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Fumigation-extraction and substrate-induced respiration derived microbial biomass C, and respiration rate in limed soil of Scots pine sapling stands

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Abstract The effect of liming on microbial biomass C and respiration activity was studied in four liming experiments on young pine plantations. One of the experimental sites had been limed and planted 12 years before, two 5 years before, and one a year before soil sampling. The youngest experimental site was also treated with ash fertilizer. Liming raised the pH_{KCl} of the humus layer by 1.5 units or less. Microbial biomass was measured using the fumigation–extraction and substrate-induced respiration methods. Liming did not significantly affect microbial biomass C, except in the experiment which had been limed 11 years ago, where there was a slight biomass increase. Basal respiration, which was measured by the evolution of CO_2, increased in the limed soils, except for the youngest experiment, where there was no effect. Ash fertilization raised the soil pH_{KCl} by about 0.5 unit, but did not influence microbial biomass C or basal respiration. Fumigation–extraction and substrate-induced respiration derived microbial biomass C values were correlated positively with each other ($r = 0.65$), but substrate-induced respiration gave approximately 1.3 times higher results. In addition, the effect of storing the soil samples at +6 and −18 °C was evaluated. The effects were variable but, generally, the substrate-induced respiration derived microbial biomass C decreased, and the fumigation–extraction derived microbial biomass C and basal respiration decreased or were not affected by storage.

Key words Basal respiration · Fumigation–extraction · Humus layer · Lime · Microbial biomass · *Pinus sylvestris* L. · Storage · Substrate-induced respiration

Introduction

Coniferous forest soils in Finland are naturally acidic. The average pH of the humus layer is 4.2 (Tamminen and Starr 1990) and acid deposition can further decrease soil pH. Increased acidification may lead to the release and leaching of nutrients and mobilization of toxic Al^{3+} in soils. Soil acidification can be countered by increasing the acid-neutralizing capacity of the soil. Practical methods of achieving this include liming, ash fertilization, and prescribed burning. In old Finnish liming experiments on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) stands, liming raised the pH of the humus layer, increased base saturation, and decreased the amount of extractable Al (Derome et al. 1986; Derome 1990/1991).

The soil microbial biomass is responsible for the mineralization and cycling of nutrients in soil. There are several methods of taking microbial biomass measurements, including fumigation–incubation (Jenkinson and Powlson 1976) and substrate-induced respiration (Anderson and Domsch 1978). In acid forest soils, however, fumigation–incubation has been shown to underestimate the microbial biomass (Williams and Sparling 1984; Sparling and Williams 1986; Vance et al. 1987a, b). The fumigation–extraction method involves extraction of total N (Brookes et al. 1985) or organic C (Vance et al. 1987c) after fumigation with chloroform, and it has been shown to give reliable estimates of microbial biomass C and N in acid soils. Fumigation–extraction is thought to measure the total microbial biomass C in soils. With the substrate-induced respiration method, which is based on the initial respiratory response of microbes to an excess energy source, dormant microorganisms may not be included in the measurement.

The aim of the present study was to assess the effect of liming on soil microbial biomass C and basal respiration in the humus layer of Scots pine sapling stands. One experiment had also been treated with ash fertilizer. Fumigation–extraction and substrate-induced respiration were chosen as biomass measurements, and a further aim was to compare these methods. In addition, the effect of storage of the samples on microbial biomass and respiration activity was evaluated, because it is often not possible to analyse fresh soil samples.

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Materials and methods

Field experiments and sampling

The material for this study was collected from four liming experiments representing the sapling stage of Scots pine plantations (Table 1). The soil type was a podsol, and the type of organic matter was mor. Experiments 607, 621, and 623 contained four replicates of both treatments; i.e., control and liming. Experiment 624 contained three replicates of each treatment; i.e., control, liming, and wood ash fertilization. The treatments consisted of spreading finely ground limestone or wood-bark ash on the soil surface before planting.

Twenty-eight random samples (core diameter 7.2 cm) were taken from the humus layer of each plot (30×30 m) in summer, 1991. The samples were combined plotwise and taken to the laboratory. Green plant material was removed and the samples were sieved (mesh size 2.8 mm), and stored in plastic bags at +6 °C.

Determination of physical and chemical characteristics of soils

The soil moisture content was determined by drying the soil samples overnight at 105 °C. The fresh bulk density was determined by weighing a volume of fresh soil. The soil organic matter content was measured as loss on ignition at 550 °C. Soil pH was measured from soil : water and soil : 1 *M* KCl suspensions (3 : 5 vol : vol). Total nutrients (N, P, K, Ca, Mg, B) and extractable nutrients (P, K, Ca, Mg) were determined as described by Halonen et al. (1983).

Microbial biomass measurements

The fumigation–extraction method of Vance et al. (1987c), as modified by Martikainen and Palojärvi (1990), was used. Three replicate samples (2 g dry matter) of field-moist soil were fumigated with chloroform for 24 h at 28 °C. The fumigated samples and three unfumigated samples were shaken in 0.5 *M* K_2SO_4. After shaking, the extract was filtered through a membrane filter and frozen for C analysis. Total organic C was determined from the extracts with a total organic carbon analyzer (TOC-5000, Shimadzu). The conversion used to obtain the microbial biomass C (C_{mic}) was:

$$C_{mic} = (1.9\ C_f + 428)\ \mu g\ g^{-1}\ \text{dry mattter}$$

where C_f is the difference in the amount of C between the fumigated and unfumigated samples (Martikainen and Palojärvi 1990).

Substrate-induced respiration was determined essentially according to West and Sparling (1986). A Glucose–water solution was added to three replicate samples (2 g dry matter) of soil in 125-ml glass bottles in order to achieve 60% water-holding capacity and a glucose concentration of 20 mg glucose ml^{-1} of soil water. The samples were allowed to stabilize for 0.5 h, then the bottles were closed with rubber septa and incubated at 22 °C for 2 h. The CO_2 evolved was measured by gas chromatography (Varian 3600) equipped with a thermal conductivity detector and a Megapore GS-Q column, 30 m in length, using He as the carrier gas. The temperatures of the detector, injector, and column were 150 °, 120 °, and 30 °C, respectively. The results were converted to biomass C by the Anderson and Domsch (1978) equation:

$$x = 40.4\ y + 0.37$$

where y is the maximum initial rate of respiration, expressed in ml CO_2 100 g^{-1} dry matter · h^{-1} and x is mg microbial C 100 g^{-1} dry matter.

Before the substrate-induced respiration measurements, the optimal glucose concentration was determined for four humus soils. Glucose was added at 0, 2, 10, 30, 50, 100, 200, and 300 mg ml^{-1} soil water, with soil moisture at 60% of water-holding capacity. The two highest concentrations were added as powder, the others in a water solution. All soils evolved the highest amount of CO_2 at glucose concentrations of 10–30 mg. Therefore, a glucose concentration of 20 mg ml^{-1} soil water was selected for use in the measurements.

Basal respiration measurements

To measure basal respiration, the soil moisture content was adjusted to 60% of water-holding capacity and samples (2 g dry matter) were

Table 1 General characteristics of field experiments. Meteorological data for the locations are from years 1950–1980. Site type according to Cajander (1949). (*Exp* experiment, *d.d.* degree days, refers to the effective temperature sum at a threshold temperature of 15 °C, *ND* not determined)

Exp. no.	Site	Geographical location longitude/ latitude	Temp. sum (d.d.)	Mean annual rainfall (mm)	Site type	Soil texture	Fertilization treatment and date	Planting of Scots pine	Sampling date
607	Kuru	23°28′E/61°55′N	1140	559	*Vaccinium* sp. type	Fine sand till	3000 kg ha^{-1} limestone of dolomite,[a] 800 kg ha^{-1} rock phosphate[b]; Autumn 1979	Spring 1980	2 Oct 91
621	Jämijärvi	22°46′E/61°45′N	1159	550	*Calluna* sp. type	Sorted coarse sand	2000 kg ha^{-1} limestone of dolomite; Autumn 1986	Spring 1987	23 Aug 91
623	Kiikala	23°40′E/60°28′N	ND	ND	*Calluna* sp. type	Sorted coarse sand	2000 kg ha^{-1} limestone of dolomite; Autumn 1986	Spring 1987	12 Aug 91
624	Ruokolahti	28°35′E/61°23′N	1254	568	*Calluna* sp. type	Till	2000 kg ha^{-1} limestone of dolomite; 2500 kg ha wood bark ash[c]; Autumn 1990	Spring 1991	23 Jul 91

[a] Approximately 35% Ca, 10 % Mg; grain size: 98% < 2.0 mm, 50% < 0.15 mm
[b] Approximately 14.8% P, 38.0% Ca, 0.8% S, 0.4% Mg, 0.3% Na, 0.2% Fe
[c] Approximately 33.7% Ca, 2.1% Mg, 3.5% K, 1.4% P

incubated as three replicates at 14 °C for 44–48 h. CO_2 was measured as above. The results given are means of four measurements taken over 2 weeks. The samples were aerated between measurements.

Statistical analysis

The SAS program was used for statistical tests. The significances of differences between treatments were analysed by analysis of variance and subsequently, if needed, by Tukey's test (Sokal and Rohlf 1981). Correlation was determined by Pearson's correlation coefficient. The data were log-transformed if necessary.

Results

Because different amounts of mineral soil were mixed in the humus layer, most of the results are presented on an organic matter basis.

Physical and chemical characteristics of soils

Liming increased the soil pH_{KCl} in experiments 607 and 621 by an average of 1.5 units, in experiment 623 by 1 unit, and in experiment 624 by 0.5 unit (Table 2). Differences in pH_{H_2O} were smaller. The concentrations of both total and extractable Ca and Mg and the concentration of boron were significantly ($P<0.05$) increased in the limed plots, except for experiment 624 (Table 3). Liming did not affect the concentrations of other nutrients significantly. Ash fertilization raised the soil pH by about 0.5 units (Table 2). The B concentration was significantly higher in the ash-fertilized plots (Table 3), and other nutrient concentrations were also slightly increased in these plots.

Microbial biomass C

Microbial biomass C, measured by the fumigation–extraction method, ranged from 5.0 to 7.9 mg g^{-1} organic matter (Fig. 1a). Standard deviations of the means of the three fumigated and the three unfumigated replicate samples were, on average, 4%. Liming increased biomass C in experiment 607 by about 12% ($P = 0.09$) but had no marked effect in the other experiments. Ash fertilization did not affect the fumigation–extraction derived microbial biomass C.

Microbial biomass C, measured by the substrate-induced respiration method, ranged between 6.2 and 15.5 mg g^{-1} organic matter (Fig. 1b). The standard deviation between the three replicate soil samples was 5% on average. Liming did not affect the substrate-induced respiration, except in experiment 607, where the value increased by about 50% ($P = 0.10$). Ash fertilization did not influence substrate-induced respiration derived microbial biomass C.

There was a significant ($P = 0.0001$) positive correlation ($r = 0.65$) between fumigation–extraction derived and substrate-induced respiration derived microbial biomass C (Fig. 2).

Basal respiration

Basal respiration was 18–41 µl CO_2 g^{-1} organic matter, equivalent to 9–20 µg CO_2-C g^{-1} organic matter (Fig. 1c). The standard deviation between the three replicate soil samples was about 4%, but the deviation between different measurement days was larger (on average, 12%). Liming either increased or did not affect basal respiration. In experiments 607 and 621, there was a significant ($P = 0.01$) difference between the basal respiration of the control and the limed plots; liming increased the basal respiration by an average of 44 and 27%, respectively. In experiment 623, the difference was also nearly significant ($P = 0.19$), the increase being approximately 22%. Liming and ash fertilization did not affect basal respiration in experiment 624.

Metabolic quotient

The metabolic quotient of the soil microflora was calculated as the amount of CO_2-C respired per hour per unit microbial biomass C (qCO_2). The calculation was made separately for the two measurement methods. The quo-

Table 2 Some physical and chemical characteristics of experimental soils. Values are means of all plots, with standard deviations in parentheses (*Exp* experiment)

Exp. no.	Treatment	Humus layer thickness (cm)	Dry matter (%)	Fresh bulk density (g cm^{-3})	Organic matter (% dry matter)	pH (H_2O)	pH (KCl)
607	Control	3 (0.8)	24.3 (2.5)	0.92 (0.09)	74.1 (6.9)	4.5 (0.1)	3.2 (0.1)
	Lime	2 (0.1)	27.8 (6.6)	0.87 (0.16)	61.2 (1.2)	5.6 (0.4)	4.8 (0.6)
621	Control	2 (0.3)	48.9 (7.6)	0.48 (0.12)	45.5 (15.7)	4.2 (0.3)	3.0 (0.0)
	Lime	2 (0.2)	44.8 (5.4)	0.41 (0.03)	54.0 (7.6)	5.1 (0.3)	4.4 (0.2)
623	Control	3 (0.3)	54.1 (4.0)	0.31 (0.04)	51.7 (2.7)	3.9 (0.2)	3.0 (0.0)
	Lime	3 (0.3)	59.2 (2.9)	0.32 (0.09)	48.1 (8.4)	4.7 (0.2)	4.1 (0.2)
624	Control	3 (0.6)	45.0 (3.1)	0.50 (0.06)	42.4 (5.1)	4.1 (0.2)	3.2 (0.1)
	Lime	3 (0.6)	46.6 (1.1)	0.52 (0.05)	41.4 (3.6)	4.7 (0.2)	3.7 (0.1)
	Ash	3 (0.6)	48.3 (2.5)	0.51 (0.06)	39.0 (4.8)	4.5 (0.2)	3.6 (0.1)

Table 3 Total and extractable nutrients in experimental soils. Values are means of all plots, with standard deviations in parentheses (*Exp* experiment)

Exp. no.	Treatment	Total nutrients, g kg^{-1} organic mater (B in mg kg^{-1} organic matter)						Extractable nutrients (g kg^{-1} dry matter)			
		N	P	K	Ca	Mg	B	P	K	Ca	Mg
607	Control	16.57 (2.85)	1.20 (0.07)	0.82 (0.19)	6.85 (0.71)	0.51 (0.07)	5.12 (1.08)	0.09 (0.04)	0.32 (0.02)	2.66 (0.42)	0.24 (0.02)
	Lime	19.34 (2.44)	2.80 (0.67)	0.87 (0.20)	21.94 (7.48)	3.59 (2.07)	9.17 (2.77)	0.12 (0.03)	0.33 (0.07)	6.58 (0.77)	1.28 (0.57)
621	Control	17.07 (2.05)	1.10 (0.04)	0.64 (0.16)	4.63 (0.55)	0.56 (0.13)	4.71 (0.70)	0.03 (0.02)	0.07 (0.02)	0.89 (0.33)	0.11 (0.05)
	Lime	15.82 (0.95)	1.01 (0.04)	0.54 (0.05)	17.50 (2.32)	2.63 (1.46)	5.86 (0.96)	0.03 (0.40)	0.08 (0.02)	6.75 (2.72)	0.65 (0.34)
623	Control	17.52 (1.31)	1.21 (0.04)	0.69 (0.06)	5.21 (0.34)	0.83 (0.28)	3.93 (0.21)	0.02 (0.00)	0.09 (0.00)	1.22 (0.09)	0.13 (0.01)
	Lime	17.74 (0.75)	1.21 (0.07)	0.68 (0.14)	17.24 (2.82)	2.18 (0.64)	5.18 (0.31)	0.02 (0.00)	0.09 (0.02)	5.13 (1.09)	0.33 (0.02)
624	Control	14.94 (0.90)	1.26 (0.13)	1.27 (0.19)	5.74 (1.96)	1.47 (0.33)	4.84 (0.36)	0.04 (0.04)	0.20 (0.02)	1.32 (0.75)	0.10 (0.02)
	Lime	15.39 (1.05)	1.28 (0.17)	1.21 (0.17)	9.28 (1.92)	2.05 (0.43)	4.83 (0.89)	0.03 (0.02)	0.23 (0.04)	2.37 (0.59)	0.26 (0.04)
	Ash	15.33 (0.78)	1.38 (0.20)	1.55 (0.37)	7.74 (1.24)	2.11 (0.88)	7.72 (0.95)	0.02 (0.01)	0.26 (0.06)	1.63 (0.40)	0.19 (0.04)

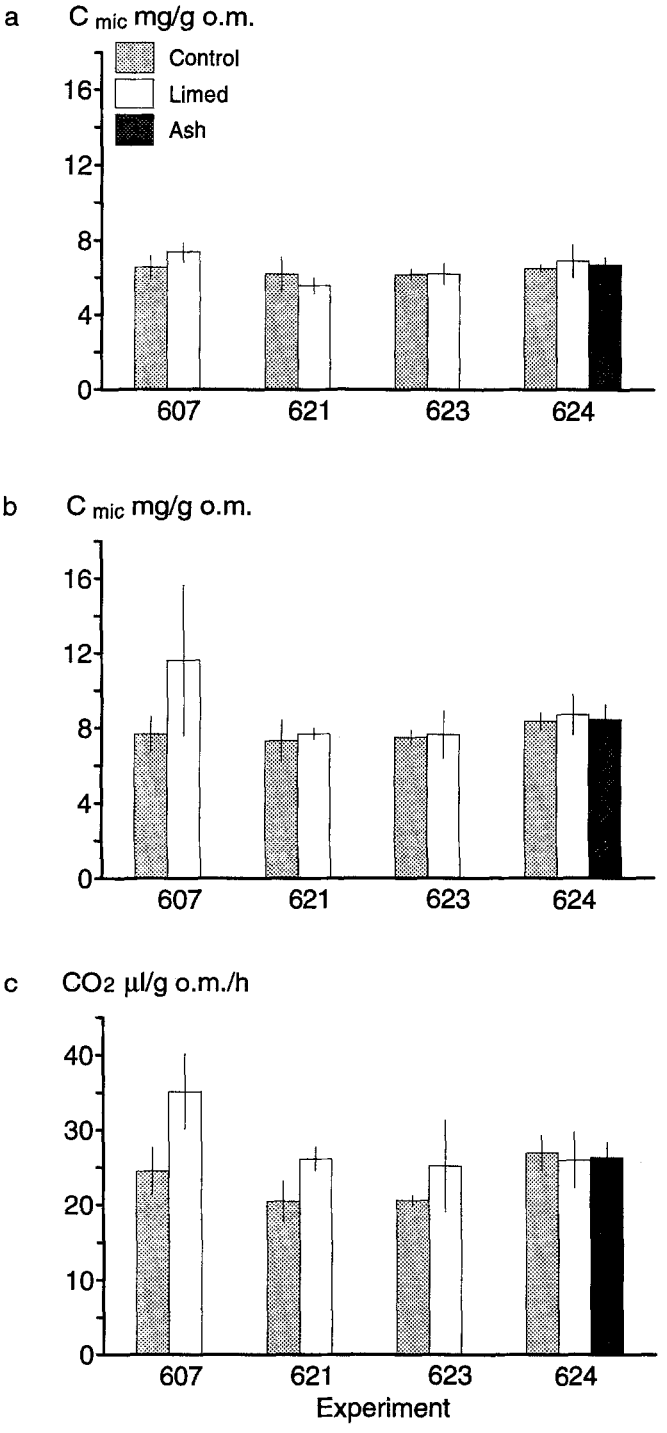

Fig. 1a–c The effect of liming on the humus layer of the experiments. **a** Fumigation–extraction derived microbial biomass C; **b** substrate-induced respiration derived microbial biomass C; **c** basal respiration. *Values* are means of all plots; *bars* show standard deviations; C_{mic}, microbial biomass C; *o.m.*, organic matter

tients obtained using the fumigation–extraction derived biomass figures were higher than those obtained with substrate-induced respiration (Table 4). Liming increased qCO_2 irrespective of the biomass determination method, except in experiment 624, where neither liming nor ash fertilization had any effect.

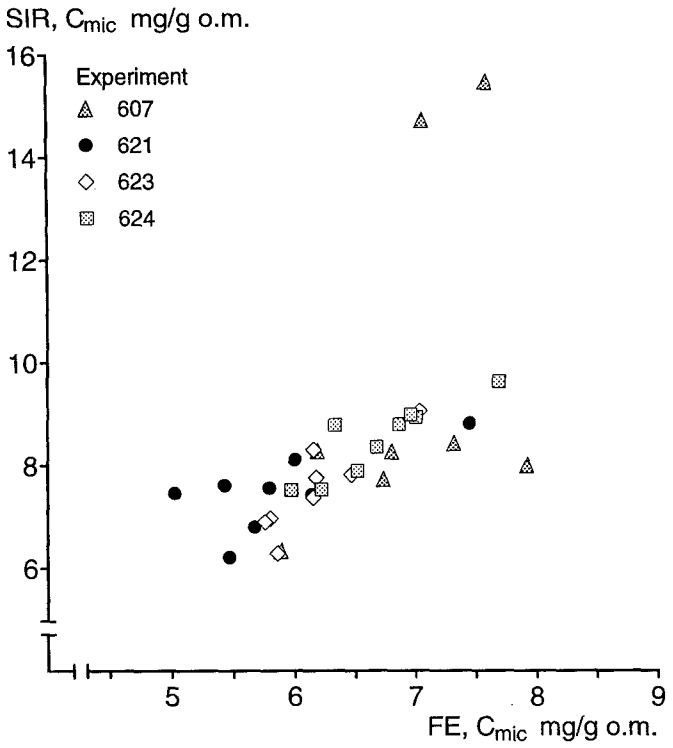

Fig. 2 The relationship between fumigation–extraction (*FE*) and substrate-induced respiration (*SIR*) derived microbial biomass C (C_{mic}) in the experiments. *o.m.*, Organic matter

Storage of soil samples

The samples from the untreated plots from experiment 623 were kept approximately 3 months at +6 °C and −18 °C in plastic bags. All samples from experiment 624 were kept approximately 2 months at −18 °C.

Neither of the storage methods affected the fumigation–extraction derived microbial biomass C in experiment 623, but in experiment 624, freezing decreased microbial biomass C by about 12% ($P = 0.002$; Fig. 3a). Storage reduced the substrate-induced respiration derived microbial biomass C in both experiments by about 14% ($P = 0.006$ and $P = 0.003$; Fig. 3b). The biomass values at +6 °C and −18 °C did not differ from each other. Basal respiration decreased by almost 25% in experiment 623 ($P = 0.001$), but in experiment 624, it was not affected (Fig. 3c).

Table 4 Metabolic quotients. Values are means of all plots, with standard deviations in parentheses (*Exp* experiment, *FE* fumigation–extraction, *S-R* substrate-induced respiration; C_{mic} microbial biomass C)

Exp.	Treatment	FE qCO_2 (μg CO_2-C mg^{-1} C_{mic})	SIR qCO_2 (μg CO_2-C mg^{-1} C_{mic})
607	Control	1.85 (0.09)	1.58 (0.09)
	Lime	2.39 (0.45)	1.66 (0.61)
621	Control	1.64 (0.09)	1.39 (0.06)
	Lime	2.33 (0.12)	1.69 (0.07)
623	Control	1.66 (0.06)	1.37 (0.04)
	Lime	1.99 (0.32)	1.62 (0.18)
624	Control	2.05 (0.22)	1.60 (0.06)
	Lime	1.86 (0.05)	1.48 (0.05)
	Ash	1.95 (0.04)	1.55 (0.03)

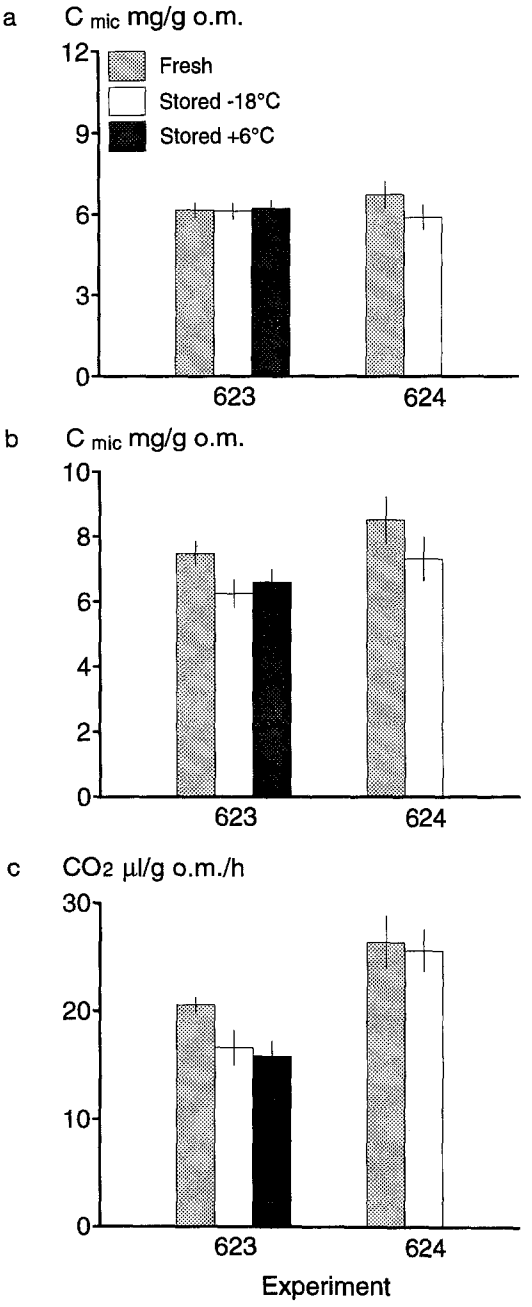

Fig. 3a–c The effect of storage of the humus samples at +6 and −18 °C. **a** Fumigation–extraction derived microbial biomass C (C_{mic}); **b** substrate-induced respiration derived microbial biomass C; **c** basal respiration. *Values* are means of all plots; *bars* show standard deviations; *o.m.*, organic matter

Discussion

The conversion factor of Martikainen and Palojärvi (1990), which had been obtained by calibrating the fumi-

gation–extraction method with direct microscopic counting, was chosen to convert the fumigation–extraction results to microbial biomass C. Various other conversion factors have been suggested (Vance et al. 1987c; Sparling and West 1988; Sparling et al. 1990). Most of these studies, however, have been done on arable soils, which differ from the typical Finnish podsol soils. The soils in the study by Martikainen and Palojärvi included three Finnish *Calluna* sp. type pine stands, which is one reason for using that factor in the present study. Furthermore, the Sparling and West (1988) equation, for instance, was obtained by calibrating fumigation–extraction against substrate-induced respiration. The use of this factor would prevent comparison of these methods in the present study. The fumigation–extraction results, when converted to microbial biomass, varied from 5.0 to 7.9 mg microbial biomass C g^{-1} organic matter (Fig. 1a). Expressed per dry matter of soil, the results were 2.2–5.8 mg g^{-1}. These values are in accordance both with Fritze (1991), who obtained a value of 4.7 mg microbial biomass C g^{-1} organic matter using fumigation–extraction, and with Martikainen and Palojärvi (1990), who obtained values of 4.0–4.3 mg g^{-1} dry matter.

The substrate-induced respiration method gave 153–383 µl CO_2 g^{-1} organic matter. The results were converted to microbial biomass C using the Anderson and Domsch (1978) conversion factor, which had been obtained by calibrating substrate-induced respiration against fumigation–incubation. Several other conversion factors have also been suggested, but they all involve uncertain factors (West and Sparling 1986; West et al. 1986; Sparling et al. 1990). The results obtained with the Anderson and Domsch conversion factor were 6.2–15.5 mg microbial biomass C g^{-1} organic matter (Fig. 1b) or 2.7–8.4 mg microbial biomass C g^{-1} dry matter. Sparling and Williams (1986) obtained a value of 1.49 mg g^{-1} dry matter for Scottish pine forest soil and Illmer and Schinner (1991) obtained 0.6–1.6 mg g^{-1} dry matter for German coniferous forest soils measured with substrate-induced respiration.

In spite of the uncertainty about conversion factors, both measurement methods gave biomass C values of the same order, though the values obtained with substrate-induced respiration were always about 1.3 times higher than those obtained by fumigation–extraction (Fig. 2). Kaiser et al. (1992) also obtained higher results with substrate-induced respiration than with fumigation–extraction. This is obviously partly due to the conversion factors used, although the correlation coefficient of 0.65 indicates that these methods do not estimate the same part of the soil microbial biomass. It is not clear whether the differences between the fumigation–extraction and substrate-induced respiration derived values for microbial biomass C are due to incorrect conversion factors, or to differences in the pool of microbial biomass which they measure, or both.

If basal respiration is assumed to reflect the actual soil situation, it is interesting to compare it with the substrate-induced potential respiration, when temperature and substrate availability are optimized. We found that basal respiration was only 11–15% of the substrate-induced value, which indicates the importance of temperature and substrate availability in the activity of microbes.

With both substrate-induced and basal respiration, there might have been some abiotic CO_2 formation due to carbonates left in the limed soils. This was obviously not a real source of error because of the small portion of abiotic CO_2 formation compared to biological CO_2 formation (Persson et al. 1989).

Storage at +6 or −18 °C affected the microbial biomass measured by fumigation–extraction and substrate-induced respiration, and basal respiration in different ways (Fig. 3). This is in accordance with the results obtained by Ross (1991), who kept soil samples for 14 months at +4 °C; the storage did not affect the fumigation–extraction derived microbial biomass, but substrate-induced and basal respiration were both significantly reduced. Measurements of microbial biomass and activity by other methods have also given variable results with storage (Ross et al. 1980; Zelles et al. 1991). Wardle (1992) concluded that the decline in the microbial biomass that is often observed during soil storage is apparently a consequence of substrate depletion, at least in temperatures above freezing point.

Liming raised the soil pH in every experiment, but not equally (Table 2). This might be explained by the time that had elapsed since liming. The longer the time, the larger the increase in pH. Limestone has to be spread as a thin layer on top of the humus layer, and its dissolution and percolation to depth takes years. This can also be seen from the concentration of calcium in the limed plots; in the youngest experiment it did not increase as much as in the older experiments (Table 3). An increase in B concentrations with liming has also been reported in other studies (Derome 1990/1991).

The changes in microbial biomass C and basal respiration appeared to be related to the time that had passed since liming and the corresponding increase in pH. Liming increased the microbial biomass as measured by both fumigation–extraction and substrate-induced respiration only in experiment 607, which had been limed 12 years previously, and which had also received 1000 kg ha^{-1} more limestone than the other experimental sites (Fig. 1). The effects of soil pH, and treatments that raise it, have mainly been studied in short-term pot experiments, and there have only been a few field experiments. In pot experiments, liming usually increases the microbial biomass (Carter 1986; Illmer and Schinner 1991; Badalucco et al. 1992), but results from field experiments have been variable. Bååth et al. (1980) found that the microbial biomass of coniferous forest soil was not affected 5–6 years after liming. Kratz et al. (1991), however, found increased biomass levels 3 years after liming. Liming may affect fungal and bacterial biomass differently. Shah et al. (1990) determined bacterial and fungal biomass separately; liming increased the bacterial biomass, but had only a short-term effect, while the fungal biomass was not affected. Zelles et al. (1990) found that liming slightly increased the bacterial biomass but decreased the fungal biomass.

In the present study, liming increased the basal respiration in all experiments, except for the youngest experiment (624). The production of CO_2 usually increases after liming, although this is often a short-term effect (Lohm et al. 1984; Zelles et al. 1987; Haynes and Swift 1988; Shah et al. 1990; Illmer and Schinner 1991; Persson et al. 1990/1991). In the soils of the present study, it was evident that the increase in CO_2 production was a long-lasting effect.

In experiment 607, P had been added with the limestone, which might affect the results. The influence of P is not well understood, because most studies on the responses of microbiological factors to fertilizers have added P and N together, to that their effects cannot be distinguished (Wardle 1992).

Liming increased qCO_2, because basal respiration increased while microbial biomass remained constant (Table 4). A similar effect was noticed in pot experiments by Badalucco et al. (1992). This may simply have been due to the rise in pH. However, according to Odum's (1985) theory of stressed ecosystems, the rise in qCO_2 can be explained by increased respiration due to microbial stress resulting from liming. Anderson and Domsch (1993), however, noticed that qCO_2 increased with decreasing pH values and explained that organisms under acidic soil conditions are stressed, which results in higher community respiration. Kratz et al. (1991) conducted a 3-year field experiment, in which liming increased the basal respiration slightly, while substrate-induced respiration was increased much more, resulting in a decrease in qCO_2. They assumed that the increase in microbial biomass on the limed plots had exhausted the easily degradable organic components.

Finnish forest soils seem to react differently from Middle European soils; liming may have increased the amount of C sources available to microbes, so that a greater proportion of the microbes was active (or at least respiring more), while the total biomass was not affected. This can be assumed to be a positive phenomenon, because the mineralization rate also increases and the cycling of nutrients is faster. Immobilization of nutrients in microbes does not seem likely because the total microbial biomass did not increase. The interpretation of qCO_2 is difficult, and it has to be considered whether the changes in qCO_2 are the result of changes in biomass or respiration or both.

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