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ECOSYSTEMS

Nutrient Addition Prompts Rapid Destabilization of Organic Matter in an Arctic Tundra Ecosystem

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Abstract

Nutrient availability in the arctic is expected to increase in the next century due to accelerated decomposition associated with warming and, to a lesser extent, increased nitrogen deposition. To explore how changes in nutrient availability affect ecosystem carbon (C) cycling, we used radiocarbon to quantify changes in belowground C dynamics associated with long-term fertilization of graminoid-dominated tussock tundra at Toolik Lake, Alaska. Since 1981, yearly fertilization with nitrogen (N) and phosphorus (P) has resulted in a shift to shrub-dominated vegetation. These combined changes have altered the quantity and quality of litter inputs, the vertical distribution and dynamics of fine roots, and the decomposition rate of soil organic C. The loss of C from the deep organic and mineral soil has more than offset the C accumulation in the litter and upper organic soil horizons. In the litter and upper organic horizons, radiocarbon measurements show that increased inputs resulted in overall C accumulation, despite being offset by increased decomposition in some soil pools. To reconcile radiocarbon observations in the deeper organic and mineral soil layers, where most of the ecosystem C loss occurred, both a decrease in input of new root material and a dramatic increase of decomposition rates in centuries-old soil C pools were required. Therefore, with future increases in nutrient availability, we may expect substantial losses of C which took centuries to accumulate.

Key words: nitrogen; phosphorus; radiocarbon; carbon dynamics; tundra; decomposition.

Introduction

Artic tundra soils hold at least 5–6% of the world's soil carbon, although recent estimates suggest that this amount is at least six times higher (IPCC 2001; Horwath 2007). In Europe, these ecosystems are subject to anthropogenic N deposition, and although the rates are generally low (0.1 g m^{-2} y^{-1}), a few places receive up to 1 g m^{-2} y^{-1} (Woodin 1997). Additionally, arctic tundra soils are warming rapidly (Overpeck and others 1997; ACIA 2004). As this warming continues, it is expected to affect soil C storage both directly, through temperature responses in microbial decomposition, and indirectly, through feedbacks associated with nutrient availability, as well as, changing surface energy balance and plant species composition (Chapin and others 1995; Hobbie and Chapin 1998; Dormann and Woodin 2002; Weintraub and Schimel 2005; Van Wijk and others 2004). Many of these feedbacks are positive, such as the observed decreases in al-

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bedo (Chapin and others 2005) and increases in snow depth during the winter months (Sturm and others 2001, 2005), which lead to further increases in air and/or soil temperatures. Another important set of feedbacks is related to the faster decomposition of organic matter in warmer soils leading to increased nutrient availability (of about 10 g N m^{-2} $y^{-1)}$, higher productivity, and changes in plant community composition (Chapin and others 1995; Mack and others 2004). Nutrient addition generally has a positive effect on primary production in vascular plants in the arctic, although which species benefits most depends on the type of system (Van Wijk and others 2004; Dormann and Woodin 2002; Hobbie and others 2005; Weintraub and Schimel 2003). In acidic tussock tundra, nutrient addition often results in a shift in plant species composition from graminoid to shrub species (Chapin and others 1995; Chapin and Shaver 1996; McKane and others 1997; Shaver and others 2001). Shrub species produce lower quality litter and wood than graminoid species, perhaps resulting in slower decomposition (Hobbie 1996) and thus a negative feedback. However, shrub soils have been found to have higher rates of mineralization than their chemistry would predict (Weintraub and Schimel 2003).

All of these feedbacks together can influence ecosystem C storage, although they may do so in opposing ways. The balance of increased aboveground production and changes in decomposition will determine the overall effect of increased temperature and nutrient contents on soil C storage. In a study of moist acidic tundra designed to isolate nutrient availability effects, Mack and others (2004) found that nutrient addition, at levels comparable to expected increases in nutrient availability with warming, prompted C losses in the lower organic and mineral layers that far surpassed the increases in productivity and C accumulation in standing biomass, litter, and the soil surface (0–5 cm) organic layers. This increase in decomposition would be associated with even greater rates of N mineralization (approximately 137 g N m^{-2} if N mineralized is proportional to the C:N ratio).

We measured radiocarbon contents of archived samples from the Mack and others (2004) study to ascertain whether decomposition dynamics were altered by nutrient addition in ways not discernible from change in C inventory alone. Radiocarbon allows us to determine whether the observed changes in C stocks reflect altered inputs, decomposition rates, or a combination of both. It is especially important to determine how vulnerable large stores of old C stored deep in northern soils could be to increased decomposition under altered nutrient and temperature conditions.

Methods

The experimental site, part of the Toolik Lake, Arctic Tundra Long Term Ecological Research site in Alaska, is located in the northern foothills of the Brooks Range (68°38′N, 149°38′W; elevation 760 m). The experiment consists of four replicate 5 × 20 m blocks. The fertilized plots have received 10 g N m^{-2} y^{-1} as NH_4NO_3 and 5 g P m^{-2} y^{-1} as P_2O_5, since 1981. Moist acidic tussock tundra dominated by the sedge *Eriophorum vaginatum* was originally present in all plots and continues in the control plots. However, the nutrient addition plots have become dominated by the deciduous shrub *Betula nana*, which was originally present as a smaller proportion of the plant community (Shaver and others 2001). Roots and soil from control and experimental plots were collected in July 2000. Roots and litter were collected within each plot from five 20 × 20 cm quadrats by cutting down to the mineral soil with a knife. The quadrats were taken 1 m from the edge of the plot and were randomly arrayed along the 20 m length of the plot. Live roots were removed and separated by hand and sorted into coarse (>2 mm) and fine (<2 mm) size fractions. Roots and soil from the mineral horizon were collected from the surface of the mineral soil to the permafrost (~5 cm) using a 2.5 cm diameter corer. A 5 × 5 cm monolith was collected from the edge of the hole for the organic soil analysis. The total organic soil was separated by depth into litter (dead recognizable plant material), 0–5 cm organic (O1), and greater than 5 cm organic (O2) layers. Samples were dried at 65°C, ground, and stored. Further details are reported in Mack and others (2004).

Samples were combusted and the evolved CO_2 was cryogenically purified and converted to graphite using sealed zinc tube reduction and analyzed for radiocarbon content at the W.M. Keck Carbon Cycle Accelerator Mass Spectrometer facility at UC-Irvine (Southon and others 2004; Xu and others 2007). Radiocarbon data are reported as $\Delta^{14}C$, the deviation in parts per thousand (permil, ‰) of the $^{14}C/^{12}C$ ratio from that of a standard of fixed isotopic composition (0.95 times the $^{14}C/^{12}C$ of the oxalic acid I standard, decay-corrected to 1950). As reported, $\Delta^{14}C$ values are corrected for mass dependent isotope fractionation using the measured $^{13}C/^{12}C$ ratio and normalizing to a $\delta^{13}C$ value of −25‰ (Stuiver and Polach 1977). Negative $\Delta^{14}C$ values represent C old enough for radioactive

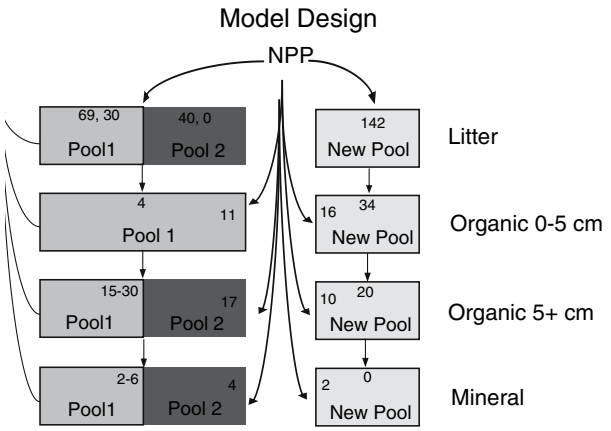

Figure 1. Model design. Pool 1 represents the entire pre-treatment C pool in the 0–5 cm organic horizon and the faster cycling C pool in the other layers. Pool 2 represents the slower cycling C pool. The New Pool contains C inputs following N + P addition. The *numbers above* represent NPP and SOM/DOC inputs in g C m^{-2} y^{-1}. Where there are *two numbers*, they represent pre- and post-treatment inputs, respectively.

decay to have occurred. Due to atomic weapons testing, the $\Delta^{14}C$ signature of atmospheric CO_2, and hence fresh vegetation inputs to litter and soils, reached a high in 1963 near about 900‰ in the northern hemisphere and has been declining since. Between 1981 and 2000, these values declined from 257 to 90‰ at a rate of approximately 6–10‰ y^{-1} (Levin and Kromer 2004). Consequently, differences in $\Delta^{14}C$ within ecosystem C pools reflect differences in the timing of when C was fixed, as well as differences in decomposition time. The accuracy of radiocarbon analyses is ±0.3% (or 3‰). The turnover time of soil organic matter (SOM) was determined from a model that tracks C additions to and losses from organic and mineral soil horizons, and best reproduces the observed C inventory and $\Delta^{14}C$ content of SOM in control and fertilized soils in 2000 (Gaudinski and others 2000; Figure 1). For the control site, we assumed steady state conditions over the past 19 years (that is, no net gain or loss of carbon in each horizon), and represented organic matter as either a single, homogeneous pool (upper organic layer), or, where required to match observations, multiple organic matter pools with different characteristic turnover times (other layers). Inputs for the steady state model (control) were calculated as the C in each SOM pool divided by its turnover time.

Organic matter in fertilized plots was assumed to have the same inputs, turnover times, and pool structure as the steady state model up to and including 1981, the initial year of simulation (Figure 1). To allow for changes in litter quality associated with vegetation change in fertilized plots, inputs in subsequent years were added to a separate ''New'' pool, except in the litter, where inputs into the graminoid pool (Pool 1) continued at a rate determined from measured aboveground net primary production (NPP). The post-fertilization increase in inputs was calculated as the overall observed increase in NPP (Mack and others 2004) divided by the length of the experiment. For tracking this new C, we assumed a 5-year transition period during which inputs into the original pools dropped to zero and inputs into the new pool increased to their constant final value.

Radiocarbon values in SOM reflect both the time spent in living plant tissues and the residence time of dead plant material in soils. Thus, failure to account for plant residence times can result in overestimation of decomposition rates from $\Delta^{14}C$ data (Perruchoud and others 1999). For model inputs into the litter layer, time spent in living plant tissues was set to be 3 years for the graminoid-dominated system and 7 years for the shrub-dominated system [estimates derived from Shaver and Chapin (1991)], with the increase in plant tissue lifetimes occurring gradually following fertilization at a rate of 1 year y^{-1} over 4 years. In all other soil horizons, the $\Delta^{14}C$ value of plant litter inputs was derived from the amount and age of root C at the time of input, as determined by the mean age of live roots in that layer derived from $\Delta^{14}C$ of live roots (Gaudinski and others 2001) and the amount of root production in that layer, assuming the amount of production was proportional to the root biomass in that layer (Nadelhoffer and others 2002). Although the root ingrowth cores used to produce these estimates have a number of biases (Vogt and Persson 1991; Fahey and Hughes 1994; Majdi and others 2005), this method of calculating root production produces deep horizon values more similar to estimates from minirhizotrons used in a nearby nutrient addition study (Sullivan and others 2007). Additional carbon inputs were required to satisfy the mass balance requirements of the model, as estimated root inputs were insufficient to support observed C inventories given the turnover times necessary to explain observed $\Delta^{14}C$ values. In these cases, we assumed the process involved downward transport of soil (SOM) or dissolved (DOM) organic matter, with the amount of material assumed to equal the difference between root inputs and the total C input required to support observed C stocks for the control plots at steady state. We assumed the time lag associated with these addition inputs was the same as for root inputs because the lags

associated with SOM, DOC, and root exudate inputs were not precisely known. Lastly, in the soil horizons where a two-pool model was necessary to reproduce the observations, Pool 1 represents the graminoid (litter layer) or faster cycling C pool (deep organic and mineral layers) and Pool 2 represents the shrub/moss (litter layer) or slower cycling C pool (deep organic and mineral layers). Inputs into the graminoid pool (Pool 1) continue after fertilization because there continues to be some graminoid production, but, to match observations, new shrub/moss litter had to go into a separate pool than old shrub/moss litter.

We ran the model iteratively for the upper organic, lower organic, and mineral horizons using the range of possible values for the turnover time and pool size for Pools 1 and 2 and the ''New'' Pool (which accumulated during the experiment). We report the range of values which best predict observed C and $\Delta^{14}C$ values for each soil layer. In the litter horizon, we used the 1982 ratio of graminoid to shrub NPP to determine the pool sizes and allowed only solutions with input values within 25% of those measured. We report the range of values that match the observed C inventory in 1981 and 2000 and $\Delta^{14}C$ content in 2000 within 1% for all control layers, 2% for the fertilized litter, and 6% for all other layers. We include only the steady state values that allowed us to match observations in both control and fertilized cases. The effects of fertilization on root radiocarbon were analyzed by horizon using one-way ANOVAs. Soil carbon changes were analyzed using a two-way ANOVA, with depth and treatment as the independent variables. Statistical analysis was performed using SPSS statistical software.

Results

Roots: Root biomass distribution and radiocarbon signatures changed in response to nutrient additions (Figure 2A). Mack and others (2004) found that depth-integrated root biomass did not change, but a large portion of root biomass shifted from the lower horizons to the upper horizons in response to nutrient addition. In the litter layer, ^{14}C of live roots, which we infer reflects root age (Gaudinski and others 2001), was consistent with ages that increased from 1 year in the control plots to 7 years in the fertilized plots ($P = 0.10$, $F_{1,4} = 4.40$). No significant change in ^{14}C-derived root age was observed in the surface organic horizon (13 years in the controls and 11 in the fertilized plots). In contrast, the ^{14}C-derived root age in the deeper organic layer decreased from 15 (control) to 8 (fertilized)

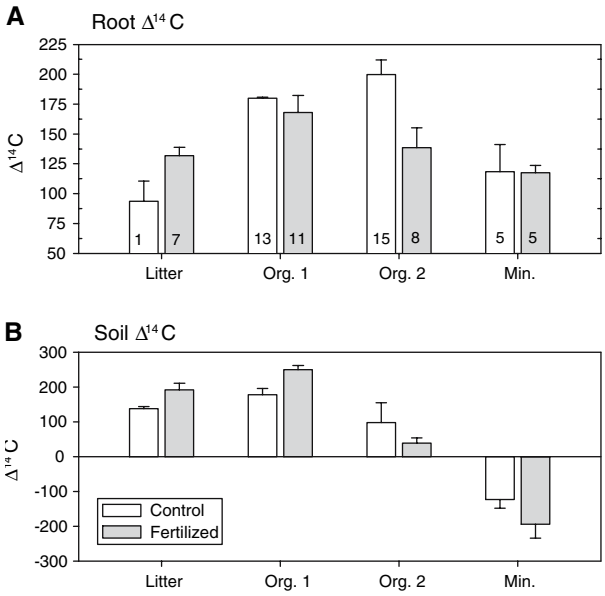

Figure 2. (**A**) $\Delta^{14}C$ values of bulk roots from Toolik. Overall there were no whole profile changes in root age, but in the litter fertilized roots were older ($P = 0.10$, $F_{1,4} = 4.40$) and in the deep organic soil fertilized roots were younger ($P = 0.04$, $F_{1,4} = 8.81$). The *numbers in the bars* represent the mean age (in years) of root C. (**B**) $\Delta^{14}C$ values of bulk soil from Toolik. Treatment × depth effects were significantly different (depth $P < 0.001$, $F_{3,24}$=65.92, treatment $P = 0.960$, $F_{1,24}$=0.00, treatment*depth $P = 0.036$, $F_{3,24}$=3.33, two-way ANOVA). The $\Delta^{14}C$ value for atmospheric CO_2 in the year of sampling (2000) was 90‰.

years ($P = 0.04$, $F_{1,4} = 8.81$). Root ages in the mineral soil were unchanged (5 years).

Soil: Changes in SOM stocks in fertilized plots greatly exceeded those for roots (Mack and others 2004). Both C content and ^{14}C decreased with depth in soils (Figure 2B). We found higher positive ^{14}C in the litter and the surface organic horizon in response to fertilization, whereas in the deeper organic and mineral horizons ^{14}C levels were lower in the fertilized plots (Figure 2B). There was a significant relationship between ^{14}C and treatment when changes in ^{14}C with depth were accounted for (depth $P < 0.001$, $F_{3,24} = 65.92$, treatment $P = 0.960$, $F_{1,24}$=0.00, treatment × depth $P = 0.036$, $F_{3,24}$=3.33, two-way ANOVA).

Explaining the high ^{14}C values observed in the upper layers of the treatment plots requires both increased stores of recent organic matter and decreased decomposition of pre-treatment shrub/moss organic matter (Table 1). The litter layer originally had a turnover time of about 4 years for graminoid litter and 6 years for shrub/moss litter. Following N

addition, turnover times of pre-treatment shrub/moss litter increased to 20–30 years, whereas the turnover times for graminoid material remained similar to control values. Post-treatment shrub inputs had slightly faster turnover times (3–4 years) than the controls (6 years) (Table 1). Due to increased input rates, there was a build-up of recent organic matter, despite the similar or even faster turnover times for most of the pools (Figure 3). Additionally, to match the measurements, it was necessary for post-fertilization shrub inputs to have different turnover times than pre-treatment shrub inputs (that is, to be modeled as a separate pool).

The surface organic horizon initially had a turnover time of 45 years, but after fertilization, the turnover times of the original material had to drop to 29–32 years to reproduce both the observed C and ^{14}C values (Table 1, Figure 4). To explain the measurements, nearly all of the post-fertilization inputs had to be retained in the model; that is, most of what accumulated between 1981 and 2000 remained relatively undecomposed (Table 1, Figure 3).

In the deeper organic horizon (>5 cm), a two-pool model was necessary to reproduce the observations. Solutions were found when the proportion of C in the younger pool (Pool 1) ranged from 0.5 to 0.9, whereas in the mineral horizon solutions were found when Pool 1 C proportional abundance ranged from 0.5 to 0.7. The remainder of the C is assumed to be in Pool 2 prior to treatment. In the deeper organic soil, the average turnover time was approximately 90 years, which was divided into a faster pool (Pool 1) with turnover time of 25–75 years and a slower pool (Pool 2) with turnover time of 100–900 years. After fertilization, Pool 2 remained unchanged, whereas the turnover time of Pool 1 dropped from 25–75 to 5–30 years, thus decreasing dramatically in size since 1981 (Table 1, Figure 3). Like the upper organic horizon, most of the newly added C was retained (Table 1).

Similarly, the mineral horizon had a mean turnover time of 1,200–1,300 years. To match post-treatment observations, it was divided into two pools with turnover times of 150–600 years (Pool 1), and 2,000–4,000 years (Pool 2). Again, reproducing observed C losses and ^{14}C values in the fertilized plots required dramatic decreases in turnover times, to 10–20 years (Pool 1), whereas turnover times for Pool 2 remained long (100 + years). As in the layer above it, most of the newly added C was retained (Table 1). In both layers, it was the pool with the faster turnover (decades-centuries vs. centuries-millennia) which experienced the dramatic C losses (Figure 3).

Given the reduction in soil C inventory, SOM influxes to the lower layers following fertilization were reduced as much as possible, but rapid acceleration of decomposition in Pool 1 was still necessary to explain observations. In this model, SOM inputs are indistinguishable from root inputs and use the same time lag. We did not know the exact rate of root inputs, thus some of the assumed SOM inputs could be an underestimation of root production. Given the amount of C in these layers relative to inputs, the assumed time lag was inconsequential and, when changed, did not alter the overall findings.

Discussion

C inventory and ^{14}C content measurements integrate multiple processes. For example, the decline in C storage and ^{14}C content in the deeper soil may result from a combination of: (1) a decline in root litter inputs into these layers, (2) changing root turnover times, and (3) the loss of the more labile C, leaving behind the older, recalcitrant C. Therefore, we used our radiocarbon measurements and model results along with previously published data from this experiment to distinguish between

Table 1. Estimated Turnover Times (years)

Layer	Pool 1 Control	Pool 1 Fertilized	Pool 2 Control	Pool 2 Fertilized	New Pool	Roots control	Roots fertilized
Litter	4	1–7	6	20–30	3–4	1	7
<5 cm depth organic	45	29–32	–	–	200 + (C stored)	13	11
>5 cm depth organic	25–75	5–30	100–900	100+	5 + (most C stored)	15	8
Mineral	150–600	10–20	2,000–4,000	100+	5–100 + (most C stored)	5	5

Pool 1 represents the entire pre-treatment C pool or, when 2 pools are present, the faster cycling C pool, whereas Pool 2 represents the slower cycling C pool. The control is assumed to be in steady state (Pools 1 and 2 do not change inventory with time). In the control scenario, Pool 1 contains 50–70% of the total C in the mineral horizon and 50–90% in the >5 cm organic horizon. Pool 2 contains the remaining C. The New Pool represents post-1981 C inputs in the fertilized treatment. Numbers greater than 20 y in the New Pool do not reflect actual turnover times, but rather, indicate C is being retained. The amounts of C in these pools are seen in Figure 3.

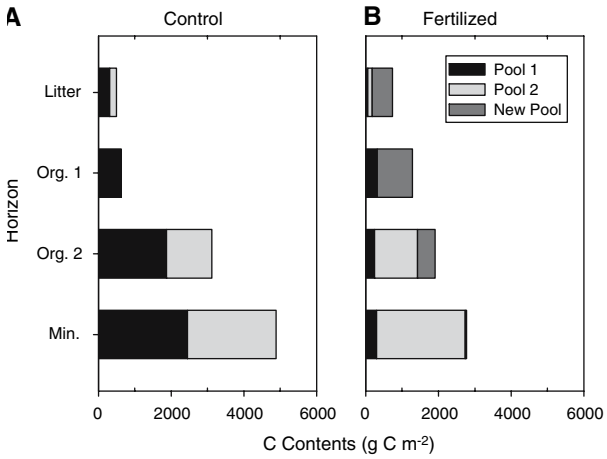

Figure 3. Soil C contents. The graph on the left represents the unfertilized plots and the graph on the right represents the fertilized plots. Turnover times are shown in Table 1. For the litter Pool 1 N + P's turnover time was 2 years, Pool 2 N + P's was 26 years, and New Pool's was 4 years. For the deep organic Pool 1 SS's turnover time was 50 years, Pool 2 SS's was 280 years, Pool 1 N + P's was 15 years, Pool 2 N + P's was 210 years, and New Pool's was 25 years. For the mineral soil organic Pool 1 SS's turnover time was 440 years, Pool 2 SS's was 3,000 years, Pool 1 N + P's was 10, Pool 2 N + P's was 4,000 years, and New Pool's was 40 years.

changes in inputs and those due to altered decomposition of the pre-1981 material.

Our analysis was constrained by the fact that C accumulation in litter and surface organic horizons since fertilizer treatment began in 1981 will have ^{14}C contents reflecting both decomposability of the added litter and changes in plant biomass lifetimes. For example, fast turnover (<10 years for combined plant + decomposition times) means that the most recently added material forms the bulk of the C pool because additions in the first decade following 1981 having largely decomposed. The accumulated SOM pool would have a ^{14}C value close to average atmospheric values over the last decade (1990–2000), between 90 and 110‰. In contrast, accumulation of all litter added since 1981, without any decomposition, would result in a SOM radiocarbon value close to the two-decade atmospheric mean of approximately 140‰. To produce the same carbon inventory in 2000 would require substantially higher C inputs in the fast turnover case, compared to the slow decomposition case. Our radiocarbon measurements incorporate both the changes in the SOM present prior to the fertilizer treatments and the accumulation of post-fertilization plant inputs to the SOM pool (tracked as New Pool in our model). Changes in the decomposition rate of SOM from either of these pools will affect the overall C and ^{14}C inventories.

Upper soils: The C storage and ^{14}C values in both the litter and surface organic soil increased with fertilization. Other studies have shown that nutrient additions in acidic tussock tundra caused increased litterfall (Mack and others 2004) and a species shift (Chapin and others 1995; Chapin and Shaver 1996; McKane and others 1997; Shaver and others 2001) associated with decreased litter quality (Hobbie 1996), which both lead to C accumulation in the litter layers. Shifting patterns of belowground allocation, including increased root biomass in the upper layers of fertilized plots and decreased biomass in the lower layers, have also been documented (Mack and others 2004). Changes in root biomass and depth distribution likely reflect the change in plant species composition, whereby shrubs have different belowground C allocation strategies than their graminoid predecessors (Jackson and others 2000). The increase in root inventory in the surface layer was coupled with a possible increase in the radiocarbon values of live root C (Table 1, Figure 2A), suggesting an overall increase in root longevity and a longer time lag for inputs from woody/shrub root litter sources to SOM. In consequence, overall root inputs to this horizon would be lower following fertilization, despite the increase in biomass. It is unclear what the actual inputs would be in any horizon because radiocarbon values reflect the mean age of the root C at a given time point. From minirhizotron studies, we know that some roots live several years, whereas others live days and are not captured in a biomass harvest, thus skewing the data toward lower production estimates and higher turnover times (Tierney and Fahey 2002; Madji and others 2005). However, root ingrowth cores also miss any production or mortality that occurs between sampling dates (Nadelhoffer and others 2002; Madji and others 2005). Using the radiocarbon estimates, assuming that productivity is equivalent to biomass × turnover time^{-1}, litter layer root production in the fertilized plots was only 36% of that in the controls. Like the litter layer, root biomass in the upper organic soil was increased, but little change was seen in the turnover times, suggesting an increase in root C inputs proportional to the change in biomass (Table 1, Figure 2A).

The SOM radiocarbon signatures were higher in the fertilized litter and upper organic horizons (Figure 2B), reflecting a combination of increased time spent in living plant tissues, accumulation of C, since 1981, and changes in decomposition rates of the SOM present before treatment began (Ta-

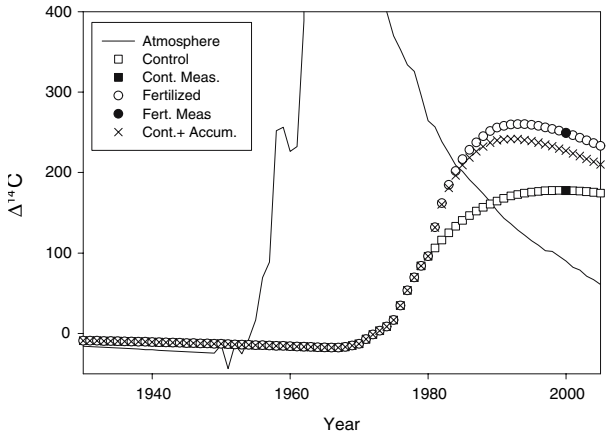

Figure 4. Modeled $\Delta^{14}C$ curves for the O 0–5 cm horizon. *Open squares* represent the organic 0–5 cm horizon $\Delta^{14}C$ in the control plots, *open circles* represent the fertilized plots, and Xs represent what $\Delta^{14}C$ would be if turnover times for Pools 1 and 2 stayed the same and new C simply accumulated. The *filled circle* represents the measured fertilized value and the *filled square* represents the measured control value. To obtain the appropriate fertilized $\Delta^{14}C$ value, we must assume some enhancement of decomposition of pre-1981 material.

ble 1, Figure 4). A decrease in decomposition of pre-treatment shrub/moss litter was necessary to explain the changes observed in the litter, whereas decomposition rates of newer more labile material either remained the same or increased. A decline in old shrub litter decomposition is consistent with frequent observations that high quality (low lignin) materials are destabilized by N additions, whereas lignin-rich litter is stabilized (Berg 1986; Fog 1988; Berg and Matzner 1997; Carreiro and others 2000; Sinsabaugh and others 2002; Knorr and others 2005). Berg and Matzner (1997) suggest that the stage of decomposition is critical in determining the overall effects of N addition. They found that N enhanced decomposition in early stages where it is dominated by cellulose and solubles, whereas in later stages, where it is dominated by more recalcitrant compounds, N hindered decomposition (Berg and Matzner 1997). Direct observations of lignin-degrading and cellulose-degrading enzymes also support this claim (Carreiro and others 2000; Sinsabaugh and others 2002; Frey and others 2004). If microbial activity is experiencing N limitation, N addition would clearly result in enhanced decomposition of easily decomposable C. There are at least two possible reasons why N may lead to increased storage of recalcitrant compounds: (1) White rot fungi have the ability to down-regulate the production of lignolytic enzymes in the presence of N, and (2) N may react with lignin and aromatic compounds making more recalcitrant compounds (Berg and Matzner 1997; Nommik and Vantras 1982). In tundra soils, where decomposition is limited by both nutrient availability and temperature, it appears that deeper soil horizons contain substantial amounts of accessible carbon, despite their age.

However, moss decomposition tends to proceed more slowly than lignin-content alone would indicate (Hobbie 1996) and may not be affected by nutrient additions in the same way. Moss production virtually ceased following fertilization, but given moss decay rates, some pre-treatment material could have remained in the litter layer, thus explaining the long turnover times of litter in Pool 2 following treatment, as well as why it was necessary to treat post-fertilization shrub inputs as a separate pool. The decrease in turnover times of the post-treatment shrub litter pool compared to the control shrub/moss pool could be due to the loss of slow-decaying mosses following N + P addition or an increase in decomposition, either due to fertilization, or to the loss of mosses, which can reduce overall decomposition rates due to the production of tannins (Painter 1991).

To match measured ^{14}C values in the upper organic horizon following treatment, it was necessary to accelerate decomposition of the pre-treatment material (Table 1, Figure 4). Therefore, the increased C inventory in the upper organic layer occurred despite increased decomposition of pre-treatment litter and indicates that inputs into this layer were higher than suggested by the change in C inventory alone. Turnover times of the New pool were very long, which implies that nearly all new C inputs were stored and also suggests that inputs into this layer following treatment were likely higher than we assumed here. Nonetheless, even when we increased new inputs, it was still necessary to accelerate decomposition in the pre-treatment material to explain the observations.

Deep soils: C stocks as well as ^{14}C values in the lower organic and mineral horizons declined substantially in response to N + P addition. Declines in root inventory in the deep soils were accompanied by either a decrease in apparent root lifetime or no change (Table 1, Figure 2A). In nutrient addition plots, fewer roots with shorter lifetimes were found in the deep organic horizon. The combination of a smaller pool with faster turnover suggests that total C allocation to this horizon could remain unchanged. In the fertilized plot mineral horizons, fewer roots with no change in lifetimes indicate C allocation to this layer has decreased. Because root production was low in relation to the SOM storage

in these horizons, any changes in C inventory resulting from shifts in root allocation were relatively small. As a result, we were unable to match measured and modeled C and ^{14}C values without assuming additional inputs. SOM/DOC input rates tended to be similar to root input rates in most horizons. This suggests that either SOM/DOC transport is an important C transfer pathway in these soils or that root inputs are decoupled from root stocks and are thus greater than calculated here.

Radiocarbon signatures in SOM from the lower soil horizons decreased with fertilization (Figure 2B), which could reflect a combination of the loss of high ^{14}C root inputs, altered root turnover times, and the loss of C through changes in SOM decomposition rates. As roots, like leaves, are comprised of recently fixed C, a reduction in root inputs into the deeper soil horizons would result in less C with the ^{14}C signature of the recent atmosphere entering the deep SOM pools. However, root production supplies only 34 g C m^{-2} y^{-1} to the whole profile (Nadelhoffer and others 2002). Only 74 g C m^{-2} of root biomass were lost in response to fertilization in the deep organic soil and 20 g C m^{-2} were lost in the mineral soil, as compared to total SOM losses of 1,169 and 2,046 g C m^{-2} from these layers, respectively. Although the changes in root production, distribution, and turnover must have contributed to the changes in ^{14}C of the soil organic matter, the direct effect of decreased root inputs alone is insufficient to explain the loss of SOM or the change in ^{14}C signature in the deeper soil horizons. To explain the amount of C loss and changes in ^{14}C signatures, it was necessary to dramatically accelerate decomposition, in spite of using the lowest allowable input rates in the calculations.

Modeling C and ^{14}C requires some acceleration of decomposition rates of pre-treatment organic matter in response to fertilization in all horizons, even ones in which C inventory increased. What caused increased decomposition in treatment plots and might the same results be expected in other ecosystems? Nitrogen concentration directly influences decomposition when there is enough labile C to support microbial demands (Haynes 1986). As microbial activity in this system is normally considered to be N limited (Hobbie and others 2002) and labile C compounds are abundant in this system due to conditions unfavorable to decomposition (Weintraub and Schimel 2003), increased N abundance can accelerate decomposition, especially of plant residues which have not yet lost their cellulose or been humified (Haynes 1986).

The dramatic acceleration of decomposition rates in deep soil OM is interesting because one would expect decomposition there to be more limited by low temperatures and high moisture levels than the layers above it and, therefore, nutrient limitation would play a lesser role. Why should the nutrient additions affect the lower layers so much more than the upper layers? Laboratory incubations of grassland soils have found that deep soils were more responsive to N and P addition than surface soils; however, they are also more sensitive to temperature (Fierer and others 2003). Therefore, the C loss may be a result of nutrient limitation or a change in the soil environment. Winter warming of soils, particularly deep soils, beneath the shrubs has been observed and increased CO_2 efflux during the winter is possible (Sturm and others 2001, 2005). However, winter CO_2 efflux rates in shrub tundra range from 20–50 mg/m^2/d (Sturm and others 2005), and with an average winter length of 235 days (NOAA/NCDC), therefore soil respiration can only account for 90–225 g C m^{-2} loss over the course of the experiment. Assuming graminoid tundra respires an equal or smaller amount, even a doubling of the maximum rate (which we might expect with 5–10°C warming) is insufficient to account for observed C loss rates in fertilized plots. Therefore, although temperature may play a small role, the primary reason for enhanced decomposition rates is probably the alleviation of N limitation on microbial activity.

Conclusions

Increased nutrient availability accelerated decomposition of labile pre-treatment organic matter. Adding ^{14}C measurement to changes in C stocks following fertilization allowed us to quantify changes in decomposition that were not observed from C inventory alone. The majority of C lost was not the youngest, most labile C, nor was it the oldest, most stabilized C, but instead, losses were dominated by the C in deep layers with an average age of approximately 300 years. Although not the most recalcitrant C in the soil, it has accumulated over several centuries and is being lost at greatly accelerated rates following fertilization, which could also prove a positive feedback to accelerated C loss under a scenario of warming and increased soil nutrient turnover. As 90% of the vast amount of C stored in arctic regions is in the soil (McKane and others 1997) and these regions are experiencing significantly increased temperatures (Serreze and others 2000), N turnover will increase, leading to additional losses of centuries-old soil C above

those due to warming alone. These losses will offset, and perhaps exceed, expected increases in NPP.

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