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Pulse-labeling studies of carbon cycling in arctic tundra ecosystems: Contribution of photosynthates to soil organic matter

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[1] To increase our understanding of carbon (C) cycling and storage in soils, we used ^{14}C to trace C from roots into four soil organic matter (SOM) fractions and the movement of soil microbes in arctic wet sedge and tussock tundra. For both tundra types, the proportion of ^{14}C activity in the soil was 6% of the total ^{14}C-CO$_2$ taken up by plants at each of the four harvests conducted 1, 7, 21, and 68 days after labeling. In tussock tundra, we observed rapid microbial transformation of labile C from root exudates into more stable SOM. In wet sedge tundra, there appears to be delayed or indirect microbial use of root exudates. The net amount of ^{14}C label transferred to SOM by the end of the season in both tundra types was approximately equal to the amount transferred to soils 1 day after labeling, suggesting that transfer of ^{14}C tracer from roots to soils continued through the growing season. Overall, C inputs from living roots contributes 24 g C m^{-2} yr^{-1} in tussock tundra and 8.8 g C m^{-2} yr^{-1} in wet sedge tundra. These results suggest rapid belowground allocation of C by plants and subsequent incorporation of much of this C into storage in the SOM. *INDEX TERMS:* 1615 Global Change: Biogeochemical processes (4805); 1851 Hydrology: Plant ecology; 1890 Hydrology: Wetlands; 9315 Information Related to Geographic Region: Arctic region; *KEYWORDS:* soil organic matter, microbial biomass, roots, photosynthates, Arctic tundra, ^{14}C-labeling

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1. Introduction

[2] Our understanding of the dynamics of carbon (C) cycling and storage, especially in soils, is incomplete and must be improved before we can make accurate predictions of ecosystem responses to climate change scenarios. An important aspect of the soil C cycle that is poorly understood is the fate of C inputs from roots to soil. Uncertainties include: (1) rates of transfer from plants to soils and soil microbes; (2) pathways of movement between roots, microbes, and soils; (3) and contributions to long-term storage via incorporation into recalcitrant soil organic matter (SOM) fractions.

[3] Determining the rate at which C is allocated belowground is critical to our understanding of the contributions of root exudates to C cycling and storage. If new C is readily available to soil microbes, then we would expect that these inputs may be driving rates of microbial respiration and that older SOM C may be a less important substrate. Previous research in agricultural and natural ecosystems has revealed rapid belowground allocation and incorporation of ^{14}C into soil microbes and bulk soils [*Norton et al.*, 1990; *Wieder and Yavitt*, 1994; *Rattray et al.*, 1995; *Minoda et al.*, 1996; *Megonigal et al.*, 1999], indicating that root-derived C is in fact an important substrate for microbes. Furthermore, several studies have shown that plants grown under elevated CO$_2$ significantly increase belowground allocation in association with increased plant biomass as well as higher microbial respiration [*Zak et al.*, 1993; *Cotrufo and Gorissen*, 1997; *Mikan et al.*, 2000; *Van Ginkel et al.*, 2000]. These patterns of belowground C allocation suggest a direct relationship between rates of plant productivity and microbial assimilation of C.

[4] Clearly, soil microbes living in the rhizosphere are likely to play a critical role in determining the fate of new C inputs from roots and to be an important intermediary pathway in C cycling and storage. Carbon inputs to soils in the form of root exudates have been characterized as primarily consisting of labile carbohydrates [*Curl and*

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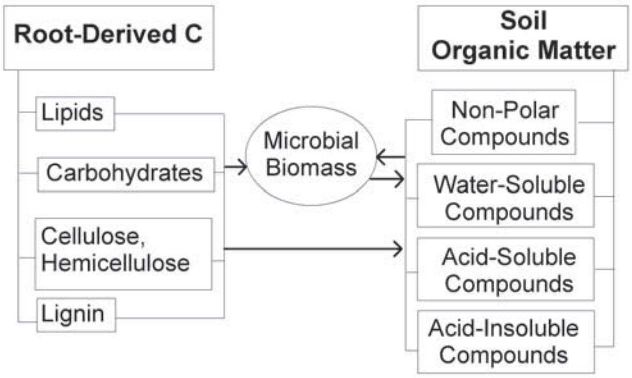

Figure 1. Conceptual diagram showing potential pathways of C flow from roots into and through the soil microbes and SOM in tundra soils.

Truelove, 1985]. On the other hand, the majority of the C in SOM tends to be predominantly in the form of intermediately to highly complex C compounds. If new C inputs in the form of root exudates are important to C storage, then this root exudate C must eventually be transformed into complex compounds, presumably as a result of the production of microbial metabolites binding with existing organic [*Hedges*, 1988] and mineral compounds in the soil [*Torn et al.*, 1997]. However, in addition to microbial processing, it is also likely that direct incorporation of new C inputs from roots into SOM also occurs, resulting in either storage or cycling through the microbial biomass at a later time.

[5] Elucidating the dynamics of C cycling and storage in soils is particularly important in the Arctic, which has been predicted to experience the greatest and most rapid effects of global climate change [*Lashof*, 1989]. Arctic soils account for 13–20% of the global soil C [*Post et al.*, 1982; *Billings*, 1987; *Michaelson et al.*, 1996] as a result of C accumulation in thick organic soil horizons at rates of 10–100 g C m^{-2} yr^{-1} [*Chapin et al.*, 1980; *Oechel and Billings*, 1992].There is concern that warmer conditions in the Arctic could stimulate mineralization of this C, resulting in significant fluxes of CO_2 and CH_4 to the atmosphere and creating positive feedbacks to greenhouse gas accumulation [*Shaver et al.*, 1992]. However, until we achieve a better understanding of C dynamics in soils, including the fate of root-derived C, we will not be able to accurately predict the impacts of global climate change on the C cycle.

[6] To improve our understanding of C dynamics in arctic ecosystems, we conducted a ^{14}C pulse-labeling experiment to investigate the contributions of recently fixed plant C to soil C pools in plant-soil mesocosms of two tundra types: moist tussock tundra and wet sedge tundra. These two tundra types account for most soil C in the Arctic [*Bliss and Matveyeva*, 1992]. Our objectives were to quantify rates of C transfer from living plants into soils, to determine the pathways through which C enters the SOM, and to quantify the proportion of C inputs stored in recalcitrant SOM pools. A conceptual model depicting the pathways that we hypothesized i.e., C would move between roots, soil microbes, and SOM is presented in Figure 1. Additional data on the distribution of ^{14}C among C pools in this experiment are presented in the companion paper on CH_4 (J. Y. King et al., Pulse-labeling studies of carbon cycling in Arctic tundra ecosystems: The contribution of photosynthates to methane emission, submitted to *Global Biogeochemical Cycles*) as well as in plants (K. J. Nadelhoffer, et al., manuscript in preparation, 2002), and in CO_2 and soil water (G. W. Kling, et al., manuscript in preparation, 2002).

2. Methods

2.1. Study Materials

[7] Intact cores of soil and vegetation from tussock tundra and wet sedge tundra were collected at the Toolik Lake Long Term Ecological Research site on the North Slope of Alaska in August 1997. Tussock tundra cores were collected from moist hillslopes, and were centered around mature tussocks of *Eriophorum vaginatum*, the dominant sedge, with a minor component of evergreen and deciduous shrubs, forbs, and moss. Cores from wet sedge tundra were collected near the outlet of Toolik Lake where conditions are supersaturated, and were dominated by *Carex* species. Soils collected from both tundra types were comprised entirely of organic horizons. Detailed descriptions of the tundra types are given by *Shaver and Chapin* [1991]. Twelve cores of each tundra type were collected using a stainless steel corer with a diameter of approximately 27 cm. Soils were sampled down to permafrost, with an average depth of 31 cm, and placed in 20-l polyethylene buckets. These mesocosms were transported to Woods Hole, MA, where the ^{14}C-labeling experiment was conducted in controlled environment growth chambers.

2.2. Growth Chamber Conditions

[8] After placing the mesocosms in growth chambers, we induced plant senescence by gradually reducing air temperature from 10° to −4°C and decreasing photoperiod from 12 to 0 hour. The mesocosms were then held in continuous darkness at −4°C for 1 week, during which time soils froze completely. To simulate the start of the growing season, temperature and light were gradually increased to 10°C and 24 hour daylight over the course of a week. Full-light conditions were maintained for 2.5 weeks, and then the chamber was placed on a diurnal schedule of 10°C and full lights for 16 hours, followed by a gradual reduction to 5°C and 50% full light. After subjecting the mesocosms to these conditions for 9.5 weeks, the end of the growing season was simulated by lowering the temperature and light levels. Over a period of 3 weeks, the photoperiod was gradually reduced to 10 hours of light and air temperature was reduced to 6°C with overnight freezes.

[9] Full-light conditions in the chambers produced photosynthetically active radiation (PAR) levels between 800 and 1000 μmol photons m^{-2} s^{-1} at the surface of the plants, approximately the light saturation level for tundra plants. With these full-light conditions and growth chamber air temperatures of 10°C, the average soil temperature was 15.2°C. Air temperatures in the field averaged 11°C in July at 3 m above the ground, and soil temperatures at 10 cm depth averaged 7°C in tussock tundra and 9°C in wet sedge tundra (Shaver et al., unpublished data 1997, 1999, 2000).

Thus our soil temperatures were considerably warmer than field conditions. In tussock tundra mesocosms soil, water levels were maintained at approximately 5 cm below the surface and in wet sedge mesocosms at approximately 2 cm above the soil surface.

2.3. ^{14}C Pulse-Labeling

[10] Labeling began on the 52nd day of the growing season, when plants were near maximum biomass. Three replicate mesocosms of each tundra type were assigned to four harvest periods. Mesocosms in each block were labeled on the same day, with all labeling occurring within a 10-day period. Prior to labeling, photosynthesis and ecosystem respiration were measured using a LI-COR 6200 Infrared Gas Analyzer to calculate gross primary production (GPP). The mesocosms were pulse-labeled under a gas-tight, transparent Plexiglas cuvette by introducing 8 MBq of ^{14}C as $^{14}CO_2$ to the headspace and allowing the plants to assimilate the labeled CO_2 over a 1.5-hour period. The $^{14}CO_2$ was pumped into the cuvette after evolving from acidification of $NaH^{14}CO_3$ (55 MBq g^{-1} C) with 1 M HCl. During labeling, CO_2 concentrations were monitored with a LI-COR attached to the cuvette. CO_2 levels were maintained at or above 400 ppm by evolving CO_2 from an unlabeled bicarbonate solution. Following the labeling period, the $^{14}CO_2$ remaining in the cuvette was trapped by pumping the air through a 1 M NaOH solution while maintaining the headspace CO_2 level with additions of unlabeled CO_2. Samples of the headspace air were analyzed for $^{14}CO_2$ to determine the quantity of ^{14}C uptake.

2.4. Harvests and Soil Analyses

[11] Three mesocosms of each tundra type from different blocks were harvested 1, 7, 22, and 68 days after the ^{14}C labeling. The first three harvest periods occurred during peak growing season conditions with chambers set on a diurnal schedule. The final harvest of mesocosms, 68 days following labeling, occurred after mesocosms were senesced by reducing photoperiod and temperature. Soils and roots were subsampled by taking eight 2.5 cm diameter cores from each mesocosm. Roots were removed from soil cores for separate analysis, and root-free soil from all cores was combined and homogenized. A 5 g subsample of soil was taken to determine gravimetric soil water content on an oven-dried basis (reweighing after drying at 105°C for 48 hours).

[12] Microbial biomass C was determined by the fumigation-extraction method [*Vance et al.*, 1987]. In brief, approximately 15 g (wet weight) of root-free soil was extracted for 2 hours with 75 ml of 13.6 M K_2SO_4, while a second sample of similar mass was fumigated with purified chloroform for 24 hours prior to extraction. Extracts were filtered (Gelmen matricel membranes, 0.45 μm) and stored in polypropylene bottles at 4°C. Levels of ^{14}C in the extracts were determined by scintillation counting following addition of extract and Fisher Scintiverse II scintillation cocktail to 20 ml glass scintillation vials, overnight storage in the dark, and subsequent analysis on a Beckman Instruments LS 3801 liquid scintillation counter. Microbial ^{14}C was determined as the difference between the quantity of ^{14}C in the fumigated and unfumigated sample. No correction factor for extraction efficiency (K_{ec}) was applied to microbial ^{14}C calculations because the rate of incorporation of ^{14}C into the unextractable portion of the microbial biomass is unknown.

[13] Analysis of total organic carbon (TOC) in the extracts was performed on a Shimadzu TOC 5000. Microbial C was calculated as the difference between the TOC in fumigated samples and TOC in unfumigated samples. For comparisons with other estimates of microbial biomass, microbial biomass C was estimated using a K_{ec} value of 0.35 [*Sparling et al.*, 1990]. Specific activity was then calculated as the activity of ^{14}C in Bq g^{-1} C.

[14] Bulk soils were analyzed for total C and ^{14}C for each of the four functionally defined SOM fractions, following the methods outlined by *Ryan et al.* [1990]. As the soils sampled for our mesocosms comprised only organic horizons, we chose this proximate fraction analysis typically applied to plant tissues and detritus. The fractions included: nonpolar extractives (NPE), hot water-soluble (WS), acid-soluble (AS), and acid-insoluble (AIS). In brief, triplicate subsamples of approximately 2 g of finely ground, oven dried (50°C) soil were fractionated for each mesocosm. Each sample was taken through four sequential extractions, with residual soil dried at 60°C for 48 hours, weighed, and subsampled for C and ^{14}C analysis between extractions. Methylene chloride was used first to extract NPE compounds, including fats, oils, and waxes. The remaining soil was then extracted with hot water to remove the WS fraction containing bioactive carbohydrates and soluble phenolics. Finally, 13.6 M sulfuric acid was used to remove the AS fraction, comprising carbohydrates and cellulose, from the remaining soil. The remaining organic matter is considered to be the AIS fraction, or lignin. For each fraction, total C was measured on a Perkin-Elmer CHN Analyzer and ^{14}C activity was determined through oxidation on a Harvey Instruments OX-500 Biological Oxidizer and scintillation counting.

2.5. Data and Analysis

[15] The experiment was set up as a randomized complete block design, and data were tested using a mixed-model ANOVA in PROC MIXED [*SAS*, 2000], using LSD tests to identify where significant differences occurred when the main effect (harvest period) was significant. Means are presented with 1 standard error (SE). The statistical significance of all the tests was considered at the 95% confidence interval.

3. Results

3.1. Bulk Soils

[16] One day after labeling, ^{14}C was detected in soils in both tundra types (Figures 1a and 1b). For tussock tundra mesocosms, the ^{14}C recovered in soils did not change significantly over the course of the experiment, averaging 5.8 ± 0.4% of the total ^{14}C assimilated by plants during the 1.5 hours pulse-labeling period (Figure 1a). Rates of GPP for tussock tundra mesocosms at the time of labeling were 4.5 ± 0.37 g C m^{-2} d^{-1}. Therefore transfer of assimilated C to bulk soils occurred at a rate of 0.3 g C m^{-2} d^{-1} or 24 g C m^{-2} yr^{-1} (if similar rates of belowground allocation occur across an 80-day growing season). For wet sedge tundra

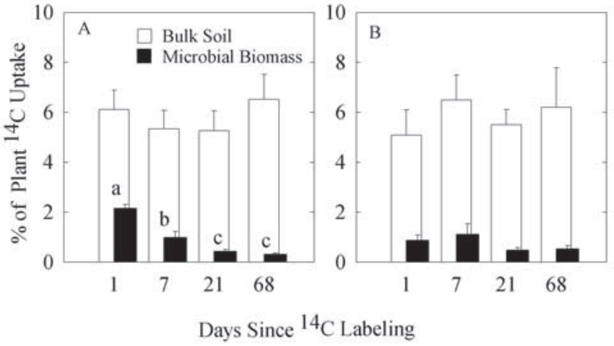

Figure 2. Distribution of ^{14}C in bulk soils and soil microbes as a percentage of total ^{14}C assimilated by plants during pulse-labeling with ^{14}CO in (a) tussock tundra and (b) wet sedge tundra for four harvest dates following pulse-labeling. Values are means (n = 3) with 1 SE. Significant differences ($P < 0.05$) within microbial biomass pools in tussock tundra among harvest dates are indicated by different letters. No significant differences were found within bulk soils in either tundra type or wet sedge microbial biomass among harvest dates.

mesocosms, similar percentages (5.8 ± 0.5%) of the total ^{14}C assimilated were recovered in soils during all the harvest periods (Figure 2b). Due to lower GPP rates in wet sedge mesocosms (1.8 ± 0.13 g C m^{-2} d^{-1}), transfer of assimilated C to soils occurred at a rate of 0.11 g C m^{-2} d^{-1} or 8.8 g C m^{-2} yr^{-1}, which was significantly lower than in tussock tundra.

[17] Some soil properties (e.g., C:N) differed between tundra types (Table 1). There were, however, no statistically significant difference in total organic soil C, soil C:N ratios, percent C in each SOM fraction, or microbial biomass C within tundra types across the four harvest periods (Table 1).

3.2. Soil C Fractions

[18] For tussock tundra soils, distributions of the soil C within each of the four different fractions remained stable over the course of the experiment (Table 1). AS and AIS fractions accounted for the greatest proportions of total soil C, which together amounted to 88% of total soil C. Water soluble and NPE fractions together accounted for the remaining 12% of the soil C. Comparisons of the specific activity across fractions within a harvest period (Table 2) provide information on the relative distribution of ^{14}C among compounds of varying complexity by harvest dates. Most of the ^{14}C was found in AS fractions across all the harvest dates in tussock tundra as well as wet sedge tundra. Initially, NPE and AIS fractions had approximately equal specific activity in tussock tundra, but by the 7-day harvest, the specific activity of the AIS fraction increased relative to the NPE fraction, presumably ^{14}C lost from the WS fraction was incorporated into AIS compounds. By the 21- and 68-day harvests, AS and AIS had approximately equal specific activities in tussock tundra. However, in wet sedge tundra, the NPE and AIS fractions remained equal throughout the experiment.

[19] To examine the dynamics of ^{14}C within fractions across the harvest periods, the percent of ^{14}C activity found within that fraction relative to the bulk soil activity was determined (Figure 3). Significant differences in the ^{14}C activity in tussock tundra soils were detected in three of the carbon fractions over the course of the experiment (Figure 3a). One day after labeling, about 40% of the ^{14}C in tussock soils was detected in the WS fraction. After 7 days, the percent of soil ^{14}C activity in the WS fraction decreased to half that of day 1 levels, suggesting losses of labile C during the first week at a rate of 8.3×10^{-3} g C m^{-2} d^{-1}. The AS pool also acquired 40% of total soil ^{14}C after 1 day. Increases in ^{14}C in the AIS fraction occurred simultaneously, as the percent of soil ^{14}C activity increased significantly from 12 to 22% between the first and second harvests, and then peaked at 33% of the soil ^{14}C activity by the end of the experiment. The ^{14}C activity in the NPE fraction was unchanged over the course of the experiment, and averaged 11% of the total soil ^{14}C activity. By the final harvest, the greatest percentages of soil ^{14}C activity were found in the AS (41%) and AIS fractions (33%).

[20] In contrast to tussock tundra, only one difference in ^{14}C activity within a wet sedge tundra soil fraction was detected with time (Figure 3b). Activity increased in the AIS pool from day 1 to day 21. As in tussock tundra, the mean percent of soil activity in the WS fraction at day 1 was nearly double that of day 7, but the decrease was not statistically significant in wet sedge. The NPE fraction contained approximately 16% of the activity, which was significantly greater than the percentage found in tussock tundra. The proportion of bulk soil ^{14}C activity found in the AS fractions did not change significantly over the course of the experiment.

3.3. Microbial Biomass

[21] Microbial biomass C in the tussock tundra mesocosms averaged 4.7 mg C g^{-1} soil C over the course of the experiment (Table 1). We found 35% of the ^{14}C transferred

Table 1. Soil Properties for Tussock Tundra and Wet Sedge Tundra Mesocosms[a]

				Soil C Fractions (% of Total C)			
Vegetation Type	Total C, mg C g^{-1} soil	C:N, g	Microbial Biomass, mg C g^{-1} soil C	Nonpolar Extractables	Water-Soluble	Acid-Soluble	Acid-Insoluble
Tussock tundra	35 (0.9)^{b}	35 (3.9)^{b}	4.7 (0.8)	6.4 (0.3)^{b}	5.6 (1.0)^{b}	38 (2.0)	50 (1.6)^{b}
Wet sedge tundra	38 (0.3)^{c}	16 (0.3)^{c}	3.3 (0.7)	8.0 (0.5)^{c}	3.5 (0.5)^{c}	42 (0.9)	47 (1.1)^{c}

[a] Values are means (n = 12) with 1 SE in parentheses. Different superscript letters within columns indicate significant differences ($P < 0.05$) between ecosystems types. No differences were detected within tundra types across harvest dates (four dates, three mesocosms per tundra type on each date).

Table 2. Specific Activity in Bulk Soils and SOM Fractions and in Microbial Biomass of Tussock Tundra and Wet Sedge Tundra Mesocosms at Harvest Dates Following ^{14}C Pulse-Labeling[a]

				Soil C Fractions, Bq g^{-1} soil C			
Tundra Type	Harvest Period	Bulk Soil, Bq g^{-1} soil C	Microbial Biomass, Microbial Bq g^{-1} soil C	Nonpolar Extractables	Water-Soluble	Acid-Soluble	Acid-Insoluble
Tussock tundra	1 day	1517 (35)	546 (112)^b	182 (105)^c	602 (37)^b	552 (56)^b	177 (17)^c
	7 day	1146 (95)	213 (45)^c	113 (65)^d	246 (63)^c	539 (5)^b	247 (30)^c
	21 day	1066 (137)	85 (22)^c	149 (86)^c	160 (14)^c	420 (59)^b	338 (78)^b
	68 day	1552 (108)	73 (21)^c	147 (85)^c	252 (57)^c	634 (36)^b	519 (48)^b
Wet sedge tundra	1 day	578 (120)	194 (38)^b	101 (65)^b	193 (32)	209 (58)	75 (11)
	7 day	676 (92)	79 (57)^c	169 (40)^c	84 (49)^c	304 (58)^b	119 (9)^c
	21 day	626 (67)	37 (19)^c	95 (60)^c	108 (30)^c	306 (44)^b	115 (26)^c
	68 day	797 (120)	37 (14)^c	152 (46)^c	145 (99)^c	349 (29)^b	151 (87)^c

[a] Values are means ($n = 3$) with 1 SE in parentheses. For microbial biomass activity, different superscript letters within columns indicate significant differences ($P < 0.05$) between harvests within tundra types. For soil C fractions, different letters within rows indicate significant differences ($P < 0.05$) between fractions within tundra types. No significant differences were found in the bulk soil activity across harvest within a tundra type.

to the bulk soil within the first day in the microbial biomass (Figure 2a), resulting in C uptake rates by microbes on the order of 8.4×10^{-2} g C m^{-2} d^{-1}. This was equivalent to 2.1% of the total ^{14}C uptake during labeling. The proportion of microbial ^{14}C decreased to 18% of the bulk soil activity after 7 days. Additional decreases in microbial biomass ^{14}C occurred between the second and third harvests, reducing the proportion of ^{14}C remaining in the microbial biomass to 8% of bulk soil activity, and it remained as such for the rest of the growing season.

[22] For wet sedge mesocosms, total microbial biomass C averaged 3.3 mg C g^{-1} soil C with no significant difference between harvests (Table 1). No significant difference in ^{14}C activity in the microbial biomass was detected between any of the four harvest periods (Figure 2b). Microbial biomass ^{14}C activity averaged 13.1% of the total soil ^{14}C activity, or 0.7% of the total ^{14}C assimilated.

4. Discussion

4.1. Rates, Quantities, and Time Course of Photosynthate Allocation

[23] Both tussock and wet sedge soils appear to be an immediate sink for recent photosynthate C. Belowground allocation of ^{14}C to roots and subsequent release into soils was detected within 24 h after labeling. Other researchers have detected ^{14}C tracers in soils and microbes between 0.5 and 24 hours after labeling [*Wieder and Yavitt*, 1994; *Minoda et al.*, 1996; *Megonigal et al.*, 1999].The proportion of total ^{14}C assimilated by tussock and wet sedge plants, which was found in the soils 1 day after labeling (6%) is within the range of most other ^{14}C tracer experiments. Between 1 and 10% of recent photosynthate C is allocated to soils in agricultural systems [*Keith et al.*, 1986; *Merckx et al.*, 1987; *Johansson*, 1992; *Swinnen et al.*, 1994; *Rattray et al.*, 1995], trees [*Gorissen and Van Veen*, 1988; *Mikan et al.*, 2000], and wetland plants [*Megonigal et al.*, 1999]. While C allocation to roots and soils in some annual crops has been found to decrease well below this level as the plants reach peak biomass and resources are instead allocated to reproduction [*Keith et al.*, 1986; *Jensen*, 1993], it seems reasonable that a large proportion of C fixed by perennial, clonal tundra plants at peak biomass would be allocated to roots. This would promote ramet expansion and acquisition of nutrients that can be stored over winter [*Berendse and Jonasson*, 1992; *Kielland and Chapin*, 1992] and support early spring growth [*Chapin*, 1980]. This late-season root growth is consistent with the findings of *Chapin et al.*

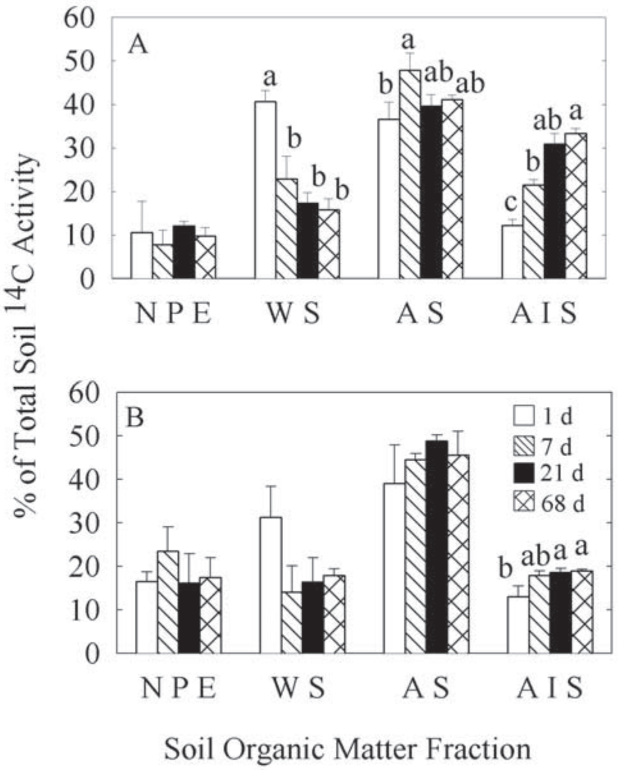

Figure 3. Distribution of ^{14}C in soil C fractions as a percent of bulk soil ^{14}C activity by harvest date for (a) tussock tundra and (b) wet sedge tundra mesocosms. Fractions are as abbreviated in Table 1. Values are means ($n = 3$) with 1 SE. Different letters indicate significant differences ($P < 0.05$) in ^{14}C activity within a fraction for each tundra type across harvest dates.

[1979], who observed a two- to four-fold increase in *E. vaginatum* root biomass as plants reached peak biomass in subarctic Alaska. Increases in belowground allocation to roots and soils over the course of the growing season have been found in trees as well [*Gorissen and Van Veen*, 1988].

[24] The proportion of total ^{14}C that was found in the soil remained unchanged for both tussock tundra and wet sedge tundra (Figures 2a and 2b) over the course of the experiment. Thus it appears that after the initial pulse of ^{14}C into the soils within the day after labeling, additional inputs are in balance with soil respiration for the remainder of the growing season. During the final harvest, 68 days after labeling and after plant aboveground biomass had senesced, the roots appeared to have just begun to senesced, suggesting that significant root turnover had not yet occurred. Therefore it appears that C inputs to soils likely occur in three phases: (1) an initial pulse following fixation in photosynthesis, (2) gradual release of complex compounds associated with growing roots over the remainder of the season, and (3) incorporation of structural material associated with root turnover and litterfall [*Shaver and Billings*, 1975; *Kummerow et al.*, 1988].

4.2. Movement of C From Labile to Recalcitrant SOM Fractions

[25] One day after pulse labeling, ^{14}C activity was found in all fractions (Figures 3a and 3b). The WS fraction, defined as containing primarily nonstructural carbohydrates and phenolics [*Ryan et al.*, 1990], is considered to be the most labile or biologically active fraction of the SOM. Given the rapid loss of ^{14}C activity in this fraction between the 1- and 7-day harvests, it appears likely that this fraction contains a large proportion of labile carbohydrates that fuel microbial activity, resulting in the production of CO_2, microbial tissue, and metabolites [*Johansson*, 1992]. The AS fraction, containing cellulose and hemicellulose [*Ryan et al.*, 1990], is likely to be formed in part by root mucilages associated with growing root tips. These secretions contain highly hydrated, complex polysaccharides, including pectin and hemicellulose [*Miki et al.*, 1980]. Therefore significant increases in the proportion of ^{14}C activity in the AS fraction between the 1- and 7-day harvests may be associated with allocation of ^{14}C to root growth. The trend toward decreases in the AS fraction in the 21- and 68-day harvests indicates that allocation of ^{14}C to root growth declines by 21 days following assimilation, likely as a result of overall loss of ^{14}C activity in the plants over time.

[26] By the end of the experiment, 2% of the ^{14}C assimilated by plants is stored in the AIS fraction. This fraction is defined as containing lignin [*Ryan et al.*, 1990] and other complex compounds that may result from secondary products formed during microbial decomposition [*Johansson*, 1992]. It therefore represents the most stable SOM. Significant increases in the percent of soil ^{14}C activity in the AIS over the course of the experiment suggest movement of C from other pools into this more recalcitrant pool. Therefore it appears that recent photosynthate C contributes to long-term soil C storage in tussock tundra ecosystems, which is in agreement with the findings by *Johansson* [1992] who showed that inputs of all forms of root derived material, including glucose, eventually contribute to stable SOM.

[27] The NPE fraction, containing fats, oils, and waxes [*Ryan et al.*, 1990], contained a consistent amount of ^{14}C label throughout the experiment. Sources of this ^{14}C activity likely include compounds found in root exudates [*Curl and Truelove*, 1985], as well as labeled microbial cell wall lipids [*Paul and Clark*, 1996]. The absence of observed movement of ^{14}C in this fraction obscures the turnover rate, and it is unclear if this pool remains stable over the growing season or if rapid turnover is obscured by replenishment from other C pools. Further investigation is needed to better understand the importance of this C fraction in the soil C cycle in tundra soils. Soil C movement between different fractions appears to be less dynamic in wet sedge tundra than in tussock tundra. In wet sedge tundra soils, we saw less microbial assimilation of ^{14}C over the course of the experiment (Figure 2b), as well as very little change in ^{14}C activity in the soil fractions (Figure 3b). A trend toward decreases in ^{14}C activity in the WS fraction and significant increases in the AIS fraction over the course of the experiment is consistent with the data shown for the tussock tundra. These changes may also be due to microbial metabolism of labile photosynthates and incorporation into stable SOM. However, the proportion of soil ^{14}C found in the AIS fraction is smaller, suggesting that the rate and/or quantity of root-derived C stabilized in more recalcitrant SOM is lower in wet sedge tundra than in tussock tundra. This may be attributed to lower microbial biomass (Table 1) or soil conditions less favorable for decomposition [*Gebauer et al.*, 1996].

4.3. Processing of Root C Exudates by Soil Microbes

[28] The microbial biomass accounts for small pools of C in tussock tundra and wet sedge tundra soils. Microbial biomass C in our mesocosm experiment was substantially lower than that reported by those who found seasonal means of 22.6 mg C g^{-1} soil C for tussock tundra and 21.3 mg C g^{-1} soil C for riparian C*arex* soils (which are similar to our wet sedge soils). These differences may be attributed either to differences in the depth of soil sampled or to differences in the soil conditions. *Cheng et al.* [1998] determined microbial biomass for the upper 5 cm of soil, which may have higher microbial activity than deeper soils, whereas we sampled the entire active layer (30 cm). Roots were abundant throughout the soil profile but most abundant at depth, as roots of Arctic grasses and sedges tend to follow the progress of thaw and accumulate at impenetrable permafrost or mineral soil layers [*Shaver and Billings*, 1975]. Furthermore, the absence of water fluctuations and drainage in mesocosms may have altered the soil environment from natural conditions. If in fact microbial biomass was lower due to experimental conditions, our data for ^{14}C uptake by microbes would likely be a minimum estimate for what would be expected in the field. Furthermore, an unknown amount of ^{14}C was likely incorporated into the unextractable portion of the microbial biomass, also potentially resulting in an underestimate of microbial ^{14}C uptake.

[29] In tussock tundra, it appears that at least a third of the ^{14}C released to soils was assimilated by soil microbes, while

decreases in ^{14}C activity in the microbes 1 week later indicate that much of this C is quickly turned over (Figure 2a). This rapid assimilation and turnover of recent photosynthate is consistent with results from pulse-labeling experiments on agricultural and forest systems [*Minchin and McNaughton*, 1984; *Merckx et al.*, 1985; *Norton et al.*, 1990]. The persistence of ^{14}C activity in the microbial biomass throughout the experiment in both tussock tundra and wet sedge tundra may indicate that some C may be incorporated into structural lipids or that microbes continue to assimilate labeled C from SOM and roots.

[30] In wet sedge soils, the ^{14}C taken up by plants appears to enter the microbial biomass in lower amounts and at lower rates than in tussock tundra. The absence of a peak in ^{14}C activity in the microbial biomass of wet sedge may indicate that either there is no peak in ^{14}C assimilation by microbes or that peak allocation occurred prior to or after the first harvest. Another possible explanation for the consistently lower level of microbial ^{14}C uptake and absence of a peak is that wet sedge microbes play a less direct role in C transfer from roots into SOM than they do in tussock tundra. Microbes may be nutrient limited, and unable to completely use newly available C substrates [*Merckx et al.*, 1987]. Lower microbial uptake might also be attributed to differences in root structure and soil porosity between the two tundra types. Wet sedge tundra plants typically have an abundance of very fine root hairs interwoven throughout the fibrous, water-saturated soil, whereas *E. vaginatum*, the dominant species of tussock tundra, generally has thicker roots with few root hairs penetrating more porous soils. These larger roots may allow tussock tundra to support a more active rhizosphere community of microbes [*Curl and Truelove*, 1985]. Therefore it appears that differences in pathways of C transfer between plants, soil, and microbes exist between the two tundra types.

5. Conclusions

[31] Use of the ^{14}C tracer has revealed that the C cycle in arctic tundra is a dynamic system, with immediate belowground allocation and root exudation of recently derived photosynthate C. The soil microbes appear to play a direct role in the movement of C from labile to recalcitrant SOM fractions in tussock tundra, whereas in the absence of a peak in microbial uptake of labeled C in wet sedge tundra, it appears that microbial assimilation of root exudates C is indirect, with less C transferred to recalcitrant pools. Accumulation of C in recalcitrant SOM fractions suggests long-term storage of these inputs. The quantity of C stored in soils at the end of the growing season derived from new photosynthates amounts to the minimum C annual accumulation estimates [*Oechel and Billings*, 1992]. However, these estimates do not include C from complete root turnover or leaf litter, which are likely to contribute an even greater amount of C to SOM in these systems.

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