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Carbon storage in forest soil of Finland

1. Effect of thermoclimate

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Abstract. A total of 30 coniferous forest sites representing two productivity classes, forest types, were investigated on a temperature gradient (effective temperature sum using +5 °C threshold 800–1300 degree-days and annual mean temperature −0.6–+3.9 °C) in Finland for studying the effect of thermoclimate on the soil C storage. Other soil forming factors were standardized within the forest types so that the variation in the soil C density could be related to temperature. According to the applied regression model, the C density of the 0–1 m mineral soil layer increased 0.266 kg m^{-2} for every 100 degree-day increase in the temperature sum, and the layer contained 57% and 28% more C under the warmest conditions of the gradient compared to the coolest in the less and more productive forest type, respectively. Accordingly, this soil layer was estimated to contain 23% more C in a new equilibrium with a 4 °C higher annual mean temperature in Finland. The C density of the organic layer was not associated with temperature. Both soil layers contained more C at the sites of the more productive forest type, and the forest type explained 36% and 70% of the variation in the C density of the organic and 0–1 m layers, respectively. Within the forest types, the temperature sum accounted for 33–41% of the variation in the 0–1 m layer. These results suggest that site productivity is a cause for the large variation in the soil C density within the boreal zone, and relating the soil C density to site productivity and temperature would help to estimate the soil C reserves more accurately in the boreal zone.

1. Introduction

Twice as much carbon is stored in soil organic matter as in the atmosphere at present (Schlesinger 1977; Post et al. 1982; Watson et al. 1990). The amount of the soil C is likely to change in response to climatic warming, because processes defining the soil C balance, net primary production and decomposition, are regulated by environmental conditions (e.g. Anderson 1992). Owing to the large amount of the soil C, even small changes in the soil C storage may significantly affect the CO_2 concentration of the atmosphere. These changes may either enhance the greenhouse effect and cause further warming, if C is released from the soils to the atmosphere, or retard the increase in the atmospheric CO_2 concentration, if C is accumulated in the soils.

Because the soils of the boreal zone contain a considerable proportion of the soil C storage worldwide, some 15% even excluding wetlands (Schlesinger 1977; Post et al. 1982), and climatic warming is predicted to be greatest in high latitudes (Mitchell et al. 1990), the changes in the C storage of the boreal soils may notably affect the global soil C balance.

The changes in the soil C storage in response to climatic warming depend on how the rate of net primary production of plants is altered in relation to the rate of decomposition of soil organic matter. In the boreal zone, the changes in the rates of these both processes and, consequently, in the soil C storage are suggested to be largely regulated by the potential replacement of coniferous forests by broadleaved ones (Emanuel et al. 1985; Anderson 1992; Smith et al. 1992; Van Cleve & Powers 1995). This replacement may lead to a decrease in the soil C storage, despite an increase in the rate of net primary production, because litter of broadleaved trees decomposes more quickly than litter of conifers (Mikola 1960; Melillo 1983; Flanagan & Van Cleve 1983). The suggestion of the decreasing soil C storage is supported by a generally observed decrease in soil C content with increasing temperature from one vegetation zone to another (Kira & Shidei 1967; Post et al. 1982; Johnson 1995) and when shifting from coniferous forests to broadleaved forests within the boreal zone (Van Cleve & Powers 1995). Applying the conclusion for the whole boreal zone is, however, not straightforward, since broadleaved trees will probably replace the present coniferous vegetation only in the southern regions of the boreal zone (Pastor & Post 1988; Kellomäki & Kolström 1992; Smith et al. 1992).

According to Pastor & Post (1988), the response of the boreal forests to climatic warming depends strongly on latitude, controlling mainly the replacement of conifers by broadleaved trees, and water balance, controlling the growth of the trees. In their model simulations, climatic warming increased productivity and the soil C storage at northern boreal sites, where the present spruce forests were not replaced by broadleaved forests. At southern boreal sites hardwoods replaced conifers, but the soil C storage still increased in the presence of sufficient water, while a lack of water led to a decrease in the soil C storage. Similarly, Townsend et al. (1992) predicted a slight increase in the soil C storage in the boreal zone over a limited range of warming, but emphasized that the results of their model simulations were very sensitive to the applied dependence of decomposition on environmental conditions.

The dependence of decomposition on environmental conditions is known only for the most easily decomposable compounds (Mikola 1960; Meentemayer 1978; Berg et al. 1993), which represent only a small percentage of soil organic matter (Jenkinson & Rayner 1977; Parton et al. 1987). This lack of knowledge impairs the confidence in the model simulations in particular for high latitudes, because in warmer conditions substrate availability more rapidly limits the loss of C from the soils (Townsend et al. 1992). Making appropriate manipulative experiments to parameterize the models and validate the simulation results is difficult, because, owing to the stable nature of the majority of soil organic matter, the actual response of the soil C storage to climatic warming is likely to be very gradual (Kirschbaum 1993).

In the present study, we investigated coniferous forest sites of two productivity classes, forest types, along a temperature gradient in Finland for the purpose of assessing the effect of thermoclimate on the soil C storage. In order to relate the variation in the soil C content to temperature, other soil forming factors were standardized among the sites of the same forest type. Equilibrium of the soil C storage with the prevailing conditions at the sites, an important prerequisite to using the gradient approach for studying the association between the soil C and temperature, is discussed.

2. Materials and methods

2.1 *Selection of the study sites*

Four study areas, sized 30 km $\times$ 30 km, were established along the largest temperature gradient in Finland on which forest sites with similar soil forming factors other than temperature, i.e. time, parent material, vegetation and topography, could be found to relate the variation in the soil C storage to temperature (Figure 1). In other words, we intended to select sites which were similar when they emerged at the same time after the most recent glaciation, but thereafter have been exposed to different thermoclimates. For objectively selecting such sites in the study areas for the study, criteria were first set for the soil forming factors as described below. The actual study sites were picked up randomly among all the sites meeting this criteria in the study areas.

To select soils of the same age, the study areas were established inside the region that was subaquatic after the latest glacial retreat 10 000–11 500 years ago (Figure 1, Eronen & Haila 1981; Kramer & Becker 1993). Soils from 9000 to 11000 years of age were chosen in the areas using applicable diagrams of shore-line displacement which express the soil age as a function of the height above the present sea level (Donner 1969; Saarnisto 1981; Glückert 1989). The ^{14}C-ages of the diagrams were converted to actual ages according to Kramer & Becker (1993) and Pearson et al. (1993).

To standardize parent material, the sites were selected on more than 1 m thick sorted deposits or till low in stone content. The parent material needed also to be formed of acidic bedrock material. For further standardization,

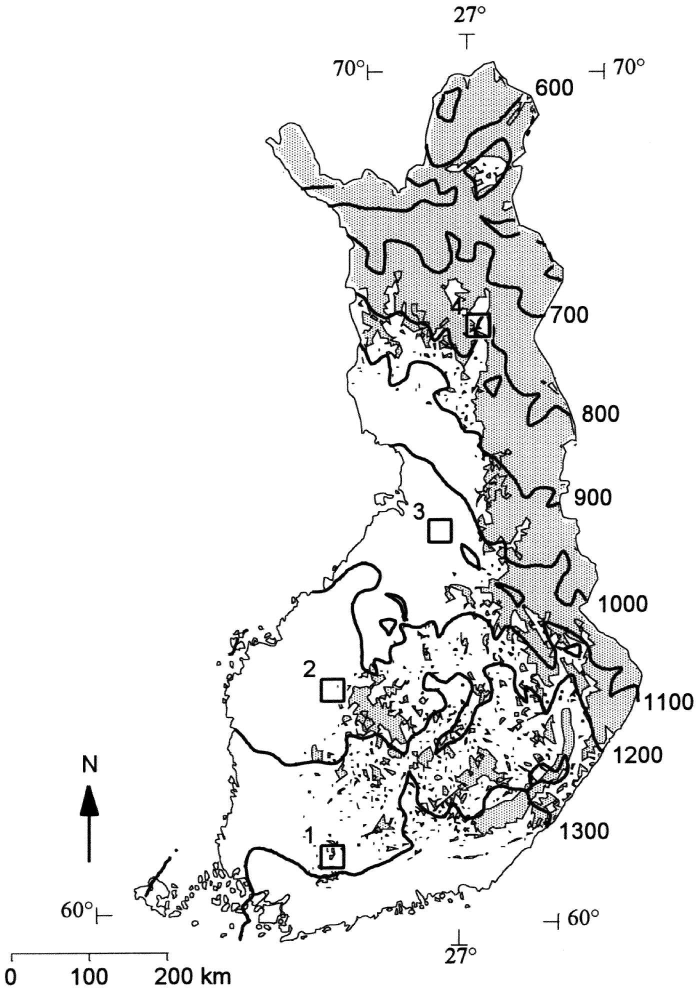

Figure 1. Location of the study areas, isolines indicating the effective temperature sum (degree-days using +5 °C threshold) and the sub- (unshaded) and supra-aquatic (shaded) areas in Finland (latitude and longitude indicated). The sub- and supra-aquatic areas are redrawn after Eronen & Haila (1981); areas covered by ice-dammed lakes, except the Baltic Ice Lake, have been included in the supra-aquatic area.

the Finnish classification of forest types was utilized (Cajander 1925). This classification system divides sites into a few forest types on the basis of the composition of ground vegetation. Corresponding types have been defined for four regions in Finland to account for the effect of climate on ground vegetation (Kalela 1961). The forest types generally differ in productivity, reflecting properties of the parent material (Viro 1947, 1951; Ilvessalo &

Ilvessalo 1975; Westman 1990; Liski & Westman 1995). The parent material of more productive types usually contains more fine particles and nutrients. Common forest types at both ends of the fertility range were chosen for the study, i.e. low productivity *Calluna* type and the corresponding types (CT sites), and more productive *Myrtillus* type and the corresponding types (MT sites). Only sites with well-drained soils, which in the study areas were also podzolized, were accepted. Comparable topography was obtained by selecting the sites on flat surfaces.

To standardize vegetation at the sites, Scots pine (*Pinus sylvestris* L.) was selected for the dominating tree species at the CT and Norway spruce (*Picea abies* (L.) Karst.) at the MT sites. These tree species are typical for the forest types and dominating on 90% of the total forest area in the country (Anonymous 1994). Only mature tree stands and sites, where no cuttings had been done for at least 10 years before the field work, were accepted to minimize the effects of forest harvesting on the soil C storage at the study sites.

In practice, all the sites meeting the criteria described above were first located in the maps of the study areas to form the basic population of suitable sites. The information on the soil age and topography was obtained from maps of height above sea level, the information on the parent material from maps of prequaternary rocks and quaternary deposits, and the information on the forest type, tree species, stand volume and stand age from satellite images. To select the actual study sites randomly, the sites meeting the criteria in each study area were first sorted in a randomized order. These sites were then inspected for the criteria in the field following the randomized order, and the four CT and four MT sites that first satisfied the criteria after the field inspection were chosen in each area. However, in area no. 2 only three MT sites and in area no. 4 only one CT site were accepted after the field inspection. The procedure of study site selection was therefore applied for an additional 30 km $\times$ 30 km area south of area no. 4 and two more CT sites were found. Consequently, a total of 15 CT and 15 MT sites were chosen as the actual study sites.

2.2 *Climate at the study sites*

For characterizing climate at the study sites, climatological data of years 1961–1990 in Finland was utilized (anonymous 1991). The data have been interpolated by the Finnish Meteorological Institute into a 10 km $\times$ 10 km grid to cover the whole country. Four points closest to a given study site were averaged for climatological records at the site. Annual mean temperature, effective temperature sum using a +5 °C threshold (degree-days, dd), annual precipitation and evapotranspiration are reported as averages for the forest types in the study areas in Table 1. The effective temperature sum was chosen to describe temperature when studying the association between the soil C storage and thermoclimate, because it summarizes the length of the active period of the involved processes, net primary production and decomposition, and the amount of energy for these processes during the active period better than, for instance, the annual mean temperature or the length of the growing season.

2.3 *Soil sampling and laboratory analysis*

An area of 30 m $\times$ 30 m was investigated at the study sites. To collect spatially independent samples in respect to the soil C density (kg m^{-2}) with pre-estimated precision for the mean C density, the soil sampling was based on a preliminary study on the variation of the soil C density (Liski 1995). A total of six soil cores (45 mm in diameter) were taken from a systematic, randomly placed grid, where the distance between the sampling points was 10 m and 15 m in perpendicular directions. The cores were manually taken using a steel corer that samples the profile in its natural form in a plastic tube (Westman 1995). The soil cores were intended to be 1 m deep, but the compactness of the soil physically constrained the actual mean depth to 79 cm. After the sampling, the tubes were sealed with plastic covers and stored cool (+1 °C – +8 °C) for no longer than a month before the laboratory work.

In the laboratory the cores were divided by horizon for the organic (F/H) and mineral soil horizons (Ah, E, B1, B2). Parent material (C horizon), was divided for 20 cm layers from the top and for the remaining part. If the morphological mineral soil horizons were indistinguishable, the mineral soil was divided by depth for 0–10 cm, 10–20 cm layers and thereafter for 20 cm layers as the C horizon. Mineral contamination in the organic horizon sample as well as organic contamination in the uppermost mineral soil sample were carefully avoided. After the division, the samples were dried to a constant weight at room temperature, weighed for the bulk density (Bd, kg m^{-3}), sieved to $<$2 mm and weighed again for the density of the $<$2 mm fraction (Bd $<$2 mm, kg m^{-3}). The $<$2 mm fraction was used for the further analysis.

Total C concentration (C_C, kg kg^{-1}), which in these acid soils (pH $<$5.15 soil:0.01 M $CaCl_2$ = 1:2.5 (v/v)) equals the concentration of organic C, was measured using a Leco CSN-1000 analyser (Leco Corporation, St. Joseph, MI, USA). In order to reduce analytical variability, the organic samples and 50 ml of the mineral soil samples were ground before the measurements using a grinder (Reutch, GmbH & Co.KG, 5657 Haan 1, Germany). The coefficient of variation for replicate measurements averaged 2.9% in the 200 mg organic samples and 4.2% in the 400 mg mineral soil samples used for the analysis

Table 1. Characteristics describing soil forming factors at the CT and MT sites in the study areas numbered from 1 to 4 respectively from south to north (mean ± standard deviation, $n = 4$ for the sites in the areas, except $n = 3$ for the CT sites in the area 4 and MT sites in the area 2).

	CT sites				MT sites			
	1	2	3	4	1	2	3	4
Effective temperature sum, dd [1)]	1285 ± 3	1130 ± 6	1062 ± 17	844 ± 30	1287 ± 1	1138 ± 4	1028 ± 9	807 ± 1
Annual mean temperature, °C	3.9 ± 0.0	2.6 ± 0.1	1.4 ± 0.1	−0.3 ± 0.3	3.9 ± 0.1	2.6 ± 0.0	1.2 ± 0.1	−0.6 ± 0.0
Precipitation, mm	613 ± 9	586 ± 3	545 ± 15	519 ± 3	623 ± 11	602 ± 15	568 ± 0	520 ± 3
Evapotranspiration, mm	371 ± 2	315 ± 3	336 ± 2	279 ± 0	372 ± 2	306 ± 6	335 ± 4	276 ± 1
Precipitation – evapotranspiration, mm	243 ± 8	270 ± 6	209 ± 13	240 ± 2	251 ± 9	295 ± 21	234 ± 4	244 ± 4
Soil age, years	11025 ± 320	10350 ± 100	9500 ± 0	9667 ± 115	10650 ± 289	10233 ± 208	9350 ± 100	9950 ± 342
Silt concentration of parent material, % [2)]	1.8 ± 0.8	1.5 ± 0.6	1.9 ± 0.7	6.7 ± 5.9	26.5 ± 10.3	17.2 ± 2.1	28.8 ± 20.8	18.0 ± 6.5
Ca concentration of parent material, mg g^{-1}	1.6 ± 0.2	0.8 ± 0.1	1.0 ± 0.2	2.8 ± 1.2	2.8 ± 0.6	2.5 ± 0.5	3.2 ± 1.7	3.9 ± 1.3
Mg concentration of parent material, mg g^{-1}	3.0 ± 0.2	1.4 ± 0.1	1.0 ± 0.4	2.4 ± 1.1	3.7 ± 1.1	1.8 ± 0.7	2.3 ± 1.3	3.7 ± 0.5
pH of parent material	5.00	4.90	4.75	4.81	4.84	4.72	4.63	4.54
	−0.11 + 0.14	−0.03 + 0.03	−0.04 + 0.04	−0.09 + 0.11	−0.07 + 0.08	−0.05 + 0.06	−0.14 + 0.20	−0.13 + 0.18
Basal area of trees, m^2 ha^{-1}	17.9 ± 3.8	20.7 ± 3.8	17.4 ± 2.0	18.1 ± 5.9	33.6 ± 3.9	31.2 ± 4.5	27.9 ± 3.6	15.7 ± 2.6
Basal area of Scots pine, m^2 ha^{-1}	17.9 ± 3.8	20.7 ± 3.8	17.4 ± 2.0	18.1 ± 5.9	11.2 ± 6.3	3.5 ± 2.2	2.7 ± 2.0	0.3 ± 0.3
Basal area of Norway spruce, m^2 ha^{-1}	0.0	0.0	0.0	0.0	22.3 ± 5.6	27.8 ± 4.5	24.9 ± 4.8	13.3 ± 1.0
Basal area of birches, m^2 ha^{-1}	0.0	0.0	0.0	0.0	0.1 ± 0.3	0.0	0.3 ± 0.2	2.2 ± 1.9
Site index H100, m	22.6 ± 0.4	16.5 ± 0.8	15.2 ± 1.0	13.9 ± 0.8	25.7 ± 3.9	23.9 ± 2.8	16.2 ± 0.5	10.2 ± 2.4
Age of dominant trees, years	87 ± 18	130 ± 16	131 ± 19	131 ± 19	114 ± 55	103 ± 13	151 ± 28	219 ± 50

[1)] +5 °C threshold
[2)] particle size fraction 2–60 μm

(a total of 3 organic and 3 mineral soil samples tested, 5 measurements per sample).

The mass of C per unit of surface area (C density, kg m^{-2}) in a given soil layer was calculated by multiplying the C_C by the Bd <2 mm and thickness of the layer. The C density of the 1 m deep mineral soil layer was calculated by summing up the C densities of the sublayers and extrapolating the volumetric C density of the deepest C horizon sample to the depth of 1 m.

To characterize physical and chemical properties of the parent material at the study sites, the two uppermost C horizon samples of each site were composited by layer for analysing particle size distribution, Ca and Mg concentrations and pH; averages of the two layers are reported. The particle size distribution was measured by laser diffraction method using a Helos 12 LA diffraction spectrometer after removing organic matter with 30% H_2O_2 as described by Elonen (1971). The Ca and Mg concentrations were determined by ICP after digestion with conc. HNO_3, H_2SO_4 and $HClO_4$. The pH was measured in 1:2.5 (v/v) soil:0.01 M $CaCl_2$ suspension.

2.4 *Vegetation measurements*

To characterize tree stands at the study sites, diameter at 1.3 m height of every tree (diameter $>=5$ cm) in the 30 m $\times$ 30 m area was measured and basal areas were calculated by species. For describing productivity of the sites, height and age of the six trees with the largest diameter at 1.3 m height was measured and the site index (H100) was calculated (Gustavsen 1980).

Coverage of ground vegetation species was estimated on four 2 m^2 squares at the study sites. The squares were placed systematically, 15 m and 15 m from each other in perpendicular directions, in a random location in the 30 m $\times$ 30 m area at the sites. The coverage of the species was estimated using classes 0, 0–1, 1–2, 2–4, 4–8, 8–16, 16–32, 32–64 and 64–100% cover. Reindeer grazing had caused almost a complete loss of lichens in the northernmost study area and, therefore, coverage of the area denuded by reindeer was also estimated and included as such in the ground vegetation data.

2.5 *Data analysis*

For illustrating sources of variation in the C densities of the organic and 0–1 m mineral soil layers, the total variance was divided into components by the soil layer and forest type using the NESTED procedure of SAS (Anonymous 1988). Means of the C densities at the study sites were used to investigate associations of the C densities with the forest type as a class variable and the effective temperature sum as a continuous variable. The GLM procedure of SAS was used for this analysis. The statistical models were parameterized and confidence limits for the model predictions were calculated using GLM, too. Confidence limits for the slope of the regression (CLb), were calculated using the formula

$$\text{CLb} = z_{0.95} \times \text{SEb},$$

where $z_{0.95}$ is the 95% fractile of students t-distribution and SEb is the standard error of the regression slope. Homogeneity of variances in the C densities of the forest types was tested using an F test.

The ground vegetation data was coded using central values of the coverage classes and the values were log-transformed after taking an average of each study site. An ordination analysis, detrended correspondence analysis (DCA), was performed on the data for interpreting variation in the ground vegetation and illustrating the composition of ground vegetation at the study sites (Jongman et al. 1987). The CANOCO program was used for the DCA (Ter Braak 1988).

3. Results

3.1 *Characteristics of soil forming factors at the study sites*

Characteristics of temperature decreased systematically from south to north along the gradient. The effective temperature sum decreased from about 1300 dd to 800 dd and the annual mean temperature from about 3.9 °C to −0.6 °C (Table 1). Humidity, measured as the difference between the annual precipitation and evapotranspiration, varied only moderately and unsystematically, since both the precipitation and evapotranspiration decreased towards the north.

Mean soil ages of the CT sites varied from about 9500 years to 11000 years in the study areas and those of the MT sites from about 9400 years to 10700 years (Table 1). The highest standard deviation for the variation in the soil age between sites of the same forest type within a study area was 340 years.

Characteristics describing physical properties, i.e. silt concentration, and chemical properties, i.e. calcium and magnesium concentrations and pH, of parent material varied fairly little and unsystematically along the gradient between the sites of the same forest type (Table 1). At the more productive MT sites the parent material contained more nutrients and substantially more fine particles than at the less productive CT sites.

Tree stands of the CT sites consisted only of Scots pines, and Norway spruce was the dominating tree species at the MT sites (Table 1). The basal a

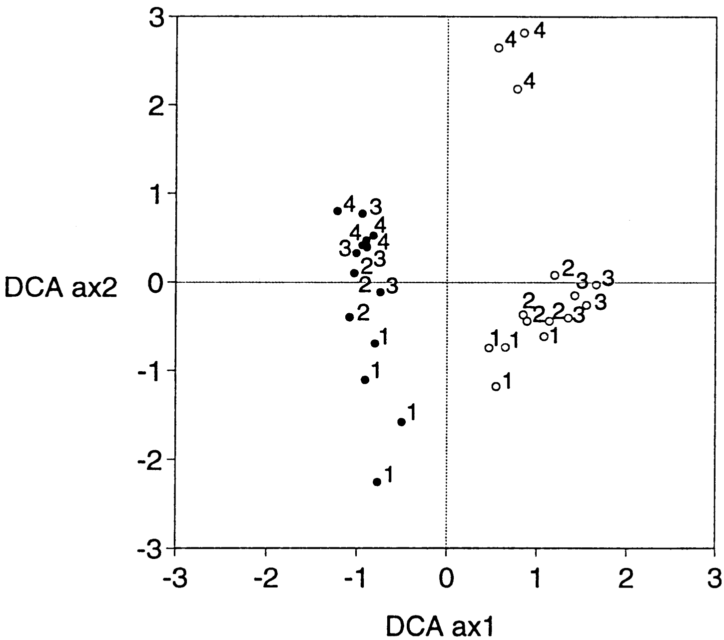

Figure 2. DCA ordination diagrams of the ground vegetation composition at the study sites: a) site scores and b) species scores. In the diagram of the site scores the CT sites are marked with the open dots and the MT sites with the filled dots; the numbers from 1 to 4 indicate the study areas respectively from south to north. In the diagram of the species scores the species names are abbreviated: *Calamagrostic arundinacea* (CALAARUN), *Calluna vulgaris* (CALLVULG), *Cladonia arbuscula* (CLADARBU), *C. rangiferina* (CLADRANG), *C. stellaris* (CLADSTEL), *Deschampsia flexuosa* (DESCFLEX), *Dicranum majus* (DICRMAJU), *D. scoparium* (DICRSCOP), *Empetrum nigrum* (EMPENIGR), *Hylocomium splendens* (HYLOSPLE), *Ledum palustre* (LEDUPALU), *Maianthemum bifolium* (MAIABIFO), *Pleurozium schreberi* (PLEUSCHR), *Trientalis europea* (TRIEEURO), *Vaccinium myrtillus* (VACCMYRT), *V. uliginosum* (VACCULIG), *V. vitis-idaea* (VACCVITI); REINDEER stands for ground cover denuded by reindeers.

area of trees varied little between the sites of the same forest type, excluding the MT sites in the northernmost study area. There the small basal area was caused by selective cuttings until some decades ago and slow recovery of the tree stands. The site indexes decreased and the age of the dominant trees increased from south to north reflecting the effect of temperature on tree growth.

The ordination analysis clearly separated the CT and MT sites on the first axis, and the first-axis-scores varied moderately little within the forest types (Figure 2a). The second axis, in turn, seemed to reflect climate-related variation in ground vegetation, since the scores tended to increase from south to north inside both forest types. Separation of the CT sites in the northernmost b

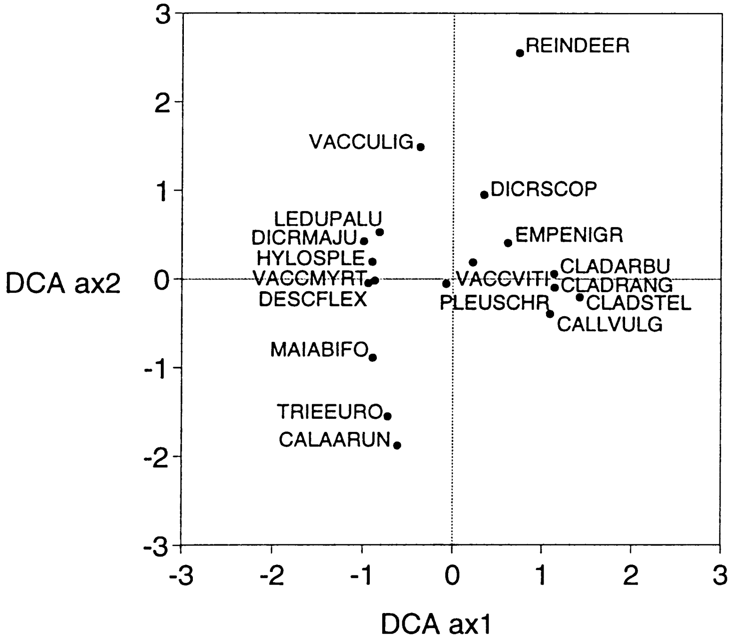

Figure 2. Continued.

study area was due to the lack of lichen cover caused by reindeer grazing. Examination of the site and species diagrams together illustrates composition of ground vegetation at the sites (Figures 2a and b). *Cladonia* lichens were common in the bottom layer of the CT sites with an increasing coverage towards the north. The most frequent shrub species at the forest type were *Calluna vulgaris* (L.) Hull., *Vaccinium vitis-idaea* L. and *Empetrum nigrum* L. the last one especially in the north. Of mosses, *Pleurozium schreberi* (Brid.) Mitt. occurred commonly at both the CT and MT sites, whereas *Hylocomium splendens* (Hedw.) B.S.G. was found almost exclusively at the MT sites. Various grasses and *Vaccinium myrtillus* L. were common in the ground layer of the MT sites and the coverage of *Ledum palustre* L. and *Vaccinium uliginosum* L. increased towards the north.

In conclusion, of the investigated characteristics describing the soil forming factors, i.e. climate, time, parent material, vegetation and topography, only temperature and temperature-associated characteristics of vegetation, such as tree growth, site index and the composition of ground vegetation, varied considerably and systematically along the gradient.

a

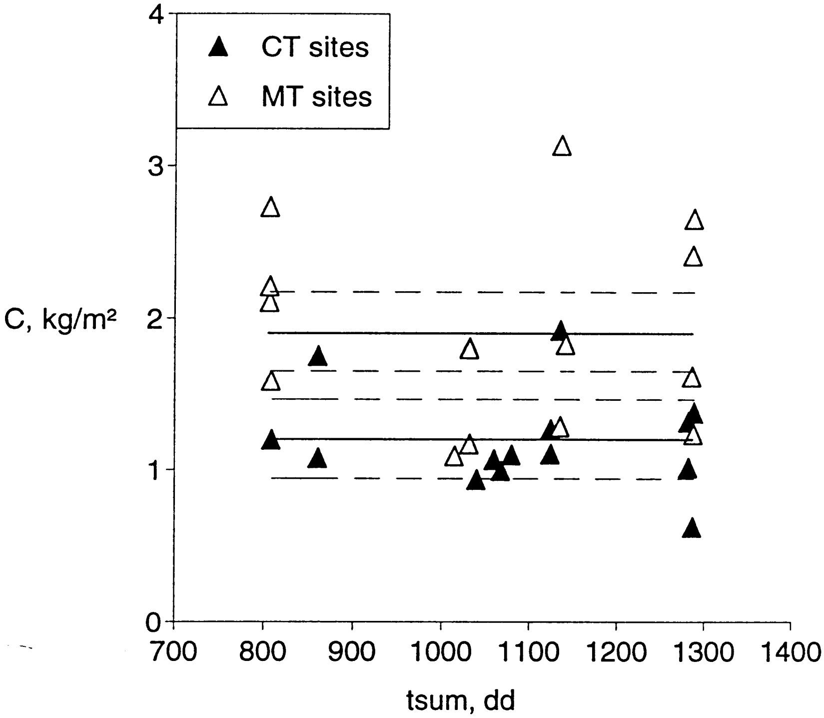

Figure 3. The C density of the a) organic and b) 0–1 m mineral soil layers at the CT and MT sites plotted against the effective temperature sum (+5 °C threshold). The solid lines represent the models fitted in the data: the C density of the organic layer explained by the forest type and that of the 0–1 m layer by the forest type and the temperature sum. The dashed lines show the 95% confidence limits for the model predictions.

3.2 *Variation of the C densities*

The C density of the organic layer was significantly higher at the more productive MT sites than at the less productive CT sites, but not associated with temperature (Table 2, Figure 3a). The mean C density was 1.20 kg m^{-2} at the CT sites and 1.91 kg m^{-2} at the MT sites (Table 3). The forest type explained 36% of the variation (Table 2). The 95% confidence limits for the C density, as predicted by the forest type, are shown in Figure 3a.

In the 0–1 m mineral soil layer the C density was also significantly higher at the more productive MT sites (Table 2, Figure 3b). The mean C density was 3.13 kg m^{-2} at the CT sites and 5.51 kg m^{-2} at the MT sites (Table 3). In addition, the C density increased significantly with the temperature sum (Table 2). The risk level for this increase was 0.0013 when including both forest types simultaneously for the test, and 0.010 among the CT sites and b

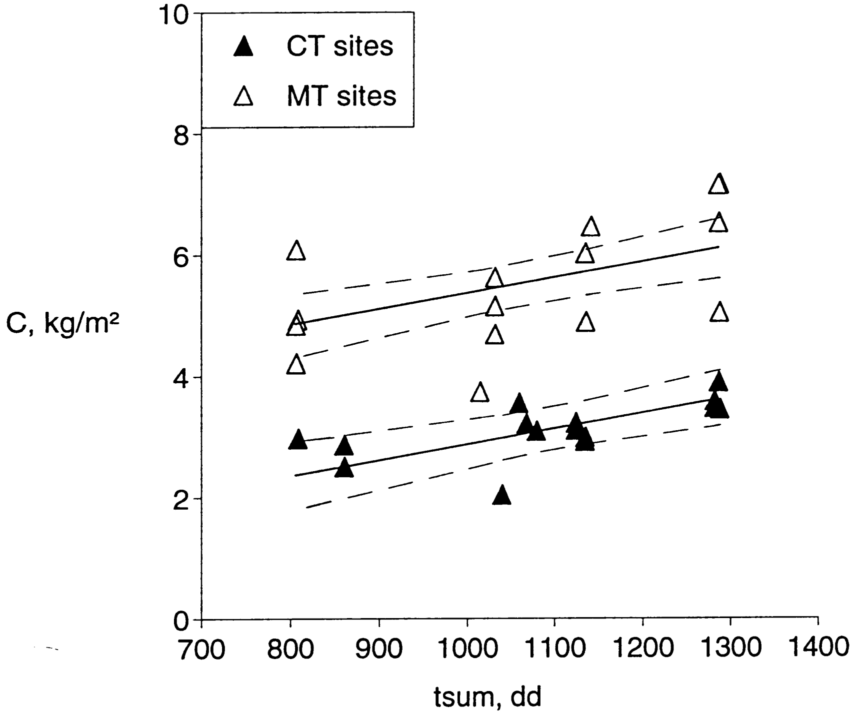

Figure 3. Continued.

0.025 among the MT sites when testing separately inside the forest types. The interaction of the temperature sum and the forest type was, however, insignificant (Table 2), and thus the data does not give support for different association of the C density and the temperature sum in the forest types. Consequently, to quantify the relation between the temperature sum, the forest type and the soil C density, a linear regression with a common slope and different intercepts for the forest types was fitted in the data:

$$MC_{CT} = 0.218 + 0.00266\text{tsum},$$

$$MC_{MT} = 2.69 + 0.00266\text{tsum},$$

where tsum is the temperature sum, and MC_{CT} and MC_{MT} are the C densities of the 0–1 m mineral soil layer respectively at the CT and MT sites (Figure 3b). The 95% confidence limits for the regression slope were ± 0.00151, and the limits for the model predictions, i.e. the C density predicted by the forest type and the temperature sum, are shown in Figure 3b. The model explained 80% of the variation in the C density, while the forest type alone accounted

Table 2. Statistical models for the C densities (kg m^{-2}) of the organic and 0–1 m mineral soil layers with *p*-values for the independent effects (forest type and the effective temperature sum with +5 °C threshold, tsum) and R^2-values for the models (n = 30).

Dependent variable	Independent effect	*P*-value	R^2
Organic layer	Forest type	<0.0001	0.356
Organic layer	Forest type	<0.0001	0.361
	tsum	0.6430	
Mineral soil layer	Forest type	<0.0001	0.702
Mineral soil layer	Forest type	<0.0001	0.798
	tsum	0.0013	
Mineral soil layer	Forest type	<0.0001	0.804
	tsum	0.0014	
	tsum∗forest type	0.3846	

for 70% of the variation (Table 2). Inside the forest types the temperature sum explained 41% of the variation among the CT sites and 33% of the variation among the MT sites.

The variances of the C densities were significantly larger for the MT than for the CT sites in both soil layers; the risk levels for the differences were less than 0.01. Therefore, the given confidence limits for the model predictions and the regression slope are in fact too wide for the CT sites and too narrow for the MT sites. This explains why so many MT sites fall outside the confidence limits in Figure 3. Still, we find the limits reasonable to illustrate the overall magnitude of the confidence of the model predictions and the regression slope.

In terms of the coefficients of variation, the C density varied equally within the same soil layer in both forest types, but for the organic layer the coefficients were twice as high, some 50%, as for the 0–1 m mineral soil layer (Table 3). Most of the variance in the C densities, from 56% to 85% depending on the soil layer and the forest type, was found inside the study sites. The differences between the study areas accounted for only a negligible proportion of the total variance in the organic layer, while in the 0–1 m mineral soil layer this proportion was 14% for the CT sites and 20% for the MT sites.

4. Discussion

An important prerequisite to using the gradient approach applied in this study for investigating the association between the soil C content and temperature

Table 3. Mean, coefficient of variation (CV) and variance divided into different components for the C densities (kg m^{-2}) of the organic and 0–1 m mineral soil layers at the CT and MT sites (n = 4 for areas, n = 4 for sites within the areas and n = 6 for profiles within the sites, except n = 3 for sites within one of the areas).

	Mean	CV	Variance components				Proportion of total			
			Total	Between areas	Between sites within areas	Between profiles within sites	Total	Between areas	Between sites within areas	Between profiles within sites
CT sites oganic layer	1.20	49%	0.351	0.010	0.043	0.298	100%	2.9%	12.2%	84.9%
CT sites mineral soil layer	3.13	25%	0.635	0.086	0.063	0.486	100%	13.5%	9.8%	76.6%
MT sites organic layer	1.91	50%	0.929	0	0.279	0.650	100%	0%	30.0%	70.0%
MT sites mineral soil layer	5.51	27%	2.175	0.426	0.534	1.216	100%	19.6%	24.5%	55.9%

is the equilibrium of the soil C with the prevailing conditions at the study sites, i.e. with respect to the soil age and the present climate. According to the data reviewed by Birkeland (1984), soil C storage first increases rapidly with the soil age for some tens or hundreds of years, thereafter the increase gradually slows down, and the storage reaches equilibrium at an age ranging from as little as 200 years to some 10000 years, depending on conditions. On a 5000 year chronosequence of soils on the west coast of central Finland near study areas 2 and 3 (see Figure 1), the C content of the topmost 30 cm mineral soil layer stabilized at the age of about 1500 years (Starr 1991, the C data unpublished). ^{14}C datings in similar soils in Sweden gave ages that ranged from 140 years to 1260 years with an average of some 500 years suggesting that the mean residence time of the organic C in the soils is some hundreds of years (Tamm & Östlund 1960; Tamm & Holmen 1967). Temperatures, in turn, have remained somewhat at the present level in Finland for the last 2500 years (Eronen 1990). The knowledge of changes in humidity in the past is much more limited, because the lack of water has not restricted the distribution of plant species, which is an important tool of the paleoclimatic studies. Consequently, it is unlikely that the minor changes in humidity have affected the processes of the soil C balance, net primary production and decomposition, which in boreal forests on well-drained soils are regulated mainly by temperature (Mikola 1960; Koivisto 1970; Schlesinger 1977; Moore 1984). There is also no evidence for that the difference of climate between southern and northern Finland has been considerably different in the past after the most recent glaciation. On these bases we conclude that the C storages of the studied soils have reached equilibrium with respect to both the soil age and the present climate.

Relating the variation in the soil C density along the gradient to temperature also presupposes similarity of the other soil forming factors at the study sites, i.e. features of climate other than temperature, parent material, vegetation, and topography. The investigated characteristics describing these factors revealed either little or moderate, but unsystematic variation along the gradient. Only some properties of vegetation, such as the site index and the composition of ground vegetation, varied systematically, but these reflected the differences in thermoclimate.

In conclusion, on basis of 1) the suggested equilibrium of the soil C storage with respect to the soil age and the prevailing climate at the study sites, 2) the similarity of the soil forming factors other than temperature at the study sites, 3) the objective selection and sampling of the study sites and 4) knowledge of temperature being an important regulator of the processes controlling the soil C balance in boreal forests (Mikola 1960; Koivisto 1970; Schlesinger 1977;

Moore 1984), we related the systematic variation in the soil C density along the gradient to the present temperature.

In the 0–1 m mineral soil layer the C density increased with temperature, and, on the basis of the regression model, the increase was 0.266 kg m^{-2} for every 100 dd increase in the effective temperature sum in both studied forest types. Consequently, 57% more C at the CT and 28% more C at the MT sites had accumulated in the layer under the warmest conditions of the gradient compared to the coolest. The increase suggests a shift in the present equilibrium soil C content towards a larger storage in response to climatic warming. The soils would thus act as sinks for the atmospheric CO_2 and provide a negative feedback for the predicted CO_2-induced climatic warming.

For illustrating the potential significance of this feedback, let us first assume that the predicted increase in the annual mean temperature in Finland, about 4 °C due to doubling of atmospheric CO_2 (Mitchell et al. 1990), causes a 400 dd increase in the effective temperature sum. For a new equilibrium with the predicted temperature, the C density of the 0–1 m mineral soil layer would increase by about 1.06 kg m^{-2}, and, subsequently, the soil C storage in forests on mineral soil in Finland (land area 199130 km^2 according to satellite image based land use and forest classification data by the National Land Survey of Finland) by 212 Tg. This would be a 23% increase in the present amount of about 900 Tg in the 0–1 m layer (Liski & Westman 1997). Assuming that the increase in the soil C storage is linear and the new equilibrium is reached in 100 years, the annual C sink in the Finnish forest soils is about 10% of the current annual CO_2 emissions of the country, 19 Tg of C during the year 1988 (Boström et al. 1990). This kind of comparison of the present and future equilibrium states serves only as a first approximation of the changes in soil C storage, since the actual dynamics of the changes will probably be more complicated.

The conclusion of the increasing soil C storage in response to climatic warming presupposes that the present type of coniferous vegetation remains at the sites also under the warmer conditions. This assumption is probably reasonable except for southernmost Finland, where the coniferous forests at the southern regions of the boreal zone are predicted to be replaced by broadleaved forests (Kellomäki & Kolström 1992). The change of the vegetation type may result in a decrease of the soil C storage despite an increase in net primary production, since litter of broadleaved trees decomposes more rapidly than litter of conifers (Anderson 1992; Van Cleve & Powers 1995). On the other hand, the production of conifer stands with broadleaved mixture has been observed to be generally higher than the production of either pure conifer or broadleaved stands (Mielikäinen 1985). The potential formation of such mixed species stands of higher productivity would therefore compensate for the possible losses due to the change in the litter type. Moreover, the gradient approach accounts only for the effects of temperature and ignores the interaction of the increased temperature and atmospheric CO_2 concentration, which may further enhance net primary production and increase the soil C storage (Rastetter et al. 1991; Gifford 1992; Kirschbaum 1993). For this reason, the soil C storage may actually increase more in the remaining coniferous forests than predicted on the basis of the temperature association alone.

The suggested increase in the soil C storage in response to climatic warming agrees with a model simulation study by Pastor & Post (1988), in which the soil C density of boreal spruce sites increased as a consequence of the warming if the coniferous vegetation remained at the sites and there was enough water. Also Townsend et al. (1992) concluded that the soil C storage of the boreal zone may increase at least over some limited range of warming, whereas the C storage of tropical soils is likely to decrease. Kirschbaum (1993, 1995) showed that theoretical equilibrium soil C density decreases with temperature from 5 °C to 35 °C and climatic warming leads to losses of the soil C. Similarly, Burke et al. (1989) observed that the soil C content of grasslands decreases with temperature in North America. On the basis of these studies, even the direction of the change in the soil C storage in response to climatic warming may be different in different ecosystems, i.e. the amount of C may increase in some soils while decreasing in others. Therefore, it is essential to consider different ecosystems separately when predicting the changes in the global soil C balance. Furthermore, it seems that soil C gradients across different vegetation zones (e.g. Post et al. 1982; Johnson 1995) are not necessarily appropriate for predicting the response of the soil C storage to climatic warming.

In the organic layer the C density was not found to be associated with temperature. One reason for the lack of the association could be different past events at the sites, for instance the frequency and intensity of forest fires and forest harvest that especially affect the organic layer. Another reason for the lack of the association could be that the sampling and measurements were not effective enough to detect the trend, even if it actually existed. In the study used to design our sampling, the coefficient of variation for the C density of the organic layer within a CT site was 28% (Liski 1995). In this study the coefficient of variation for all the variation in the organic layer was substantially larger, about 50% for both forest types, and most of this variation was found within the study sites. Consequently, the study site means for the C densities of the organic layer were not as accurate as planned, and probably a larger number of study sites and samples from the sites would have been needed to detect the trend.

On the other hand, if the association between the C density and temperature was really weaker for the organic layer than for the mineral soil and the C storages of both soil layers were in equilibrium, it implies that the dependence of C input and decomposition rates on temperature are different in these two soil layers. Either the C input to the organic layer is not increased as much with temperature as is that to the mineral soil or the decomposition in the organic layer is increased more with temperature than in the mineral soil. On the basis of this study, it is not possible to judge which one of these alternatives is true. However, the result suggests that the C storage of different soil layers containing different organic matter may change differently in response to climatic warming.

The division of the variance into different components highlighted the large within-site variation in the soil C density. It is noteworthy that well over half of the variance, from 56% to 85% depending on the forest type and the soil layer, found along a 1000 km transect among sites of the same forest type was due to the small-scale variation over a few meters. This emphasizes the importance of the sampling design within the sites in order to sample efficiently for the soil C density.

Both in the organic and 0–1 m mineral soil layers the C density was higher at the more productive MT sites than at the less productive CT sites, and the forest type explained a substantial proportion of the variation in the C densities, 36% in the organic layer and 70% in the 0–1 mineral soil layer. This result supports our earlier suggestion (Liski & Westman 1995) that site productivity is a cause of the large variation in the soil C density within the boreal zone observed in worldwide studies (Schlesinger 1977; Post et al. 1982). Within the forest types the temperature sum explained a considerable proportion of the variation in the C density of the 0–1 m mineral soil layer: 41% among the CT sites and 33% among the MT sites. Therefore, classification of sites into more homogenous subgroups according to their productivity, and applying temperature as another explanatory variable within the subgroups could provide a useful means for reducing unexplained variation in the estimates of the soil C reserves in appropriate regions in the boreal zone and also for investigating regional patterns of the C reserves.

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