	0.061	cd	0.0014	ab	0.91	0.103	cd	0.0026	ab	0.93
	Oh	Desert	0.0092	bc	0.00052	b	0.93	0.021	b	0.0014	a	0.93	0.051	c	0.0028	ab	0.93
	A1	Thézan	0.0122	cd	0.00057	bc	0.92	0.030	bc	0.0016	ab	0.91	0.054	c	0.0028	ab	0.93
	A1	Desert	0.0172	d	0.00057	bc	0.94	no convergence					no convergence				

Table 2. Continued

Soil	Horizon	Host site*	Independent variable														
			x = time (days)					$x = \tau_{sum}$ (days)					$x = \tau \mu_{sum}$ (days)				
			k_a		k_b		R^2	k_a		k_b		R^2	k_a		k_b		R^2
Calcareous sequence																	
Friston	A1	Friston	0.0187	d	0.00115	e	0.95	0.077	d	0.0043	e	0.96	0.105	d	0.0050	d	0.97
	A1	La Clape	0.0121	cd	0.00079	cd	0.96	0.043	cd	0.0022	bc	0.97	0.052	c	0.0035	bc	0.96
La Clape	Oh	La Clape	0.0023	a	0.00066	bcd	0.94	0.006	a	0.0020	abcd	0.93	0.010	a	0.0029	ab	0.93
	Oh	Maials	0.0032	ab	0.00056	abc	0.84	0.006	a	0.0017	ab	0.76	0.035	bc	0.0022	a	0.96
	A1	La Clape	0.0249	bcd	0.00089	d	0.95	0.112	d	0.0025	c	0.96	0.106	bcd	0.0040	bc	0.96
	A1	Maials	0.0303	d	0.00097	de	0.95	0.056	cd	0.0024	bc	0.96	0.162	d	0.0052	de	0.96

*Sites where the soils were incubated.

**Different letters indicate significant differences within a column ($p < 0.05$).

Table 3. Annual climatic response functions cumulated at each site for the 1st and 2nd year of incubation

		Boreal		Atlantic		wet Mediterranean		dry Mediterranean	
		Vindeln	Jädraås	Haldon	Friston	Thézan	La Clape	Desert	Maials
τ_{sum}	1st year	46	52	81	95	128	132	141	147
	2nd year	52	60	87	94	87	128	141	140
	mean	49	56	84	95	107	130	141	144
$\tau\mu_{sum}$	1st year	44	48	77	88	90	88	57	72
	2nd year	42	58	78	69	64	67	70	62
	mean	43	53	77	78	77	78	63	67

Results are expressed in days.

to the optimal value at the boreal and Atlantic sites, whereas it was reduced by summer drought at the Mediterranean sites (data not shown). In addition, the seasonality of moisture content was less pronounced in the northern sites. Considering that the moisture response function equals zero during the frost periods, only the Atlantic sites showed a low seasonal pattern of decomposition. Annual $\tau\mu_{sum}$ values were higher at the host sites than in the donor sites for boreal and Atlantic sites. At the Haldon-Thézan and Friston-La Clape site pairs, the $\tau\mu_{sum}$ values were similar (77–78 days) but at Haldon and Friston, temperature was responsible for the reduction factor, while at Thézan and La Clape, it was moisture. For the Mediterranean sites, the mean annual $\tau\mu_{sum}$ values were also lower at the host sites (dry Mediterranean) than at the donor sites (wet Mediterranean) even though the mean annual temperature was similar (Table 1).

The fast-decomposing 'A' compartment

The daily decomposition rate of the A fraction (k_a) had high fitting errors especially in southern countries (Figure 2(a)). This could be attributed to the few sampling occasions compared to the high ^{13}C loss during the early stage of decomposition.

The k_a value, when x = time, generally increased from north to south. It was unaffected by translocation from Vindeln to Jädraås but decreased by a factor of 1.6, 2.8 and 2.5, respectively when Jädraås, Haldon, and Thézan Oh soils were moved to the south (Table 3). The decrease was significant for the Haldon and Thézan soils ($p < 0.05$). The largest decrease in k_a occurred when the Haldon soil was moved from the Atlantic to the Mediterranean conditions at Thézan.

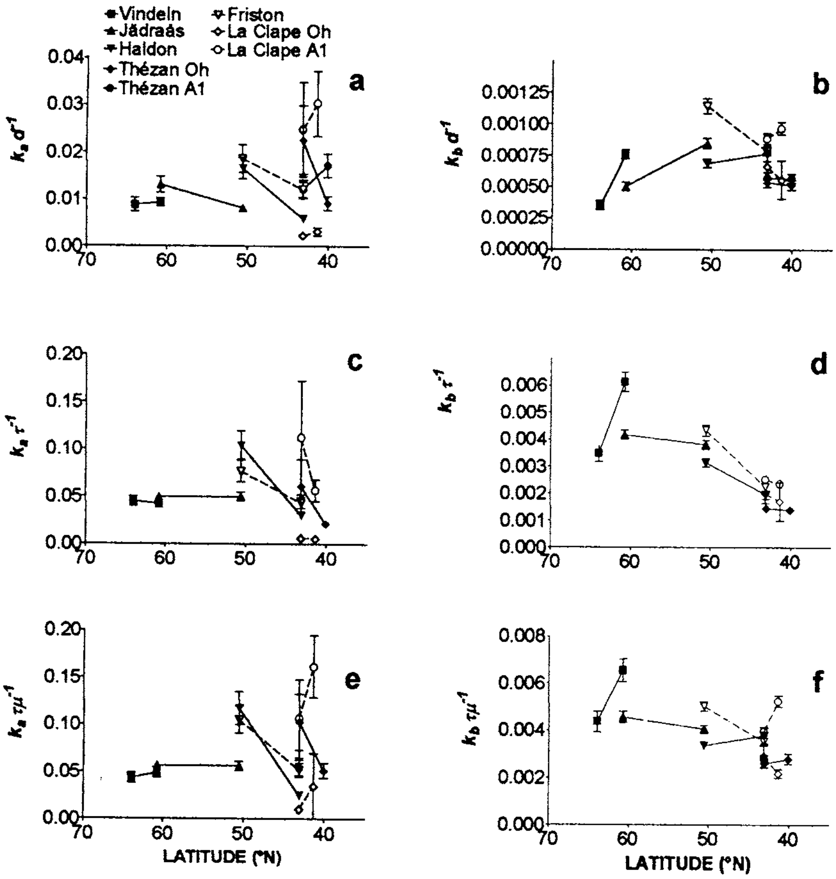

Figure 2. Relationships between the latitude of soil column incubation and decomposition rate constants (k_a and k_b) for the double exponential function when x = time (a, b), $x = \tau_{sum}$ (c, d), and $x = \tau\mu_{sum}$ (e, f). Error bars are 95% confidence intervals.

When the cumulative daily van't Hoff function τ_{sum} was used as x value, the temperature corrected k_a values (0.006 to 0.112 day^{-1}) were 3 to 4 times higher than the k_a values obtained using time alone as the independent variable (0.002–0.03 day^{-1}). The distribution pattern of these values was comparable (Figures 2(a) and (c)), with generally higher values for the limestone soils compared to the acid soils. The distribution range of values was not reduced. Thus the temperature optimisation improved the k_a estimation in boreal translocations, whereas it had little effect in the other translocations.

When the cumulated daily value $\tau\mu_{sum}$ (sum of the products of the van't Hoff function and the moisture response function) was taken as the x value (Eq. (1); Table 3, Figure 2(e), Figure 3), the range of variation in k_a was of the same amplitude as when τ_{sum} was used. This indicates that moisture

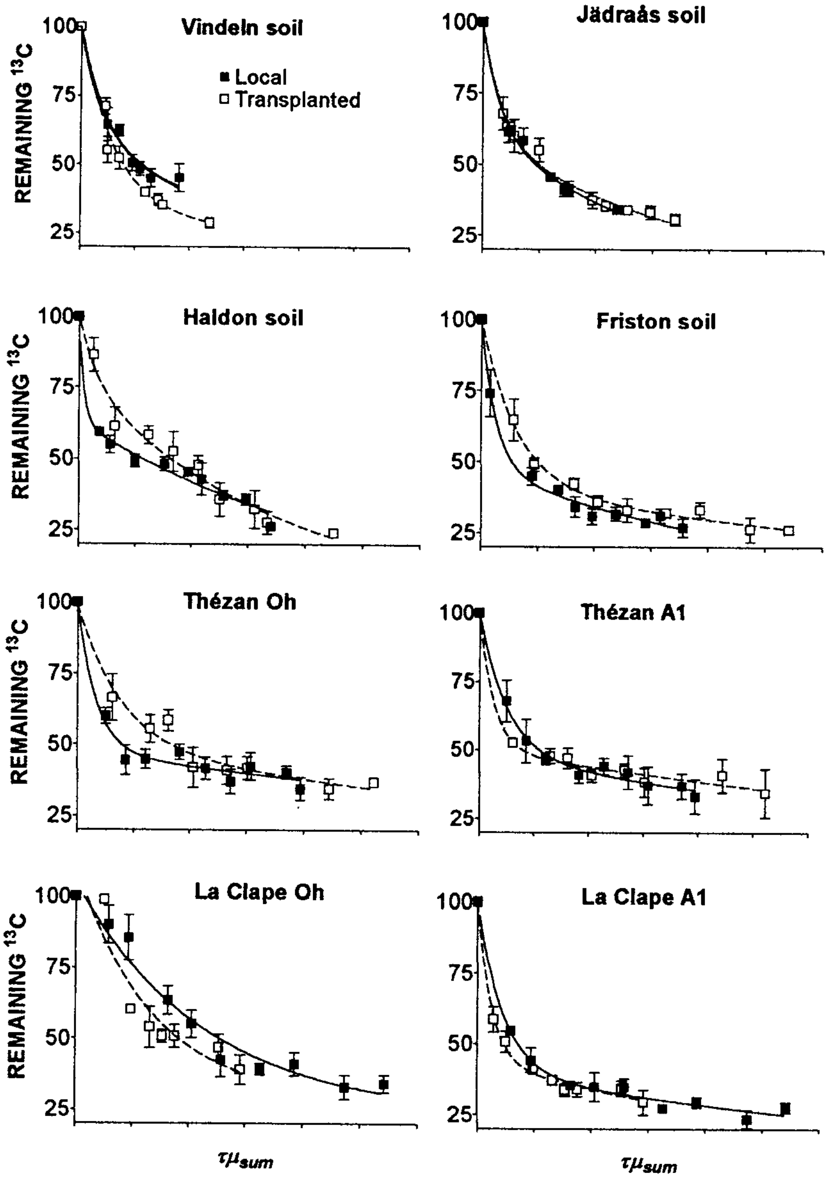

Figure 3. Remaining ^{13}C *vs* $\tau\mu_{sum}$ for each soil. Closed symbols are measured data at donor site. Open symbols are measured data at host site. Solid lines are predicted values at donor site, dashed lines are predicted values at host site using a double exponential model. Error bars are standard deviations.

may have contributed much less than temperature in determining the rates of decomposition. However, the use of the combined coefficients decreased the fitting errors compared to the van't Hoff function alone, indicating an improved explanation of the climatic effect by the $\tau\mu_{sum}$ variable although for most soils, the k_a variations due to translocation were poorly explained by climate.

The slow-decomposing 'B' compartment

The values for k_b, when x = time, of the most northern soils were increased significantly ($p < 0.05$) by translocation. For Vindeln the increase was a factor of 2.1 and for Jädraås 1.7. There was a non-significant increase for Haldon soil and the value was unchanged for Thézan Oh and A1 soils (Table 3, Figure 2(b)).

In the calcareous sequence, the k_b values of Friston and La Clape A1 soils showed significantly higher loss rates than in the acid sequence. The Mediterranean soil at La Clape is of special interest because its upper horizon, Oh (a xeromoder), had the lowest k_a value and its deeper organic horizon (A1) the highest k_a value. Unlike the acid sequence, the calcareous sequence did not show any trend as a consequence of translocation except for the translocation of the Friston soil to La Clape where there was a significant reduction of k_b (times 0.69, $p < 0.05$).

The k_b values were 4–5 times higher than those obtained with time as independent variable. They displayed two different patterns: (i) the boreal and Atlantic soils with the highest values and (ii) the Mediterranean soils with the lowest values (Figure 2(d)). For the Vindeln soil, the translocated/local k_b ratio was reduced from 2.2 to 1.7 for x = time and $x = \tau_{sum}$ respectively. This indicates that although the difference between the local and translocated k_b constants was reduced, temperature did not completely explain the translocation effect. In contrast, values of k_b converged for local and translocated Jädraås soils. Both Atlantic soils showed a significant decrease of k_b when translocated to the Mediterranean conditions, again illustrating that temperature alone did not explain the response to translocation. The translocation from wet to dry Mediterranean climate did not significantly modify k_b values. The values were very close regardless of the soil type (acid or calcareous), of the kind of horizon (Oh or A1) and of the origin of the soils (local or translocated).

Statistical significance of the soil translocation

The differences between the residuals of the data for the local and the translocated samples compared to the common fitted curve adjusted to the combined data set for x = time, τ_{sum} and $\tau\mu_{sum}$ are shown in Table 4. If

Table 4. Mean differences between the residuals of the local or translocated ^{13}C data compared to the common fitted curve

Soil		x = time (days)	t-test	$x = \tau_{sum}$ (days)	t-test	$x = \tau\mu_{sum}$ (days)	t-test
Acid sequence							
Vindeln	Oh	9.43 ± 2.20	***	6.69 ± 1.97	**	6.10 ± 2.07	*
Jädraås	Oh	4.75 ± 2.12	*	−1.03 ± 1.05	ns	−1.38 ± 1.11	ns
Haldon	A1	–3.21 ± 2.17	ns	–9.92 ± 2.12	***	–4.74 ± 2.66	ns
Thézan	Oh	–3.41 ± 2.15	ns	–3.86 ± 2.24	ns	−1.39 ± 2.05	ns
	A1	1.52 ± 1.77	ns	1.07 ± 1.99	ns	3.57 ± 1.78	ns
Calcareous sequence							
Friston	A1	–6.89 ± 1.81	**	−11.1 ± 1.58	***	–6.98 ± 1.61	***
La Clape	Oh	0.64 ± 4.11	ns	–3.98 ± 4.56	ns	4.85 ± 3.95	ns
	A1	1.45 ± 2.03	ns	−1.97 ± 1.92	ns	4.34 ± 1.90	*

the climate optimised independent variable explained the variation in the amounts of remaining ^{13}C, the differences should decrease. This was the case for Vindeln and Jädraås soils. For these, temperature had a dominant effect on decomposition. For the Haldon and Friston soils translocated into a wet Mediterranean climate, introducing temperature into the independent variable increased the difference showing that the temperature effect was less important than some other factor. As shown by the decrease of the differences, the introduction of a moisture effect reduced the variation in decomposition coefficients. For the Mediterranean soils, the differences were not significant, with all independent variables showing that the effect of changing the climate was low. However, the effects of drought limitation of microbial processes is already strong in the south of France and the translocation did not change the moisture effect to any great extent. Nevertheless, significant differences between local and translocated Vindeln, Friston and La Clape A1 soils indicated the effect of other factors than climate when soils were translocated.

Discussion

Temperature and moisture response functions

The sum of the daily temperatures above zero has been used as a heat unit (Andrén & Paustian 1987; Van Cleve et al. 1990; Sparrow et al. 1992; Vreeken-Buijs & Brussaard 1996). For example, Honeycutt et al. (1988)

showed, in laboratory studies, that a single line could described soil respiration at different temperatures when cumulative CO_2 efflux was plotted against degree-days. Hence a single parameter collectively accounted for the temperature effects on the microbial decomposition processes.

The exponential Q_{10} rate function based on the van't Hoff law is widely used in modelling the response of soil C pools to temperature. Das et al. (1995) showed that Q_{10} integrates oscillating temperature effects and suggested the use of a rate unit accumulation rather than heat unit accumulation. We used the sum of the daily van't Hoff function (τ_{sum}) with an optimal daily temperature of 30 °C and a fixed Q_{10} of 2.2. This value is close to the median value 2.4 given by Raich and Schlesinger (1992) for respiration of a large range of soils. However, Q_{10} appears to vary with temperature and Schleser (1982) and Kirschbaum (1995) calculated low values under high temperatures and high values (up to 6) under low temperatures. From 149 values given in the literature (Table 5), we calculated a linear relationship between Q_{10} and temperature: $Q_{10} = -0.0708T + 3.61$ and based on this relationship, we calculated τ using a variable Q_{10}. τ_{sum} was increased for all treatments with higher increases for the warm sites than for the cold ones. However the fit was not improved (results not shown). Kätterer et al. (1998) also found that a constant Q_{10} was adequate for describing the temperature dependence in the intermediate temperature range (about 5–35 °C).

At Jädraås, air temperature was recorded at the same time as soil temperature (0 to 10 cm). The calculation of τ and the model fits were not improved by using soil temperature and we therefore consider that air temperature may be used for modelling SOM decomposition.

We assumed that the response function to moisture was linear with the water deficit between 0 ($\mu = 1$) and a limit water deficit (DEF_{lim}) above which the decomposition stops ($\mu = 0$). For high moisture contents, soil conditions become anaerobic and decomposition rates decrease. In these sequences, soils were located in well-drained areas and we assumed that the anaerobic threshold was generally not reached. Under field conditions, good predictions of soil respiration or decomposition for moisture control were obtained by Schlentner and Van Cleve (1985) using the GRESP model (Bunnel & Tait 1974) and by Jansson and Berg (1985) using the ratio of the current moisture content or the water potential to an optimal threshold.

Several authors (Wildung et al. 1975; Casals et al. 2000) have shown, from field data, that the moisture effect on microbial respiration is temperature dependent. At low temperatures, the increase in moisture content has a small effect on soil respiration whereas the range of response to moisture increases at higher temperatures. In order to take the interactive effects between temperature and moisture into account, the authors generally use the product of the temperature and moisture response functions (e.g. Jansson

Table 5. Source data for Q_{10} values for CO_2 production or mass loss

Date source	Temperatures	Measurement	Ecosystem	Country
Donnelly et al. 1990	4, 12, 24	mass loss	forest	Oregon, USA
Holland et al. 1995	15, 25, 45, 55	CO_2 efflux	pasture, forest	Hawaii, USA
Joergensen et al. 1990	15, 25, 35	CO_2 efflux	grassland	UK
Nadelhoffer et al. 1991	3, 9, 15	CO_2 efflux	tundra	Alaska, USA
O'Connell 1990	4, 20, 35	CO_2 efflux	Eucalypt forest	south-western Australia
Peterjohn et al. 1993	+5	CO_2 efflux	mixed deciduous forest	Massachusetts, USA
Pöhhacker & Zech 1995	5, 15	mass loss	beech forest	Germany
Ross & Cairns 1978	0, 5, 10, 15, 20, 25	CO_2 efflux	tussock grassland	New Zealand
Seto & Yanagiya 1983	15, 20, 30	CO_2 efflux	volcanic forest	Japan
Stott et al. 1986	0, 5, 10, 15, 20	CO_2 efflux	wheat residue	
Townsend et al. 1997	20, 30, 40	CO_2 efflux	pasture, forest	Hawaii, USA
Winkler et al. 1996	4, 15, 22, 38	CO_2 efflux	mixed forest	North Carolina, USA
Wolters & Ekschmitt 1995	5, 15	CO_2 efflux	beech litter	Germany

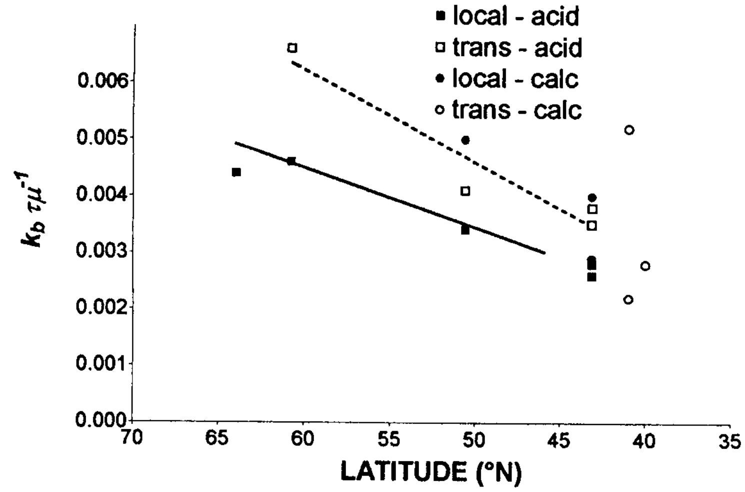

Figure 4. Linear regression between k_b and latitude (LAT) for local (k_b = 0.9.10^{-4} LAT − 1.2.10^{-3}, R^2 = 0.96, $p < 0.01$, solid line) and translocated soils (k_b = 1.6.10^{-4} LAT − 3.5.10^{-3}, R^2 = 0.91, $p < 0.05$, dashed line).

& Berg 1985; Parton et al. 1987; Rodrigo et al. 1997; Kätterer et al. 1998). Although the balance between both response functions is arbitrary, there is a consensus about the validity of this simple combination.

In the present study, the effect of the translocation on ^{13}C decomposition was largely explained by the combined response function for the Jädraås soil indicating that the variation of decomposition rates due to the translocation was almost exclusively due to the climate. However, for the other soils, discrepancies between the measured and expected data indicate that other factors must be involved.

Deviation from expected trends

If both climate components completely explain the observations, the temperature × moisture optimised k_a and k_b parameters should reach similar respective values (1) amongst the sites and (2) for the local and transplanted soils, regardless the climatic condition of the sites. This was not generally the case. The value of k_a was similar for both boreal soils (Vindeln & Jädraås) (Figure 2(e)) and for donor and host sites but for more southerly soils, k_a was different in both Atlantic local soils (Haldon & Friston) and in the local Mediterranean soils of La Clape Oh and A1. Thus the k_a values of most of the local and translocated Atlantic and Mediterranean soils differ and were unexplained by the climate variables alone. From Figures 2(a) to 2(c) to 1(e) only the fitting errors were improved. The range of variation of k_b was reduced for the $\tau\mu_{sum}$ optimised values (Figure 2(f)). Nevertheless, despite the overlap of the fitting errors, the k_b showed a trend of lowering from north to south in the acid sequence as indicated by the linear regression for both the local and the translocated soils (Figure 4). The slope of this regression was significantly different from 0, thus the temperature × moisture optimised k_b values decreased from north to south. No trend appeared in the calcareous sequence.

By the end of the experiment (after 3–3.5 years), the ^{13}C remaining in the soils was 30–25% of the initial amount, reaching similar levels of mineralisation at all sites, and for local and translocated soils and may indicate that the stabilised fraction was insensitive to climate variation. Giardina and Ryan (2000) have shown that responses of soil-C turnover along mean annual temperature gradients to increased temperatures are small, ephemeral or non-existent. However, the amount of C stabilisation occurred earlier in the warmer southern sites than in the colder northern sites. This was reflected by the overall decline in k_b and increase in k_a values as towards the south. This also implied (and was observed when the measured data were plotted against τ_{sum}) that the northern soils required less temperature units than the southern soils to reach the same mineralisation level, even if τ_{sum} is corrected by μ_{sum} (Figure 3). Using soils from the same sites as in the present experiment, McTiernan (1998) showed under laboratory conditions, that soil microbial inocula originating from Mediterranean coniferous forests induced lower decomposition rates at all temperatures than inocula originating from boreal forests. He concluded that the decomposer community differed either in composition or in efficiency with respect to climate. Dalias et al. (2001a,b), incubating soils at different temperature found that the magnitude of the temperature response function was related to the period of soil incubation. Initial temperature responses of microbial communities were different to those shown after a long period of laboratory incubation and may have reflected shifts in microbial species composition in response to changes in the temperature regime. The amount of material that can be readily decomposed, at a given decomposition stage, was higher in samples incubated at 4 °C than at 30 °C. It was concluded that in addition to temperature controlling rates of C mineralisation in soil it also affects the processes of decomposition so that material produced at higher temperatures was more recalcitrant than at lower temperatures. These results support the hypothesis that there is probably not a single decomposition response function to climate as confirmed by the overall lowering of k_b in Figure 2(f).

Finally for k_b, three results deviate from the general distribution pattern: the translocated Vindeln soil and limestone Friston and La Clape soils (Figure 2(f)). The translocation of the Vindeln soil stimulated the decomposition of the B fraction to an extent not directly explained by the climate parameters (Figure 2(b), (d) and (f)). At Vindeln the top organic soil may be temporarily under anaerobic conditions at snowmelt when the sub-soil is still frozen with a high ground water, thus preventing the normal drainage. At Jädraås, under warmer conditions, with deep ground water and well-drained soil, this phenomenon is expected to be less pronounced and of a shorter duration. Thus the deviation of the translocated Vindeln soil may be explained by a climate effect that was not reflected by the response functions.

The temperature effect prevailed at the northern sites. The Mediterranean sites were dominated by prolonged water stress (Table 1) and the temperature effect was counteracted by μ close to 0 during summers. This is illustrated by comparing data in Figure 2(d) and (f) for the boreal and Atlantic sites, where the k_b values were not modified when the moisture factor was integrated, in contrast, moisture reduced the generally sinking of k_b values for the Mediterranean sites.

Soil physico-chemical characters, given by Bottner et al. (2000), can in some cases explained the higher and climate-independent dispersion of k_a rates. Bottner et al. (1998) found, for some soils of these series that mineralisation rates in the laboratory were generally higher for the calcareous soils, possibly because the microbial activity was stimulated by neutral or basic pH and more nutrient-rich soils. This may explain the higher k_a values for La Clape A1, and Friston (local soil) but also the higher k_b values of these calcareous soils. Thus soil pH may be considered as a factor determining decomposition parameters. The Oh horizon at La Clape deserves special consideration. The humus type is morphologically recognised as a 'xeromoder', where the raw humus accumulates and remains largely undecomposed, probably due to the extreme dry conditions of the top horizon. In such Mediterranean soils, the top organic horizon is isolated from the mineral soil by a layer of stones (Bottner et al. 2000; Casals et al. 2000) which was simulated in the soil columns. Nevertheless the particular conditions of this horizon does not completely explain the k_a and k_b, since the climate optimised k_a and k_b are still deviated toward the lowest values (Figure 2(e) and (f) compared to (a) and (b)). Obviously, in these 'xeromoders', the microbial composition and efficiency are different from the other soils. The Haldon soil (the Atlantic site of the acid sequence) also shows a high k_a value unexplained by climate. All the other acid soils, developed on granite or sandstone, are sandy soils. The Haldon soil, developed on chalk, is characterised by a much higher clay content which should reduce the ^{13}C mineralisation rate. Thus for the climate optimised k_a values, the local Haldon soil and the significant differences after translocation of Friston, Haldon and La Clape Oh soils remain unexplained. The translocation effect of the Mediterranean wet soils to the dry Mediterranean zone was generally significant neither for k_a nor for k_b. This is may be explained by the fact that the climate differences are too small especially for temperature (Table 1).

The k_b parameter was expected to be more closely related to the soil characteristics than k_a, since the stabilised B pool is closely linked to the soil mineral part and this is confirmed for the limestone soils. Nevertheless, in general, our results show that k_a was less explainable by the climate components than k_b suggesting for k_a a higher contribution from the soil physico-chemical environment. The specific temperature response of A and B pools is another possible explanation. Despite Kätterer et al. (1998) and Lomander et al. (1998) assumption that the decomposition rates of different SOM compartments are equally affected by temperature, the results of this study suggest, as mentioned also by Trumbore et al. (1996), that the pools may not have responded in the same way to climate conditions.

Conclusions

This experiment, using standard ^{13}C labelled plant material, showed that none of the effects on decomposition, due to changes in temperature and moisture produced by translocating soil between sites, were explained by a single climatic response function.

1. Estimates of k_b values were better than for the k_a values;
2. except for boreal sites, the slow-decomposing compartment B was more sensitive to climate than the fast-decomposing compartment A;
3. except for the Jädraås soil, the climate response functions did not fully explain the translocation effect;
4. the k_b values optimised for climate decreased with latitude indicating that the SOM stabilisation occurred earlier in warmer sites; and
5. some indirect effects of climate are not taken into account by the response functions. For example, the anaerobic conditions that may occur during the spring when permafrost smelt in the boreal site of Vindeln, or the strong water stress that occurred in xeromoder laying on a stone layer in the Mediterranean site of La Clape.

Acknowledgements

This study was performed within the VAMOS programme funded by the European Union (Climate and Environment programme, DG XII, EV5VCT920141). We thank G Billès, H Casabianca, V Coûteaux, J Cortina, P Cox, P Dalias, F Picasso, P Rovira, L Sanger, P Splatt and MJ Whelan for their contributions to the experiment. We are also grateful to Prof V Meentemeyer for providing the WATERBUD model. Financial support for this work was also provided by German Ministry for Education, Science, Research and

Technology (BMBF, Grant No PT BEO-51-0339476) to Dr Björn Berg, while working as a guest scientist at BITÖK, University of Bayreuth.

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