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ORIGINAL PAPER

Fast assimilate turnover revealed by in situ $^{13}CO_2$ pulse-labelling in Subarctic tundra

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Abstract Climatic changes in Arctic regions are likely to have significant impacts on vegetation composition and physiological responses of different plant types, with implications for the regional carbon (C) cycle. Here, we explore differences in allocation and turnover of assimilated C in two Subarctic tundra communities. We used an in situ ^{13}C pulse at mid-summer in Swedish Lapland to investigate C allocation and turnover in four contrasting tundra plant communities. We found a high rate of turnover of assimilated C in leaf tissues of *Betula nana* and graminoid vegetation at the height of the growing season, with a mean residence time of pulse-derived ^{13}C of 1.1 and 0.7 days, respectively. One week after the pulse, c. 20 and 15%, respectively, of assimilated label-C remained in leaf biomass, representing most likely allocation to structural biomass. For the perennial leaf tissue of the graminoid communities, a remainder of approximately 5% of the pulse-derived C was still traceable after 1 year, whereas none was detectable in *Betula* foliage. The results indicate a relatively fast C turnover and small belowground allocation during the active growing season of recent assimilates in graminoid communities, with comparatively slower turnover and greater investment in belowground allocation by *B. nana* vegetation.

Keywords Carbon cycle · GPP partitioning · Stable isotopes · Tundra biome

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Introduction

Tundra vegetation is a heterogeneous cover of different vegetation types occurring in patches throughout the landscape, reflecting a harsh climate and well-adapted, but species-poor, communities. Changes in the frequency and extents of different vegetation types are likely to result from altered climatic conditions (Street et al. 2007). There is already abundant evidence for an increase in shrub expansion in Arctic tundra over the past 50 years (Tape et al. 2006), with direct consequences on the albedo (Chapin et al. 2005), hydrology and cycling of C and nutrients (Post et al. 2009; Wookey et al. 2009). Process models indicate that this 'greening' of the tundra (Wookey et al. 2009) has led to an increase in net primary productivity (NPP), which is predicted to persist into the near future (Sitch et al. 2007). However, these process models are based predominantly on leaf area relationships and therefore lack the necessary level of detail for the partitioning of assimilated C (i.e. gross primary productivity, GPP) to accurately predict changes in the net C balance and cycling of nutrients in tundra ecosystems (Street et al. 2007; Euskirchen et al. 2009; Hudson and Henry 2009; McGuire et al. 2009; Roberts et al. 2009). NPP modelling approaches are necessarily based on generalisations of GPP

to NPP ratios, with a range of assumptions regarding the apportioning of assimilated C to either respiratory loss or biomass gain, and ultimately turnover rates of C in ecosystems (Waring et al. 1998; Gifford 2003; Trumbore 2006). Moreover, ecophysiological responses used in ecosystem models often lack the necessary detail and have treated vegetation characteristics uniformly (Williams et al. 2001; Shaver et al. 2007), ignoring unique responses of different plant functional types (PFTs) and their individual C allocation patterns. Likely changes in vegetation structure and hence shifts in nutrient input and cycling (van Wijk et al. 2004) following climatic change require new modelling approaches that can capture these dynamic variations. Consequently, there is a need to obtain direct measurements of C allocation and turnover in different tundra vegetation communities, in order to parameterise ecosystem models considering separate PFTs (Williams et al. 2006). So far, little is known about the PFT-specific C partitioning and turnover in tundra vegetation (Shaver et al. 2006; Douma et al. 2007; Woodin et al. 2009; Street et al. 2011), but an understanding of the partitioning of GPP into either respiration or biomass is crucial, as this ultimately determines the long-term fate of assimilated C and likely differs between PFTs.

Pulse-labelling experiments using stable isotope tracers have become a standard tool in ecophysiology to investigate the fate of assimilated C in the plant–soil–atmosphere continuum. They are frequently used to unravel processes of assimilation, allocation and respiration (Dawson et al. 2002; Bowling et al. 2008). We used the stable carbon isotope ^{13}C to quantify, in situ, the amount of C incorporated into plant biomass and the rate of respiration of labelled C in relation to the total amount of label uptake during photosynthesis. This approach has previously been successful in forest and shrubland ecosystems (Carbone and Trumbore 2007; Carbone et al. 2007; Högberg et al. 2008). Whilst C partitioning in tundra vegetation has been addressed in a radiocarbon (^{14}C) pulse-labelling experiment (Olsrud and Christensen 2004), there are no published results of GPP partitioning and C turnover for specific plant functional types representative of vascular vegetation. The aims of our study were to apply an in situ stable isotope ($^{13}CO_2$) pulse in representative tundra vegetation to (1) trace assimilated C into different biomass pools, (2) estimate the turnover of assimilated C and (3) assess the long-term fate of these assimilates within different PFTs. The presented work concentrates on vascular plant communities but also includes representative lichen-dominated plots, whilst an accompanying experiment conducted at the same site and over the same period as this study investigated GPP/NPP partitioning and C turnover in bryophyte communities (Street et al. 2011).

Materials and methods

Site description

The study site was located in northern Sweden near Abisko at 68°18′N, 18°51′E at about 700 m asl (Fig. 1). The mean annual temperature in the Abisko Valley is −1°C (recorded at the Abisko Research Station situated 6 km north of the research site at 400 m asl), with mean July air temperatures of +11°C (http://www.linnea.com/~ans/ans.htm). Three replicated plots (0.55 × 0.55 m) were established for each of four contrasting vegetation types, representing typical tundra heath communities dominated by key species or plant types (Table 1): (1) dwarf birch (*Betula nana* L.), (2) crowberry (*Empetrum nigrum* L.), (3) graminoid communities (dominated by sedges) and (4) exposed ridges (dominated by lichen). All 12 plots were located within an area of 15 × 20 m. Soils comprised organic horizons developed on glacial till deposits. Organic layer depth varied between 5 and 30 cm for the three vascular plant communities, whilst there were only small 'pockets' of soil material in lichen plots. The patchwork of vegetation communities over relatively short distances relates mostly to the micro-topography between small rocky outcrops and resulting variability in soil drainage. Whilst graminoid communities tended to occur in areas of lower drainage, *E. nigrum* and *B. nana* patches were generally situated in more mesic locations. Areas dominated by mosses also co-occurred where soil moisture was highest; these were not part of this study (but see Street et al. 2011).

$^{13}CO_2$ labelling

Isotope pulse labelling was carried out on 4th July 2007 between 13:20 and 16:00 h. For pulse labelling, we placed custom-made Perspex covers (0.55 × 0.55 m, 0.2 m high; York Plastics, York, UK) over the 12 individual vegetation patches without inserting a soil frame, thus preventing potential damage to the branch and root systems, a particular concern in these dwarf shrub communities (Fig. 2a). Larger gaps between the cover edge and the vegetation or ground were filled using clear plastic film. Remaining gaps were small and not significant for an incursion of ambient air given the over-pressured chamber conditions during the labelling gas flow. The pulse gas (artificial air with 371–375 µl l^{-1} CO_2 with 98% ^{13}C atom enrichment; Spectra Gases Ltd., Littleport, UK) flushed the Perspex covers at a flow rate of 5 l min^{-1}, resulting in a mean residence time of pulse gas within the covers of 12 min. Weather conditions during the pulse period were sunny with air temperatures averaging 20.2°C, i.e. relatively warm but not an unusual July air temperature for daytime maxima in the region (Fig. 3). Tests under comparable

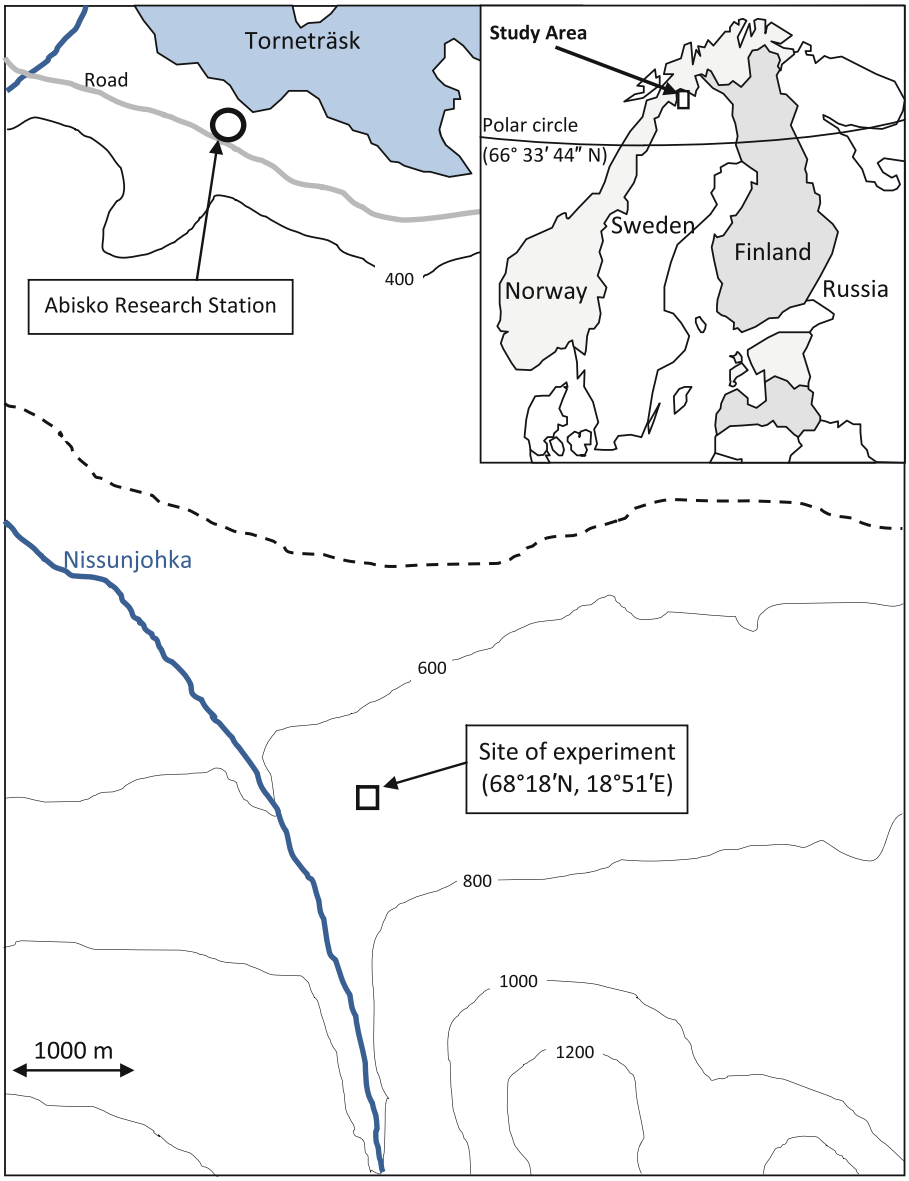

Fig. 1 Map of the study area in Swedish Lapland (*inset map*). The experiment was sited at about 700 m asl on the slope from the Nissoncorru mountain in the south-east to lake Torneträsk in the north. The *hatched line* indicates the approximate position of the altitudinal tree line of mountain birch (*Betula pubescens* Ehrh.)

Table 1 Four contrasting plant communities studied during $^{13}CO_2$ pulse-labelling experiment

Community	Dominant species	LAI
Dwarf birch	*Betula nana* (*Empetrum nigrum*)	2.09 ± 0.31
Empetrum heath	*Empetrum nigrum*	1.66 ± 0.13
Graminoid	*Carex nigra* (*Tofieldia pusilla*, *Scirpus cespitosus*)	1.60 ± 0.32
Exposed ridge	Lichen (predominantly *Cetraria* and *Cladonia* spp.)	0.27 ± 0.15

All plots ($n = 3$ per community type) were located within an area of 15 × 20 m. Species names in brackets indicate subdominant species. LAI estimates are mean ± 1 SD, and in the 'exposed ridge' community refers to vascular plants located within the plot; biomass sampling in these plots following the isotope pulse was carried out for lichen biomass only

meteorological conditions and with identical gas flow rates showed a mean increase in 2.7°C inside the labelling hood compared with ambient temperatures, so that temperature conditions inside the sampling hoods are not likely to have exceeded 25°C.

Pulse-chase sampling

Leaf and lichen materials were sampled before the pulse, and then at 0.25, 0.75, 1, 2, 3, 5 and 7 days following the pulse. At each sampling occasion, approximate equivalents

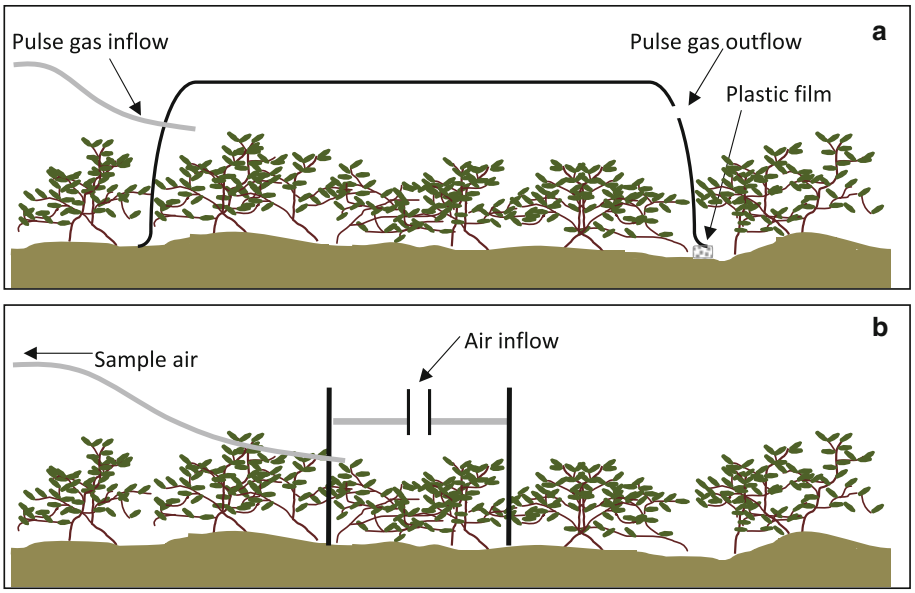

Fig. 2 Schematic of a Perspex hood used for $^{13}CO_2$ pulse labelling (**a**) and a PVC respiration chamber (**b**). $^{13}CO_2$ pulse gas was flushed through Perspex hoods at approximately 5 l min^{-1}. Sample air from PVC respiration chambers was drawn from two points in the chamber (only one shown here) to the York Mobile Lab, and ambient air entered the chamber headspace via a central vent. Plastic film ('bubble wrap') was used to fill larger gaps of both the pulse hoods and the respiration chambers

of 1 g dry mass of foliage of the dominant plant species (or lichen on exposed ridges) were collected, ensuring an even representation of plants within the area covered by the cover. Senesced foliage was removed, and samples were transferred into paper envelopes at the field site and subsequently transferred to the laboratory and oven-dried at 60°C. The remoteness of the site meant that oven drying of samples occurred between 3 and 12 h of sampling in the field for individual samples. As we can not exclude the possibility that some of the labelled assimilates were lost as respiration in this period, we treat our estimates of C turnover as low estimates of actual turnover. Soil samples were taken initially before the pulse, and again at 1 and 7 days postpulse, to a depth of 5 cm using a 5-cm-diameter corer. Sampling to this depth resulted in obtaining mainly organic soil material, with only small amounts of mineral content in individual samples. All samples were stored in plastic bags in soil pits at below 5°C before transportation to the laboratory (within less than 5 h), where samples were frozen.

$^{13}CO_2$ monitoring

Immediately after the end of the pulse, opaque PVC chambers (20 cm diameter, 10 cm high; Fig. 2b) were placed on the vegetation at the centre of the 0.55 × 0.55 m pulse areas. Chambers were operated in flow-through mode, with air being drawn at 0.3 l min^{-1} laterally from the headspace, and ambient air entering the chamber space through a central chamber lid inlet (1 cm diameter) (Subke et al. 2009). Gaps between chamber base and soil were filled using plastic film, whilst any remaining small leaks at the chamber base being considered insignificant for measurements made in flow-through mode. The CO_2 concentration and ^{13}C:^{12}C isotopic ratio in sample lines from soil chambers were measured directly in the field using a mobile laboratory containing an isotope ratio mass spectrometer (IRMS), referred to here as the York Mobile Lab (see Subke et al. (2009) for more detail of chambers and laboratory). The laboratory comprises a gas handling unit for switching between the 16 input lines, connected to a Continuous-Flow Gas Chromatograph IRMS (CF-GC-IRMS). A standard laboratory gas chromatograph is coupled to a 12-cm-radius magnetic sector mass spectrometer (SIRAS Series2, Micromass, UK), NIER (Non-Ionising Electromagnetic Radiation) type ion impact source, triple faraday collector system, rotary/turbo-molecular pumping vacuum system, interfaced to Microsoft Windows™ data system (model name 'PVS12', built by Pro-Vac Services, Crewe, UK). The CF-GC-IRMS, together with a temperature control system and gas supplies for CO_2 reference and helium carrier gas, has been custom built to fit a modified twin-axle trailer unit (Model 'Tow-A-Van', Indespension Ltd., Bolton, UK), thus providing the unique opportunity to conduct isotope ratio measurements in real time and under field conditions, with no need for off-line sampling and associated problems of gas handling and storage. Transportation of the York Mobile Lab to the field site was by helicopter. Power for running the instrumentation was provided by two propane fuelled generators (Honda EU10*i*, converted for propane use; Honda Motor Co Ltd., Tokyo, Japan) with a total power output of 1.8 kW.

The air drawn continuously from all chambers was directed sequentially to the CF-GC-IRMS. One measuring cycle (length of 1 h) consisted of measurements from all 12 respiration chambers as well as one reference gas injection,

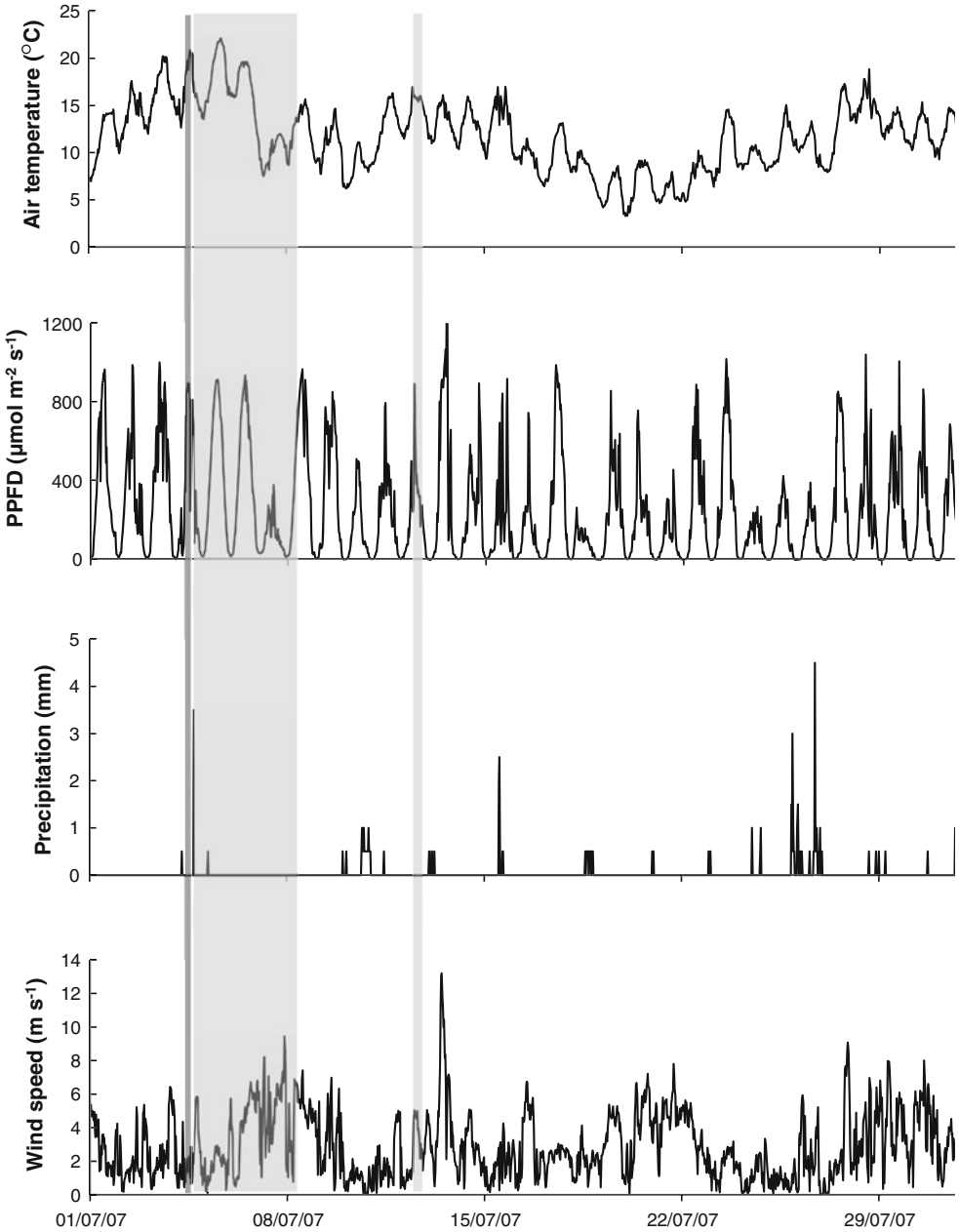

Fig. 3 Meteorological conditions during July 2007 at the research site. The *dark-shaded area* indicates the period of the 3-h pulse period on the 4th July 2007, *whilst lighter shaded areas* represent the CO_2 flux monitoring periods

one measurement of ambient air, and two measurements from respiration chambers placed on un-pulsed control vegetation to measure natural abundance (NA) isotope ratios of respired CO_2. Whilst the respiration chambers on the labelling plots remained in place for the entire duration of the monitoring period, the two NA chambers rotated between different locations to capture all four vegetation types. The continuous CO_2 monitoring chambers remained in place for four full days following the pulse, and an additional 8-h period 7 days after the pulse.

The isotope ratio of the CO_2 flux was calculated using a 2-source mixing model:

$$\delta_F = \frac{\delta_{\text{Sample}} C_{\text{Sample}} - \delta_{\text{Air}} C_{\text{Air}}}{C_{\text{Sample}} - C_{\text{Air}}} \quad (1)$$

where C and δ are, respectively, the CO_2 concentration and $^{13}C/^{12}C$ isotopic mixing ratio of a gas, and the suffixes relate to ecosystem respiration flux CO_2 (F), CO_2 in ambient air (Air), and CO_2 in the sample line (Sample). Weather conditions during the pulse-chase period, with high wind speeds over extended periods (Fig. 3), meant that there was significant leakage of air from the chamber head space. Since the ambient air concentrations of ^{12}C and ^{13}C were subtracted from the sample gas, this leakage had

no effect on the observed isotope ratio detected in the CO_2 enrichment above ambient concentrations. However, the absolute amount of C recorded in the sample lines cannot be regarded as an accurate estimate of respiration from the area enclosed by the chamber, as we cannot correct for the amount of air that leaked from each chamber over time under high winds. We, therefore, concentrate here on isotopic ratio changes of respiration-derived CO_2. For quality control purposes, $\delta^{13}C$ estimates were only considered valid if the respiration-derived CO_2 in the sample gas amounted to more than 50 μmol mol^{-1} (an apparent CO_2 flux of 0.2 μmol m^{-2} s^{-1}). This requirement led to the exclusion of isotopic data from lichen plots, which had very low CO_2 flux rates, and therefore, only small CO_2 concentration increases compared with ambient air in the sample gas.

Solid sample $\delta^{13}C$ analysis

Coarse and fine roots and stones were removed from soil cores by sieving. The organic soil material was mixed with any mineral soil fractions present, and sub-samples of homogenised soil samples were ground for isotopic analyses. Fine roots (<1 mm) were separated from coarser root material and also ground. For plots with mixed communities, leaf material was sorted and analyses performed for the dominant species only. For leaf samples, only green parts were used for sample processing (i.e. excluding senesced leaves). For lichen plots, where only small biomass quantities could be obtained, soil particles were carefully removed prior to sample processing. Dried and ground leaf, root and soil samples were analysed for their isotopic composition on an elemental analyser (EA: FlashEA1112, ThermoFinnigan, Germany) linked to a custom built IRMS (with components identical to those described above for the IRMS in the 'York Mobile Lab', and also constructed by Pro-Vac Services Ltd., Crewe, UK). The instrumental output was calibrated against certified isotopic material (NIST sucrose ANU 8542). Isotope results relate to the organic matter contained in samples, i.e. they exclude mineral components present in soil samples. All isotopic ratios are expressed in the delta notation (in ‰) and reported relative to the Vienna Pee Dee Belemnite standard.

Turnover calculations of assimilated C

In order to assess differences in C turnover, we consider two general pools of C turnover within the vegetation: (1) a labile C pool, and (2) leaf biomass C. All assimilated C initially forms part of the labile, non-structural C pool (Pool 1), which includes all water-soluble forms of carbohydrates (i.e. also sugars stored in cell vacuoles). As this labile pool turns over, a small fraction of it becomes incorporated into leaf biomass (Pool 2), whilst the remainder is either exported to other plant parts via the phloem, or respired by the leaf. In order to derive the fraction of assimilated C built into structural biomass (carbon use efficiency, CUE), as well as calculating the rate of turnover of labile C, we fitted the following exponential decay function to isotopic enrichment results of both the biomass and respiration data:

$$\delta = \delta_0 + ae^{-bt}, \tag{2}$$

where δ is the $\delta^{13}C$ value of either biomass or respired CO_2, t is the time since pulse labelling (in days), and δ_0, a and b are fitted parameters. In doing so, we assume that the overall pool sizes do not change over the observation period, i.e. that the reduction in ^{13}C abundance in Pool 1 is caused by respiratory loss, phloem export or incorporation into Pool 2 and not by dilution due to an increase in (unlabelled) C subsequent to the 13C pulse. From this, we estimate the mean residence time (MRT) of labile C in foliage and total respiratory substrate as the inverse of the decay constant (b):

$$\mathrm{MRT} = b^{-1}. \tag{3}$$

For foliage data, MRT refers to labile C in leaves, whilst the MRT calculated for ecosystem respiration is indicative of the turnover of labile C pools in both plants and soil. The asymptote of the exponential decay function (δ_0) indicates the amount of labelled C not affected by the exponential decay, i.e. the amount of C that would remain in the leaf once the labile pool of labelled C is completely turned over. We consider this to represent C fixed in more permanent molecular structures, mainly structural components of the plant biomass. We, therefore, calculate the fraction of C fixed as GPP during our pulse period and subsequently allocated to leaf biomass within each plot according to:

$$f_{SC} = (\delta_0 - \delta_{NA})/(\delta_i - \delta_{NA}), \tag{4}$$

where f_{SC} is the fraction of GPP allocated to structural carbon, δ_i is the initial abundance of ^{13}C measured in the leaf biomass, δ_0 is the asymptote value obtained from Eq. 2, and δ_{NA} is the NA $\delta^{13}C$ value of the vegetation obtained from samples taken before the pulse. We note that this calculation relates to leaf biomass only and does not represent the CUE of the whole plant. For biomass data harvested 1 year after the pulse, we also applied Eq. 4, substituting δ_0 with measured isotopic abundances in the biomass for each plot.

Statistical methods

Differences between average MRTs and f_{SC} values were assessed using two-way ANOVA for vegetation type and C

pool (MRT) and vegetation type and sampling time (f_{SC}) as independent variables. Differences between vascular plant communities in $\delta^{13}C$ values of root tissue and SOM were analysed using a repeated-measures ANOVA (within-subjects factor = time postpulse; between-subjects factor = plant community). Where ANOVAs indicated significance, differences between means were assessed post hoc, using the Holm–Sidak t test. Although the assumption of normality (i.e. Kolmogorov–Smirnov test) was not always within the $P > 0.05$ threshold (i.e. $n = 3$), we report those data as significance levels were high. All statistical tests and regression parameter fittings were carried out using Sigma plot 11.0 software (Systat Software Inc., San Jose, California).

Results

Short-term $\delta^{13}C$ changes in foliage samples

Initial foliage enrichment in ^{13}C was found to be highest in *Betula*, indicating greater assimilation rates per leaf biomass in these dwarf shrubs than in the other vegetation types. Despite considerable spatial variation in leaf tissue enrichment, $\delta^{13}C$ values in *Betula* leaves were significantly greater than all other vegetation types until 48 h after the pulse (Fig. 4). A sharp decline in enrichment over the following days meant that this difference disappeared after this period. $\delta^{13}C$ values in both *Betula* and graminoid foliage showed a consistent trend of diminishing ^{13}C abundance, following an exponential decay curve over the sampling period (Fig. 4). In contrast to these communities, no consistent trend was observed for either *Empetrum* or lichen plots, the latter lacking any considerable increase in $\delta^{13}C$ (Fig. 4). C turnover tended to be higher in *Betula* leaves, compared with graminoid foliage, but differences were not statistically significant (Table 2). In contrast, the fraction of GPP allocated to plant biomass in leaves was higher in graminoid compared with *Betula* plots. One year after the pulse, less than 25% of pulse-derived C found after 1 week could be detected in graminoid leaf biomass, whilst none was detected in *Betula* foliage (Table 2).

Short-term $\delta^{13}C$ changes in ecosystem respiration

Given the remoteness of the site and resulting logistical problems of transportation and power provision, the York Mobile Lab performed consistently, enabling measurement of the isotope ratio and CO_2 flux rates at frequent time resolution, with data loss occurring on two separate occasions due to failure of the generators. This caused data gaps of about 12 h over the total monitoring period of 134 h.

Figure 4 shows the changes in isotopic abundance of respiration over the 8-day period for all *Betula*, graminoid and *Empetrum* plots. Since total respiration on the lichen plots was very low, no significant increase in CO_2 concentration in the sample gas was recorded, and all data were removed by the data quality requirement. Isotope ratios immediately after the pulse showed extremely high values with a sharp decline lasting about 16-h postpulse. This pattern of a sharp decline from extreme values, followed by a moderate increase, has been reported in other pulse-chase experiments (Högberg et al. 2008) and has been shown to result from physical tracer diffusion in and out of soil pores (Subke et al. 2009). We included only data after this initial period for the exponential decay regression in order to capture the return of C allocated belowground by plants only. Given the shallow depth of soils, its comparatively low porosity and the likelihood of high rates of flushing of soil pores under the windy conditions following the pulse (Fig. 3), we consider the abiotic tracer return after this period to be insignificant.

Similar to the results found in leaf biomass, despite *Betula* vegetation tending to show higher values than graminoid communities, there were no significant differences between the mean residence times of labile C as evidenced in enrichment of ecosystem respiration for these two vegetation types (Table 2).

Root and SOM results

Fine root tissue of the three vascular plant plots showed only a slight isotopic enrichment, with no statistical differences between either plant communities or sampling day (Fig. 5a). SOM results indicated significantly higher $\delta^{13}C$ values for lichen plots, which are independent of the pulse treatment (Fig. 5b). Grouping all results of vascular communities (i.e. excluding lichen plots), the $\delta^{13}C$ signal of SOM across all communities was significantly enriched 7 days and still after 365 days postpulse labelling.

Discussion

With a mean residence time of less than 1 day, our results document a fast rate of C cycling at the peak of the short growing season at this site representing two key tundra PFTs. The CUE of less than 20% at the leaf level is lower than observed in previous experiments including herbaceous plants (Van Iersel 2003) and perennial grass species (Lehmeier et al. 2010a, b). These leaf sample-based estimates mean that our CUE estimates are conservative, as phloem export and C storage in other plant organs is not included in this estimate. However, the rapid decline in the ^{13}C label detected in plant respiratory substrate (i.e. as

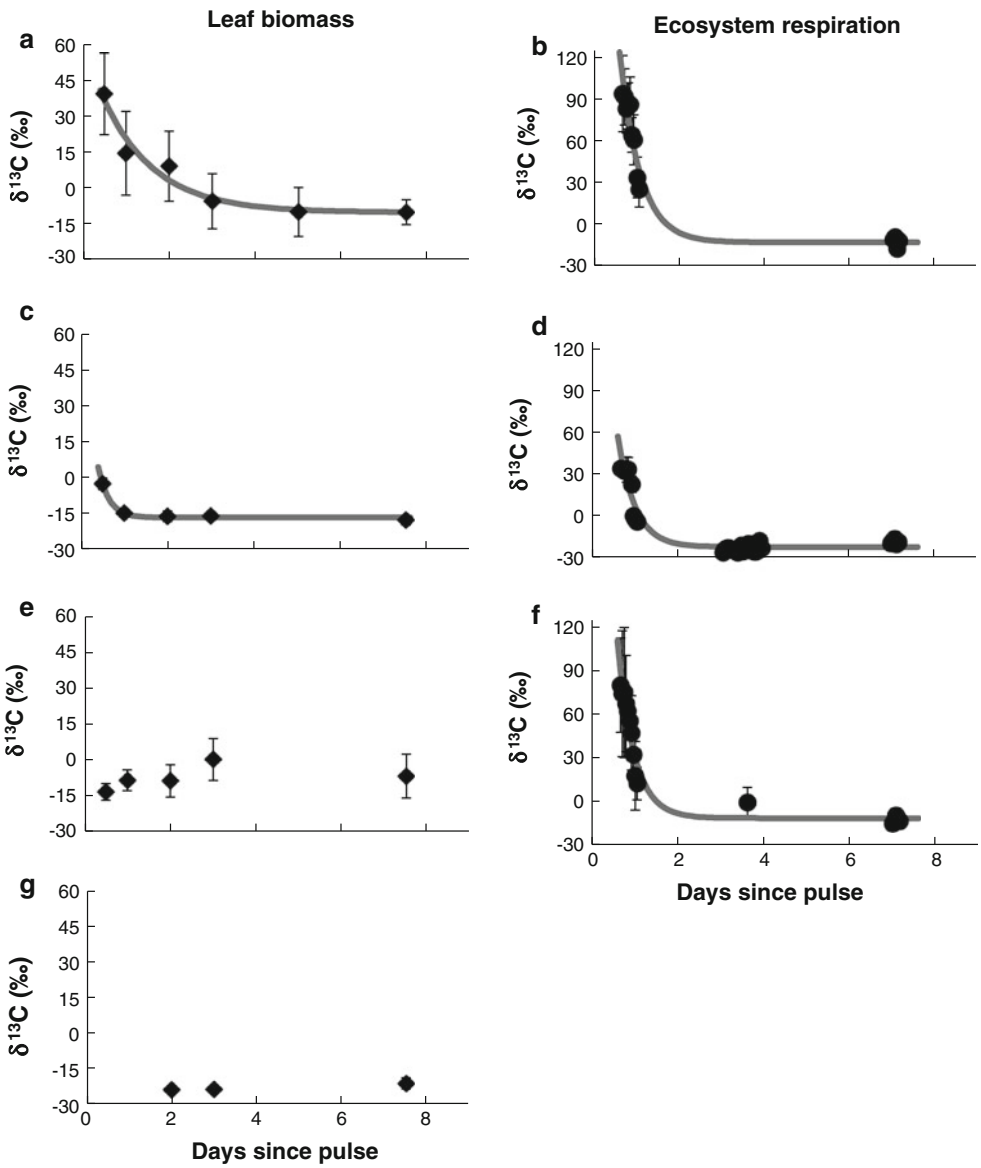

Fig. 4 Carbon isotope ratios following the 3-h pulse period in leaf biomass (*left column*) and ecosystem respiration (*right column*). Results are means and *error bars* indicate Standard Errors for three replicate plots of *B. nana* (**a**, **b**), graminoid vegetation (**c**, **d**), *E. nigrum* (**e**, **f**), and lichen plots (**g**). *Lines* are fitted exponential decay curves for means. No meaningful isotope ratios were obtained for lichen plots due to the low CO_2 flux (see text). Enrichment was significantly greater in *Betula* foliage until 48 h after the pulse ($p = 0.016$ ANOVA with Tukey's post hoc test at 48-h postpulse). Note difference in *y*-axis scale between graphs in *left-hand* and *right-hand* columns

Table 2 Carbon turnover in foliage of *B. nana* and graminoid spp

		Betula nana	Graminoid
MRT (leaf biomass)	Days	1.093 ± 0.223	0.667 ± 0.164
MRT (respiration)	Days	0.456 ± 0.007	0.394 ± 0.025
f_{SC} (1 week)	–	0.160 ± 0.020	0.207 ± 0.054
f_{SC} (1 year)	–	−0.002 ± 0.002	0.046 ± 0.016

Mean residence times (MRTs) and fractions of GPP incorporated into structural carbon (f_{SC}) derived from isotopic results. Data are mean ± 1 SE ($n = 3$). Two-way ANOVA showed significant differences in MRT between C pools (i.e. between leaf biomass and respiration substrate pools, $p = 0.011$) across vegetation types, but no differences between vegetation types or interactions between pools and vegetation ($p = 0.117$ and $p = 0.226$, respectively). The amount of GPP incorporated into biomass differed between time points (1 week or 1 year; $p = 0.001$), with no significant difference between vegetation types or interaction between both ($p = 0.163$). However, a post hoc Hiolm–Sidak test revealed a significant difference between vegetation types 1 year after the pulse ($p = 0.007$)

$^{13}CO_2$) supports the observation that the majority of assimilated C cycles through plants at a high rate. Our findings contrast with results reported from $^{13}CO_2$ pulse-labelling in temperate peatland communities of 1.9 and 4.7 days, respectively (Fenner et al. 2007; Ward et al. 2009). A critical factor affecting the turnover of C between

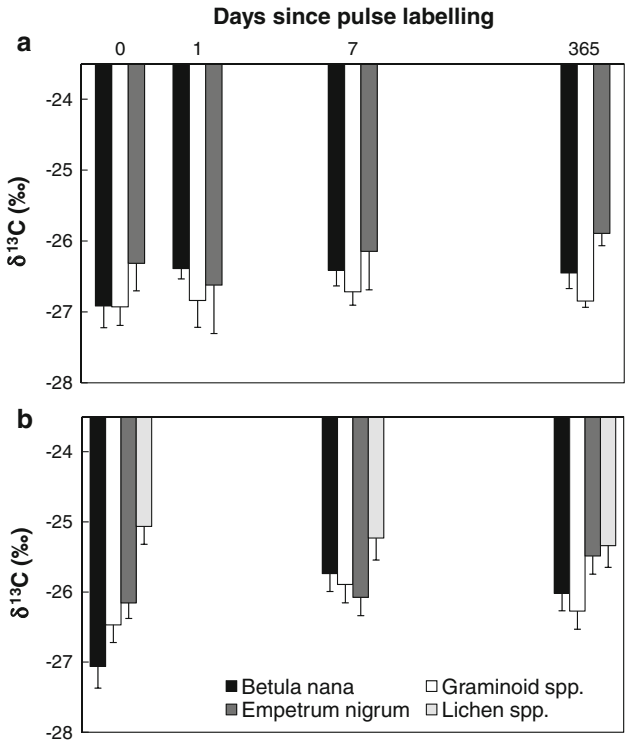

Fig. 5 $\delta^{13}C$ values of **a** fine root tissue from soil cores sampled in the three vascular plant communities and **b** soil organic matter in all plots. Data show isotopic abundance immediately before the pulse (day 0, representing natural isotopic abundance), and at 1 (roots only), 7 and 365 days after the pulse. There were no significant differences or interactions between sampling days and plant species for root tissue. For SOM results (**b**), a 2-way ANOVA indicate a significant effect of plant community ($p < 0.001$), with lichen plots having significantly enriched values compared with all other plots ($p < 0.02$, Holm–Sidak post hoc test). A two-way ANOVA performed for SOM data grouping all vascular plant communities (i.e. excluding the lichen plots) showed a significant influence of the sampling day ($p = 0.018$), with values on day 0 being significantly lower than either of the other days across all vascular communities

these contrasting systems is likely to be the seasonality of GPP as well as NPP. The already considerable difference between the two cited temperate peatland studies may relate to the different seasons during which the ^{13}C pulse experiment was conducted (June in Fenner et al. 2007 and October in Ward et al. 2009). Our results are representative for conditions at the height of the arctic summer, and it is likely that the high rate of diurnal assimilation combined with a very N limited system (Michelsen et al. 1996) resulted in the observed high turnover of C, with the majority of initially fixed C being respired. During periods of relatively lower diurnal GPP, a higher proportion of fixed C may be turned into plant biomass (NPP), resulting in a longer overall MRT and higher CUE of C in the ecosystem.

Our results further indicate that C available for respiration (which is likely to include respiration from all plant organs as well as rhizospheric respiration involving heterotrophic organisms) turns over at a faster rate than labile C found in leaves (Table 2). Whilst both community types show the same pattern of shorter MRTs of the respiratory substrate pool, the difference in turnover tended to be greater in the dwarf birch plots compared with the graminoid communities. Such differences in turnover both between PFTs and between different substrate pools within a particular PFT require further investigation, as a better understanding of these rates is required in order to enable meaningful process modelling of anticipated vegetation distribution and shifts in environmental conditions (Dorrepaal 2007; Nobrega and Grogan 2008).

Our treatment of the labile C pool, which includes recent assimilates as well as carbohydrates in other storage forms (e.g. sugars stored in cell vacuoles) is simplistic compared with other schemes (Lehmeier et al. 2008; 2010b) and may confound effects of carbon use efficiency (NPP/GPP) with rates of respiratory processing of different substrates. However, whilst we acknowledge this limitation, the results nonetheless allow a comparative investigation of C allocation in different PFTs. This is likely to relate to differences in C transport to belowground plant organs. Despite lacking statistical significance, a trend towards faster allocation of recent assimilates to roots in *B. nana* emerges, which is not observed in the graminoid community (Fig. 5a). This is corroborated by the trend of slightly faster turnover of labile C in graminoid plots compared with *B. nana* dominated vegetation, as evidenced in the marginally shorter mean residence time of labile substrates, even if here also the differences are not significant. Whilst the low level of replication ($n = 3$) means that these trends show statistical significance in only a few instances, a general difference in C allocation pattern emerges, with fast C turnover and a relatively small belowground allocation of recent assimilates in graminoid communities, and comparatively slower turnover and greater investment in belowground allocation by the dwarf shrub communities. Previous work by Shaver and Chapin (1991) has shown that distinct differences in allocation patterns and C turnover between vegetation forms in the tundra at leaf level can be compensated by storage processes in stems, resulting in similar C turnover dynamics between communities. The results for label retention in foliar biomass after 1 year are consistent with the deciduous habit of *B. nana*, where no label-derived ^{13}C could be detected, whilst the graminoid communities still showed significant enrichment. These findings corroborate results reported on the basis of biomass and nutrient abundances for characteristic divergence in plant C pools above- and belowground between PFTs, and seasonally different allocation patterns related to growth form and leaf habit (Chapin et al. 1980).

The absence of significant enrichment in *Empetrum* leaf samples was a surprising result. The CO_2 flux results clearly showed a respiratory return of ^{13}C similar to the other vascular plots, indicating that significant amounts of the isotopic tracer were assimilated by the vegetation. This is corroborated by CO_2 gas exchange measurements obtained by automated NEE chambers at the same site, where *Empetrum*, *Betula*, and graminoid communities show similar assimilation values (both in terms of mean daily NEE or peak daytime peak NEE rates; data not shown; R. Poyatos Lopez, *pers. com.*). The results suggest that only small amounts of assimilated C were stored in the foliage of *E. nigrum*. We suspect that the inconsistent temporal pattern of enrichment in *E. nigrum* foliage results from a high degree of heterogeneity in photosynthetic activity, particularly during relatively dry conditions, as in our case. Whilst care was taken to sample representative parts of the *Empetrum* canopy, the absence of significant tracer assimilations in the sampled foliage could therefore be caused by an inadvertent preference for less active areas within the canopy.

Notwithstanding the small-scale experimental work, this study shows different rates of C turnover and belowground allocation of recent assimilates between key tundra plant communities and warrants further long-term validation in relation to C pool turnover modelling in such mosaic landscapes containing considerable C stocks.

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References

Bowling DR, Pataki DE, Randerson JT (2008) Carbon isotopes in terrestrial ecosystem pools and CO_2 fluxes. New Phytol 178:24–40

Carbone MS, Trumbore SE (2007) Contribution of new photosynthetic assimilates to respiration by perennial grasses and shrubs: residence times and allocation patterns. New Phytol 176:124–135

Carbone MS, Czimczik CI, McDuffee KE, Trumbore SE (2007) Allocation and residence time of photosynthetic products in a boreal forest using a low-level C-14 pulse-chase labeling technique. Glob Change Biol 13:466–477

Chapin FS, Johnson DA, McKendrick JD (1980) Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem—implications for herbivory. J Ecol 68:189–209

Chapin FS, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in Arctic summer warming. Science 310:657–660

Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. Annu Rev Ecol Syst 33:507–559

Dorrepaal E (2007) Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? J Ecol 95:1167–1180

Douma JC, Van Wijk MT, Lang SI, Shaver GR (2007) The contribution of mosses to the carbon and water exchange of arctic ecosystems: quantification and relationships with system properties. Plant, Cell Environ 30:1205–1215

Euskirchen ES, McGuire AD, Chapin FS, Yi S, Thompson CC (2009) Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: implications for climate feedbacks. Ecol Appl 19:1022–1043

Fenner N, Ostle NJ, McNamara N, Sparks T, Harmens H, Reynolds B, Freeman C (2007) Elevated CO_2 effects on peatland plant community carbon dynamics and DOC production. Ecosystems 10:635–647

Gifford RM (2003) Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Funct Plant Biol 30:171–186

Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol 177:220–228

Hudson JMG, Henry GHR (2009) Increased plant biomass in a high Arctic heath community from 1981 to 2008. Ecology 90:2657–2663

Lehmeier CA, Lattanzi FA, Schaeufele R, Wild M, Schnyder H (2008) Root and shoot respiration of perennial ryegrass are supplied by the same substrate pools: assessment by dynamic C-13 labeling and compartmental analysis of tracer kinetics RID A-5609-2009. Plant Physiol 148:1148–1158

Lehmeier CA, Lattanzi FA, Gamnitzer U, Schaufele R, Schnyder H (2010a) Day-length effects on carbon stores for respiration of perennial ryegrass. New Phytol 188:719–725

Lehmeier CA, Lattanzi FA, Schaeufele R, Schnyder H (2010b) Nitrogen deficiency increases the residence time of respiratory carbon in the respiratory substrate supply system of perennial ryegrass. Plant, Cell Environ 33:76–87

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo LD, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79:523–555

Michelsen A, Schmidt I, Jonasson S, Quarmby C, Sleep D (1996) Leaf N-15 abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53–63

Nobrega S, Grogan P (2008) Landscape and ecosystem-level controls on net carbon dioxide exchange along a natural moisture gradient in Canadian low arctic tundra. Ecosystems 11:377–396

Olsrud M, Christensen TR (2004) Carbon cycling in subarctic tundra; seasonal variation in ecosystem partitioning based on in situ ^{14}C pulse-labelling. Soil Biol Biochem 36:245–253

Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Hoye TT, Ims RA, Jeppesen E, Klein DR, Madsen J, McGuire AD, Rysgaard S, Schindler DE, Stirling I, Tamstorf MP, Tyler NJC, van der Wal R, Welker J, Wookey PA, Schmidt NM, Aastrup P (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325:1355–1358

Roberts P, Newsham KK, Bardgett RD, Farrar JF, Jones DL (2009) Vegetation cover regulates the quantity, quality and temporal dynamics of dissolved organic carbon and nitrogen in Antarctic soils. Polar Biol 32:999–1008

Shaver GR, Chapin FS (1991) Production—biomass relationships and element cycling in contrasting arctic vegetation types. Ecol Monogr 61:1–31

Shaver GR, Giblin AE, Nadelhoffer KJ, Thieler KK, Downs MR, Laundre JA, Rastetter EB (2006) Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. J Ecol 94:740–753

Shaver GR, Street LE, Rastetter EB, Van Wijk MT, Williams M (2007) Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. J Ecol 95:802–817

Sitch S, McGuire AD, Kimball J, Gedney N, Gamon J, Engstrom R, Wolf A, Zhuang Q, Clein J, McDonald KC (2007) Assessing the carbon balance of circumpolar Arctic tundra using remote sensing and process modeling. Ecol Appl 17:213–234

Street LE, Shaver GR, Williams M, Van Wijk MT (2007) What is the relationship between changes in canopy leaf area and changes in photosynthetic CO_2 flux in arctic ecosystems? J Ecol 95:139–150

Street LE, Subke JA, Sommerkorn M, Ineson P, Heinemeyer A, Williams M (2011) Turnover of recently assimilated carbon in Arctic bryophyte communities. Oecologia 167:325–337

Subke JA, Vallack HW, Magnusson T, Keel SG, Metcalfe DB, Högberg P, Ineson P (2009) Short-term dynamics of abiotic and biotic soil $^{13}CO_2$ effluxes after in situ $^{13}CO_2$ pulse labelling of a boreal pine forest. New Phytol 183:349–357

Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. Glob Change Biol 12:686–702

Trumbore S (2006) Carbon respired by terrestrial ecosystems—recent progress and challenges. Glob Change Biol 12:141–153

Van Iersel M (2003) Carbon use efficiency depends on growth respiration, maintenance respiration, and relative growth rate. A case study with lettuce. Plant, Cell Environ 26:1441–1449

van Wijk MT, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS, Cornelissen JHC, Gough L, Hobbie SE, Jonasson S, Lee JA, Michelsen A, Press MC, Richardson SJ, Rueth H (2004) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Global Change Biol 10:105–123

Ward SE, Bardgett RD, McNamara NP, Ostle NJ (2009) Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. Funct Ecol 23:454–462

Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 18:129–134

Williams M, Rastetter EB, Shaver GR, Hobbie JE, Carpino E, Kwiatkowski BL (2001) Primary production of an arctic watershed: an uncertainty analysis. Ecol Appl 11:1800–1816

Williams M, Street LE, van Wijk MT, Shaver GR (2006) Identifying differences in carbon exchange among arctic ecosystem types. Ecosystems 9:288–304

Woodin SJ, van der Wal R, Sommerkorn M, Gornall JL (2009) Differential allocation of carbon in mosses and grasses governs ecosystem sequestration: a ^{13}C tracer study in the high Arctic. New Phytol 184:944–949

Wookey PA, Aerts R, Bardgett RD, Baptist F, Brathen KA, Cornelissen JHC, Gough L, Hartley IP, Hopkins DW, Lavorel S, Shaver GR (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Glob Change Biol 15:1153–1172