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Density of organic carbon in soil at coniferous forest sites in southern Finland

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Abstract. More detailed knowledge of the density of organic carbon in soils of boreal forests is needed for accurate estimates of the size of this C stock. We investigated the effect of vegetation type and associated site fertility on the C density at 30 mature coniferous forest sites in southern Finland and evaluated the importance of deep layers to the total C store in the soil by extending the sampling at eight of the sites to the depth of ground water level (2.4–4.6 m). The C density in the organic horizon plus 1 m thick mineral soil layer ranged from 4.0 kg/m^2 to 11.9 kg/m^2, and, on the average, increased towards the more productive vegetation types. Between the depth of 1 m and the ground water level the C density averaged 1.3–2.4 kg/m^2 at the studied vegetation types and these layers represented 18–28% of the total stock of C in the soil. The results emphasize the importance of also considering these deep layers to correctly estimate the total amount of C in these soils. At the least fertile sites the soil contained about 30% more C than phytomass, whereas at the more fertile sites the amount of C in soil was about 10% less than the amount bound in vegetation.

Key words: boreal forests, carbon cycle, carbon pools, podzols, soil carbon

Introduction

Worldwide, carbon in soil organic matter constitutes two thirds of the C stored in terrestrial ecosystems (Post et al. 1990). The amount of C in soil is shown to be dependent on climate; the cooler and more humid is the climate the larger is the C density in soil (Post et al. 1982). Therefore, climatic changes may induce alterations in the soil C reserves (Post et al. 1982; Prentice & Fung 1990; Bonan & Van Cleve 1992). These changes may affect carbon dioxide concentration of the atmosphere and, consequently, enhance the greenhouse effect. In order to assess the potential changes in the soil C storage, one of the fundamental factors is the current amount of C in different soils.

A considerable proportion, 12–13%, of the C reserves in the soils of the world are found in boreal forests owing both to the large land area covered by boreal forests and high C density in these soils (Schlesinger 1977; Post et al. 1982). Accuracy of these estimates, made by extrapolating a mean C density over the area covered by boreal forests, is impaired by the large variation in the C density within the boreal zone (Schlesinger 1977; Post et al. 1982). Post et al. (1982) related the variation to factors, such as aspect, topography, parent material, age of soil profile, climate and vegetation, which do not appear at the life zone level of organization. Better estimates for boreal forests, as well as for smaller regions, could, therefore, be produced by stratifying sites into more homogenous groups and using different C densities for the groups. For this reason, more detailed knowledge of the density and co-varying factors are needed.

In Finland, data on the density of organic C in forest soils is limited. Density of organic matter in surface soil layer, no deeper than 60 cm in mineral soil, has been analyzed by the loss-on-ignition method in few studies, which have concentrated on the biomasses of forest stands (e.g. Mälkönen 1975; Havas & Kubin 1983). However, these studies are not very useful when estimating the total amount of organic C in the soil. First, in these soils also the deeper layers may contain large quantities of organic C (Schlesinger 1977) and secondly, conversion of loss-on-ignition to organic C is problematic in mineral soil samples (Huntington et al. 1989).

The objective of this study was to investigate the effect of vegetation type and associated site fertility on the density of organic C and evaluate the importance of deep layers in respect of the total C content in forest soils in southern Finland. The amount of C in the soil is compared to the amount bound in vegetation at the study sites.

Materials and methods

Study area and study sites

A total of 30 sites, scattered over an approximately 400 km^2 area surrounding the Helsinki University Forestry Station in Hyytiälä in southern Finland (61°48′ N, 24°19′ E), were studied. Climate is uniform throughout the area. The annual mean temperature is +2.9 °C; January is the coldest month (mean −8.9 °C) and July the warmest (mean +15.3 °C). The annual precipitation averages 709 mm (Anonymous 1991).

Bedrock of the area consists mainly of acidic granite, granodiorite and mica gneiss; basic gabro and periodite rocks occur only rarely. The most recent glacier in the area melted 9500–10000 years ago and the highest post-glacial shore-line is 160 m above the present sea level (Eronen & Haila 1981). As the height of the study sites ranged from 115 m to 180 m above the present sea level, both sub- and supra-aquatic sites were chosen for the study. Parent material at the study sites consisted of either glacially deposited till or parent material sorted by wind or glaciofluvial action.

The Finnish classification of forest types (Cajander 1925) was utilized to select sites of different vegetation types and fertilities in the area. The classification system divides sites into a few types, forest types, on the basis of the composition of the ground vegetation; these types generally differ in productivity. Scots pine (*Pinus sylvestris* L.) is usually the dominating tree species at the less fertile *Calluna* type (CT) and *Vaccinium* type (VT), whereas Norway spruce (*Picea abies* (L.) Karst.) is often the most common tree at the more fertile *Myrtillus* type (MT) and *Oxalis-Myrtillus* type (OMT). The different fertility of the types is reflected in their yield capacities. The total stemwood production of naturally developed (naturally regenerated and no forest harvest) Scots pine stands average 310 m^3/ha and 528 m^3/ha at the age of 100 years at typical CT and VT sites, respectively; similar production figures for Norway spruce are 614 m^3/ha at MT sites and 658 m^3/ha at OMT sites (Ilvessalo & Ilvessalo 1975).

A total of five CT sites, nine VT sites, eleven MT sites and five OMT sites were selected for the study. An area of 10 m $\times$ 30 m was studied at the sites. Soils at these study sites were podzols or at least clearly podzolized. Some properties of the soils are reported in Table 1. The topography of the sites was flat or very slightly southward sloping. The tree stands were mature, dominated by Scots pine (*Pinus sylvestris*) or Norway spruce (*Picea abies*) and aged approximately 100 years. The stands were in a good silvicultural condition and no harvesting had been done during the 10 years prior to the sampling and measurements. Field measurements were made and soil samples taken during the summers of 1987 and 1988, except for the soil collection to ground water level, which was carried out in May 1992.

Soil carbon density

For soil sampling, three pits were excavated on the longitudinal axis of each site. Thicknesses of the soil horizons were measured, and a sample of known volume from the organic horizon (F/H) and a 150 cm^3 sample from the top of the E horizon, from the top of the upper and bottom halves of the B horizon and from the parent material were collected from each pit. To get comparable parent material samples in relation to different thicknesses of the soil horizons at the sites, the sampling depth for the parent material sample was determined by multiplying the sum of E and B horizon thicknesses by 1.5 which resulted in the sampling depths of 31–82 cm (average 51 cm). In addition, at one CT, four VT and three MT sites on sorted parent material soil sampling was extended to the depth of ground water level (2.4–4.6 m) using hydraulic drilling equipment. From these deep layer core samples (one per site), 130 cm^3 subsamples at approximately 1 m intervals (3–5 subsamples) were taken for further analysis.

In the laboratory the samples were dried to a constant weight at 105 °C, passed through a 2 mm sieve, and weighed. Bulk density (Bd, kg/m^3) of the

Table 1. General properties of the soil layers at the *Calluna* type (CT), *Vaccinium* type (VT), *Myrtillus* type (MT) and *Oxalis-Myrtillus* type (OMT) sites (average values; $n = 5$, $n = 9$, $n = 11$ and $n = 5$ for CT, VT, MT and OMT sites, respectively). B1 refers to the top half of the B horizon and B2 to the bottom half.

	CT					VT					MT					OMT				
Soil layer	F/H	E	B1	B2	C	F/H	E	B1	B2	C	F/H	E	B1	B2	C	F/H	E	B1	B2	C
Thickness, cm	3.5	3.1	23.4[1)]			4.8	5.3	26.6[1)]			4.8	7.0	29.1[1)]			5.1	6.1	33.1[1)]		
Density, kg/dm^3	0.13	1.08	1.25	1.47	1.59	0.11	1.18	1.22	1.47	1.60	0.13	1.16	1.17	1.35	1.57	0.12	1.20	1.27	1.35	1.57
Silt conc., % [2)]		9.9	9.9	7.7	1.7		18.4	15.2	13.5	7.6		27.0	27.1	27.7	35.9		24.6	21.9	21.1	29.8
pH$_{CaCl2}$ [3)]	3.01	4.07	4.60	4.72	4.94	3.1	3.59	4.49	4.78	4.88	3.22	3.58	4.34	4.64	4.76	3.35	3.49	4.15	4.62	4.64
CECe, cmol(+)/kg [4)]	8.9	1.7	0.82	0.53	0.29	9.7	1.6	1.1	0.48	0.31	9.4	1.9	1.5	0.75	0.52	9.0	1.6	1.9	1.2	0.63
Base saturation, % [5)]	18.9	9.9	9.9	15.9	28.9	30.9	7.2	8.4	19.0	29.8	37.8	8.3	10.3	19.2	29.2	45.2	10.8	9.2	13.6	18.4

[1)] of the entire B horizon;

[2)] particle size fraction 2–60 μm; determined according to Elonen (1971);

[3)] soil : 0.01 M CaCl2 = 1 : 2.5 (v/v);

[4)] Ca + Mg + H + Al extracted by 1 M KCl;

[5)] (Ca+Mg)/CECe.

parent material samples and density of the soil fraction with particle size of less than 2 mm (Bd<2mm, kg/m^3) were calculated for the samples of each pit before the samples of the same horizon at a given study site were combined for the C analysis. The average of the density measurements for each horizon at a site was used for the calculations. The Bd<2mm for the deep layer samples was calculated by multiplying the Bd of the parent material at the site by the gravimetric concentration of < 2 mm fraction (kg/kg) in the deep layer sample.

The total C concentration of the < 2 mm fraction (C_C, kg/kg) was measured by Leco CHN-600 analyzer (pit samples) or Leco CR-12 analyzer (deep layer samples). In these acid soils (pH 2.9–5.9, soil : 0.01 M $CaCl_2$ = 1 : 2.5) the total C concentration equals the concentration of organic C.

The amount of organic C per volume of soil (volumetric C density, D_C, kg/m^3) in the samples was calculated by multiplying the C_C by the Bd<2mm. The D_C between the samples of the different layers was interpolated linearly; earlier continuous sampling through the profile suggest the assumption of linearity is appropriate (unpublished data). The D_C between the parent material sample of the pits and the depth of 1 m in mineral soil was extrapolated assuming a constant D_C from the parent material sample to the depth of 1 m; the extrapolation seems also appropriate, since the extrapolated D_C and the D_C of the deep layers match well at the 1 m depth (see Figs. 2 and 3). The amount of C in the soil per unit of surface area (surface density of C, M_C, g/m^2) in a given soil layer was then calculated by integrating the D_C over depth.

Stone volume

The rod testing method, developed by Viro (1952), was modified to estimate stone volume at different depths in the 0–50 cm mineral soil layer at the study sites. A 1 cm thick steel rod was forced into soil at 30 systematically selected locations (3.3 m between the measurements at the 10 m × 30 m sites) and the penetration depth was recorded as 5, 15, 25, 35, 45 and > 50 cm. Each of the measurements represented thus 10 m^2 (1/30 × 300 m^2) of land area. The horizontal surface area of stones at the recorded depths was then calculated by multiplying the penetration frequency to the depth by 10 m^2. Because the vertical dimension of a stone encountered by the rod could not be known, any stone was assumed to extend to the depth of 50 cm. This enabled us to convert the horizontal surface area of stones to stone volume. The estimate of stone volume was included in the C densities, where noted so, by multiplying the M_C in each soil horizon by 1-Si, where Si is the volume fraction of stones in the soil horizon i.

When developing the rod testing method, Viro (1952) found a linear correlation of 0.8 between the mean penetration depth of the rod and measured volume of stones in 0–30 cm soil layer at the 134 Finnish forest sites studied. Because the soil C density decreased clearly with depth in the soil profiles (see Fig. 2), we found it necessary to modify the method for estimating the stone volume at different depths. Our assumption of any stone met by the rod extending to the 50 cm depth may be unrealistic in a number of cases and the approach most likely overestimates the actual stone volume and, consequently, underestimates the C density. On the other hand, if the stone volume is ignored, the C densities of stony soils are overestimated. Comparison of these two estimates, then, provides us with certain minimum and maximum estimates for the actual C density.

Amount of carbon in vegetation

For estimating the amount of C bound in vegetation at the study sites, diameter at 1.3 m height of every tree (diameter $\geq$ 5 cm) was measured. The biomasses of the trees, excluding the biomass of fine roots, were then calculated by species using Marklund's (1988) allometric regression equations and transformed to organic C by multiplying by 0.5 (Hakkila 1989). The error in the tree C caused by leaving out the small trees was negligible, because there were only few such trees at the mature stands studied. According to the studies by Mälkönen (1975) and Havas & Kubin (1983), the error in the vegetation C caused by excluding the fine roots and ground vegetation was less than 10%.

Composition of ground vegetation

Coverage of ground vegetation species at the study sites was estimated using 0, 0–1, 1–2, 2–4, 4–8, ..., 64–100% classes. An ordination analysis (detrended correspondence analysis, DCA) was performed on the data to objectively interpret the variation between the sites, aside the forest type classification. The idea of the analysis is that environmental factors determining fertility are difficult to characterize exhaustively. Therefore, the species composition may summarize the environmental information better than any set of measured variables (Jongman et al. 1987). The iterative algorithm constructs theoretical variables, ordination axes, best explaining the variation in the species composition between the sites; eigenvalues of the axes are measures for their importances. Sites with similar species composition get similar scores, site scores, on the ordination axes and occur close to each other in the ordination diagram. CANOCO program was used for the analysis (Ter Braak 1988). Spearman rank correlation coefficients were used for studying associations

Table 2. Spearman rank correlation coefficients between the site scores on the first and second axes of the DCA ordination, silt and total Mg+Ca concentrations of the parent material, base saturation and N concentration of the organic horizon and C content in the organic horizon plus 0–1 m mineral soil layer (n = 30, *p < 0.05, **p < 0.01).

	Ax1	Ax2	Silt[1)]	Ca+Mg[2)]	BS[3)]	N[4)]	C
Ax1	1.00						
Ax2	−0.32*	1.00					
Silt	0.76**	−0.10	1.00				
Ca+Mg	0.59**	−0.18	0.77**	1.00			
BS	0.76**	0.11	0.58**	0.52**	1.00		
N	0.46**	−0.10	0.44**	0.46**	0.37**	1.00	
C	0.77**	−0.29	0.58**	0.50**	0.49**	0.14	1.00

1) particle size fraction 2–60 μm; determined according to Elonen (1971);
2) determined using wet digestion with conc. HNO_3, H_2SO_4 and $HClO_4$;
3) (Ca+Mg)/CECe, CECe = Ca + Mg + H + Al extracted by 1 M KCl;
4) determined by the Kjelldahl method.

between the site scores and soil characteristics. To compare differences in the C densities between the forest types, we carried out ANOVA and used Tukey-Kramer HSD test for pairwise comparisons (Anonymous 1992).

Results

A major proportion of the variation in the composition of ground vegetation between the sites was included in the first ordination axis (eigenvalue 0.52), while the second axis explained substantially less of the variation (eigenvalue 0.24) (Fig. 1). The first axis also correlated significantly with soil characteristics related to fertility; i.e. both with primary characteristics, like silt and nutrient concentrations of the parent material, and characteristics formed through soil formation, like base saturation and nitrogen concentration of the organic horizon; the correlations with the second axis were weak (Table 2). Nevertheless, none of the soil characteristics correlated as strongly with the soil C content as the first ordination axis. The first axis also agreed with the classification of the forest types (Fig. 1), which have been shown to differ in productivity (Ilvessalo & Ilvessalo 1975). Therefore, we conclude that the composition of ground vegetation reflects site fertility and the forest types are a useful means for grouping the sites in relation to fertility and to the soil C storage.

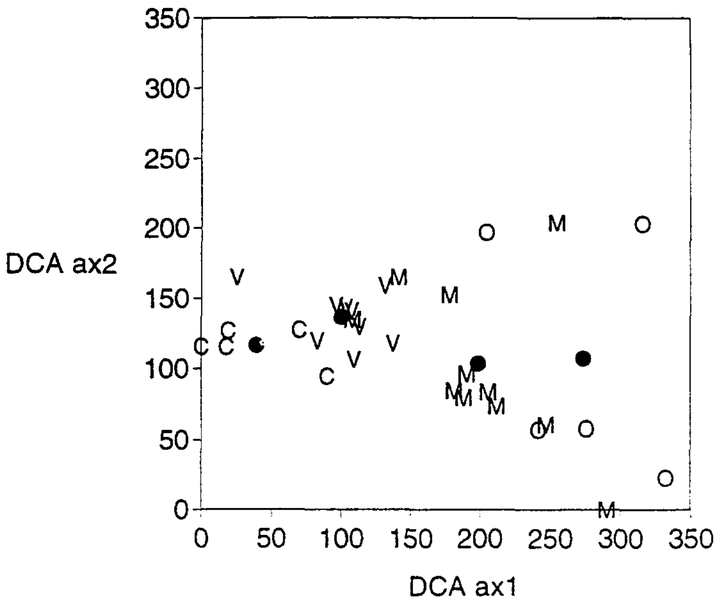

Fig. 1. DCA ordination diagram of the ground vegetation composition at the study sites. Scores of the *Calluna* type, *Vaccinium* type, *Myrtillus* type and *Oxalis-Myrtillus* type sites marked with C, V, M and O, respectively. The dots indicate means for the CT, VT, MT and OMT sites from left to right.

The amount of organic C per unit of surface area in the organic horizon and in mineral soil to the depth of 1 m ranged from 4.0 kg/m^2 to 11.9 kg/m^2 (Table 3). On average, the soil C content varied with the forest type and increased with site fertility; the means for the CT, VT, MT and OMT sites were 5.8 kg/m^2, 6.0 kg/m^2, 8.0 kg/m^2 and 9.6 kg/m^2, respectively. The average for the OMT sites differed statistically very significantly from both the CT (p = 0.003) and VT (p = 0.002) sites. The p-values for the differences between the MT and CT sites and between the MT and VT sites were 0.062 and 0.038, respectively. The proportion of that C amount found between the depths of 0.5 m and 1 m in mineral soil also increased with site fertility; the percentages averaged 7.6% at the CT sites, 8.2% at the VT sites , 18% at the MT sites and 22% at the OMT sites. The estimate of stone volume in the 0–0.5 m mineral soil layer lowered the estimates for the C densities in that layer by 16%, 6%, 14% and 23% at the CT, VT, MT and OMT sites, respectively. It did not, however, alter the trend towards higher C densities at the fertile sites.

C content in the deep layers (1 m to ground water level) was 1.3 kg/m^2 at the studied CT site and averaged 2.4 kg/m^2 at the VT sites and 2.3 kg/m^2 at the MT sites (Table 3). These deep layers accounted for 18%, 28% and 22%

Table 3. Average amount ± standard deviation (min - max) of organic C in the different soil layers for the *Calluna* type (CT), *Vaccinium* type (VT), *Myrtillus* type (MT) and *Oxalis-Myrtillus* type (OMT) sites. ANOVA carried out for the layers above 1 m; averages marked with different letters differ at less than 5% risk level. Percentages of the total stock indicated only for the CT, VT and MT sites, because the layers below 1 m were not studied at the OMT sites. The depth of ground water level (gwl) averaged 4.1 m, 4.3 m and 2.5 m at the CT, VT and MT sites, respectively.

	CT		VT		MT		OMT
Soil layer	kg/m^2	%	kg/m^2	%	kg/m^2	%	kg/m^2
F/H [1)]	1.6a	23	1.9a	23	2.0a	20	2.2a
0–0.5 m [1)]	3.7ab	53	3.6a	42	4.5ab	44	5.3b
0.5–1 m [1)]	0.5a	6	0.5a	6	1.5b	14	2.1b
F/H-1.0 m [1)]	5.8ac ± 1.1 (4.0–6.9)	82	6.0a ± 0.9 (4.6–7.5)	72	8.0bc ± 1.7 (5.7–10.4)	78	9.6b ± 2.5 (6.9–11.9)
1–2 m [2)]	0.5	7	0.9	11	2.0	19	
2 m-gwl [2)]	0.8	11	1.5	17	0.3	3	
1 m-gwl [2)]	1.3	18	2.4	28	2.3	22	
Total F/H-gwl	7.1	100	8.4	100	10.3	100	

[1)] $n = 5$, $n = 9$, $n = 11$ and $n = 5$ for CT, VT, MT and OMT sites, respectively;
[2)] $n = 1$, $n = 4$ and $n = 3$ for CT, VT and MT sites, respectively.

of the total amount of C in soil at CT, VT and MT sites, respectively. The total store of organic C in soil averaged 7.1 kg/m^2 at CT sites, 8.4 kg/m^2 at VT sites and 10.3 kg/m^2 at MT sites.

The amount of organic C per volume of soil decreased with depth in the soil profiles until the depth of 2 m (Figs. 2 and 3). Below that depth no depth-dependent trend was observed and the volumetric C density varied between 0.2 kg/m^3 and 1.3 kg/m^3 (Fig. 3). The organic and mineral soil horizons contained about equal amounts of C per volume of soil at sites of different fertilities. The larger amounts in the soil horizons at the fertile sites were due to the thicker horizons (Fig. 2; Table 3). However, in the parent material, above that depth of 2 m, the volumetric C density increased clearly with site fertility leading to the larger amounts of C in the parent material at the fertile sites (Figs. 2 and 3; Table 3).

Total C content (soil to the depth of ground water plus vegetation) averaged 12.6 kg/m^2, 17.1 kg/m^2, 21.9 kg/m^2 at the CT, VT and MT sites, respectively (Fig. 4). At the OMT sites, where the deep soil layers below the depth of 1 m were not studied, the amount of C averaged 23.1 kg/m^2. At the least fertile

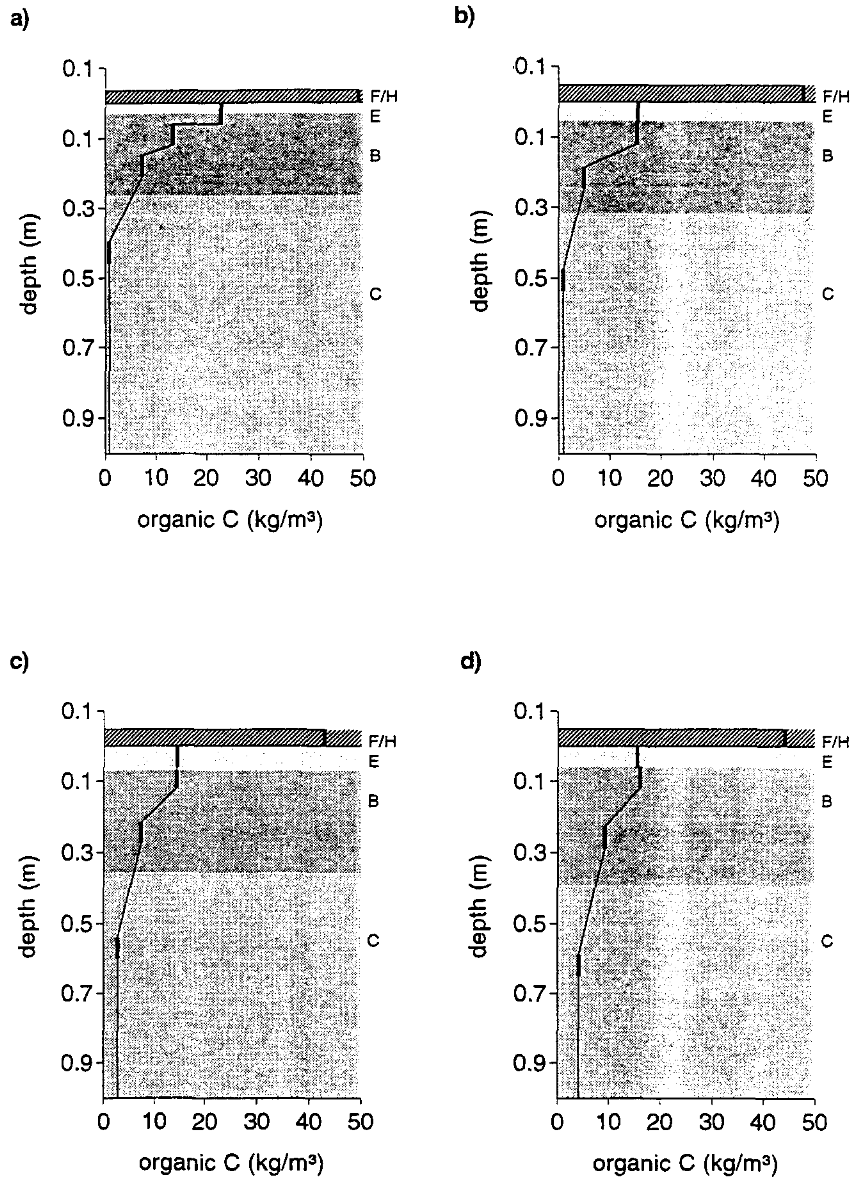

Fig. 2. Volumetric density of organic C in the soil profiles at the a) *Calluna* type (n = 5), b) *Vaccinium* type (n = 9), c) *Myrtillus* type (n = 11) and d) *Oxalis-Myrtillus* type (n = 5) sites (averages for the forest types). Mean sample depths are indicated by the thicker vertical lines and mean thickness of the soil horizons by the shadings.

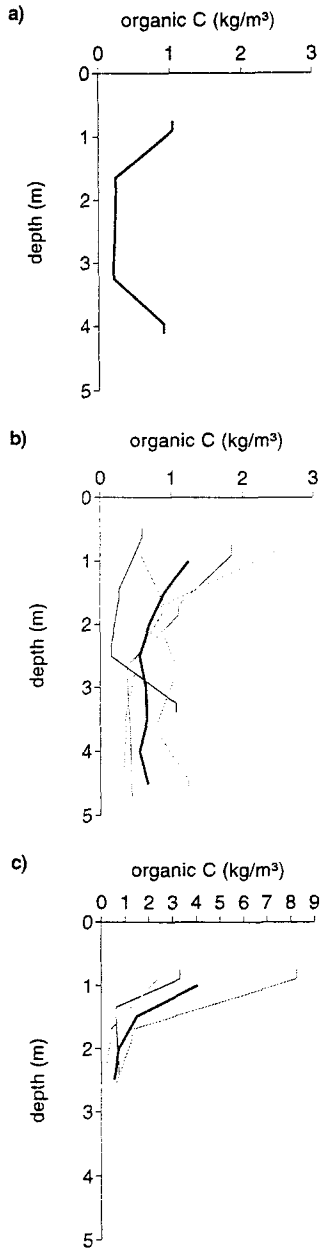

Fig. 3. Volumetric density of organic C in the deep layer samples collected from a) *Calluna* type, b) *Vaccinium* type and c) *Myrtillus* type sites. The thin lines represent the individual profiles; the thick lines are calculated by averaging the volumetric carbon densities of the individual profiles at 0.5 m intervals.

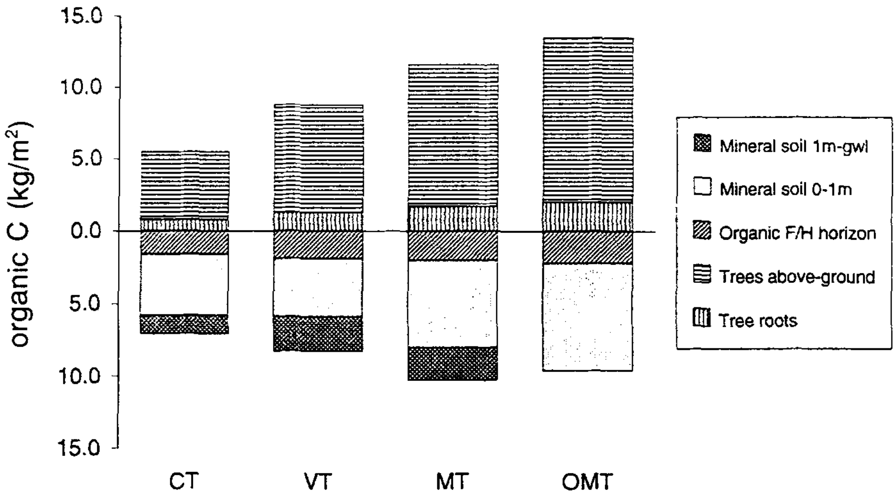

Fig. 4. Total store of organic C at the *Calluna* type (CT), *Vaccinium* type (VT), *Myrtillus* type (MT) and *Oxalis-Myrtillus* type (OMT) sites divided into different pools (averages for the forest types; $n = 5$, $n = 9$, $n = 11$ and $n = 5$ for CT, VT, MT and OMT sites, respectively). The depth of ground water level (gwl) averaged 4.1 m, 4.3 m and 2.5 m at the CT, VT and MT sites, respectively.

CT sites soil organic matter accounted for 56% of that total amount, whereas at the more fertile sites the proportion in the soil was about 45%.

Discussion

Soils of boreal forests contain large quantities of organic C, but the C density varies considerably within the boreal zone (Schlesinger 1977; Post et al. 1982). Therefore, more detailed knowledge of the density and covarying factors are needed to accurately estimate soil C reserves in different regions within the boreal zone as well as in boreal forests on the whole. In this study, we investigated the effect of vegetation type and associated site fertility on the soil C density and evaluated the importance of deep soil layers in respect of the total stock of C in the soil at coniferous forest sites in southern Finland.

At the studied forest types the mean amount of organic C per unit of surface area in the organic horizon plus 1 m thick mineral soil layer ranged from 5.8 kg/m^2 to 9.6 kg/m^2. These C densities are lower than the mean value 11.6 kg/m^2 used by Post et al. (1982) for 1 m deep soil layer in moist boreal forests in their study of the C reserves in soils worldwide. However, bearing in mind the large variation in the density, a standard deviation of 8.2 kg/m^2 for the 222 profiles studied by Post et al. (1982), our results fit well within their range.

The soil C density varied considerably also within our study area; the largest difference between the study sites was three-fold. Forest type, however, explained part of this variation; at the most fertile OMT sites the C density was, on average, 1.7 times the density at the least fertile CT sites. We suggest that site fertility, and the associated variation in vegetation types and productivity, are causes for the large variation in the soil C density within the boreal zone. On the other hand, the C density did not differ between sub- and supra-aquatic sites or between sites on till and sorted parent material.

Accuracy of estimates of soil C reserves for a given region within the boreal zone is certainly impaired by the large variability in the C density, especially when the estimates are made by extrapolating mean C density over the area in question. More accurate estimates could most likely be made by dividing the region into more homogenous subgroups and using then different C densities for these subgroups. Recently, in the USA, Davidson and Lefebvre (1993) compared estimates of soil C reserves calculated by extrapolating a mean C density over the state of Maine to estimates made by stratifying the state according to soil maps and using different C densities for the different strata. They ended up with estimates that differed by 49%. Because the soil C density varied with vegetation type within our study area, classification of sites according to their forest type, reflecting their fertility, could provide a useful means for the classification in Finland and perhaps elsewhere.

Considerable quantities of organic C were found in soil layers deeper than 0.5 m and the amount increased, both in absolute and relative terms, with site fertility. Therefore, if only surface soil layers are taken into account when estimating C reserves in these soils, the largest underestimation occurs for fertile sites. Even the layer between the depth of 1 m and the ground water level (2.4–4.6 m) contained significant quantities of organic C. In fact, these layers contained about as much C as the organic soil horizon. The considerable quantity was due to the large mass of the soil layer despite of the low volumetric C density in the material itself.

The importance of the deep layers to cycling of C in soil needs further study. It is, however, most likely that the C has accumulated in the deep layers after the latest glaciation. The deep layer samples were taken from sorted deposits, where the parent material has been derived from bedrock and pre-glacial deposits by the most recent glacier and sorted then by glaciofluvial action. For this reason, the material is thought to be free of pre-glacial organic C. In addition to the flow from the soil layers above, the C seems to originate, at least to some extent, from direct input to the deep layers by trees, because we have found living roots of trees even at the depth of 3 m in the study area. Most of the C compounds accumulated in the deep layers are most likely extremely resistant to decomposition. Therefore, even slow input to these layers may lead to an increasing stock, which may be significant when considering the C balance of these ecosystems in a long time scale.

At the least fertile sites 56% of the total stock of C was found in soil organic matter, whereas at the more fertile sites this proportion was about 45%. These percentages slightly overestimate the proportion in soil organic matter, because C in fine roots of trees and surface vegetation is omitted from the total amount. However, we assume the error is quite small, less than 10% in the vegetation C (Mälkönen 1975; Havas & Kubin 1983), and, therefore, does not alter the general pattern that at the least fertile sites the soil organic matter contained a little more and at the more fertile sites a little less C than the phytomass.

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