

Pine Forest Floor Carbon Accumulation in Response to N and PK Additions: Bomb ^{14}C Modelling and Respiration Studies

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ABSTRACT

The addition of nitrogen via deposition alters the carbon balance of temperate forest ecosystems by affecting both production and decomposition rates. The effects of 20 years of nitrogen (N) and phosphorus and potassium (PK) additions were studied in a 40-year-old pine stand in northern Sweden. Carbon fluxes of the forest floor were reconstructed using a combination of data on soil ^{14}C , tree growth, and litter decomposition. N-only additions caused an increase in needle litterfall, whereas both N and PK additions reduced long-term decomposition rates. Soil respiration measurements showed a 40% reduction in soil respiration for treated compared to control plots. The average age of forest floor carbon was 17 years. Predictions of future soil carbon storage indicate an increase of around 100% in the next 100 years for the N plots and 200% for the NPK plots. As much as 70% of the increase in

soil carbon was attributed to the decreased decomposition rate, whereas only 20% was attributable to increased litter production. A reduction in decomposition was observed at a rate of N addition of 30 kg C ha⁻¹ y⁻¹, which is not an uncommon rate of N deposition in central Europe. A model based on the continuous-quality decomposition theory was applied to interpret decomposer and substrate parameters. The most likely explanations for the decreased decomposition rate were a fertilizer-induced increase in decomposer efficiency (production-to-assimilation ratio), a more rapid rate of decrease in litter quality, and a decrease in decomposer basic growth rate.

Key words: carbon accumulation; decomposition rate; decomposition theory; forest fertilization; forest floor model; nitrogen deposition; soil respiration.

INTRODUCTION

It has been suggested that the soils of large areas of coniferous forests of the Northern Hemisphere act as a carbon sink (see, for example, Valentini and others 2000; White and others 2000). Environmental changes are likely to affect this process because the forest floor is the part of the soil that is most

active and responsive to environmental changes (Townsend and others 1995). The existence and magnitude of the net carbon uptake of boreal forests depends on a delicate balance between ecosystem production and carbon loss (Valentini and others 2000), which occurs mainly through microbial and root respiration (Högberg and others 2001). Production and respiration both depend on nutrient availability, particularly the availability of nitrogen.

Nitrogen (N) modifies organic matter decomposition, often reducing the rates of decay at later stages (Berg 1993, 1991), mainly through effects on

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the decomposer community (Ågren and others 2001). As N deposition to forests continues, N effects on the carbon balance are likely to become increasingly important. However, the potential effect of N-induced changes in decomposition and litter inputs on the carbon balance of a boreal forest soil is still uncertain.

Due to the peak in atmospheric ^{14}C concentrations caused by nuclear testing in the 1950s and 1960s, it is possible to trace recent carbon in organic soil layers. Combining this information with data on litter production and decomposition, carbon flows can be estimated using budget models. Models for this purpose usually rely on assumptions of a steady state and homogenous pools (for example, see Harrison and others 2000). However, non-steady-state carbon flows and N availability may require a different model—that is, a model that can account for heterogeneity of the processes and the effects of nutrient additions. Failure to account for the heterogeneity of soil organic matter could result in erroneous estimations of soil carbon storage responses to environmental changes (Trumbore 2000). The nutrient effects on long-term decomposition need especially careful examination for analyses beyond simple empirical extrapolations of short-term data.

One feasible way to address these questions is to combine long-term experimental data on carbon inputs with a theory that can adequately account for the effects of nutrient additions. From the Norrliden site in northern Sweden there are extensive data sets on soil carbon and tree development (Holmen and others 1976; Tamm and others 1999), as well as decomposition and respiration studies at different levels of NPK additions. Furthermore, measurements of ^{14}C of different horizons in the forest floor provide a unique opportunity to study carbon turnover.

Ågren and Bosatta have developed a decomposition theory that explains the effects of nutrients on litter decomposition (Ågren and Bosatta 1998; Ågren and others 2001). In this paper, we combine their theory with estimates of litter quality and temporal distributions of litter carbon and ^{14}C inputs in a non-steady-state model of forest floor carbon dynamics. Our aim was to reconstruct the litter production and decomposition during stand development to evaluate the effect of nutrient additions on these processes. Using the theory formulated by Ågren and Bosatta (1998), the effects on decomposition were interpreted in terms of decomposer and substrate properties. The carbon fluxes were extrapolated to predict potential future carbon storage. In addition to the modeling, field soil res-

Table 1. Summary of Experimental Treatments

Treatment	N	P K	B
C	—	—	2.5 (1980)
N1	60 (1971–73)	—	=C
N2	2.N1	—	=C
N3	3.N1 ^a	—	=C
		P 40 + K 76 (every 3rd year 1971–97)	
PK	—	—	=C
N1PK	= N1	= PK	=C
N2PK	= N2	= PK	=C
N3PK	= N3 ^a	= PK ^a	=C

^aThe N3 and N3PK treatments were discontinued in 1990. N (urea and ammonium nitrate), PK (triple super-phosphate + potassium chloride), and boron (B) additions are given in kg element ha⁻¹ y⁻¹. Years of fertilizer application are shown in parentheses. There are six replicate plots for treatments C and N1–N3, and four replicate plots for PK and N1PK–N3PK.

piration was measured to further assess the effects on soil respiration and to compare them with the model predictions.

SITE CHARACTERISTICS AND NUTRIENT TREATMENTS

The Norrliden site is located in northern Sweden and has the following geographical and climatic characteristics: latitude N 64°21', longitude E 19°45', altitude 260–275 m, mean annual temperature 1.2°C, mean annual precipitation 595 mm, annual N deposition 2.5–5 kg ha⁻¹ y⁻¹. The soil is classified as till with a distinctly developed iron podzol (Holmen and others 1976).

Before 1953, the whole area was an old-growth stand dominated by Norway spruce (*Picea abies* Karst). The stand was clear-cut and the ground vegetation removed by prescribed burning. Thereafter, the area was planted in 1953 with 2-year-old Scots pines (*Pinus sylvestris* L.). Ground vegetation was mainly dwarf shrubs (*Vaccinium* spp.), grass (*Deschampsia flexuosa*), and mosses (mainly *Pleurozium schreberi*). In 1971, the nutrient treatments with N (in the form of urea and ammonium nitrate) and PK (triple superphosphate and potassium chloride) fertilizer started. The stand was divided into 30 × 30 m plots (20 × 20 m net plots used for sampling) where different amounts of nutrients were applied (Table 1). The stand was thinned in 1984 and 1989. Detailed descriptions of the experiments and the site are given in Tamm and others (1999) and Holmen and others (1976).

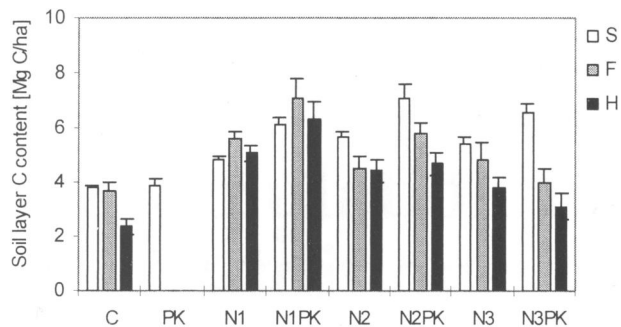


Figure 1. Measured carbon amounts in the S, F, and H layers. Bars show standard errors. Number of plots per treatment are $n = 6$ (treatments: C, N1, N2, N3) or $n = 4$ (treatments: PK, N1PK, N2PK, N3PK). Treatments in Table 1.

EXPERIMENTAL MEASUREMENTS: METHODS AND BASIC RESULTS

Soil Carbon Measurements

In 1992, in six (N treatments) or four (NPK treatments) replicate plots per treatment, 10 soil cores per plot of the organic horizon were sampled and divided into S, F, and H layers. The S layer included litter and living moss and lichens. Carbon content was measured for each layer in each core. For ^{14}C analysis, the cores for each treatment (40–60 cores per treatment) and layer were pooled into one homogenized sample, which was analyzed using accelerator mass spectrometry (AMS). ^{14}C is expressed as percent of a standard concentration (% modern) of prebomb levels. In all samples, coarse material, such as branches and cones, which often belonged to several horizons, was removed. ^{13}C was measured along with the ^{14}C and used to correct the ^{14}C values for isotopic discrimination after carbon fixation based on the average value of $\delta^{13}\text{C} = -25.95$ for new needles in Norrliden during the period 1970–94 (P. Högberg unpublished). Measured amounts of forest floor carbon and ^{14}C enrichment are shown in Figures 1 and 2. Owing to the failure of AMS analysis of samples from the PK plot, this treatment was not included in the modeling.

Field Respiration Measurements

Soil respiration measurements were made on three different occasions, 20 and 21 August 1996, 4 and 5 September 1997, and 2 and 3 September 1999. The average temperatures in the mor layer were 11.8, 13.8, and 11°C, respectively, at the time of the three different samplings. Twelve of the $30 \times 30 \text{ m}^2$ plots were studied (including the C-, PK-, N1-, and N2-

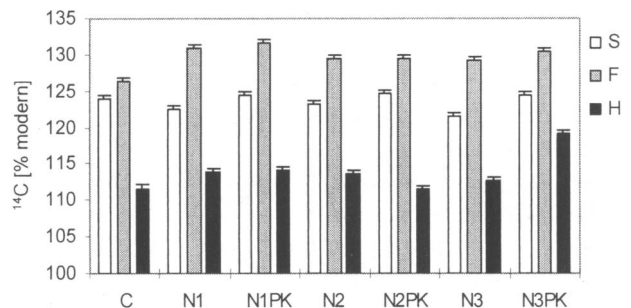


Figure 2. Measured ^{14}C enrichment in the S, F, and H layers. Composite samples of 40–60 soil cores per treatment. Bars show precision of measurements = $\pm 0.5\%$ modern. Treatments in Table 1.

treated ones, but excluding the N3 treatments). The respiration rate from each $30 \times 30 \text{ m}^2$ plot was determined as the mean respiration of four 243-mm diameter plots that were randomly laid out within the central 10 m^2 of each of the $30 \times 30 \text{ m}$ plots. The distance between each of the 243-mm diameter plots was 1–2 m. Basal soil respiration and substrate-induced respiration measurements (SIR) (respiration rate 1 h after addition of 300 ml sucrose solution to the mor layer; concentration 33 mg ml^{-1}) were made from each 243-mm diameter plot in situ as described previously (Högberg and Ekblad 1996; Ekblad and Högberg 2000). Each 243-mm diameter plot was used only once for basal respiration and SIR determinations. The SIR technique gives a measure of microbial biomass (Anderson and Domsch 1978) and has usually been applied under laboratory conditions. Our assumption in the present study was that the increase in respiration following sucrose addition corresponds to the nonsymbiotic microbial biomass in the soil and that roots and/or mycorrhizal fungi do not respire the added substrate or increase their respiration of endogenous carbon in response to the sucrose addition. There are several direct and indirect lines of evidence supporting this assumption (Ekblad and Nordgren 2002).

FOREST FLOOR MODEL

Model Structure

Our aim was to make a budget model that balances measured carbon and ^{14}C content in the organic soil layers (Figures 1 and 2) with past litter inputs and decomposition. The site has previously been extensively studied, including measurements of stand development (Tamm and others 1999) and litter decomposition (Berg and others 1991). These detailed

input data made it possible to limit degrees of freedom in the model to a few unknown carbon fluxes (ground vegetation litter production, root litter production, and long-term decomposition) and to separate effects on these carbon fluxes. Estimated carbon fluxes could then be extrapolated to predict potential future carbon storage.

A key assumption in the model is the representation of soil as a series of consecutively deposited cohorts of litter with no vertical mixing, an assumption applicable in this soil type, where there is relatively little activity of burrowing soil animals (for example, earthworms). The soil layers (S, F, and H) in our model are not represented by pools; instead, they represent points of measurement along a continuous (yearly cohorts) gradient of increasingly decomposed organic material. This contrasts to many other models, where the soil carbon is represented by completely mixed pools (see for example, Harrison and others 2000).

Litter input to the S layer comes from pines and from ground vegetation. In the F and H layers, there is also an influx of root litter, which is assumed to be distributed in the soil profile, decreasing exponentially with depth. The model equations describe carbon and ¹⁴C of each layer as sums (or integrals) of yearly litter cohorts, where the amount of C in each cohort is determined by the amount deposited to the soil and its stage of decomposition (Figure 3). Each type of litter (needle, root, ground vegetation) has separate input and decomposition functions. The litter cohort ages at the divisions between layers (S, F, and H) result from the fitting of the model to the measured data. Litter cohort age in Figure 3 is defined as the age of the remaining aboveground litter content in each cohort, although each cohort in the F and H layer contain root material of different ages. The model has no reference to actual soil depth (in cm), and the only difference between layers—assumed a priori—is that roots enter only the F and H layers.

The model is represented by a system of equations for the amounts of carbon and ¹⁴C enrichment in each of the S, F, and H layers (C and ¹⁴C for three layers in seven treatments = 42 equations). The parameters determined by fitting the model to measured soil C and ¹⁴C are, for each treatment, ground vegetation litter production (assumed to be equal for all treatments), root litter production, long-term decomposition, and age spans of soil layer material (S, F, and H).

A simplified mathematical representation of a model equation of one soil layer is given in Eqs. (1) and (2). The decomposition functions of the model

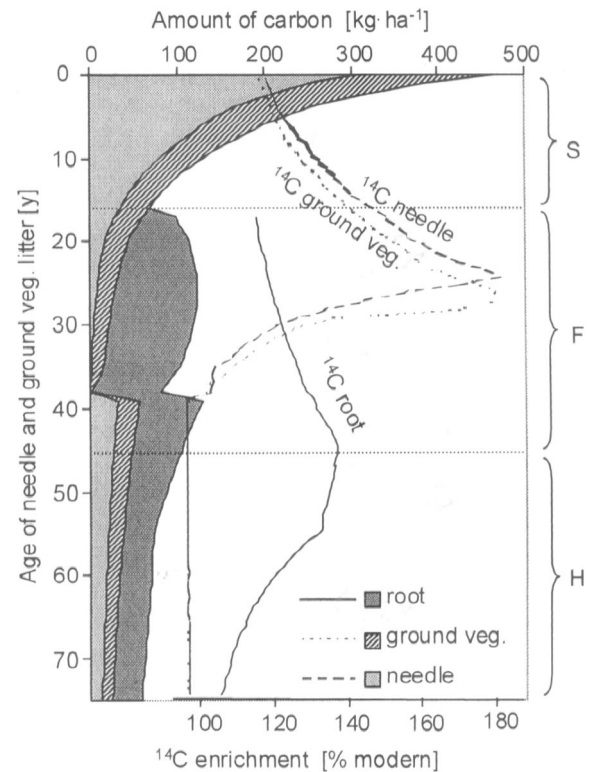


Figure 3. Modeled amount of carbon (shaded areas) and ¹⁴C enrichment (lines) in each cohort of litter input versus the age of its needle litter content. The C and ¹⁴C for root material is a result of yearly inclusions of new roots in each litter cohort. C and ¹⁴C content of each layer (S, F, and H) are obtained by integration of the curves over the cohort ages spanned by each layer. Ages at layer divisions are obtained by fitting of the model to measured soil layer C and ¹⁴C. The abrupt change in remaining litter C amounts at age = 39 marks the clear-felling and burning of the stand. Figure based on control plot model results (see Table 4 and Figure 5).

and the litter input data are described in detail below.

$$C = \sum_{\text{needle root ground veg.}} \int_{\text{age}_{\text{layer bottom}}}^{\text{age}_{\text{layer top}}} C_{\text{litterfall}}(a) \cdot g(a) da \tag{1}$$

$$E_{14c} = \frac{1}{C} \sum_{\text{needle root ground veg.}} \int_{\text{age}_{\text{layer bottom}}}^{\text{age}_{\text{layer top}}} C_{\text{litterfall}}(a) \cdot {}^{14}C_{\text{litterfall}}(a) \cdot g(a) da \tag{2}$$

where C = amount of carbon in a soil layer (S, F, or H) consisting of litter cohort ages between age_{layer top} and age_{layer bottom}; E_{14c} = ¹⁴C enrichment of a soil

layer; $C_{\text{litterfall}}(a)$ = amount of carbon in litter deposited at time a ago; $^{14}C_{\text{litterfall}}(a)$ = ^{14}C enrichment in litter deposited at time a ago; and $g(a)$ = decomposition function describing the remaining fraction of litter carbon after a time a of decay.

Decomposition Submodel

A detailed decomposition submodel was needed to include and interpret the effects of fertilization on decomposition. A model based on separate properties of decomposers and substrate and the interaction between them has been developed by Ågren and Bosatta (1998). In this theory, carbon from the substrate is respired or incorporated in decomposer biomass, and dead decomposer biomass is returned to the substrate. Substrate carbon is characterized by its quality, which is a measure of how easily it can be consumed by the decomposers. When passing from decomposers to substrate, the quality of the remaining carbon is decreased. From this theory, an equation for the change in remaining carbon can be derived (Eq. [3]). A parameter of initial leaching (L) was added to the model because for some litters, a significant fraction of newly deposited litter is lost through leaching (Nykqvist 1963; Bogatyrev and others 1983).

$$g(t) = L \cdot (1 + \beta \eta f_c u_0 q_0^{\beta} t)^{\frac{e_0 - 1}{\eta \beta e_0}} \quad (3)$$

or by aggregating parameters,

$$g(t) = L \cdot (1 + P_1 t)^{-P_2} \quad (4)$$

where q_0 = initial quality of the substrate; e_0 = efficiency—that is, production to assimilation ratio of the decomposers; u_0 = growth rate parameter of decomposers; f_c = fraction of carbon in decomposer biomass; η = change in quality of carbon passing through the decomposer biomass; β = interaction between quality and decomposer growth; L = fraction remaining after initial leaching; and P_1 , P_2 = aggregated parameters.

In Eq. (3), all parameters except q_0 and L are associated with the decomposers. This separation of decomposer and substrate parameters makes it possible to separate effects of decomposers and substrate. The decomposer parameters are affected only by the treatment of the plot and not by litter substrate (for example, mosses, dwarf shrubs, pine needles, or roots).

Because it is not necessary to estimate all parameters of the decomposition model separately, the parameters have been aggregated in Eq. (4). The same P_2 (Eq. [4]) is used for all litters in the same treatment (or plot) because P_2 is only dependent on

decomposer properties. Different litters are defined by different initial qualities (q_0) and different initial leaching (L). Relative q_0 and L of each litter type as well as initial decomposition rates ($P_1 \cdot P_2$) were determined from litterbag decomposition studies (see below and Table 2), while P_2 for each treatment is an unknown parameter fitted by the forest floor model. P_2 largely determines the long-term decomposition—that is, the proportion of remaining carbon after many decades.

Initial decomposition parameter estimations. Although long-term decomposition, regulated by P_2 (Eq. [4]), is estimated in the forest floor model, initial decomposition rates ($P_1 \cdot P_2$) and relative qualities of different litters are input parameters that need to be determined beforehand. Needle litter decomposition parameters were estimated from litterbag studies from the Norrliden site (Berg and others 1991). Decomposition parameters of litters other than pine needles (fine roots, moss, and dwarf shrubs) were calculated using data from other sites (Berg 1984a, 1984b; Johansson 1993), and parameter values were determined relative to those of local pine needles (Table 2). For a given site, decomposer parameters P_2 (Eq. [4]) was determined from local pine needle decomposition. This P_2 was then used for other litters at the same site, while substrate parameter (q_0) and initial leaching (L) were fitted to litterbag data. A nonlinear least-squares method was used to fit the model (Eqs. [3] and [4]) to the litterbag data, which had been corrected for local climatic variation (see Appendix).

The relative value of $q_0 \text{ substrate} / q_0 \text{ pine needle} = (P_1 \cdot P_2)_{\text{substrate}} / (P_1 \cdot P_2)_{\text{pine needle}}$ was used to translate the relative q_0 values for substrates measured in other sites to corresponding values for the same species in Norrliden. Because P_1 and P_2 are dependent (see Eqs. [3] and [4]), the product $P_1 \cdot P_2$ is used when relative values of substrate parameters (q_0) are calculated. This product also equals the initial decomposition rate.

Nutrient effects on initial decomposition. From Norrliden, there are litterbag experimental data where the same litter ("standard litter" originating from control plots) has been used in differently treated plots and where different litters (local litter originating from fertilized plots) have been used in its plot of origin (Berg and others 1991). This makes it possible to test the assumptions of separate effects of nutrient treatment and substrate on the decomposition function.

If the model describes the decomposition process, adequately, the following hypotheses about the model behavior should hold: (a) There is no difference in decomposer parameters (P_2) between de-

Table 2. Summary of Assumptions and Parameters of the Forest Floor Model

Process/Variable	Model Input Data and Basic Assumptions	Nutrient Treatment Effects a priori Assumptions	Model Output (Fitted Parameters)
Soil layer ages	—	—	S, F, and H -layer age spans for each treatment
Pine needles	Production calculated from basal area measurements, biomass allocation functions, and needle survivorship curves	Input based on separate measurements for all treatments. Needle life span dependent on treatment.	—
Ground vegetation	Includes dwarf shrubs, grass, and mosses with different life spans	No mosses on fertilized plots. No treatment effect on total ground vegetation production.	Yearly production common to all treatments
Roots	Exponentially decreasing with depth. Temporally proportional to needle production in each treatment (no relation assumed between treatments).	—	Production estimated for each treatment
¹⁴ C	Litter ¹⁴ C concentrations calculated from needle and atmospheric measurements and seasonal growth pattern	—	—
Decomposition	Relative substrate quality and initial leaching for all litters calculated from litterbag experiments	Fixed initial decomposition rates dependent on N level: C, N1, and N2-N3	Decomposer parameters (regulating long-term decomposition) for each treatment

composition curves of different substrates decomposing in the same plot, and (b) there are differences in decomposer parameters but no difference in the substrate parameter q_0 where the same substrate has been used in different treatments. These hypotheses were tested using analysis of variance (ANOVA).

Litter Inputs

Pine needles. From tree basal area data of the stand (Gay and others 1994; Tamm and others 1999), needle biomass for every year from 1953 to 1993 was estimated using empirical biomass functions for each treatment (Tamm and others 1999). The amount and age distribution of the needle litterfall of each year were calculated using needle maximum life span (5 years for fertilized plots, 6 years for control plots), needle growth (10% per year linear weight increase), and needle survivorship curves (Flower-Ellis and others 1994; Jalkanen and others 1995; Tamm and others 1999). This calculation also took into account a 20% resorption of needle carbon before abscission (J. G. K. Flower-Ellis personal communication).

Ground vegetation. Ground vegetation was mainly dwarf shrubs (*Vaccinium* spp.), grass (*Deschampsia flexuosa*), and mosses (mainly *Pleurozium schreberi*). The distribution of species was different depending on treatment. Mosses disappeared and grass cover increased on fertilized plots, whereas dwarf shrubs were dominant on control plots. Moss production was assumed to be one-third of total ground vegetation production in controls (C. O. Tamm personal communication). Despite changes in species composition, a field estimation of ground vegetation production done in 1985 showed similar total production on the N2PK fertilized plot and the control (C. O. Tamm personal communication). Ground vegetation has also been studied by Johansson and others (1999).

Production of ground vegetation was assumed to increase linearly during the 4 years after the burning of the site in 1953 and then remain at a constant level. This level was determined as one of the fitted parameters of the model.

Roots. Because coarse roots were removed from the soil samples, only fine-root production was in-

cluded in the model. The temporal development of fine-root litter production was assumed to be proportional to needle production development within each treatment. The constants of proportionality—that is, the absolute amounts of root production—were estimated independently for each treatment in the model. The vertical distribution of root input was assumed to be an exponentially decreasing function of soil cohort age ($r = e^{-0.07 \text{ soil cohort age}}$). Fine-root life span was assumed to be 1-year (Persson 1980). However, recent studies have shown that fine-root life span is variable and may be longer than previously estimated (Gaudinski and others 2001; J. Gaudinski personal communication). The effect of longer fine-root life span was investigated using a 3-year fine-root life span in the model.

¹⁴C input. A ¹⁴C enrichment input curve for carbon fixation was derived from measurements of ¹⁴C in new local pine needles and from atmospheric measurements (Nydal and Lövseth 1983; Olsson 1993) combined with the expected seasonal growth pattern (Bergh and others 1998). This curve was then combined with the data on needle growth, needle C resorption, and needle life span to obtain the ¹⁴C enrichment of the litterfall of each year. This resulted in a litterfall ¹⁴C enrichment curve, which was shifted a few years and somewhat flattened out compared to the atmospheric curve. Fine roots were assumed to be formed from carbon fixed in the previous year (Gaudinski and others 2001). In Figure 3, the soil ¹⁴C curves of needle litter and ground vegetation litter correspond to their respective litterfall ¹⁴C curves, whereas ¹⁴C enrichment of root material is a result of the continuous inclusion of new C in each soil age cohort. The ¹⁴C data were corrected for radioactive decay between carbon fixation and soil sampling.

Pre-1953 conditions. Because the forest floor contains material deposited before 1953, estimates of litter inputs before the current stand was planted were needed. Before 1953, the whole area was an old-growth spruce-dominated stand (Holmen and others 1976) with no records of litter production and species composition. An estimate of 800 kg C ha⁻¹ y⁻¹ needle litter production and a ground vegetation production of 350 kg C ha⁻¹ y⁻¹ with a moss fraction of one-third and two-thirds dwarf shrubs were used for model input.

The lack of information about the vegetation history before 1953 is not as serious as might be expected. First, because decomposition progresses very rapidly in the beginning, the remaining fraction of carbon deposited before 1953 is very small and will not have much influence on calculated

properties. Second, because all plots were alike before the experiments started in 1971, the earlier history should not have a great effect on relative differences between treatments.

Calculation Method

Using the predetermined (fixed) input parameters and unknown (fitted) output parameters (summarized in Table 2), the model equation system (compare Eqs. [1] and [2]) was fitted to the measured C and ¹⁴C of each layer and treatment. For this, we used MathCad 8 mathematical software (MathSoft Engineering & Education, Inc., Cambridge, MA), which uses a conjugate gradient optimization method. The results obtained for the past carbon fluxes were also extrapolated forward in time to assess potential impact of nutrient additions on future forest floor carbon accumulation. Because ¹⁴C measurements were made on one composite sample for each treatment and layer, variation could be calculated based only on the variation in carbon amounts between replicate plots. The effects of uncertainty in ¹⁴C measurements as well as estimates of root life span and root decomposition rate were evaluated in a sensitivity analysis.

RESULTS

Basic Soil Measurements

From the soil C measurements (Figure 1), it is clear that carbon storage has increased in response to the nutrient additions. Possible reasons for this are increased litter production and/or reduced decomposition. The ¹⁴C enrichment values are highest in the F layer, which indicates that this layer contains much of the material formed during the atmospheric ¹⁴C bomb peak in the 1960s. However, inferring treatment effects directly from C and ¹⁴C values is not straightforward or even possible. The age span of material in the layers of different treatments is not necessarily similar, and the root production in the F and H layers is a complicating factor (compare Figure 3). These factors can only be untangled by modeling.

Initial Decomposition Rates: Litterbag Studies

The ANOVA analysis of parameters (Eq. [4]) for standard litter placed in plots with different treatments showed significant differences in both P_1 , P_2 and $P_1 \cdot P_2$ (initial decomposition rate) between fertilized and control plots ($P < 0.008$).

The effects of different substrates placed in the same plot showed no significant differences in the

Table 3. Estimated Relative Litter Initial Qualities (q_0), Initial Leaching (L), and Initial Decomposition Rates

Litter	Relative Initial Quality (q_0 litter/ q_0 pine needle)	Initial Leaching ($1 - L$)	Initial Decomposition Rates in Different Treatments (% C- γ^{-1})		
			1(I-L)-(%)	C	N1PK
Pine needles	1.00	0	28	39	42
Dwarf shrubs, Grass	1.02	28.3	28	40	43
Mosses	0.42	4.1	12	16	18
Roots	0.31	16.8	9	12	13

Initial qualities are given relative to that of pine needles.
 q_0 and L refer to Eqs. (3) and (4). Treatments in Table 1

decomposer parameters represented by P_2 between standard and fertilized local litter ($P = 0.18-0.84$). Given no difference in P_2 , there were differences in P_1 —that is, q_0 , between litters originating from different treatments ($P < 0.022$).

We conclude that this analysis supports the assumptions of separate fertilization effects on decomposer community and substrate, described by changes in their respective parameters. P_2 is only dependent on decomposer properties, whereas P_1 depends both on substrate and decomposer properties. However, given the short time span of the litterbag studies (4–5 years), the fitting of the forest floor model provides more confident estimates of the long-term decomposition rate than the litterbag results.

Estimated initial quality, initial leaching, and initial decomposition rates for different litters are shown in Table 3.

Modeled Nutrient Effects on Past Litter Production and Long-term Decomposition

The model fit to measured data is shown in Figure 4. Table 4 summarizes the soil layer ages and decomposition properties derived from the model. The mean ages of soil layers are calculated through integration over all ages of material included in each layer. Average ages for S, F, H, and the whole forest floor are 5.2, 13, 38.4, and 17.1 years, respectively. However, inferring treatment effects from mean layer ages is not meaningful because layers are not separate entities and the age span and composition of layer material differ between treatments (results not shown).

Estimated needle litter production was based on extensive measurements by Tamm and others 1999, which showed that N level had significant

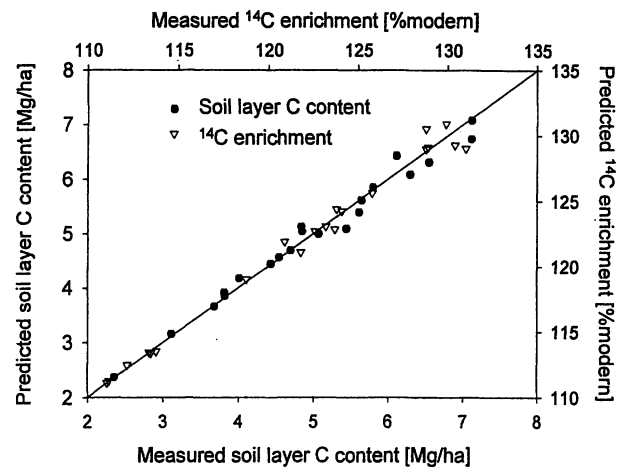


Figure 4. Measured and predicted forest floor carbon amounts and ^{14}C enrichment for all treatments and all soil layers.

effects on stemwood production and its relation to needle biomass. As expected, our estimated needle litter production matches the results for stemwood production and needle biomass, showing an increase on fertilized treatments. The root-above ground litter production ratio decreased with increasing nutrient addition. Decomposition was radically changed by the treatments. The results indicate that both N and PK additions had negative effects. Although the initial decomposition rate increased (Table 3), a reduction in the long-term decomposition rate is the main consequence of nutrient additions. In agreement with reduced long-term decomposition rates, modeled percentage forest floor carbon respired per year was also reduced in the fertilized treatments compared to the control (Table 4).

Table 4. Forest Floor Model Results

Treatment	Mean Age of Organic Soil Layers (y) ^a				Decomposition Pars ^b		Decomposition 50 y ^c (% C)	Respiration ^d %C y
	S	F	H	S+F+H	P ₁	P ₂		
C	5.5 (0.39)	13.7 (0.96)	42.0 (0.46)	17.3 (0.57)	0.19	1.48 (0.040)	96.9 (0.2)	7.6 (0.21)
N1	3.9 (0.10)	11.1 (0.36)	37.7 (0.45)	17.6 (0.42)	0.55	0.70 (0.014)	90.5 (0.3)	6.7 (0.11)
N1PK	5.4 (0.14)	11.6 (0.49)	38.4 (0.98)	18.3 (1.16)	0.82	0.47 (0.054)	82.4 (2.7)	5.1 (0.41)
N2	5.3 (0.07)	11.9 (0.46)	37.8 (0.71)	17.2 (0.88)	0.67	0.62 (0.050)	88.9 (1.4)	6.6 (0.36)
N2PK	6.0 (0.09)	14.6 (0.91)	46.5 (1.09)	19.6 (0.66)	1.08	0.39 (0.066)	79.1 (3.9)	4.7 (0.56)
N3	4.1 (0.08)	13.9 (0.67)	39.4 (0.67)	17.0 (0.90)	0.68	0.62 (0.046)	89.2 (1.3)	6.5 (0.31)
N3PK	5.9 (0.07)	14 (0.97)	26.7 (0.37)	13.1 (0.70)	0.9	0.47 (0.034)	83.8 (1.4)	5.4 (0.25)
mean	5.2 (0.13)	13.0 (0.69)	38.4 (0.68)	17.1 (0.76)			96.9 (1.6)	6.1 (0.32)

Standard errors (based on carbon amounts in replicate plots) given in parentheses.

Number of plots per treatment are $n = 6$ (treatments: C, N1, N2, N3) or $n = 4$ (treatments: N1PK, N2PK, N3PK)

^aAges are integrated values of all material in each layer.

^bParameters of Eq. (4) for pine needles

^cThe fraction of pine needle litter C lost after 50 years

^dRespiration is % forest floor carbon mineralized 1993

Treatments in Table 1.

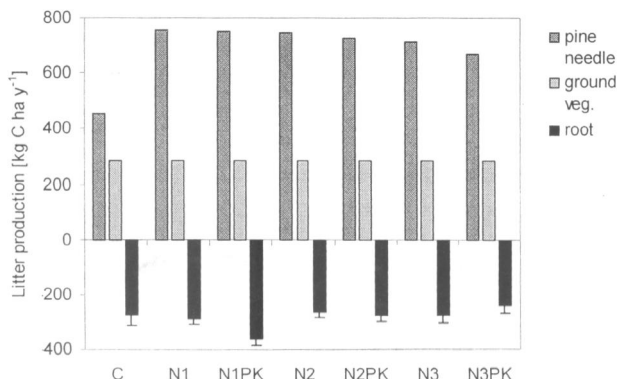


Figure 5. Pine needle, ground vegetation, and fine-root litter production for all treatments. Needle production is average yearly litterfall 1983–93; ground vegetation and root litter production is for 1993. Bars show standard errors for root production based on carbon amounts in replicate plots. Number of plots per treatment are $n = 6$ (treatments: C, N1, N2, N3) or $n = 4$ (treatments: N1PK, N2PK, N3PK). Treatments in Table 1.

Prediction of Future Forest Floor Carbon Accumulation

Predictions of future forest floor carbon are highly dependent on future litter inputs. The estimates used were based on a conservative extrapolation of calculated litter inputs (Figure 5). For needle litter inputs, the values used were (in $\text{kg C ha}^{-1} \text{y}^{-1}$) 500 for C; 700 for N1, N1PK, N2, and N2PK; and 600 for N3 and N3PK. Root and ground vegetation inputs were the same as those calculated for 1993 (Figure 5). Based on these litter inputs, soil carbon amounts

of 1993, and estimated decomposition parameters for the different treatments (Table 4), the model was extrapolated 100 years forward in time (122 years of nutrient effects in total).

The forest floor carbon future predictions showed large differences in carbon accumulation between treatments with a potential increase in forest floor carbon of about 100%–300% (10,000–30,000 kg/ha) compared to the control under the present conditions at the Norrliden site (Figure 6).

The predicted changes in soil carbon storage are consequences of nutrient effects on both decomposition and litter production. These two effects were separated by including each effect exclusively in separate model runs. The relative effects of decomposition and production were then calculated from differences in predicted carbon storage between control and treatments (Figure 6). Averaging all treatments, the nutrient effect on decomposition and production explained 69% and 21%, respectively, of the increase in soil carbon. The fraction of soil carbon accumulation that could be attributed to reduced decomposition increased with increasing nutrient addition.

Field Respiration Measurements

Nutrient additions reduced the basal respiration rate on average to only 60% of the control (mean for all treatments and all years). The N2 and N2PK treatments showed the lowest basal respiration rates compared to the control; overall, the respiration rates in these two treatments were reduced to 50%–35% of that of the control (Figure 7A). In-

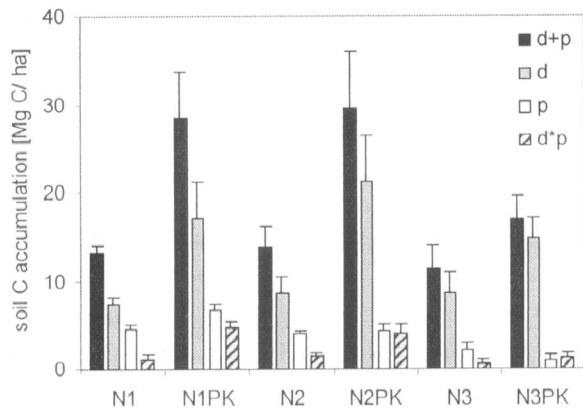


Figure 6. Effects of decomposition and production changes on organic (S+F+H layers) soil carbon. Carbon storage is extrapolated 100 years forward in time (since 1993) using separated effects of reduced decomposition and increased production. Treatment effects: d, decomposition effect; p, litter production effect; d*p, interaction effect. Soil carbon in the control plot was 12,490 kg C ha⁻¹. Bars show standard errors based on carbon amounts in replicate plots. Number of plots per treatment are $n = 6$ (treatments: C, N1, N2, N3) or $n = 4$ (treatments: N1PK, N2PK, N3PK). Treatments in Table 1.

deed, multiple regression analysis showed that both N and P had significant negative effects on basal respiration [statistically significant model Y (basal respiration/basal respiration for control) = 0.909 ± 0.047 (SE) - N $\cdot 0.187 \pm 0.031$ ($P < 0.001$) - PK $\cdot 0.132 \pm 0.051$ ($P = 0.014$) mg C m⁻² h⁻¹; $R^2_{adj} = 0.55$; $P < 0.001$ for the model; $n = 35$; data from all 3 years together].

The SIR increase 1 h after sucrose addition varied greatly between treatments and years (Figure 7B). However, multiple regression analysis showed that PK had a negative effect on the respiration increase [statistically significant model Y (respiration increase) = 58.8 ± 5.6 - PK $\cdot 28.4 \pm 8.1$ mg C m⁻² h⁻¹; $P = 0.001$; $R^2_{adj} = 0.25$; $n = 35$], hence suggesting a negative effect on soil microbial biomass.

Sensitivity Analysis

The estimate of fine-root litter initial quality was assumed to be relatively less confident compared to other parameter estimates because of the small amount of measured data available and the high variability in size and distribution of roots. Because the measured root decomposition rate and initial litter quality (q_0) was lower than expected (Table 2), the effect of increasing root litter quality was investigated. In addition, the effects of increasing root life span from 1 to 3 years were evaluated.

Changing the root initial quality to the same as

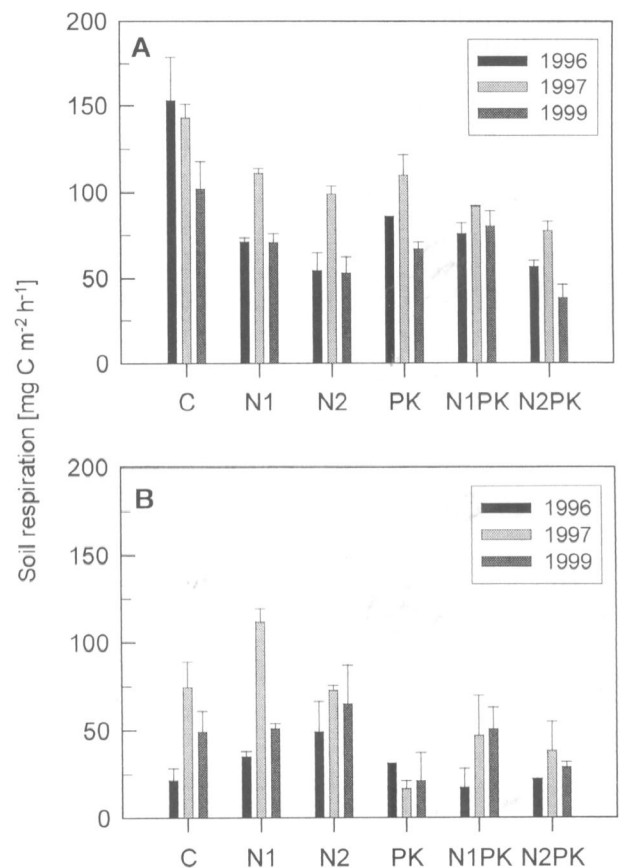


Figure 7. Measured field respiration rates. A Basal respiration. B SIR (increase in respiration after sucrose addition). Bars show \pm standard error for $n = 2$ plots per treatment. Treatments in Table 1.

for pine needles (60% increase in root initial decomposition rate) caused a slight compensatory increase in root production and a decrease (15%) in ground vegetation production. The effects on other results, such as long-term decomposition, were very small, resulting in almost no change in predictions of future carbon accumulation (Table 5). Thus, the prediction of long-term decomposition is not sensitive to initial litter quality and initial decomposition rate. Also, the effects of an increased root life span were modest, with only a slight increase in the long-term decomposition rate and a small reduction in nutrient effects on carbon accumulation.

The sensitivity to variation in ¹⁴C data was evaluated by randomly increasing or decreasing each measured ¹⁴C value by 1%—that is, 1.12%–1.35% modern, which is comparable to the difference between most of the treatments. This procedure was repeated for 10 model runs; the resulting coefficients of variation in selected results are shown in Table 6. Relative to the differences between treat-

Table 5. Change in Selected Results Caused by Increase in Root Life Span (from 1 to 3 years) and Root Litter Quality Increase to the Same as for Pine Needles

	Treatments ^a	Root prod ^b (kg C ha ⁻¹)	Decomp. 50 y ^c (%)	Soil C Acc. ^d (kg C ha ⁻¹)	C Acc from Decomp. Red ^e (%)
Original model	C	276	96.9		
	N	277	89.7	13,515	59
	NPK	318	80.8	29,020	66
Root lifespan increase	C	262	99.1		
	N	271	95.1	10,257	60
	NPK	312	89.3	23,462	72
Root decomposition Increase	C	481	95.2		
	N	380	87.1	16,030	54
	NPK	410	78.6	33,225	68

^aC = control, N = N1 and N2 combined, NPK = N1PK and N2PK combined treatments in Table 1.

^bFine-root production

^cFraction of carbon lost after 50 years of decomposition of pine needles

^dPredicted increase of soil C relative to control after 100 years

^e% soil C increase relative to control caused by decomposition rate reduction

Table 6. Sensitivity of Selected Results to Random Change in ¹⁴C Soil Enrichment Values by 1% (1.1%–1.3% Modern)

Treatments	Root Prod.	Decomp. 50 y	Soil C Acc.	% C Acc. from Decomp. Red.
C	7.7	3		
N	11.4	5.7	13.5	4.8
NPK	10.0	7.5	12.9	8.0

Columns as in Table 5

Values are coefficients of variation (%).

ments, root production is sensitive to ¹⁴C variation, whereas the sensitivity of the predictions of nutrient effects on carbon accumulation is low compared to the treatment differences. Thus, uncertainty in ¹⁴C measurements would result in uncertainty in estimates of root production and the long-term decomposition rate of single treatments, whereas the general pattern of carbon accumulation as a result of reduced decomposition in nutrient treatments would remain.

DISCUSSION

Alternative Models, Validity, and Limitations

There is always a question as to how many parameters and how much complexity should be included in a model to get the most useful results. In this

case, the minimum set of parameters needed to explain the observations satisfactorily was chosen. The introduction of additional degrees of freedom for treatment effects on ground vegetation litter input and root distribution did not produce significant improvements in the model fit to the data.

Because of the high cost, ¹⁴C was analyzed for one pooled sample per treatment and layer; thus, the presented SEs in the results are based on the variability between replicate plots in carbon amounts only. However, there are reasons to expect a low variation in ¹⁴C enrichment compared to variation in carbon amounts. Possible sources of variation in ¹⁴C values are differences in decomposition and proportions of different litter inputs (compare Figure 3). On the other hand, variation in the total amount of litter production should not affect the soil ¹⁴C values. Because the stand is very uniform (Tamm and others 1999) and the only tree species is pine, the replicate plots differ mainly in number of trees. Consequently, the main difference between replicate plots should be in total litter production, which affects amounts of soil carbon but not ¹⁴C enrichment. In a mixed natural stand of mainly *Pinus sylvestris* and *Picea abies* in Åheden in northern Sweden (Persson and others 2000b; Harrison and others 2000), the coefficient of variation in ¹⁴C in the L + F layer was 1% (A. F. Harrison personal communication), which is comparable to the variation introduced in our sensitivity analysis.

The sensitivity analysis (Table 6) shows that random changes in ¹⁴C comparable to the differences

between treatments do not refute the main conclusions of the original results. Small treatment differences in ^{14}C values combined with larger differences in carbon amounts are compatible with different carbon accumulation but similar soil ages of different treatments.

Alternative Models, Soil Pools, and Mean Residence Times

In addition to our model, a commonly used pool model (Harrison and others 2000) was tested. This model is based on assumptions of a steady state and homogenous soil carbon pools—in this case, represented by our organic soil layers (S, F, and H). Estimated soil layer ages and total carbon fluxes of this three-pool model were on average similar to the predictions by our model, but the ranking of treatments was different, with no clear relation to nutrient addition level. One reason for this is the concept of soil pools, which means that a continuous quality distribution of soil material must be approximated with a pool represented by a single mean residence time (MRT). This is especially problematic for the F and H layers, where new roots enter older decomposed material. Furthermore, to make treatments comparable would require very careful definition and sampling of the pools—for example, division of the F and H layers. These problems are largely avoided in our continuous model.

One serious problem of using the pool model with our data is that root litter input could not be included in the F and H soil layer due to its mathematical structure. When the approach followed by Harrison and others (2000) is used, roots are removed from the samples before analysis of ^{14}C , but this was not done for our samples.

The assumption of a steady state used in the pool model is not valid and the concept of MRT is not very useful in the investigated type of disturbed (fertilized) ecosystem. Because carbon is accumulating partly as a consequence of retarding late-stage decomposition, MRTs become very large and sensitive to asymptotic decomposition rates, which are uncertain.

Modeled Litter Production

Nutrient additions seem to have increased needle litter production on all treated plots, with relatively small differences between nutrient levels, indicating that above the lowest level of nutrient addition, other factors were limiting to litter production (see also Tamm and others (1999) Figure 5).

Carbon stocks and fluxes in comparable stands in Finland have been studied by Mäkipää (1995).

Their results (Mäkipää 1995) for soil carbon were similar to this study, but for ground vegetation biomass they found a decrease on fertilized plots. Although it has not been shown in this study, a reduction of ground vegetation on fertilized plots may also take place in Norrleden as the tree canopy becomes more closed.

Results for root–shoot litter production ratios show the expected negative relation with amount of added N. The amount of root production can be compared to a study of a younger pine stand in central Sweden, where Persson (1980) estimated a total annual root production in the F/H layer of about $1000 \text{ kg C}^{-1} \text{ ha}^{-1}$. However, a reevaluation of that result indicated that it is likely a considerable overestimate (Högberg and others 2002). Furthermore, the results presented here are based on integrated inputs over decades that suffer less from temporal variation and other problems of more direct methods.

Decomposition and Soil Respiration

A comparison of the results for the different N levels shows that differences in respiration and decomposition (Figure 6) are relatively small compared to the differences between NPK and only N treatments. Even at the lowest N addition level—between 30 and $60 \text{ kg N ha}^{-1} \text{ y}^{-1}$ (Table 1)—the nutrient effects seem to have almost reached a maximum. At this level of N input, the availability of P and K have a greater influence on decomposition than further N additions.

In accordance with the model results, the field respiration measurements showed a 40% reduction in respiration on the fertilized plots compared to the control. This might be a result of reduced respiration by saprotrophic microorganisms, and/or a reduced respiration by roots and their mycorrhizal fungi. In support of the first assumption, the model showed only minor nutrient effects on root production (Figure 5). Furthermore, in combination with the increase in forest floor carbon, the SIR results indicated a reduction in microbial biomass per unit soil carbon in fertilized plots (Figures 1 and 7B). The SIR results also suggested that the effect of PK was strong even without N addition. However, since mycorrhizal root respiration is a large component of soil respiration in boreal pine forests (Högberg and others 2002), nutrient effects on tree belowground C allocation may also be important and thus warrant further study.

One year after the soil samples used in this study were taken, laboratory respiration measurements on root-free samples from the plots were conducted (M. Sjöberg and T. Persson personal communica-

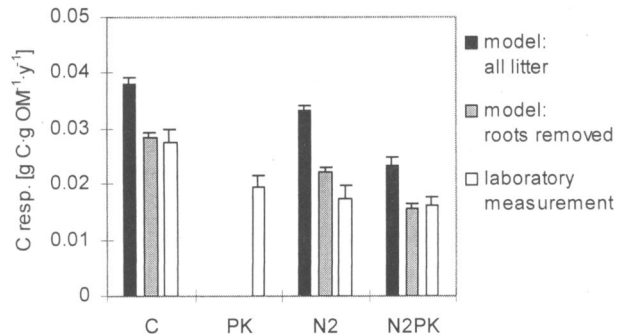


Figure 8. Forest floor microbial respiration. Model results, with and without root litter, compared to laboratory incubation measurements of samples where fresh and dead roots had been removed (T. Persson, personal communication). Bars show standard error for laboratory measurements n (plots per treatment) = 2 for C and PK and $n = 4$ for N2 and N2PK; for model results SE based on carbon amounts in replicate plots, $n = 6$ for C, $n = 4$ for N2 and N2PK. Treatments in Table 1

tion). Measured respiration was converted to average yearly field conditions using a conversion factor from Persson and others (2000a). The measured respiration per unit of organic matter for the organic layers are close to the predictions by our model (Figure 8).

Although nutrient additions on the whole reduce decomposition rates and thus microbial respiration, there is an increase in the initial decomposition rate (Table 3). Furthermore, using the estimated fertilization-induced changes in decomposition parameters in Eqs (3) and (4), decomposition rates initially increase after nutrient addition, regardless of how much decomposition has proceeded before nutrient addition. However, the initial increase is followed by a decline, resulting in the observed overall reduction in decomposition in the fertilized plots (Figure 6). Thus, the time span of litter decomposition studies is crucial for the interpretation of long-term consequences.

Although this study cannot provide numbers for all separate parameters of the decomposition process (Eq. [3]), the long time span of integration ensures a more confident estimation of the combination of parameters that determine long-term decomposition than what could be obtained from extrapolation of short-term litterbag studies. The consequences of deviations in different parameters when decomposition is extrapolated from short-term data can be substantial (Hyvönen and others 1998).

Mechanisms of Decomposition Changes

In terms of the decomposition theory (Eq. [3]), the exact mechanisms of the interaction between added

nutrients and the decomposition process cannot be fully explained from the aggregated parameters P_1 and P_2 (Eq. [4]). One possible combination of parameter changes that can explain these results is that both the decomposer parameters e_0 and η have increased together with q_0 (Eq. [3]). A similar response of the decomposition parameters to nutrient additions was observed by Ågren and others (2001). In other terms, this means that the microbial growth to assimilation ratio (e_0), the substrate quality degradation rate (η), and the substrate initial quality (q_0) all are increased by nutrient additions. Possibly, there has also been a decrease in the decomposer basic growth rate (u_0), which would agree with the decreased decomposer biomass suggested by field SIR measurements. The suggested changes in microbial properties could be a result of shifts in microbial species composition, which have been discussed in depth by Ågren and others (2001).

Persistence of Nutrient Effects

Are the nutrient effects on decomposition persistent? Or will they reverse if nutrient inputs stop? An indication of recovery is given by the relatively small effects in the highest levels of nutrient treatments (N3 and N3PK) compared to the low-dosage treatments. This result may reflect the recovery of the decomposer community after the discontinuation of the N3 and N3PK treatments in 1990 (3 years before sampling). Resilience of the decomposers would imply that if nutrient additions cease, a reduction in soil nutrient availability due to reduced decomposition and N mineralization would not be persistent.

Potential Effects on Future Carbon Storage

Our results suggest that nutrient additions substantially increase forest floor carbon in this type of ecosystem (Figures 1 and 6). In fact, nutrient additions are already occurring through N deposition at for example, about 30 kg N ha⁻¹ y⁻¹ in central European sites (Persson and others 2000b). Although the N levels used in this study were high, the results of an almost maximum effect at the N1 level indicate that lower N inputs also would have effects. The addition of 15 kg N ha⁻¹ y⁻¹ gave rise to similar effects on decomposition, as has been shown in this study (Ågren and others 2001). The effect of a reduction in the long-term decomposition rate caused by NPK additions is stronger than the increase in production as a mechanism of future soil carbon buildup (Figure 6). The effect on decomposition prevents soil carbon from reaching a steady

state, whereas a steady state is reached if only the production effect is included. Thus, the dominance of the decomposition effect would increase with a longer time span of extrapolation. A steady state of soil carbon is never reached in the fertilized plots because, during the decomposition process, the rate of reduction in substrate quality is very high compared to the carbon mineralization rate (Bosatta and Ågren 1985).

A potentially important process not modeled explicitly in this study is leaching from decomposed organic matter. Although the initial leaching from litter included in our model (around 10% of litter C input) affects soil carbon accumulation only marginally, leaching from old recalcitrant material could significantly decrease predicted carbon accumulation at longer time scales. Including a 1% per year leaching rate of all ages of organic material in our modeled system reduced predicted carbon accumulation in 100 years by up to 30% in nutrient treatments. However, more knowledge is needed before we can confidently include this process in our model.

CONCLUSIONS

The combination of ^{14}C and amount of carbon data of the three subdivisions (S, F, and H) of the organic layer combined with litter initial decay rates and an elaborate decomposition theory made it possible to reconstruct the main fluxes of carbon without assumptions of steady state and completely mixed pools.

Nutrient additions increase the initial decomposition rate but reduce the long-term decomposition rate and total soil carbon mineralization, a conclusion also supported by field respiration measurements. The addition of PK augments this effect compared to N-only treatments.

A comparison of the effects on production and decomposition shows that the reduced decomposition rate is the main cause of the observed and potentially large increase in forest floor carbon storage. The results suggest that these effects may be in progress in areas where N deposition is high.

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REFERENCES

- Ågren GI, Bosatta E. 1998. Theoretical ecosystem ecology. Cambridge (UK): Cambridge University Press.
- Ågren GI, Bosatta E, Magill AH. 2001. Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia* 128:94–8.
- Anderson JPE, Domsch KH. 1978. A physiological method for the quantitative measurement of microbial biomass in soils. *Soil Biol Biochem* 10:215–21.
- Berg B. 1984a. Decomposition of moss litter in a mature Scots pine forest. *Pedobiologia* 26:5301–8.
- Berg B. 1984b. Decomposition of root litter and some factors regulating the process: long term root litter decomposition in a Scots pine forest. *Soil Biol Biochem* 16:609–16.
- Berg B, Brootink H, Breymeyer A, Ewertsson A, Gallardo A, Holm B, Johansson MB, Koivuvoja S, Meentemeyer V, Nyman P, and others. 1991. Data on needle litter decomposition and soil climate as well as decomposition characteristics for some coniferous forest sites. Part 2. Decomposition data. Reports of Department of Ecology and Environmental Research, Swedish University of Agricultural Science 42 Uppsala, Sweden.
- Berg B, McLaugherty C, Johansson MB. 1993. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites. Long-term decomposition in a Scots pine forest. VIII. *Can J Bot* 71:680–92.
- Bergh J, McMurtrie RE, Linder S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *For Ecol Manage* 110:127–39.
- Bogatyrev L, Berg B, Staaf H. 1983. Leaching of plant nutrients and total phenolic substances from some foliage litters—a laboratory study. Swedish Coniferous Forest Project. Technical Report 33. Swedish University of Agricultural Sciences.
- Bosatta E, Ågren GI. 1985. Theoretical analysis of decomposition of heterogeneous substrates. *Soil Biol Biochem* 17:601–10.
- Ekblad A, Högberg P. 2000. Analysis of $\delta^{13}\text{C}$ of CO_2 distinguishes between microbial respiration of added C_4 -sucrose and other soil respiration in a C_3 -ecosystem. *Plant Soil* 219:197–209.
- Ekblad A, Nordgren A. 2002. Is growth of soil microorganisms in boreal forests limited by nitrogen availability? *Plant Soil* 242: 115–22.
- Flower-Ellis JGK, Brown CG, Wodger GH. 1994. Vertical life-tables for Scots pine and Norway spruce needles from the forest limit in Swedish Lapland. Report in Ecology and Environmental Research 77.
- Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, Richter DD. 2001. The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. *Oecologia* 129:420–9.
- Gay C, Tamm CO, Aronsson A, Flower-Ellis JGK, Linder S. 1994. Ekologen database. Collection of data from the Forest Optimum Nutrition Program.
- Harrison AF, Harkness DD, Rowland AP, Garnett JS, Bacon PJ. 2000. Annual carbon and nitrogen fluxes in soils along the European forest transect, determined using ^{14}C -bomb. In: Schulze E-D, Eds. Carbon and nitrogen cycling in European forest ecosystems. *Ecological Studies* 142. Berlin Heidelberg: Springer-Verlag. p 237–56.
- Holmen H, Nilsson Å, Popovic B, Wiklander G. 1976. The optimum nutrition experiment Norrliden. A brief description of an experiment in a young stand of Scots pine. Research notes of

- Departments of Forest Ecology and Forest soils 26. Stockholm: Royal College of Forestry.
- Hyvönen R, Ågren GI, Bosatta E. 1998. Predicting long-term soil carbon storage from short-term information. *Soil Sci Soc Am J* 62:1000–5.
- Högberg P, Ekblad A. 1996. Substrate-induced respiration measured in situ in a C3-plant ecosystem using additions of C4-sucrose. Accelerated paper. *Soil Biol Biochem* 28:1131–8.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg M, Nyberg G, Mottosson Lövvenius, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411:789–92.
- Högberg P, Nordgren A, Ågren GI. 2002. Carbon allocation between tree root growth and root respiration in boreal pine forest. *Oecologia* 132:579–81.
- Jalkanen R, Aalto T, Kurkela T. 1995. Development of needle retention in Scots pine 1957–1991 in northern and southern Finland. *Trees* 10:125–33.
- Johannisson C, Myrold DD, Högberg P. 1999. Retention of nitrogen by a nitrogen loaded Scots pine forest. *Soil Sci Soc Am J* 63:383–9.
- Johansson MB. 1993. Biomass, decomposition and nutrient release of *Vaccinium myrtillus* leaf litter in four forest stands. *Scand J For Res* 8:466–79.
- Mäkipää R. 1995. Effect of nitrogen input on carbon accumulation of boreal forest soils and ground vegetation. *For ecol manage* 79:217–226.
- Nydal R, Klövseth. 1983. Tracing bomb ^{14}C in the atmosphere, 1962–1980. *J Geophys Res* 88:3621–42.
- Nykvist N. 1963. Leaching and decomposition of water soluble organic substances from different types of leaf and needle litter. *Studia Forestalia Suecia* 3.
- Olsson IU. 1993. A ten-year record of different levels of the ^{14}C activities over Sweden and the Arctic. *Tellus* 45:479–81.
- Persson H. 1980. Spatial distribution of fine-root growth, mortality and decomposition in a young Scots pine stand in central Sweden. *Oikos* 34:77–87.
- Persson T, Karlsson PS, Seyferth U, Sjöberg RM, Rudebeck A. 2000a. Carbon mineralisation in European forest soils. In: Schulze E-D, Eds. Carbon and nitrogen cycling in European forest ecosystems. *Ecological Studies* 142. Berlin Heidelberg: Springer-Verlag. p 257–75.
- Persson T, van Oene H, Harrison AE, Karlsson PS, Bauer GA, Cerny J, Couteaux M-M, Dambrine E, Högberg P, Kjeller A, and others. 2000b. Experimental sites in the NIPHYS/CANIF project. In Schulze E-D, editor. Carbon and nitrogen cycling in European forest ecosystems. *Ecological Studies* 142. Berlin Heidelberg: Springer-Verlag, p 14–46.
- Tamm CO, Aronsson A, Popovic B, Flower-Ellis JKG. 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. *Studia Forestalia Suecia* 266.
- Townsend AR, Vitousek PM, Trumbore SE. 1995. Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. *Ecology* 76:721–733.
- Trumbore S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on below ground C dynamics. *Ecol Appl* 10:399–411.
- Valentini R, Matteucci G, Dolman AJ, Schulze ED, Rebmann C, Moors EJ, Granier A, Gross P, Jensen NO, Pilegaard K, and others. 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–4.
- White A, Cannell MGR, Friend AD. 2000. The high-latitude terrestrial carbon sink: a model analysis. *Global Change Biol* 6:227–45.

Correction of Climatic Effects on Decomposition Data

To minimize the effect of seasonal and between-year climatic variation, we constructed a climatic compensation curve that describes the relative decomposition rate over the years of interest. First, an "average" decomposition curve was fitted using all data from the Norrliden site (36 litterbag data series) (Berg and others 1991). This curve was used on consecutive individual data points to calculate deviations in the decomposition rate from the expected rate. This calculation was done for all data series and plots of the site, and the results were summed to give the average relative decomposition rate for each day. In the summation, the calculated deviations are weighted depending on the SEs of the data points and the length of time interval between data points. The final compensation curve was used on each data series to correct the sampling intervals (time-data points) for climatic variation.

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