



Effect of temperature on humus respiration rate and nitrogen mineralization: Implications for global climate change

M. NIKLIŃSKA, M. MARYAŃSKI & R. LASKOWSKI

Department of Ecosystem Studies, Institute of Environmental Biology, Jagiellonian University, Ingardena 6, 30-060 Kraków, Poland

Accepted May 14 1998

Key words: decomposition, global warming, humus, nitrogen mineralization, respiration, Scots pine, soil organic matter, temperature increase

Abstract. Respiration and nitrogen mineralization rates of humus samples from 7 Scots pine stands located along a climatic transect across the European continent from the Pyrenees (42°40') to northern Sweden (66°08') were measured for 14 weeks under laboratory conditions at temperatures from 5 °C to 25 °C. The average Q_{10} values for the respiration rate ranged from about 1.0 at the highest temperature to more than 5 at 10 °C to 15 °C in the northernmost samples. In samples from more northern sites, respiration rates remained approximately constant during the whole incubation period; in the southern end of the transect, rates decreased over time. Respiration rate was positively correlated with incubation temperature, soil pH and C:N ratio, and negatively with soil total N. Regressions using all these variables explained approximately 71% of the total variability in the respiration rate. There was no clear relation between the nitrogen mineralization rate and incubation temperature. Below 15 °C the N-mineralization rate did not respond to increasing temperature; at higher temperatures, significant increases were found for samples from some sites. A regression model including incubation temperature, pH, N_{tot} and C:N explained 73% of the total variability in N mineralization. The estimated increase in annual soil respiration rates due to predicted global warming at the high latitudes of the Northern Hemisphere ranged from approximately 0.07×10^{15} to 0.13×10^{15} g CO_2 at 2 °C and 4 °C temperature increase scenarios, respectively. Both values are greater than the current annual net carbon storage in northern forests, suggesting a switch of these ecosystems from net sinks to net sources of carbon with global warming.

Introduction

The rate of organic matter decomposition in forest ecosystems depends primarily on temperature and humidity (e.g., O'Connell 1990). Thus, soil organic carbon is a large potential source of CO_2 , which would be released at an increased rate under the predicted global climate warming. Although a number of studies on decomposition rate versus temperature have been

published recently (e.g., Holland et al. 1995; Kirschbaum 1995; MacDonald et al. 1995), results are quite variable. For example, an exponential increase in the respiration rate up to 55 °C in soil samples originating from different ecosystems along an altitudinal gradient in Hawaii was reported by Holland et al. (1995). In contrast, O'Connell (1990) determined an optimum temperature between 33 °C and 34 °C for the respiration rate of litter originating from two species of Australian eucalyptus trees. Such variation makes it very difficult to predict global or even regional effects of climate change on soil organic matter decomposition rates, especially because, as noted by Holland et al. (1995), even minor variability in soil respiration rates due to temperature changes may make regional estimates of gas exchange uncertain. Without these predictions, however, reliable scenarios of global change are impossible: relatively minor changes in the estimated effects of temperature on decomposition can mean the difference between a net sink and a net source of CO₂ in large areas of the Northern Hemisphere.

In this work we hypothesized that the decomposition process is 'fine-tuned' to the climatic conditions under which it normally operates. This should result in different temperature/decomposition rate curves for northern and southern systems. This climatic fine-tuning may result from the specific temperature and humidity tolerance of soil microorganisms as well as differences in chemistry of litter and soil organic matter developed under different climatic regimes (Berg et al. 1995; Couteaux et al. 1995; Amelung et al. 1997). In this study we only tested the extent to which the biological activity of soils originating from Scots pine forests ranging from the Pyrenees to Northern Sweden, respond differently to temperature changes.

Materials and methods

Study sites and humus sampling

Seven Scots pine stands from the European continent along a latitudinal transect ranging from 42 °40' N to 66 °08' N were selected for this study. The plots were Scots pine monocultures, with only small admixtures of other species in the undergrowth (birch, oak). Three plots were located in Sweden: Harads (H), Jädraås (J) and Brandstorp (B); two in Poland: Czerlonka (C) and Ołobok (O); one in France: LaViale (L); and one in Spain: Biescas (E). The mean annual temperature ranged from 0.6 °C at the northernmost plot (H) to 10.6 °C at the southernmost (E). The Swedish and Polish plots were located in lowlands (below 200 m a.s.l.), and the two southernmost plots were mountainous (L, about 920 m a.s.l.; E, about 800 m a.s.l.). More detailed site data are given in Table 1.

Table 1. Main characteristics of sites used in the study.

Site	Latitude/longitude	Altitude (m a.s.l.)	Ann. mean temp. (°C)	Avg. temp. for growing season (°C)	Ann. mean precip (mm)	Actual evapo- transpiration (mm)
H	66°08' N 20°53' E	58	0.6	9.8	470	387
J	60°49' N 16°01' E	185	3.8	11.5	609	472
B	58°03' N 14°08' E	155	6.2	11.1	930	491
C	52°41' N 23°47' E	165	5.7	12.0	594	545
O	52°22' N 14°36' E	60	8.1	13.9	604	549
L	44°11' N 03°24' E	920	8.2	13.5	793	565
E	42°40' N 03°20' E	800	10.6	17.7	793	661

H – Harads (Sweden), J – Jädraås (Sweden), B – Brandstorp (Sweden), C – Czerlonka (Poland), Ołobok (Poland), L – LaViale (France), E – Biescas (Spain).

At all plots there was a well developed mor-type humus layer. At least ten randomly selected samples of the whole organic layer ($A_{0L} + A_{0F} + A_{0H}$) were sieved through a 1-cm mesh sieve at each plot, and approximately 1 kg of humus (wet weight) was collected and transported to the laboratory in perforated plastic bags. Immediately upon arrival at the laboratory the humus from each plot was thoroughly hand-mixed, and the water holding capacity (WHC) and dry weight (DWT) were measured.

Laboratory incubation, respiration measurement and chemical analyses

Five samples of 5 g DWT humus from each site were incubated at 50% WHC at 5 °C, 10 °C, 15 °C, 20 °C, and 25 °C. The samples were incubated in air-tight perspex or glass jars of about 0.5 l volume, with a small 10 cm³ container for NaOH attached to the jar lid. Respiration rates were measured every second week for 14 weeks, and in the meantime the containers were left open. The moisture of the samples was adjusted weekly gravimetrically with deionized H₂O. The respiration rates were measured for approximately 10–24 hours, depending on the incubation temperature, by CO₂ absorption in 0.2 N NaOH. The excess NaOH was titrated with 0.1 N HCl, using a digital Jencons burette with 0.01 ml precision. The incubation time was recorded to the nearest minute.

Concentrations of N-NH₄ and N-NO₃ in the litter were measured before and at the end of the experiment, after 105 days of incubation. The N-NH₄ and N-NO₃, after extraction in 2M KCl, were analyzed using distillation with Devarda's alloy (Starck modified Bremner method; Sady et al. 1994). Subsamples were analyzed also for pH_{H₂O} (digital pH-meter, Nester Instr.)

and content of dry matter (105 °C, 12 h) and organic matter (550 °C, 12 h). Total C and total N were analyzed in five replicate mixed samples per plot, using a Perkin-Elmer CHN-analyzer.

Statistical analysis

The average respiration rates for the whole incubation period were compared between plots with analysis of covariance, with incubation temperature as a covariate. More detailed analysis was performed using multiple regression technique with dummy variables (D) for plots. Using this model, the respiration rate R can be expressed as

$$R = a + bT + c \exp T + dD + eDT,$$

where T stands for the incubation temperature and *a*, *b*, *c*, *d*, *e* are the estimated parameters. The significance of *d* indicates different intercepts, and significant *e* – indicates a significant difference between plots in the slope of the relation between respiration rate and temperature.

Multiple regression analysis was used also to relate average humus respiration and nitrogen mineralization rates to the main factors besides incubation temperature potentially having significant effects on these processes, that is, pH, C:N ratio and total nitrogen (N_{tot}). The most important relations were shown as three dimensional surface plots (Figures 4 and 6). For each of these plots we calculated both linear and quadratic regressions, and the one that gave better fit (higher R^2 adjusted for degrees of freedom) was plotted.

Finally, the Q_{10} values were calculated based on the respiration rates (R) measured at 5 °C intervals, using the formula:

$$Q_{10} = \left(\frac{R_{T_2}}{R_{T_1}} \right)^2$$

where T_1 and T_2 stand for lower and higher incubation temperatures in 5 °C intervals, respectively.

Results

Humus

The humus samples differed markedly between plots in their initial moisture (DWT = 33.5% to 82.8%) and organic matter content (46.2%–95% of DWT), but these characteristics were not related to latitude or actual evapotranspiration. Similarly, no latitudinal relation was found for nitrogen concentration or

Table 2. Soil organic matter and selected chemical characteristics.

Site name	Dry matter content (%)	Organic matter content (%)*	N _{tot} ** (mg g ⁻¹)	C:N	pH _{H₂O}
H	67.6	93.1	0.71	70.4	5.6
J	29.2	92.6	1.16	43.1	5.8
B	33.5	95.1	1.05	49.2	5.9
C	42.6	46.2	0.85	33.4	6.1
O	39.6	83.1	1.67	28.1	5.9
L	82.8	84.9	0.91	53.2	6.1
E	52.2	75.0	0.93	44.7	6.3

H – Harads (Sweden), J – Jädraås (Sweden), B – Brandstorp (Sweden), C – Czerlonka (Poland), O – Ołobok (Poland), L – LaViale (France), E – Biescas (Spain)

* Organic matter content as percent dry matter

** N_{tot} on a dry matter basis.

C:N ratio (Table 2). The pH of the soil was the least variable characteristic, with the lowest values in the northern part of the transect (pH = 5.6 for H, and pH = 5.8 for J), and the highest at the southernmost location (pH = 6.3; Table 2). Such a geographical distribution may have a confounding effect on correlations between climate and decomposition.

Respiration rate

The average respiration rates for 14 weeks were related to temperature for all sites, but for particular temperatures the rates differed markedly between sites within temperature ranges (ANOVA, $p < 0.0001$). On average, the study plots could be ordered by respiration rates as follows: B < O < J < H < C ≤ E < L. However, a highly significant interaction term (plot × temperature; $p < 0.0001$) indicates different relationships between temperature and respiration rate for different plots (Figure 1). In fact, there were highly significant differences in intercepts ($p < 0.0001$) and slopes ($p < 0.0001$) of the regressions for different plots of the respiration rate on temperature. Also, a significant nonlinearity (EXP(T)) of the relation between respiration rate and temperature was found ($p < 0.0001$). The regression calculated in that way, that is, considering the between-plot differences and the nonlinearity of the relation, explained as much as 94% of the total variability in the average humus respiration rates across plots and temperatures ($n = 175$, $P < 0.0001$).

To determine the factors responsible for the between-plot variability in the respiration rates, a multiple regression analysis with temperature (T), pH, total N (N_{tot}) and C:N as independent variables was performed. All these

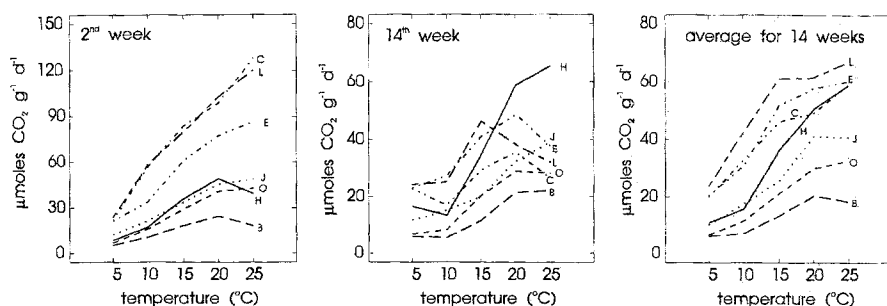


Figure 1. Relation between respiration rate and temperature for humus samples originating from Harads (H; N. Sweden), Jädraås (J; central Sweden), Brandstorp (B; S. Sweden), Czerlonka (C; N.-E. Poland), Ołobok (O; W. Poland), LaViale (L; S. France) and Biescas (E; N. Spain). Results from the 2nd and 14th weeks of the experiment are shown together with the averages calculated for the whole incubation period.

factors appeared significant (T , $p < 0.0001$; pH , $p < 0.0001$; N_{tot} , $p = 0.004$; C:N , $p = 0.0214$). The common regression model for all plots was as follows:

$$\text{CO}_2 = -226.7 + 1.79 T + 39.3 \text{ pH} - 14.01 N_{\text{tot}} + 0.28(\text{C:N}).$$

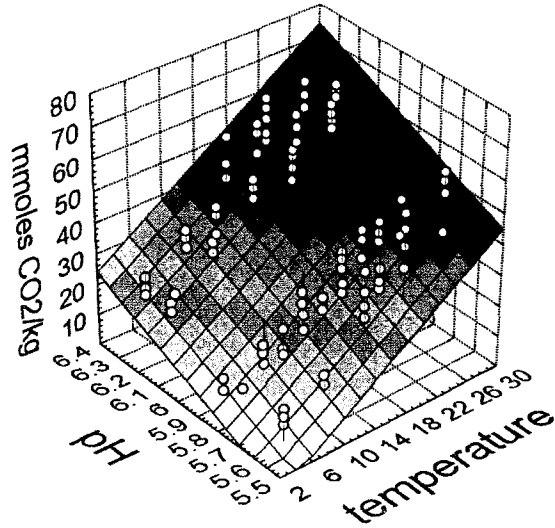
Thus, the respiration rate increased with increasing temperature, pH and C:N , and decreased with increasing concentration of total N . These relations were in agreement with the simple bivariate correlation coefficients (Table 3), and can be shown as a set of two three-dimensional surfaces (Figure 2). In terms of the standardized regression coefficients (β), the most important factor was, as expected, temperature ($\beta = 0.67$), followed by pH ($\beta = 0.45$), N_{tot} ($\beta = -0.21$) and C:N ($\beta = 0.19$). This multiple regression model explained approximately 71% of the total variability in the respiration rate.

The samples with the highest respiration rates, originating from three sites L, E and C, had relatively large increases in their respiration rates with a temperature increase from 5 °C to 15 °C, but above 15 °C the average respiration rates increased much more slowly (Figure 1). In contrast, for samples from the remaining four sites (B, O, J, H) the greatest change in average respiration rates were noted between 10 °C and 20 °C, and for two of them the average respiration rates decreased at 25 °C (Figure 1). These differences are reflected in the calculated Q_{10} values (Table 4). For those humus samples for which Q_{10} s values were below 1.0 (B and J), the optimum temperature was exceeded, and the low respiration rate increase ($1 < Q_{10} < 1.5$) for humus from other plots indicates that in those cases the highest incubation temperature was close to the optimal one (Table 4).

The dynamics of respiration during the incubation period differed considerably among plots and temperatures. The respiration rates of humus from

$$\text{CO}_2 = -188.794 + 1.793 \cdot T + 32.694 \cdot \text{pH}$$

$$p = 0.0000 \quad R^2_{\text{adj}} = 0.58$$



$$\text{CO}_2 = -19.87 + 2.18 \cdot T + 0.92 \cdot (\text{C/N}) - 0.046 \cdot T^2 + 0.022 \cdot T \cdot (\text{C/N}) - 0.011 \cdot (\text{C/N})^2$$

$$p = 0.0000 \quad R^2_{\text{adj}} = 0.48$$

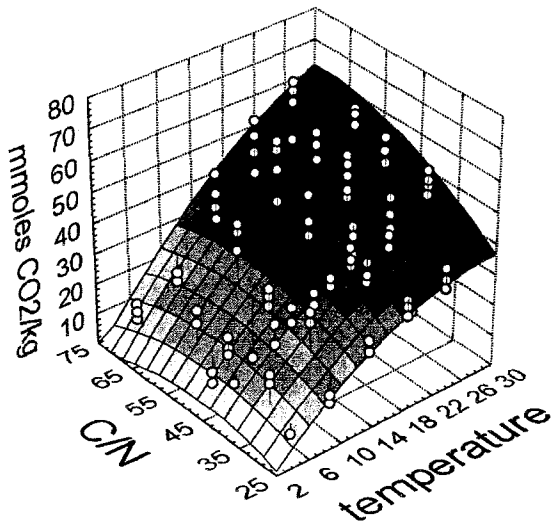


Figure 2. Three-dimensional surface plots showing combined effects of temperature and pH (upper plot) and temperature and C:N ratio (lower plot) on the humus respiration rate.

Table 3. Simple Pearson correlation coefficients between variables used in multiple regression analysis; RES – average respiration rate for the incubation period ($n = 175$).

Variable	TEMP	pH	N _{tot}	C:N	RES
TEMP	–				
pH	0.00	–			
N _{tot}	0.00	–0.06	–		
C:N	0.00	–0.47***	–0.70***	–	
RES	0.67***	0.37***	–0.38***	0.13	–
N _{min}	0.34***	0.18*	0.07	–0.52***	0.21**

* $p < 0.05$

** $P < 0.005$

*** $p < 0.001$

H, J and B were fairly constant over the whole incubation period at all temperatures. For the remaining plots (C, O, L, E), a clear decrease in the respiration rates with time was observed, at least for some incubation temperatures (Figure 3). For Olobok (site O) the pattern was less pronounced, but the respiration rates at all temperatures above 5 °C at the end of incubation were also lower than the initial rates (Figure 3). These decreases resulted in substantial differences in Q_{10} values calculated at the beginning and at the end of incubation (Table 4, Figure 1).

Nitrogen mineralization

In general, nitrogen mineralization rates were positively related to incubation temperature. However, unlike respiration, for which the greatest rate of increase was found in the lower range of temperatures, N mineralization did not respond significantly to temperature increase up to 15 °C (with the exception of plot C) (Figure 4). A significant increase in N mineralization rates was found above 15 °C for O and J, and above 20 °C for B (Figure 4). In humus from Biescas (E), negative values (net immobilization) were obtained for temperatures below 20 °C, and low positive values (net mineralization) at 20 °C and 25 °C. For LaViale (L) the changes in concentration of mineral N during incubation were in the range of analytical error (net mineralization approximately balanced by net immobilization). For most sites except C, nitrification was negligible (J, B, O, L) or very low (H), and at the end of incubation the mineral nitrogen was recovered mainly as N-NH₄ (Figure 4).

Multiple regression analysis with mineralized N as a dependent variable, and with incubation temperature, pH, C:N, N_{tot}, initial N-NH₄ and initial N-NO₃ concentrations as independent variables, resulted in a highly significant

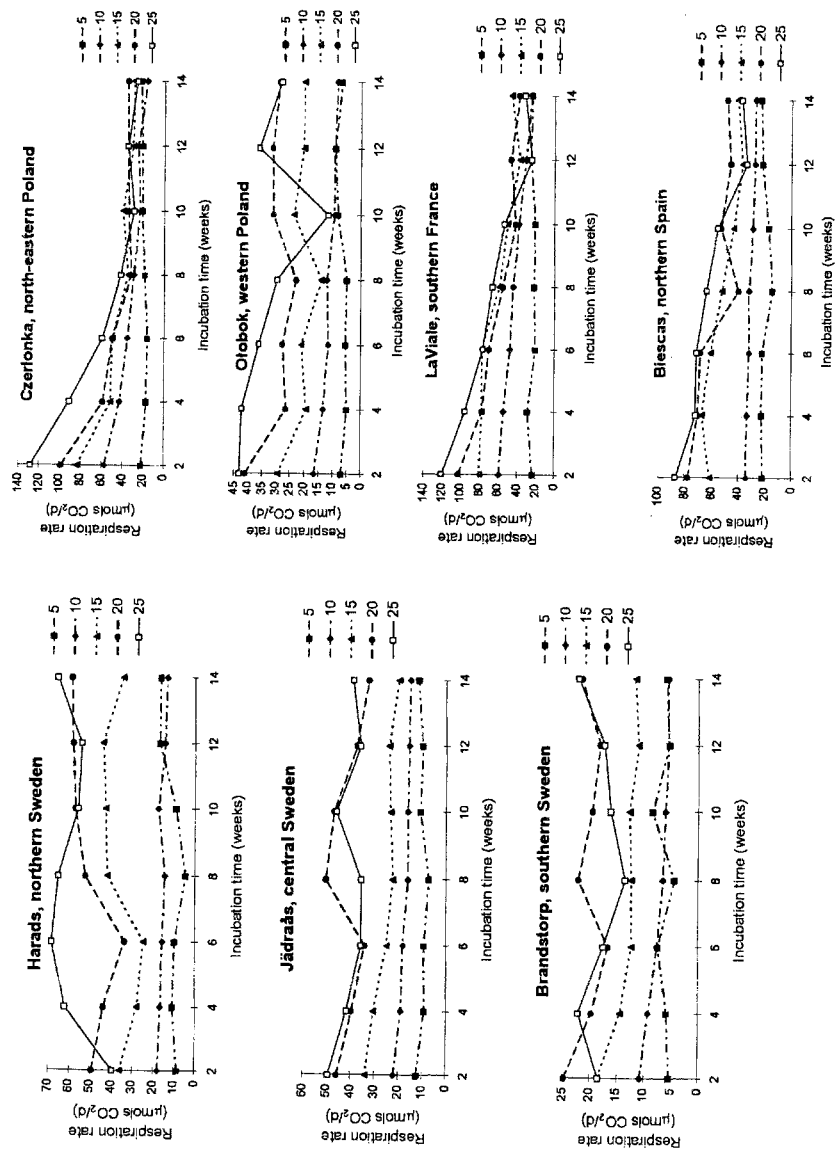


Figure 3. Dynamics of the respiration rates of humus samples originating from Sweden (Harads, Jädraås, Brandstorp), Poland (Czerlonka, Ołobok), France (LaViale) and Spain (Biescas) during 14 – week incubation; numbers in the legends stand for incubation temperatures.

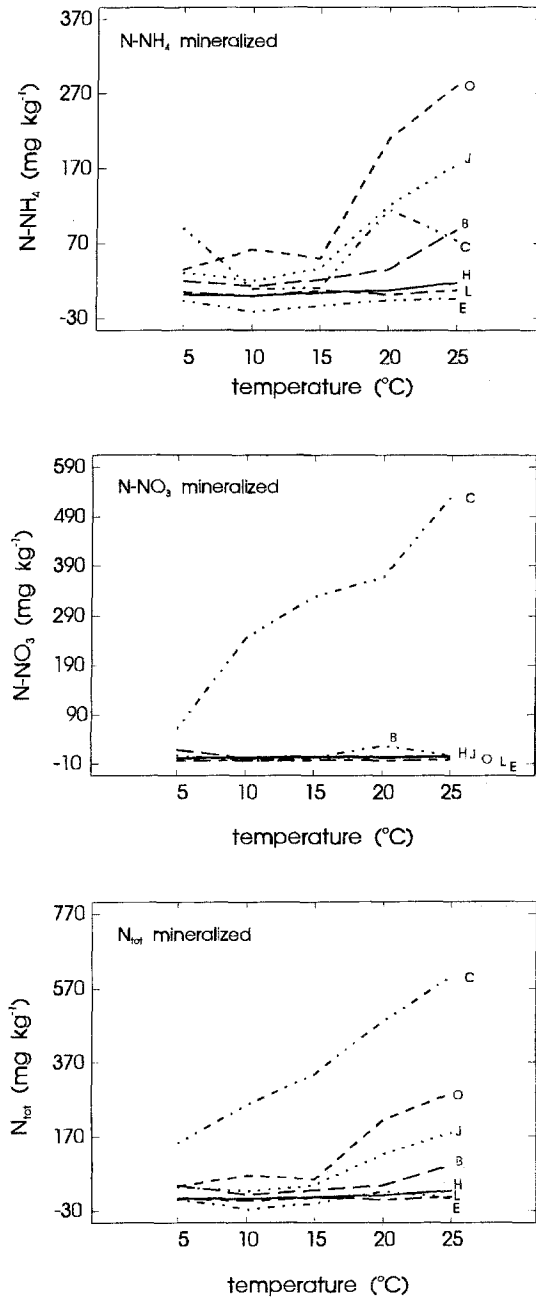


Figure 4. Relation between nitrogen mineralization rate and temperature for humus samples of different origins (H, J, B, C, O, L, E – see description for Figure 1).

Table 4. Q_{10} values based on 5 °C-intervals, calculated for the beginning of humus incubation (RES_{ini}), the last respiration measurement (105 days; RES_{end}) and the average respiration rates for the whole incubation period (RES_{avg}).

Plot	Temp. range (°C/°C)	RES_{ini}	RES_{end}	RES_{avg}
		Q_{10}		
H	10/5	4.43	0.65	2.07
	15/10	4.09	6.66	5.28
	20/15	1.87	2.89	1.96
	25/20	0.64	1.25	1.35
J	10/5	3.15	1.65	2.98
	15/10	2.38	1.75	2.15
	20/15	1.83	2.62	2.56
	25/20	1.16	1.45	0.98
B	10/5	4.04	0.87	1.39
	15/10	2.98	4.49	3.40
	20/15	1.78	3.37	2.33
	25/20	0.55	1.06	0.80
C	10/5	6.83	0.55	2.73
	15/10	2.13	5.74	1.98
	20/15	1.39	2.03	1.13
	25/20	1.68	0.95	1.42
O	10/5	5.67	1.51	3.01
	15/10	3.17	5.74	3.36
	20/15	1.95	2.03	1.99
	25/20	1.10	0.95	1.18
L	10/5	6.12	1.08	3.24
	15/10	1.84	3.40	2.04
	20/15	1.65	0.83	1.02
	25/20	1.38	0.70	1.18
E	10/5	2.52	1.40	2.28
	15/10	3.22	2.24	2.83
	20/15	1.59	1.42	1.24
	25/20	1.26	0.60	1.08

regression ($P < 0.0001$). The significant factors were temperature, pH, C:N and N_{tot} ($p < 0.0001$ for all). The final regression model,

$$N_{min} = 3823 + 6.92 * T - 414 * pH - 17.7 * (C:N) - 533 * N_{tot},$$

explained 73% of the total variability (R^2 adjusted for degrees of freedom). This multiple regression suggests that the N mineralization rate was the

highest at high temperatures in humus samples with low pH, C:N and N_{tot} . However, these results partly contradict the correlation analysis, which indicates a positive correlation between N mineralization rate and pH, and practically no correlation with N_{tot} (Table 3). The three-dimensional surfaces shown in Figure 5 also suggest a positive correlation between N mineralization rate and pH.

The most probable cause of this discrepancy was the much lower variability of pH between the studied soils ($CV = 0.036$) than of other factors ($CV_{\text{TEMP}} = 0.47$; $CV_{N_{\text{tot}}} = 0.28$; $CV_{C:N} = 0.28$). As a result, the effect of pH could have been masked by other, more variable factors. In fact, the values of the standardized regression coefficients (β) suggest that the most important factors for N mineralization were C:N ($\beta = -1.6$) and total N ($\beta = -1.1$), followed by pH ($\beta = -0.61$) and temperature ($\beta = 0.34$). Another factor possibly responsible for such an outcome is non-biological fixation of nitrogen in neutral to high pH soils (Johnson 1992): in these soils, even if mineralization rates would increase with increasing temperatures, most of the N mineralized would be fixed in non-biological processes. The data obtained for the two southernmost sites, L and E, having the highest pH, may confirm this hypothesis; on the other hand, the fastest N mineralization rate was found in humus originating from Czerlonka (C) with the same pH reaction as at L.

Discussion

Respiration rate

The calculated average Q_{10} s in our experiment ranged from values below 1.0 for some soils at the highest temperatures to above 5.0 at lower temperatures. This is a much broader range than the 1.4 to 2.0 reported by Holland et al. (1995), but these authors studied tropical soils from Hawaii, which appear to be more uniform in their sensitivity to temperature changes. For two northern peat soils, Chapman and Thurlow (1996) found Q_{10} values of 3.3 and 6.1, similar to the range obtained in our experiment, and Kirschbaum (1995) reported Q_{10} as high as about 8. He also noted that the temperature sensitivity of decomposition processes decreases with increasing temperature, with Q_{10} about 4.5 at 10 °C, and 2.5 at 20 °C. This is in agreement with our higher Q_{10} s around the lower end of the temperature gradient.

The dynamics of the respiration rates during the incubation period differed clearly between sites, and two separate groups could be distinguished: in samples from Scandinavian sites, the respiration rates remained approximately unchanged throughout the experiment, while in samples of more southern origin they clearly decreased with time. Differences in carbon

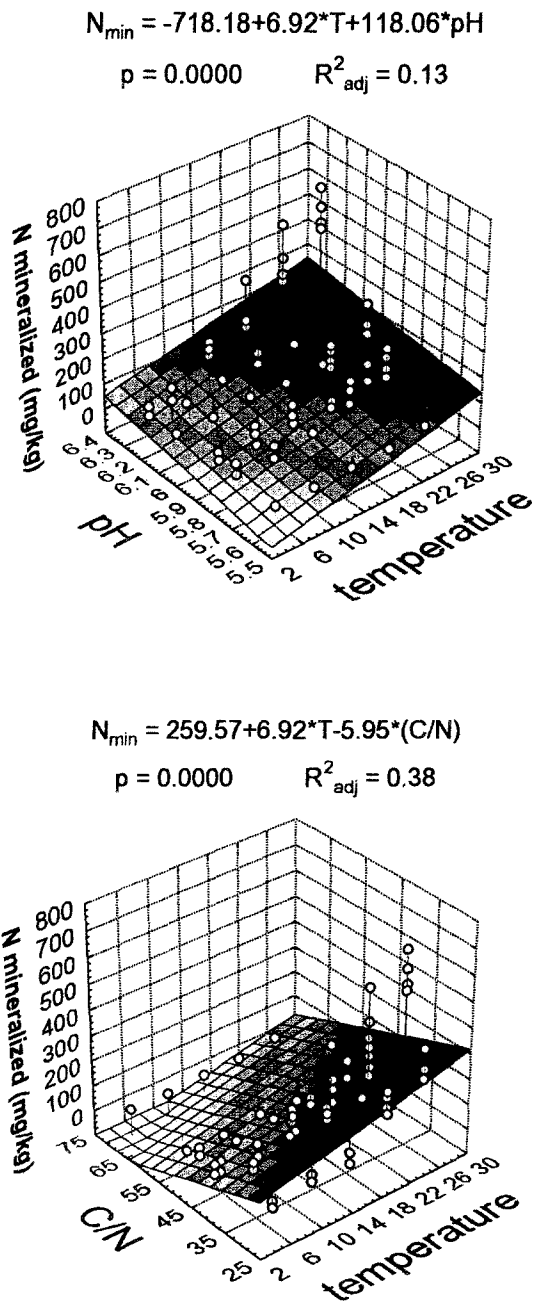


Figure 5. Three-dimensional surface plots showing combined effects of temperature and pH (upper plot) and temperature and C:N ratio (lower plot) on the nitrogen mineralization rate.

sources between these two groups may explain these differences. Relatively constant respiration rates in time suggest more uniform organic material, presumably consisting largely of compounds relatively resistant to decomposition. On the other hand, fast decrease in the respiration rate with time indicates the presence of two different pools of organic matter: an easily degradable pool that is depleted early in the incubation, and a resistant, slowly degrading pool that remains after more available carbon sources have been used.

Nitrogen mineralization

The magnitude of temperature-driven changes in nitrogen mineralization rates was not related to latitude as it was in case of respiration rates. In humus from the French site (L), net mineralization rates were generally very low, and it is difficult to estimate the possible effects of a temperature increase. The pattern is somewhat more clear for the Spanish site (E), where there was a switch from negative (that is, net immobilization) at lower temperatures to positive (net mineralization) at 20 °C. As the present temperature for the growing season at E is 17.7 °C, this could mean a switch from net immobilization or zero mineralization to positive values at increased temperatures.

Implications under climate warming

The relations between humus respiration rates and incubation temperature are complicated and nonlinear, with substantial differences between humus samples of different origin. Our estimates suggest that global warming will have a greater effect on rates of CO₂ release from humus at northern latitudes, even if the average temperature increase is the same over all of Europe. Our laboratory study indicate that 2 °C increase in temperature during the growing season will cause as much as a 17%–37% increase in the humus respiration rate in Scandinavian Scots pine forests, a 15%–22% increase at middle latitudes (e.g., Poland, Germany), and only 4%–11% in areas close to the southern boundary for Scots pine (Table 5).

Assuming a uniform increase of temperature over the whole of Europe, our estimates give a statistically significant relationship between the predicted increase in humus respiration rate and AET or latitude (Figure 6). However, Taylor and Penner (1994) predicted a surface temperature increase of 3 °C to 4 °C over the northernmost parts of Scandinavia and Great Britain, 2 °C to 3 °C over parts of northern and western Europe, and 1 °C to 2 °C over large areas of the central and southern parts of the continent. Under this scenario, the relation between the increase in CO₂ production from humus and latitude

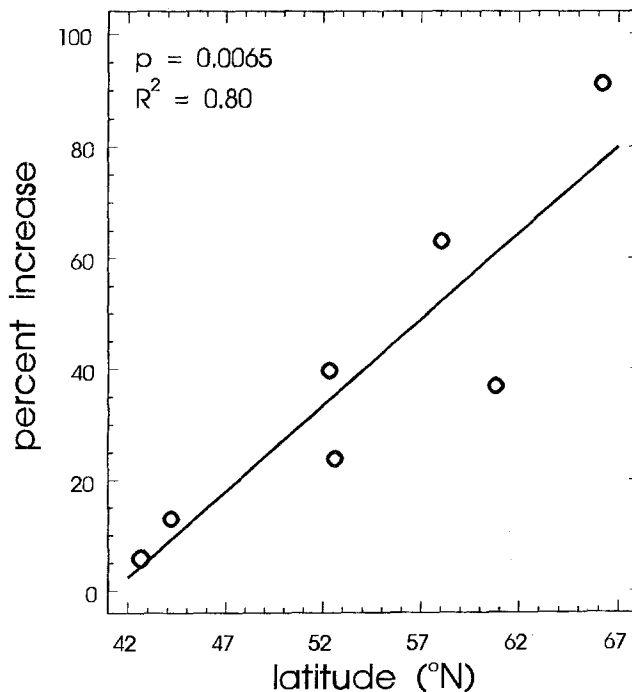


Figure 6. Relation between latitude and the estimated increase in respiration rate due to a 2 °C increase in temperature over Europe.

becomes steeper, and at the northernmost end of our transect (close to the northern timberline) the predicted increase exceeds 90% (Table 5). Using our regression equations (Figure 6), we calculate no significant increase in the humus respiration rate in Scots pine stands located below approximately 40° N, even under the “high temperature increase” scenario. This agrees with the general view that at high latitudes litter decomposition rates are influenced predominantly by climatic factors, while in climates with higher actual evapotranspiration (that is, at higher temperatures and humidities) the litter quality is the key factor (cf. Couteaux et al. 1995; Johansson et al. 1995).

To evaluate the relative importance of the predicted shifts in humus respiration rates for the global carbon budget, it is necessary to estimate the potential increase in total soil CO₂ evolution over broad geographic areas. For this purpose we combined data on the total area of temperate and boreal forests (Schlesinger 1991, and the literature cited there), estimates of the current soil CO₂ production rates (Box & Meentemeyer 1993) and our own results and calculations. In estimating the temperature-driven increase in the soil CO₂ evolution rate, we used our experimental data for humus respiration rates at current and predicted temperatures for the growing season.

Table 5. Predicted climate change-induced increases in CO₂ release rates from humus in Scots pine stands along latitudinal transect across Europe. Two climate change scenarios are considered: +2° and +4° increases in average temperature for the growing season. Calculations are for the growing season only; values calculated using average respiration rates during incubation. The respiration rates for both scenarios were calculated using the Q₁₀ values for appropriate temperature intervals.

Plot	Respiration rate $\mu\text{mol CO}_2 \text{ gorg.mat.}^{-1} \text{ d}^{-1}$			% change	
	Present temperature	+2 °C	+4 °C	+2 °C	+4 °C
H	5.48	21.2	29.6	+37	+91
J	19.6	22.8	26.9	+17	+37
B	8.13	10.6	13.5	+28	+63
C	37.7	43.3	46.8	+15	+24
O	18.5	22.5	25.9	+22	+40
L	54.9	61.1	61.3	+11	+13
E	55.0	57.4	58.5	+4	+6

This analysis has a number of limitations. First, we use CO₂ evolution from humus alone, although the soil respiration rate is the sum of a number of processes (e.g., Box & Meentemeyer 1993). Second, we use only the growing season temperatures in our calculations because data on soil respiration at temperatures below zero are limited and contradictory. However, since at low temperatures the Q₁₀ values were the highest, we believe that our estimated shifts in CO₂ production are conservative. Finally, we used data from only Scots pine forests, and litter and humus quality vary among different kinds of forests. As a consequence, our regional analysis is highly uncertain. Nevertheless, two important consequences of global warming for soil CO₂ evolution from soils can be seen in this analysis (Table 6). First, due to the higher sensitivity of humus from northern forests to a temperature increase, the present difference in the soil CO₂ evolution rate between north and south decreases under the +2 °C scenario, and almost completely disappears under the +4 °C scenario. Second, the predicted difference in carbon evolution from soils under the +2 °C scenario, $0.07 \times 10^{15} \text{ g C yr.}^{-1}$, is almost twice as high as estimates of the annual net storage of soil carbon in northern ecosystems: $0.04 \times 10^{15} \text{ g C yr.}^{-1}$ (Schlesinger 1991). Under the +4 °C scenario, the difference, $0.13 \times 10^{15} \text{ g C yr.}^{-1}$, is three times the current annual net storage. As a consequence of temperature increase in isolation from other factors, northern forests would switch from being a net sink to a net source of carbon.

Effect of changes in nitrogen mineralization rates are more unclear. The average increase in the mineralization rate for more northern sites (H, J, B,

Table 6. Current soil CO₂ evolution at the study plots, estimated using the Box and Meentemeyer power function (1993), and the predicted increase in CO₂ evolution for +2 °C and +4 °C scenarios, based on data from this study (% change from Table 5); *g CO₂ evol*, *g C evol* – estimated CO₂ and C evolution from the temperate and boreal forests of the Northern Hemisphere, *g C diff* – calculated difference in total carbon evolution under +2 °C and +4 °C scenarios.

Plot	AET (mm)	g CO ₂ m ⁻² yr ⁻¹ current	g CO ₂ m ⁻² yr ⁻¹ +2 °C	g CO ₂ m ⁻² yr ⁻¹ +4 °C
H	387	965	1301	1753
J	472	1231	1540	1912
B	491	1292	1589	1931
C	545	1468	1715	1949
O	549	1482	1723	1948
L	565	1535	1757	1941
E	661	1861	1926	1799
<i>g CO₂ evol</i>		1.40×10^{15}	1.65×10^{15}	1.89×10^{15}
<i>g C evol</i>		0.38×10^{15}	0.45×10^{15}	0.52×10^{15}
<i>g C diff</i>			0.07×10^{15}	0.13×10^{15}

C, O) was estimated to be approximately 27% under a 2 °C increase, and 78% under a 4 °C increase. The highest increases – above 100% under a 4 °C increase – were found for humuses from H and O. This would mean more than double the current rate of nitrogen turnover during the growing season in those forests. It is difficult to make reasonable predictions about the effects of such a change in nitrogen turnover on ecosystem function. Increased availability could lead to colonization of species that produce more decomposable litter (Van Vuuren et al. 1993; Van Vuuren & Berendse 1993). On the other hand, increased nitrogen availability may lead to production of litter with larger fraction of material resistant to decomposition (Berg et al. 1996) and, in consequence, to faster accumulation of undecomposed organic matter. Also, as indicated by another experiment made on six out of the seven stands used in this study (Laskowski et al., unpublished), at higher soil nitrogen concentrations a more stable secondary organic matter (humus) may develop. These latter phenomena would counteract to some extent the increased decomposition rate resulting from the shift in temperature alone.

Acknowledgments

We are grateful to all participants in the VAMOS workshop in Jädraås, Sweden, for fruitful discussions. In particular we wish to thank Jonathan Anderson, Björn Berg and Pierre Bottner for their help and comments. Special thanks are due to Marie-Madeleine Couteaux, Coordinator of the VAMOS project, for her creative work and much help during all the project work. We also wish to thank anonymous reviewers and the Editors who vastly improved the manuscript.

This study was funded by the EU Programme Environment 1990–1994 (PECO Programme agreement no. ERBCIPD-CT930010 and contract no. ERBEV5V-CT920141).

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