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# Projections of 30-year soil carbon balances for a semi-natural grassland under elevated $CO_2$ based on measured root decomposability

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**Abstract**

Long-term soil C projections were made for a semi-natural grassland under $CO_2$ elevation in Central Sweden based on treatment-induced differences in input quantity, input quality and measured microclimate. Three treatments were applied to the grassland during 6 years: Ambient and Elevated (+350 μmol $mol^{-1}$) $CO_2$ levels in open-top chambers and Control. Roots grown during the fifth experimental year were incubated under controlled conditions for 160 days and showed significant treatment differences in decomposition rates. The fraction of C lost during incubation of Elevated was 57% while only 53% for Ambient and 52% for Control. The incubation results were fit to a decomposition model and a humification coefficient was used to account for treatment-induced differences in root quality. Annual soil C input was calculated considering both root and shoot input estimates and was 103, 74 and 92 g C $m^{-2}$ $year^{-1}$ for Elevated, Ambient and Control, respectively. A climate factor represented measured microclimate differences. Due to drier conditions this factor was somewhat lower for Ambient than for Control and Elevated. The ICBM model was used for 30-year soil C projections. The input, quality and climate parameters for Control resulted in projections indicating that the present measured soil C store, 5.5 kg C $m^{-2}$ at 0–15 cm, is near steady-state. The soil C pool in Ambient was projected to lose 90 g C $m^{-2}$ in 30 years primarily due to the decreased input. Although Elevated had the greatest input, this did not compensate for the increased root decomposability and Elevated was projected to lose 70 g C $m^{-2}$. We discuss the validity of the projections and test other possible scenarios. A tentative conclusion is that the expected $CO_2$ and temperature increase during the next 30 years will have only minor effects on the soil carbon content of this system, unless plant production is severely reduced by weather irregularities or even disasters.


*Keywords:* Carbon sequestration; Modeling; Soil carbon; ICBM; Incubation; Root decomposition

## 1. Introduction

Soil C is primarily plant derived, originating from either root and shoot litter or root exudates. The amount of C present in soil organic matter (SOM) is generally determined by the balance of plant derived C inputs to the soil and outputs through decomposition, erosion and leaching. Both climate and inherent soil properties are primary determinants of both sides of this balance, however, elevated-$CO_2$-induced changes in the input litter quality or quantity will also affect the soil C cycle and eventually the long-term storage of C in SOM (Mooney et al., 1999).

Increased tissue C/N ratio is often considered to be a fundamental response of C3 plants grown in elevated $CO_2$, although the difference is less pronounced in root than shoot tissues (Cotrufo et al., 1998). Such $CO_2$-induced quality changes have been shown to retard decomposition in several studies (Gorissen et al., 1995; van Ginkel et al., 1996), but not in others (Randlett et al., 1996). In general, however, it seems that

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the C/N quality differences often seen in green plant materials are small or non-existent in naturally senesced shoot litter and that subsequent changes in decomposition rates will be small or negligible (Norby and Cotrufo, 1998; Norby et al., 2001).

Increased peak biomass is another response commonly seen in plants grown under elevated $CO_2$ (Kimball et al., 1993; Owensby et al., 1999). This holds even under natural, nutrient- or water-limited conditions (Mooney et al., 1999). However, under nutrient-limiting conditions root biomass usually increases more than other plant parts (Rogers et al., 1994). This increase in biomass production under elevated $CO_2$ together with increased plant C allocation below-ground will greatly affect soil C pools and has been viewed as more important than the quality issue in terms of C sequestration (Dukes and Field, 2000; Norby et al., 2001).

Measuring the effects of elevated $CO_2$ on soil C in short-term experiments is clouded with problems (Hungate et al., 1996). However, due to the lack of elevated $CO_2$ experiments lasting longer than a decade, predictions of the effects of $CO_2$-enrichment on long-term soil C pools are usually based on extrapolations from short-term experiments. Such extrapolations should of course be interpreted with caution, since the properties of the litter that may be decisive in the long-term cannot really be measured in a short-term experiment (cf. Hyvönen et al., 1998; Andrén et al., 2001).

In this paper, we used the ICBM soil carbon model (Andrén and Kätterer, 1997) for predicting the long-term (30-year) effects of $CO_2$ enrichment on soil C dynamics in a semi-natural grassland in central Sweden. ICBM is a relatively simple, analytically solved model that was parameterized using data from a Swedish long-term soil organic matter experiment. The model parameters can quite easily be estimated from general climate, crop and soil data or simple front-end models, and has successfully been applied to 99 long-term soil C field data sets from northern Europe (Kätterer and Andrén, 1999).

The objectives of this paper were: (1) to test the hypothesis that roots grown under elevated $CO_2$ will decompose more slowly than those grown under ambient $CO_2$, (2) to explain the decomposability difference in terms of measured root quality differences found during laboratory incubations, (3) to fit a simple decomposition model to the incubation results for parameterizing the ICBM soil carbon model and (4) to make 30-year soil C balance projections for the different treatments. The projections were to be based on treatment differences in input quantity, input quality and microclimate.

## 2. Materials and methods

### 2.1. Site description

The site was located in a semi-natural grassland at Nåntuna (59°48′N and 17°38′E), 5 km south of Uppsala in central Sweden. The climate is cold temperate with a mean annual temperature of +5.5 °C and an annual precipitation of 527 mm. The site had a long history of grazing and there were about 35 plant species $m^{-2}$. When not restricted by grazing, grasses typically constitute 30–50% of the above-ground dry biomass towards the end of the growing season. The most common grasses included *Agrostis capillaris* L., *Festuca rubra* L. and *Poa pratensis* L. The forbs were dominated by *Achillea millefolium* L., *Carum carvi* L., *Stellaria graminea* L., *Plantago media* L. and *Taraxacum* sect. *ruderalia* Kirschner, H. Øllg. & Stepanek. The prevailing legumes were *Trifolium repens* L. and *Lotus corniculatus* L. The soil was classified as Eutric Cambisol and the upper 30 cm was a loam (22% clay, 47% silt, 18% sand, 13% gravel, 3.51% C and 0.25% N) and very stony. At about 10 cm depth across the entire site, we found a layer of charcoal, which explains the high C/N ratio of 14. Normal C/N ratios for similar soils in the region are about 10 (Eriksson et al., 1997) and this indicated that ca. 25% of the C at this site was charcoal. This black carbon is essentially inert in terms of soil C dynamics on the scale of 30 years and therefore we excluded it from our calculations.

From the spring of 1995 until autumn 2000, three treatments were applied at the site: ambient $CO_2$ ($360 \pm 20$ μmol $mol^{-1}$) and elevated $CO_2$ ($700 \pm 100$ μmol $mol^{-1}$) treatments in open-top chambers (OTC), and Control in a 5 cm high chamberless ring with the same diameter as the OTCs. The OTCs were cylindrical in form (height 1 m, diameter 1.5 m) and made of thin polypropylene sheets mounted on steel frameworks. The three treatments were laid out in a randomized block design with four blocks placed down a mild southwest-facing slope. See Sindhøj et al. (2000) and Marissink et al. (2002) for a more detailed description of the site and experimental design.

### 2.2. Root material

Roots were collected from ingrowth cores installed at the site. The ingrowth cores, nylon mesh bags filled with sieved root-free soil taken from the site, were 8 cm in diameter and 15 cm deep and were installed according to Steen (1984). Two ingrowth cores per plot, i.e., 24 cores in total, were installed on 21 April 1999 and removed on 2 August 1999. The cores were gently hand washed in cold tap water to remove adhering soil while roots were recovered on a 1-mm sieve. After washing, the roots were freeze-dried, weighed and then ground to pass a 1-mm sieve.

Ground samples were pooled to form one sample per treatment and block, i.e., 12 samples. Total C and N in the root material were determined with an elemental analyzer (NA 1500 Element Analyser; Carlo-Erba Strumentazione, Milan, Italy). Ash content was determined by combustion for 6 h at 600 °C. Klason lignin was determined according to Theander et al. (1995).

### 2.3. Decomposition incubations

Grinding the roots to pass 1-mm sieve was necessary to analyze root quality differences using laboratory incubations

according to Gunnarsson and Marstorp (2002), however grinding is not generally recommended in elevated $CO_2$ litter quality and decomposition studies (Norby et al., 2001). We decided in this case it was acceptable primarily owing to the extremely fine nature of these roots (almost 90% under 0.5 mm in diameter and 25% were under 0.1 mm in diameter), and also since no treatment-induced differences in root morphology were found (see Sindhøj et al., 2004). The root samples were incubated at 20 °C in 250-ml plastic jars, each containing 40 g dw soil, with three replicates for each plot ($n = 36$) plus three blanks containing only soil. A sandy soil (12.5% clay, 25.9% silt, 51% sand, 1.63% C and 0.13% N) was used from a nearby site at Ultuna in central Sweden (60°N, 17°E) and was sieved through a 4-mm mesh. To prevent N, P and K limitation during the initial hours of incubation, when the simple carbohydrates are decomposed by soil microorganisms, a nutrient solution containing $KNO_3$ and $K_2PO_4$ with NPK totals of 1.04, 0.06 and 3 mg, respectively, was added to each jar. The soil was wetted to 40% of water holding capacity (0.173 g $H_2O$ $g^{-1}$ dw soil). At the start, 130 mg of ground roots (ash corrected) were added to each jar except the blanks, and mixed thoroughly. The $CO_2$ which evolved during decomposition was measured every hour for ca. 15 days with an automatic respirometer as described by Marstorp (1996), and then by titration (Stotzky, 1965) after 36, 65, 103 and 161 days. All measurements presented here are corrected for the background respiration measured in the soil blanks. For both root material analysis and decomposition incubations, the GLM procedure (SAS Institute, Inc., 1982) was used for analysis of variance at specific sampling times with blocks and treatments as main factors and LSD tests were used for assessing differences between means. A critical significance level of 5% was applied in all tests.

### 2.4. Model structure

In ICBM, long-term soil C dynamics within a given climate is mainly controlled by a humification quotient, $h$. Since we had high-resolution data from the early parts of the incubation, we used ICBM/2 (Fig. 1 and Table 1), which has two litter carbon pools (Kätterer and Andrén, 2001) as the model to fit to the incubation results. The three components are: Young, labile ($Y_l$); Young, refractory ($Y_r$); and Old ($O$). The first-order decay rate constants $k_{Y_l}$, $k_{Y_r}$ and $k_O$ control the $Y_l$, $Y_r$ and $O$ pools, respectively. The fraction of outflows from $Y_l$ and $Y_r$ that is transferred to $O$ is governed by a humification factor, $h$, which can range from 0 to 1 and was used here as the litter quality factor. A climate factor, $r_e$, is used to modify the decay rates of the three components according to abiotic conditions.

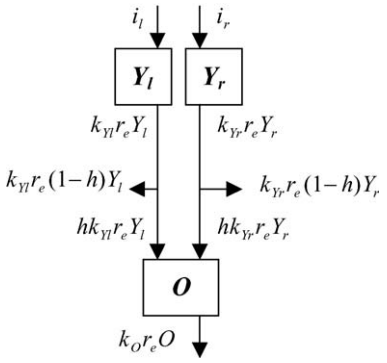


Fig. 1. ICBM/2 model structure (Kätterer and Andrén, 2001). Arrows not pointing at pools indicate $CO_2$ emission (see Table 1 for parameter definitions).

### 2.5. Model parameterization

Input labile ($i_l$) and input refractory ($i_r$) were set to 0, as was the initial size of the $O$ pool. The climate factor, $r_e$, was calculated from the laboratory conditions (+20 °C, 40% water holding capacity) compared with the default value of 1 for a field in central Sweden (cf. Andrén and Kätterer, 1997). We initially set $h$ to equal 0.125, which was calibrated for a mixture of straw and roots (Andrén and Kätterer, 1997). The decay rate constant for $O$ ($k_O$) was assumed to be equal to that calibrated for field conditions. Then we optimized the proportion of $Y_l$ and $Y_r$ and the decay rate constant for $Y_r$ ($k_{Y_r}$) simultaneously using non-linear regression analysis (SAS, Inc., 1985) to fit the results from Control. The decomposition rate constant of $Y_l$ ($k_{Y_l}$) was set manually to match the early mass loss.

Table 1
Parameter description, value and source for ICBM/2 model shown in Fig. 1

| Parameter | Short description | Unit | Value | Source |
|---|---|---|---|---|
| $Y_{0l}$[a] | Initial C mass of 'Young and labile' pool | kg | $0.42^C$, $0.42^A$, $0.41^E$ | Fit to data from Control |
| $Y_{0r}$[a] | Initial C mass of 'Young and refractory' pool | kg | $0.58^C$, $0.58^A$, $0.59^E$ | Normalized to $Y_0 = 1$ |
| $O_0$ | Initial C mass of 'Old' pool | kg | 0.000 | |
| $i_l$ | Annual C input, labile | kg $year^{-1}$ | 0.000 | |
| $i_r$ | Annual C input, refractory | kg $year^{-1}$ | 0.000 | |
| $k_{Y_l}$ | Decomposition rate constant, '$Y_l$' | $year^{-1}$ | 12.8 | Fit to data from Control |
| $k_{Y_r}$ | Decomposition rate constant, '$Y_r$' | $year^{-1}$ | 0.33 | Fit to data from Control |
| $k_O$ | Decomposition rate constant, 'Old' | $year^{-1}$ | 0.006 | Model default |
| $h$[a] | Litter quality coefficient | – | $0.145^C$, $0.141^A$, $0.10^E$ | Fit to treatment data |
| $r_e$ | External 'climate' factor | – | 3 | Calculated from incubation temperature and moisture |

[a] Individually optimized for [C]Control, [A]Ambient and [E]Elevated.

After obtaining an optimal fit of the needed parameters for Control, we used these parameters for Elevated and Ambient while optimizing for the proportion of $Y_l$ and $Y_r$ as well as for $h$ (Table 1). In other words, we tried to express the quality differences between roots from the three treatments by the difference in the proportions of $Y_l$ and $Y_r$ and as differences in $h$.

### 2.6. 30-year soil carbon projections

To make projections of soil carbon dynamics for 30 years in the three treatments we used the ICBM two-component model (Andrén and Kätterer, 1997), which differs from ICBM/2 by having only one $Y$ pool. Thus, the two rate constants $k_{Y_l}$ and $k_{Y_r}$ were aggregated into one, $k_Y$. We used the model default value for $k_Y$ (0.8) which induced almost the same decomposition dynamics in a longer time perspective as estimated here for the roots. For example, after 1 year at reference climate, about 50% of the roots would decompose regardless of which of the two models and parameter sets used. Also for $k_O$ the default value was used (0.006). The $h$ parameter was taken from the model parameterization of the incubations while $i$ and $r_e$ were calculated as described below.

Annual C input to the soil, $i$, was estimated for each treatment using the mean of yearly values taken from the 6 experimental years. Root input for the different treatments (0–15 cm depth) during this time was estimated by Sindhøj et al. (2004). Root-derived material consists of root exudates, mucilage, sloughed-off cells and tissue and is also understood to be a significant source of carbon entering the soil (Andrén et al., 1990), however it is very difficult to quantify. Therefore, we based a conservative estimate of this input on lower-end values from in-depth studies of organic C release from meadow fescue, barley, wheat and several other species (Biondini et al., 1988; Liljeroth et al., 1990; Johansson, 1992), which amounted to 10% of total plant C content measured in early August. Shoot input was estimated as 20% of the above-ground biomass measured when plots were cut in early August. This rough estimate was based partially on unpublished measurements of the regrowth which occurred after the harvest in August and then subsequently died during autumn and winter. It also accounts for the seasonal litter fall and eventual input of several species which were observed to decrease in numbers between early spring and just before cutting (Marissink and Hansson, 2002).

To account for treatment effects on microclimate, we calculated a climate factor for each treatment based on measured differences in temperature and soil moisture. The annual climate factor ($r_e$) for ICBM was originally calibrated to equal unity at a reference site situated close to Nåntuna, so we can assume the general climate is the same. However, the reference site was a fertilized barley field with a clay content of 37%, so we had to adjust for the differing crop and field properties. Temperature ($T$) and soil moisture ($\theta$) were assumed to affect $r_e$ independently, i.e., $r_e = r_T \times r_\theta$. Mean soil temperature measured at 5 cm depth inside and outside the OTCs during four growing seasons differed on average less than 0.3 °C from air temperature measurements at a nearby official meteorological station. Therefore, we used daily means of air temperature measured at this station to calculate $r_T = (T - T_{min})^2/(20 - T_{min})^2$, where 20 °C is the reference temperature and $T_{min} = -5$ °C is the minimum temperature for decomposition activity (Kätterer et al., 1998), for both the Nåntuna and the reference site for which ICBM was originally calibrated. To calculate soil moisture we fitted a simple bucket-type water balance model to soil moisture measured with TDR in the field during 3 years. The model was based on potential evapotranspiration, precipitation and soil properties, i.e., permanent wilting point and field capacity. Thereafter, we applied the calibrated model to a 26-year period, for which daily values for the climatic variables were available, to calculate soil water content. From soil water content we calculated daily values for $r_\theta$ by assuming a linear relationship between water content and $r_\theta$. The same procedure was followed for the reference site for which ICBM originally was calibrated by adjusting the soil-related properties. Mean annual values for the product $r_T \times r_\theta$ were then calculated. The lower water holding capacity and greater stoniness at the Nåntuna site resulted in a 31% lower annual $r_e$-value compared with the reference site. Further, taking into account the higher evaporative water demand of a grassland compared with the annual crop at the reference site into account, there was an additional slight reduction in $r_\theta$. The resulting mean $r_e$-value for the whole 26-year period became 0.65 in Control and Elevated and somewhat lower (0.62) in Ambient, where soil conditions were slightly drier according to the TDR measurements (Sindhøj et al., 2004).

Finally, we made three different projections of soil carbon dynamics, assuming 30 years with no change (Control), 30 years of increased temperature (Ambient) and 30 years of increased temperature and $CO_2$ (Elevated). For comparison, we also used a set of parameters for the three treatments considering a land management change, namely that the field was left in 'green fallow', i.e., without grazing or harvesting of shoot material for 30 years.

## 3. Results

### 3.1. Root chemical analysis

$CO_2$ treatment did not influence root N concentration, C/N ratio or lignin concentration (Table 2), yet Ambient had a significantly higher N concentration than Control.

### 3.2. Decomposition incubations

Respiration peaked for all treatments approximately 1 day after the start of the incubation (Fig. 2). Elevated had the

Table 2
Total C and N, C/N ratio, lignin and ash concentrations found in roots which grew into ingrowth cores during the 5th year of $CO_2$ elevation

| | Total C | Total N | C/N | Lignin | Ash |
|---|---|---|---|---|---|
| Control | 35.92[a] | 0.71[a] | 49.83[a] | 11.71[a] | 13.97[a] |
| Ambient | 35.50[a] | 0.84[b] | 42.38[a] | 11.00[a] | 14.39[a] |
| Elevated | 35.39[a] | 0.78[ab] | 46.59[a] | 11.71[a] | 13.78[a] |

C, N lignin and ash given as percent of dry mass. Different superscript letters (a and b) indicate significant differences at $p < 0.05$, $n = 4$.

lowest respiration peak while the highest was in Control. Both elevated and ambient $CO_2$ treatments peaked simultaneously, while the peak for control roots occurred somewhat later, although the differences were not significant. Between the second and fourth day, respiration from Ambient roots increased above the elevated and control treatments, and then was similar again for all treatments for the next 10 days.

During the rest of the incubation (Fig. 3), respiration increased in Elevated relative to that in Ambient and Control ($p < 0.05$). The fraction of initial C lost during 160 days was 57, 53 and 52% in Elevated, Ambient and Control, respectively.

### 3.3. Model predictions of incubations

We optimized each treatment for $Y_{0l}$, $Y_{0r}$ and $h$ (Table 1), and obtained a good model fit to the incubation data for all three treatments (Fig. 4). The proportion of $Y_{0l}$ (42%) was the same for Ambient and Control while Elevated was 41%. The quality coefficient, $h$, was greater for Control and Ambient than the standard $h$ calibrated for straw ($h = 0.125$, Andrén and Kätterer, 1997) while Elevated was somewhat lower (see Table 1).

### 3.4. 30-year soil carbon projections

To compare with soil C measurements taken from the site we calculated, using ICBM, the soil C steady-state value for Control to a depth of 15 cm based on the annual C input,

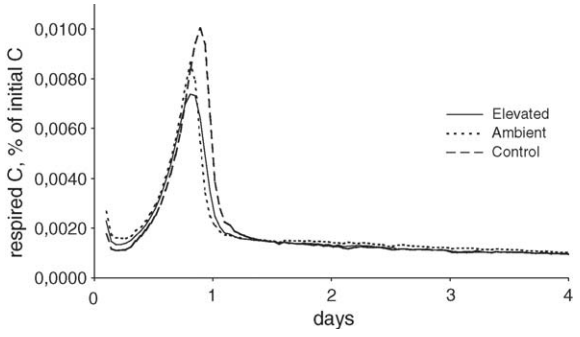


Fig. 2. Hourly respiration rate during the first 6 days of incubation, measured as percent of $CO_2$-C respired per mg of initial substrate C added ($n = 12$ per treatment). All measurements are corrected for the background respiration measured in the soil blanks.

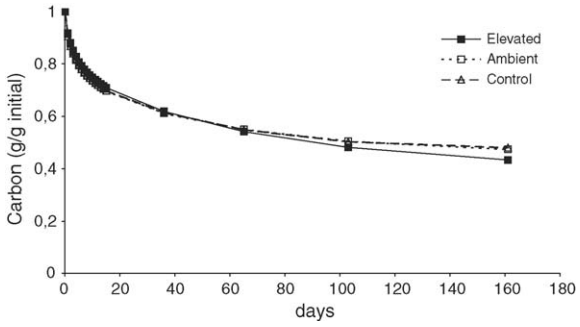


Fig. 3. Proportion of root C remaining after incubation for 160 days. Calculated from cumulative $CO_2$-C respired per milligrams of initial substrate C added and corrected for background respiration measured in the soil blanks.

quality and climate parameters (Table 3). These calculations resulted in 3.6 kg C $m^{-2}$ (excluding black C) and would give a site soil C/N ratio of 9.2. This was remarkably close to the measured value of 3.59 kg C $m^{-2}$ (soil bulk density

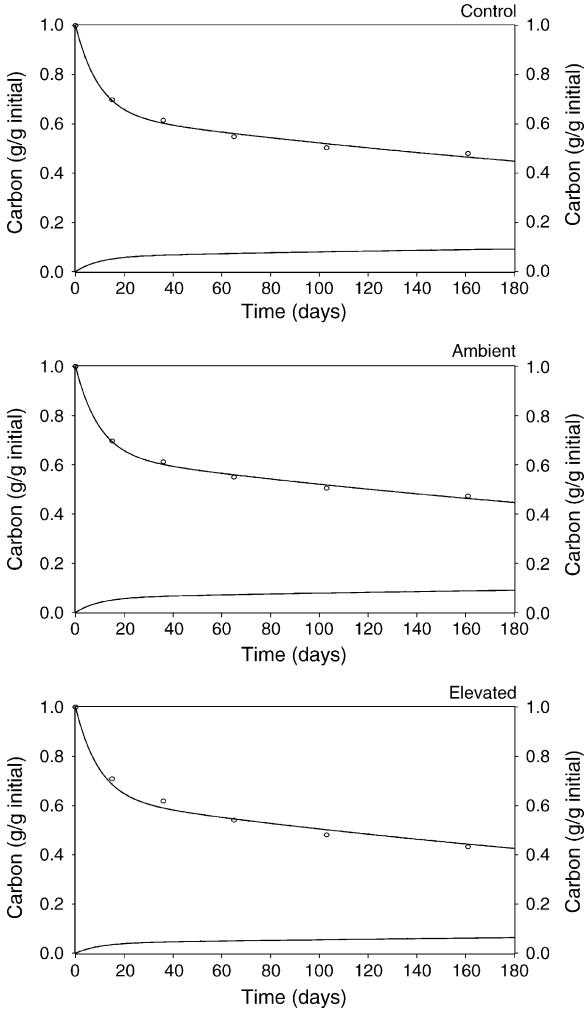


Fig. 4. ICBM/2 model fit to decomposition data (symbols) from incubation of roots from the three treatments. The top line is the total C ($Y_l + Y_r + O$) and the bottom line is the $O$ pool.

Table 3
Parameters used in 30-year projections of soil C dynamics using the ICBM model

| Parameter | Control | Ambient | Elevated |
|---|---|---|---|
| Projections from treatments | | | |
| $i$[a] | 92 | 74 | 103 |
| $Y_0$[b] | 180 | 180 | 180 |
| $O_0$[b] | 3420 | 3420 | 3420 |
| $k_Y$[c] | 0.8 | 0.8 | 0.8 |
| $k_O$[c] | 0.006 | 0.006 | 0.006 |
| $h$[d] | 0.145 | 0.141 | 0.100 |
| $r_e$[e] | 0.65 | 0.62 | 0.65 |
| Parameters changed for projections from land-use change | | | |
| $i$[a] | 178 | 157 | 205 |

Time step = 1 year. $i$ is annual C input in g m$^{-2}$. $Y_0$ and $O_0$ are initial C mass in g m$^{-2}$ of the young and old soil C pools, respectively. $k_Y$ and $k_O$ are decay rate constants for $Y_0$ and $O_0$, respectively. $h$ is the litter quality parameter and $r_e$ is the climate factor.

[a] Root and shoot litter input.
[b] Optimized for initial steady-state conditions in Control.
[c] Model default value, see Andrén and Kätterer (1997).
[d] Fitted to respiration results.
[e] Calculated by front-end climate model.

1.3 g cm$^{-3}$, 30% stoniness and 25% black C) and indicated that so far our assertions were within reason. This suggests that soil C for Control was close to steady-state at the experimental onset and will not change in 30 years time if all conditions remain the same (Fig. 5).

The long-term soil C balance for Ambient conditions, which entails increased temperature, decreased soil moisture and decreased C input from roots and shoot litter, is expected to show slightly declining soil C content (Fig. 5). Input was 74 g C m$^{-2}$ year$^{-1}$, there was a slight increase in root decomposability (lower $h$) compared with control, and the warmer and drier environment lowered $r_e$ somewhat (Table 3). This led to a soil C loss of 90 g m$^{-2}$ over 30 years which was equivalent to 2.5% of the initial soil C.

Soil C under Elevated conditions was also in decline (Fig. 5), primarily due to the increased root decomposability. Soil conditions were slightly moister in comparison with Ambient and enhanced decomposition even further. However, the increased input compensates for much of this and Elevated lost only 70 g C m$^{-2}$ over 30 years, which was equivalent to 1.9% of the initial soil C.

For the land management comparison of turning the grassland to 'green fallow' for 30 years, i.e., left without harvesting or grazing, we used essentially the same parameters as earlier, except increased the input to include the entire shoot biomass (Table 3). Thirty years after this land management change, soil C would increase with 500, 390 and 400 g m$^{-2}$ for Control, Ambient and Elevated, respectively (Fig. 5, only Elevated is shown).

## 4. Discussion

Initially, the incubation seemed to support the general findings that decomposition of plant materials grown under

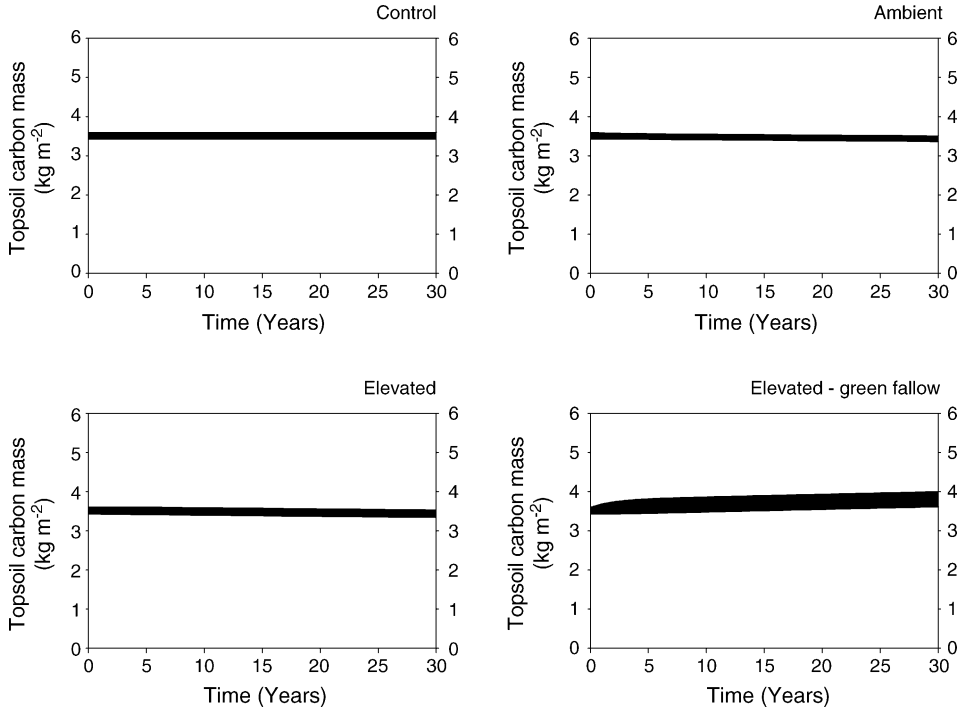


Fig. 5. ICBM 30-year soil C projections for Control, Ambient and Elevated treatments and Elevated plus land management change. Solid area represents the $Y$ pool and the white underneath is the $O$ pool. Parameters listed in Table 3.

elevated $CO_2$ will either be slightly reduced or not affected at all (Gorissen et al., 1995; Mooney et al., 1999; Norby et al., 2001). However, after 3 weeks a somewhat different picture began to take form as the rate of $CO_2$ evolution from Elevated roots increased and remained 25% greater than the other treatments ($p < 0.05$) throughout the remainder of the incubation, i.e., another 20 weeks. While this is contrary to most findings, others have reported enhanced decomposition of some grassland species when grown under elevated $CO_2$ (Coûteaux et al., 1991; Franck et al., 1997).

Greater C/N ratios in plants grown in elevated $CO_2$ is a general explanation for altered decomposition rates (Cotrufo et al., 1998; van Ginkel et al., 1996). Such a simple description of the elevated $CO_2$ effect on litter quality and decomposition did not apply to our results as there was no correlation between C/N ratios and decay rates. Since lignin concentrations did not differ between treatments either, the quality changes under elevated $CO_2$ were likely more subtle and we can make some general assumptions by looking at the detailed short-term respiration results.

Studies of the respiration pattern during decomposition of several pure plant carbohydrates and proteins have shown that different types of carbohydrates are available for decomposition at different times, and this is seen as an increase in respiration rate at different stages during decomposition (Gunnarsson and Marstorp, 2002). Regarding the initial detailed incubation period, the synchronized respiration increase in all treatments after approximately 10 h of incubation indicates that the same kind of substances with the same availability is being decomposed. This peak has been shown to correspond mainly with decomposition of simple carbohydrates such as sucrose, glucose and fructose present in the roots. The height of this initial peak also corresponds to the concentration of these simple carbohydrates in the substrate. This initial peak was lowest in Elevated during our incubations which indicates a decrease in the simple carbohydrates, although the difference was not significant. On the whole, however, our results indicate that the spectrum of C quality in the roots from Elevated was more available for decomposition compared with Ambient and Control. The significantly higher loss of C in elevated treatment from day 40 to 160 probably is related to qualitative differences in structural carbohydrates of the root materials (Gunnarsson and Marstorp, 2002).

One of the more interesting aspects of the soil C projections was that despite relatively large differences in input C quantity and quality, only minimal differences were found when extrapolating to 30-year soil C dynamics (Fig. 5). During this period total C input in Elevated was 870 g C $m^{-2}$ greater than in Ambient, yet total soil C after 30 years in Elevated was only 20 g C $m^{-2}$ greater than in Ambient. Furthermore, although total C input in Elevated was 330 g C $m^{-2}$ greater than Control, Elevated would lose 70 g C $m^{-2}$ from the Control level. These dynamics were to some extent due to the change in soil climate, but mostly due to the unexpected increase in the decomposability of roots grown under elevated $CO_2$, which essentially 'ate' almost all of the increased input.

In this study, we only measured the decomposition rates of the roots. However, it is reasonable to argue that these measurements would not necessarily apply to decomposition rates of shoot litter. Then $h$, which describes litter quality, should be weighted to account for the total input quality of both root and shoot litter. Following the general findings (Norby et al., 2001) for the purpose of this illustration, and assuming there was no $CO_2$ effect on the decomposability of shoot litter between treatments, we used the ICBM default value of $h$ for the shoot litter, which was originally parameterized for straw. Calculating a weighted $h$ from these values gave 0.111, 0.133 and 0.137 for Elevated, Ambient and Control, respectively, and resulted in 30-year projections where Elevated had 60 g C $m^{-2}$ more than Ambient and only 5 g C $m^{-2}$ less than the pre-changed Control level.

The absolute values of the soil C projections were affected by assuming that Control was more or less in steady-state. However, we think this was reasonable considering the grassland has been managed similarly for the past several hundred years or more. On the other hand, if Control was not in steady-state, it is primarily the overall soil C dynamics which would be affected most on the 30-year scale, while the relative differences between treatments would remain similar. This was also the case when excluding the charcoal C from the model calculations. Since charcoal is essentially inert in terms of soil C dynamics on the 30-year scale, excluding it seemed reasonable and was much like creating a third soil C pool considered to be very stable. If we did not remove the charcoal and instead included it in the $O$ pool, then soil C in Control would not be in steady-state and would lose 208 g C $m^{-2}$ during 30 years. Following this line, soil C in both Elevated and Ambient would have declined at greater rates than originally suggested. However, the relative difference between treatments would be similar to the original calculations. Elevated and Ambient would lose 71 and 80 g C $m^{-2}$ more than Control, respectively, compared to the original suggested (charcoal excluded) decline of 70 and 90 g C $m^{-2}$ for Elevated and Ambient. It is also worthwhile to note that the calculated steady-state soil C balance for Control was also quite similar to the actual measured soil C content, which we think indicates our assumptions were reasonable and that the input quantity, quality and climate parameters ($i$, $h$ and $r_e$, respectively) were realistic. Regardless, the values of the projections should be viewed cautiously and the focus should be placed on differences between the treatments.

One point not yet discussed concerning these projections is the possibility of treatment-induced differences in soil nutrient availability. Although not measured directly, Sindhøj et al. (2004) suggested that increasing root to shoot ratios in Elevated compared with the other treatments during 5 years of elevated $CO_2$ exposure could indicate increased nutrient limitation. The argument would be that

increased C input to the soil has increased N immobilization in Elevated soils. This N limitation in turn would slow the decomposition of the Elevated litter and result in an increase of soil C storage. However, Gill et al. (2002) reported that despite increased soil C/N ratios and decreased N mineralization in a grassland under elevated $CO_2$, increased soil C was minimal. What they did see was an increase in the particulate organic matter and a decrease in the mineral associated SOM, two SOM fractions which, more or less, correspond to the Young and Old pools in ICBM. Similar changes in these SOM fractions were reported by Cardon et al. (2001) and they suggest that in the elevated $CO_2$ system there was a decrease in the transfer of C from new to old soil carbon pools along with an increase in turnover of the new pool. In ICBM, the amount of C moving between the Young and Old pools is determined by $h$, and lowering this for Elevated, as the case in our projections, achieves the results of moving less C from the Young to Old pool. Similarly, our projections indicate that the Old C pool, $O$, was least in Elevated under all scenarios, and that any gains over Ambient were limited to the Young pool, $Y$, which has a much shorter turnover time.

Of course, long-term soil C projections based on short-term experimental results should be taken with a grain of salt considering that we do not have equally long-term $CO_2$ experiments with which to validate such projections. However, accurate projections of new soil C steady-state levels resulting from climate change and elevated atmospheric $CO_2$ level is not the intention of this work. Errors in such long-term calculations can become huge due to increased sensitivity to parameterization, and there are also uncertainties which arise from how different models partition the soil C pools (Andrén et al., 2001; Hyvönen et al., 1998). However, for periods up to 100 years, the uncertainties may be acceptable. Varying any one of the ICBM treatment-dependent parameters ±5% ($i$, $h$, $r_e$) resulted in a ±0.7% difference in the calculated 30-year soil C balance. If all three parameters were either over- or underestimated ±5% simultaneously, there was only a ±1.5% difference in the soil C balance.

The comparison scenario of changing land management to green fallow offers an interesting perspective on the effectiveness of sequestering C in the soil. The increased C input to the soil when changing management from exporting the harvest to a green fallow totals 3 kg $m^{-2}$ during 30 years, yet the increase in soil C would be less than 0.5 kg C $m^{-2}$ (see Fig. 5). The rest of the C would be respired back to the atmosphere. It should also be pointed out that over 40% of the 0.5 kg sequestered C $m^{-2}$ was in the $Y$ pool and would decompose again within a few years if the management changed back to exporting the harvest. This illustrates a point Andrén and Kätterer (2001) made on the inefficiency, and uncertainty, of trying to sequester C in the soil. It would be much more effective to reduce the decomposition rate of the C stored in the soil than to increase the input of litter C into the soil.

## 5. Conclusions

The results from this study do not support the hypothesis that $CO_2$ effects on litter quality leads to decreased decomposition rate. The fact that root material grown in elevated $CO_2$ led to increased decomposition rates is of interest in the debate as to whether soils may act as a source or sink for atmospheric $CO_2$. The plant material used was grown in a semi-natural grassland during the fifth year of elevated $CO_2$ exposure and consisted of a natural mixture of roots from up to 30 different species, a number similar to those in many natural systems. Overall, changes in soil C dynamics will be driven primarily not only by changes in the quantity and quality of plant C inputs, but also by any changes in climate, i.e., soil moisture and temperature. However, despite the treatment-induced differences we found in C input quantity and quality as well as microclimate, there was little difference in soil C dynamics between treatments on a 30-year time scale. It seems that elevated $CO_2$ will only marginally affect carbon storage in this grassland, especially in comparison with the change in soil C dynamics by a land-use change.

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