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Limited variation in proportional contributions of auto- and heterotrophic soil respiration, despite large differences in vegetation structure and function in the Low Arctic

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Abstract Arctic ecosystems contain vast stores of soil carbon (C), yet our understanding of the factors controlling CO_2 efflux from tundra soils remains poor. Partitioning soil respiration (R_S) into heterotrophic (R_H) and autotrophic (R_A) sources can help elucidate the relative contributions from microbial breakdown of soil organic matter (SOM) and root and rhizospheric activities—two processes that can have contrasting effects on long-term soil C stocks. Using two techniques, we quantified the magnitudes, relative proportions and environmental drivers of R_H and R_A in four common arctic vegetation types in West Greenland. We employed a trenching method in large patches of *Betula nana*, *Salix glauca*, mixed-shrub (equal mix of *Betula* and *Salix*) and graminoids dominated by *Poa* spp. At a nearby location, we introduced $^{13}CO_2$ to *Betula*- and graminoid-dominated plots. The difference in the autotrophic proportion (R_A/R_S) between methods was minimal, providing confidence that our more extensive trenching approach provided accurate estimates of R_A and R_H. Despite contrasting microclimate conditions, large differences in vegetation structure and wide variation in R_S, there were minimal differences in mean R_A/R_S (0.40–0.48 across all vegetation types). Our results suggest that R_A/R_S may be more conservative than previously thought for low-productivity ecosystems. We suggest that partitioning R_S into R_A and R_H may be a useful tool to identify ecosystems that have fallen out of equilibrium and may be poised to either gain or lose soil C.

Keywords Arctic · Carbon · ^{13}C labeling · Respiration partitioning

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Introduction

Soil respiration (R_S) is a major flux in the global carbon cycle. It is second only to gross primary

production (Schlesinger 1997) and accounts for as much as 70–90 % of total ecosystem respiration (Law et al. 1999; Janssens et al. 2001). Quantifying the magnitude and sensitivity of soil respiration in the northern high latitudes is of critical importance because Arctic soils contain approximately twice the amount of carbon (C) that is currently in the atmosphere (Tarnocai et al. 2009). Historically, Arctic ecosystems have been a sink for atmospheric CO_2 (McGuire et al. 2012). However, rising air temperatures in the Arctic (Kaufman et al. 2009) are expected to accelerate soil organic matter (SOM) decomposition (Schimel 2013). Given the vast amount of C in tundra soils, small changes in SOM decomposition with warming would result in substantial increases in atmospheric CO_2 concentration, if not balanced by increased primary production.

Despite the relative importance of belowground respiration, partitioning soil CO_2 efflux between autotrophic and heterotrophic sources remains a persistent challenge in ecology (Hanson et al. 2000; Kuzyakov 2006; Subke et al. 2006; Trumbore 2006; Schimel 2013). Total soil respiration (R_S) is the sum of CO_2 production from two sources: autotrophic (R_A) and heterotrophic respiration (R_H). Belowground autotrophic respiration is associated with maintenance and growth of roots and rhizosphere microbes that utilize recent photosynthate for their metabolism with no direct effect on soil C storage. Alternatively, R_H is associated with microorganisms (e.g. bacteria, fungi, protozoans) oxidizing more persistent SOM. Therefore, changes in R_S may not entirely represent changes in decomposition of SOM and alterations in C stocks if R_A dominates soil CO_2 efflux. Thus, examining the magnitude, seasonality and sensitivity of R_H in conjunction with R_S is important to our understanding of long-term C sequestration. R_H and R_A may respond differently to environmental drivers. While microbial respiration is largely influenced by soil temperature, soil moisture and SOM quality and quantity (Nadelhoffer et al. 1991; Hobbie 1996; Epron et al. 1999; Schimel et al. 1999), there is increasing evidence that R_A is tightly coupled with short-term aboveground productivity and allocation of photosynthate to the rhizosphere (Kuzyakov and Gavrichkova 2010; Vargas et al. 2011). Because R_A is influenced by plant productivity, trends and variation in the magnitude of this flux can vary in response to plant phenology and differences in community composition among sites (Rey et al. 2002; Yuste et al. 2004).

Global estimates of R_H vary across ecosystems and seasons, but range from 10 to 90 % of R_S (Hanson et al. 2000). In the Arctic, estimates of the heterotrophic contribution to soil and ecosystem respiration (R_H/R_S) range between 25 and 87 % (Billings et al. 1977; Chapin et al. 1980; Nakatsubo et al. 1998; McConnell et al. 2013); however, this range includes estimates from one growing season or a single date within a season. Few studies have partitioned R_S in low-shrub tundra, which is a dominant plant community along the west-central Greenland Ice Sheet and throughout the Arctic (Walker et al. 2005). There is a high level of uncertainty in the relative fractions of R_H and R_A in the Arctic because both respiratory components can be large. Belowground biomass can account for a significant proportion of total biomass (Dennis and Johnson 1970; Wardle 2002) and the pool of soil organic C is often large. Additionally, the strong seasonality of active layer thaw may impose a unique constraint on microbial and root activity, while differences in plant phenology may lead to contrasting patterns in seasonal contributions from R_H and R_A across vegetation types. A global synthesis of R_S partitioning studies revealed that less productive ecosystems may be associated with lower relative proportions of R_A (Bond-Lamberty et al. 2004). However, the global dataset is relatively small (54 sites) and only three sites represent Arctic tundra. The dearth of partitioning studies from high latitudes limits our understanding of belowground C cycle dynamics and may hinder efforts to accurately model long-term changes in Arctic C pools.

We had two primary goals in this study. First, we aimed to quantify and compare R_S, R_H and R_A across four common and contrasting tundra vegetation types. Second, we sought to corroborate our estimates by comparing results obtained by trenching (i.e., root exclusion) and ^{13}C pulse-chase approaches. We anticipated that the large amount of belowground biomass common to graminoid communities would result in very high R_A and R_A/R_S compared with sites dominated by woody shrubs. Finally, we examined whether the global model of Bond-Lamberty et al. (2004), which shows a logistic decline in R_A/R_S at sites with low annual R_S, accurately predicts R_A/R_S at out study sites.

Materials and methods

Site description and study design

The study area was located near Kangerlussuaq in West Greenland (67°06′N, 50°16′W). The region represents bioclimatic subzones D and E (Walker et al. 2005) and is classified as low shrub tundra, dominated by a mosaic of deciduous woody shrub patches (*Salix glauca* and *Betula nana*) and graminoid tundra (*Poa* spp, *Carex* spp.). The C content in the upper 10 cm is highest in graminoids (7.9 ± 1.2 %), followed by *Salix* (6.6 ± 1.5 %) and *Betula* (4.0 ± 0.8 %; unpublished data). The trenching component took place over a more spatially extensive area in the vicinity of a warming x herbivore exclusion experiment (Post and Pederson 2008), while the $^{13}CO_2$ pulse-chase experiment took place near the site of a more recent warming experiment (Cahoon et al. in press), approximately 2.0 km east of the exclosure site. The two locations were similar in community composition, slope and aspect. For the trenching experiment, we selected four sites that best represented the vegetation in the region. Large homogenous patches of *Betula nana*, graminoid (*Poa* spp., *Carex* spp.), *Salix glauca*, and a mixed-shrub site (equal mix of *S. glauca* and *B. nana*) were selected by visually estimating the relative aboveground contribution of each species. At the labeling site, similar patches of *Betula nana*, graminoids and *Salix glauca* and areas of mix-shrub communities were identified visually; however, only the *Betula nana* and graminoid plots received the label (see *Ecosystem* $^{13}CO_2$ *labeling* below).

Microclimate monitoring

A micrometeorological station monitored air temperature (CS215; Campbell Scientific, Logan, UT, USA) at 2 m height, photosynthetic photon flux density (PPFD, LI-190; LI-COR, Lincoln, NE, USA), and precipitation (TE 525; Campbell Scientific, Logan, UT, USA) in proximity to the trenching plots. An additional micrometeorological station was established near the labeling site in early May 2012. At this station, three soil temperature sensors (CS105E; Campbell Scientific, Logan, UT, USA) were installed each within the graminoid and *Betula* communities at 10 cm depth. All sensors were scanned every 30 s, with hourly averages stored using a CR1000 datalogger (Campbell Scientific, Logan, UT, USA). Daily and monthly totals from 2012 to 2014 are from the station nearest the trenching experiment. Handheld measurements of soil temperature at 5 and 10 cm depths (Model: 82021-156, VWR International, West Chester, PA, USA), and the average of three soil water content measurements (SWC; 0–12 cm depth, HydroSense II; Campbell Scientific Inc., Logan, UT, USA) were recorded concurrently with weekly respiration measurements.

Trenching treatment

At each vegetation type (i.e. *Betula nana*, graminoids, mixed-shrub and *Salix glauca*), nine pairs of plots (0.36 m^2) were evenly distributed across three distinct, but similar patches that were nearly homogenous in vegetation cover. At each pair, one plot was randomly assigned the trenching treatment. Paired plots were separated by at least 2 m to prevent the disturbance created by the trenching from affecting the control plots. Thus, our study consisted of nine replicates of control (untrenched plots) and nine replicates of trenched plots for each vegetation type. To prevent root growth and estimate R_H, a narrow trench was excavated along the perimeter of the plot to approximately 0.6 m depth or until permafrost prevented further excavation. Recent observations recorded 100 % of *Betula* and 80 % of graminoid root standing crop in the upper 30 cm of the soil profile (L. Radville, personal communication). Two layers of heavy construction plastic (6 mm thick) were inserted along the perimeter and soil was backfilled into the trench. All aboveground vascular vegetation was removed by hand from within the plot to prevent further root growth. The trenching process was completed in late July 2010 at the *Betula* site and July 2011 at the remaining sites. In the three sites where soil respiration was monitored before and after trenching, soil CO_2 efflux was reduced by 43 % (±2.0 SE), 40 % (±0.6 SE) and 25 % (±0.3 SE) in the graminoid, mixed-shrub and *Salix* sites, respectively, just 3 days following the disturbance (Online Resources Fig. A1). Similar trends have been noted in tree girdling (Högberg et al. 2001; Andersen et al. 2005) and other trenching experiments (Vogel and Valentine 2005). The rates immediately following trenching should be interpreted with caution, however, as the rapid decomposition of severed fine roots often contributes to overestimates of R_H by approximately 2–24 % (Subke et al. 2006).

Thus, we elected to include only data from the 2012 and 2013 growing seasons in our analyses.

Summer respiration measurements

A single respiration collar made of PVC (0.15 m diameter) was permanently installed in the center of each plot to 2–3 cm depth. Soil respiration was measured at near weekly intervals throughout the growing seasons of 2011–2013 using a LI-840A infrared gas analyzer (LI-COR Environmental, Lincoln, NE, USA) plumbed to a custom-built PVC chamber. Chamber CO_2, H_2O and temperature were logged every second for 60 s using a LI-1400 datalogger (LI-COR Environmental, Lincoln, NE, USA). Untrenched control plots were used to estimate total soil respiration (R_S), whereas trenched plots were assumed to represent CO_2 efflux from heterotrophic sources (R_H) (Hanson et al. 2000). Autotrophic respiration (R_A) was then estimated as the difference between control and trenched plots ($R_A = R_S - R_H$). Error in R_A was propagated as:

$$\sigma_{R_A} = \sqrt{\sigma_{R_S}^2 + \sigma_{R_H}^2}, \quad (1)$$

where σ_{R_S} and σ_{R_H} represent the standard deviation of R_S and R_H, respectively. Error in the relative proportion of R_A (R_A/R_S) was then propagated as:

$$\sigma_{R_A/R_S} = \sqrt{\left(\frac{\sigma_{R_A}}{\bar{\chi}_{R_A}}\right)^2 + \left(\frac{\sigma_{R_S}}{\bar{\chi}_{R_S}}\right)^2}\,\bar{\chi}_{R_A/R_S}, \quad (2)$$

where σ_{R_A} and σ_{R_S} are the standard deviation of R_A and R_S, respectively, and $\bar{\chi}_{R_A}$, $\bar{\chi}_{R_S}$ and $\bar{\chi}_{R_A/R_S}$ are the mean R_A, R_S and R_A/R_S, respectively. Aboveground vascular plants were removed by hand at least 24 h prior to all respiration measurements to prevent new root growth and eliminate any respiration contributed from aboveground biomass. When present, which was rare, moss was left intact because of its important role in regulating soil thermal and moisture conditions (Sveinbjörnsson and Oechel 1981).

Winter respiration measurements

Subnivean [CO_2] measurements were made in February 2013 and January 2014 near the labeling site. Measurements were made using a hollow stainless steel probe with a perforated tip, plumbed with 3.2 mm bev-a-line tubing (e.g., Sullivan et al. 2010). The tubing was connected to an LI-840 CO_2- and H_2O analyzer (LI-COR Environmental, Lincoln, NE, USA), and air was drawn through the optical bench using a small diaphragm pump at approximately 0.85 L min^{-1}. During each site visit, measurements were made at 6–8 plots per vegetation type. At each plot, the probe was inserted to the base of the snowpack. Once the [CO_2] stabilized, data were stored using a LI-1400 datalogger (LI-COR Environmental, Lincoln, NE, USA). At least three probe measurements were made at each plot. On each occasion, 2–3 snowpits were dug within each vegetation type to measure snow density and temperature at 10 cm intervals. Diffusion of CO_2 through the snowpack was estimated using the methods described by Musselman et al. (2005). Because winter respiration measurements were made on so few occasions, the data were used to constrain the annual CO_2 flux model (see below), but not to examine the seasonality of soil CO_2 efflux.

Ecosystem $^{13}CO_2$ labeling

Isotopic labeling was conducted on graminoid and *Betula* plots on three occasions (June 14, July 7 and July 15) in 2014. For each labeling event we established four new plots: two *Betula* and two graminoid. At each plot, a custom-built clear acrylic chamber (0.75 × 0.75 × 0.75 m) and matching base with a plastic skirt attached to the underside were lowered onto each plot and sealed to the ground using a heavy chain. Through a small port on the chamber wall, 0.4 L of 99 atom% $^{13}CO_2$ (Cambridge Isotope Laboratories, Tewksbury, MA, USA) was administered at a rate of 0.2 L min^{-1} for 2 mins. The chamber was left in place for 1 h to allow for assimilation of $^{13}CO_2$. On both occasions, the labeling occurred on sunny days between the hours of 10:00 and 16:00. Two fans ensured equal mixing of the air throughout the labeling period. The long labeling period can cause conditions within the chamber to dramatically exceed those of the ambient air, which may affect plant physiology and the fixation of ^{13}CO-$_2$ (Carbone et al. 2007). We mitigated those effects by constructing the labeling chamber with a narrow water jacket, through which cold water was circulated continuously during the labeling process. Use of the water jacket allowed us to maintain chamber air temperatures well below 30 °C during all labeling events, while ambient air temperature ranged between 12.4 and 16.2 °C.

Chasing ^{13}C in belowground respiration

We measured the efflux of $^{13}CO_2$ from the soil using PVC collars (20.3 cm diameter) inserted 2–3 cm into the soil in the center of each plot. Collars were installed at least 24 h prior to each labeling event in areas with limited aboveground plant tissue, but immediately adjacent to vascular plants. At the time of installation, the limited leaf tissue present within the collars was carefully removed. Soil $^{13}CO_2$ efflux was monitored from each plot using an opaque chamber (3.9 L) sealed to the PVC collar. The chamber was plumbed to a Picarro G2201-*i* Isotopic Analyzer (Picarro Inc., Sunnyvale, CA, USA), which was checked against an air standard with known $[CO_2]$ and $\delta^{13}CO_2$ at the beginning and end of each measurement day. There was very limited evidence of analyzer drift over the course of our measurement days. The mean change in $[CO_2]$ from the beginning to the end of a measurement day was 0.7 μmol/mol, while the maximum change was 3.2 μmol/mol. The mean change in $\delta^{13}C$ was 0.2 ‰, while the maximum change was 0.9 ‰. The soil chamber was equipped with two gas ports. One was connected to the analyzer using 30 m of 3.2 mm I.D. bev-a-line tubing. The other port was connected to a 50 cm coil of the same tubing that was left open to the atmosphere, similar to Warren et al. (2014). Sample air was drawn to the analyzer at a rate of 0.025 L min^{-1} for approximately 20 min. At the end of each measurement, the chamber was left open to the atmosphere for at least 8 min before sealing to the next soil collar. Measurements of the atmosphere between each plot provided another opportunity to check for analyzer drift at regular intervals during the measurement day. Keeling plots were constructed using $[CO_2]$ and $\delta^{13}CO_2$ data from each collar (Pataki et al. 2003). The y-intercepts were estimated using ranged major axis regression in the lmodel2 package (Legendre 2014) in R 3.1.2 (R Core Team 2014). Each collar was chased 1, 2, 7 and 14 days following the labeling event.

Chasing ^{13}C in root respiration

Measurements of $\delta^{13}C$ in root-respired CO_2 were made on the same schedule as soil $^{13}CO_2$ efflux (1, 2, 7 and 14 days following the labeling event). Immediately following soil $^{13}CO_2$ sampling, two small soil cores (2.6 cm diameter) were collected to 12 cm depth from within each labeled plot, but outside of the soil respiration collars. Roots were washed free of soil, placed in a mason jar (0.273 L) and incubated in the soil. The mason jars, which had two gas ports installed in the lid, were plumbed to the G2201-*i* using 3.2 mm I.D. bev-a-line tubing. Estimates of $\delta^{13}C$ in root-respired CO_2 were made using the same protocol as the soil chambers.

^{13}C data processing

To determine the proportion of belowground respiration that can be attributed to roots (f_A), we used a single isotope, two-source mixing model (Phillips and Gregg 2001):

$$f_A = \frac{\delta^{13}C_S - \delta^{13}C_B}{\delta^{13}C_A - \delta^{13}C_B}, \quad (3)$$

where $\delta^{13}C_S$ is the isotopic composition of belowground respiration, $\delta^{13}C_A$ is the isotopic composition of "labeled" root-respired CO_2 and $\delta^{13}C_B$ is the isotopic composition of "unlabeled" bulk soil heterotrophic respiration. The variance in f_A was estimated as:

$$\sigma^2_{f_A} = \frac{1}{\left(\bar{\delta}_A - \bar{\delta}_B\right)^2} \times \left[\sigma^2_{\delta_S} + f_A^2\sigma^2_{\delta_A} + (1 - f_A)^2\sigma^2_{\delta_B}\right], \quad (4)$$

where $\bar{\delta}_A$ and $\bar{\delta}_B$ are the mean isotopic signatures for labeled root respired CO_2 and bulk soil (unlabeled) heterotrophic respiration, while $\sigma^2_{\delta_S}$, $\sigma^2_{\delta_A}$, and $\sigma^2_{\delta_B}$ represent the variance in $\delta^{13}C_S$, $\delta^{13}C_A$, and $\delta^{13}C_B$, respectively (Phillips and Gregg 2001). We approximated $\delta^{13}C_B$ by excavating soil pits adjacent to the study area and sampling root-free soil from depths of 5, 10 and 20 cm (8 *Betula* and 8 graminoid pits). We elected to use this approach, rather than measure $\delta^{13}C$ in respiration of root-free soils, because it is nearly impossible to remove all fine roots from the soil and because $\delta^{13}C$ in respiration of physically disturbed soils may not reflect $\delta^{13}C$ in respiration of undisturbed soils. Our approach assumes that $\delta^{13}C$ of bulk soil heterotrophic respiration is equivalent to soil $\delta^{13}C$. This assumption is not entirely valid (e.g., Ehleringer et al. 2000), as microbes may preferentially break down molecules that differ isotopically from bulk soil organic matter. However, the mixing model is robust to small errors in $\delta^{13}C_B$ estimates. In our study, a fairly

large 1 ‰ difference in $\delta^{13}C_B$ would have altered our estimate of f_A by approximately 3 %. Soil samples were oven-dried at 60 °C for at least 48 h, homogenized and analyzed for $\delta^{13}C$ measured at the Environment and Natural Resource Institute's Stable Isotope Laboratory (ENRI SIL) at the University of Alaska Anchorage using a Costech 4010 Elemental Analyzer (Costech Analytical, Valencia, CA, USA) interfaced with a Delta PLUS XP continuous flow isotope ratio mass spectrometer (Thermo Scientific Inc., USA). Ambient soil $\delta^{13}C$ was averaged across depths and then across soil pits (*Betula* $\delta^{13}C_B$: -25.9 ± 0.15 ‰; graminoid $\delta^{13}C_B$: -25.2 ± 0.08 ‰).

On several of the 1- and 2-day chase events, estimates of $\delta^{13}C_S$ were more enriched than our estimates of $\delta^{13}C_A$ for a few of the plots. This is likely an artifact of isotopic equilibration between the highly enriched chamber air and soil CO_2 during the labeling event, as observed in other studies (Subke et al. 2009, 2012). Data from those plots on those sampling dates were excluded from further analyses. Estimates of f_A were then averaged across chase-dates for each plot then across vegetation type, yielding a sample size of 4 *Betula* and 4 graminoid plots.

Modeling and statistical analyses

We tested for differences in R_S, R_A, R_H and R_A/R_S between vegetation types using repeated measures analysis of variance (ANOVA). Least-squares means for each site were compared using Tukey's honest significant difference. Data were $\log_{10}$—transformed when there was evidence of non-normality and/or heteroscedasticity. Statistical analyses and modeling exercises were performed on temperature-corrected R_H values using the nlme (Pinheiro et al. 2015) and lsmeans (Lenth and Hervé 2014) packages in R 3.1.2. We anticipated that the trenching treatment would result in an increase in soil temperature, which may lead to overestimates of R_H We accounted for this treatment-induced increase in temperature by normalizing R_H to the soil temperature at 5 cm depth in adjacent control plots. To do so, we fit separate Q_{10} temperature response models to all the R_H data from each vegetation type and estimated R_H at the soil temperature observed in the adjacent untrenched area, following Litton et al. (2003). On average, the temperature adjustment reduced R_H by 0.006 ($\pm$0.001 SE), 0.05 ($\pm$0.01 SE), 0.003 ($\pm$0.0004 SE) and 0.15 ($\pm$0.02 SE) μmol CO_2 m^{-2} s^{-1} in *Betula*, graminoid, mixed-shrub *Salix* sites, respectively. We elected to correct R_H for soil temperature and not soil water content (or other abiotic conditions), because we detected much larger differences in soil temperature than soil water content in response to the trenching treatment (Online Resources, Fig. A2). Additionally, correcting for differences in SWC in previous trenching studies has resulted in minor adjustments to R_H (Ngao et al. 2007). Lastly, we found greater support in the data for the Q_{10} temperature response model (AICc = 417) than for a similar model that also included SWC (Carlyle and Ba Than 1988; AICc = 974). We recognize, however, that soil water content can sometimes mediate the relationship between temperature and soil respiration (Davidson et al. 1998; Illeris et al. 2004).

To estimate annual CO_2 efflux from each vegetation type, we fit a 3-parameter logistic model to the data from each plot (Barr et al. 2002):

$$R_S = \frac{\theta_1}{1 + e^{(\theta_2 - \theta_3 * T)}}, \quad (5)$$

where θ_{1-3} are fitted parameters and T is soil temperature measured at 10 cm depth. We included winter respiration measurements by randomly assigning 2/3 of the site-specific winter dataset to each plot. Model parameters were estimated by the nonlinear least squares function in the stats package (R Core Team 2014) in R 3.1.2. Annual R_S was estimated by driving the model using hourly soil temperature data collected at our nearest micrometeorological station.

Results

Microclimate

The 2012 growing season was warm and wet compared with 2013, which was relatively cool and dry (Table 1). Soil temperature in the control plots was warmest in 2012 at all sites (Fig. 1a, b), whereas soils were slightly wetter in 2013 ($F_{3,24} = 1.308$, $P = 0.03$; Online Resource, Table A1; Fig. 1). We did not detect a significant difference in SWC among vegetation types in either year, though there was a tendency for graminoid soils to be wetter. In contrast, there were sharp differences in soil temperature

among vegetation types in each year (Fig. 1). Soils at the *Betula* site were consistently colder than any other site, whereas the warmest soils were among the graminoid plots in 2012. In the cooler season of 2013, soils among graminoid, *Salix* and the mixed-shrub sites were similar at both 5 and 10 cm depth. The trenching treatment resulted in warmer and slightly wetter soils (Online Resource Table A1, Fig. A2).

Methodological comparison of respiration partitioning

Our estimates of R_A obtained by the trenching method were remarkably similar to the autotrophic proportion (f_A) estimated using the $^{13}CO_2$ pulse-chase method (Online Resource, Table A2; Fig. 2). The autotrophic proportion was estimated at 49.0 % (±0.24 SE) and 47.4 % (±0.12 SE) using the ^{13}C-labeling and trenching methods, respectively, in the *Betula* vegetation type. At the graminoid plots, the autotrophic contribution was 52.5 % (±0.12 SE) and 46.2 % (±0.11 SE) using the ^{13}C-labelling and trenching methods, respectively (Fig. 2). Although we were unable to directly compare methods in the same season, these results provide qualitative corroboration that the trenching method did not lead to large artifacts beyond the temperature and moisture effects addressed above.

Annual and seasonal trends in R_S, R_H and R_A

Soil respiration (R_S) was greatest during the warm and wet 2012 growing season and lowest during the cool and dry 2013 season (Fig. 3a, b). When compared across vegetation types, R_S, R_H and R_A were greatest at the *Salix* site, followed by the mixed-shrub and graminoid sites, whereas the lowest fluxes were among the *Betula* plots. When averaged across all dates, R_H and R_A were remarkably similar within each site, with the single exception of the graminoid site in 2013 when R_A was significantly greater than R_H ($F_{1,\ 41} = 5.44$, $P = 0.02$, Fig. 3b). The proportion of R_H was slightly above 0.5 in 2012 for all sites, although there were no detectable differences between sites or years (Fig. 3c). In both seasons, there was very little difference between vegetation types in R_H/R_S across sampling dates (Online Resource Fig. A3). The logistic model was a moderately strong predictor of seasonal variation in plot-level R_S ($r^2 = 0.78$; $R_{S(measured)} = 0.95 \times R_{S\ (modeled)} + 0.06$) (Online Resource Fig. A4). In the global context, our sites fit within the range published by Bond-Lamberty et al. (2004; Fig. 4), however the autotrophic contribution exceeded what the global model would predict based on annual soil CO_2 efflux.

Table 1 Monthly average air temperature and photosynthetic photon flux density (PPFD) and total precipitation for May–August in each year of the trenching (2012–2013) and isotope-labeling (2014) of our study

	May	June	July	August	Season
2012					
Air temperature (°C)	3.92	10.4	11.5	8.4	8.6
Precipitation (mm)	21.6	19.1	25.9	51.3	117.9
PPFD (μmol m^{-2} s^{-1})	457	530	468	326	445
2013					
Air temperature (°C)	−2.75	8.5	9.6	6.2	5.4
Precipitation (mm)	4.3	1.8	21.6	31	58.7
PPFD (μmol m^{-2} s^{-1})	483	569	477	345	468
2014					
Air temperature (°C)	0.39	9.5	11.1	8.6	7.4
Precipitation (mm)	11.4	3.1	2.8	51.3	68.6
PPFD (μmol m^{-2} s^{-1})	442	570	530	333	469

Data were collected at the micrometeorological station near the trenching experiment. The far-right column is the seasonal average air temperature and PPFD and total precipitation between the dates May 1 and August 31 of each year

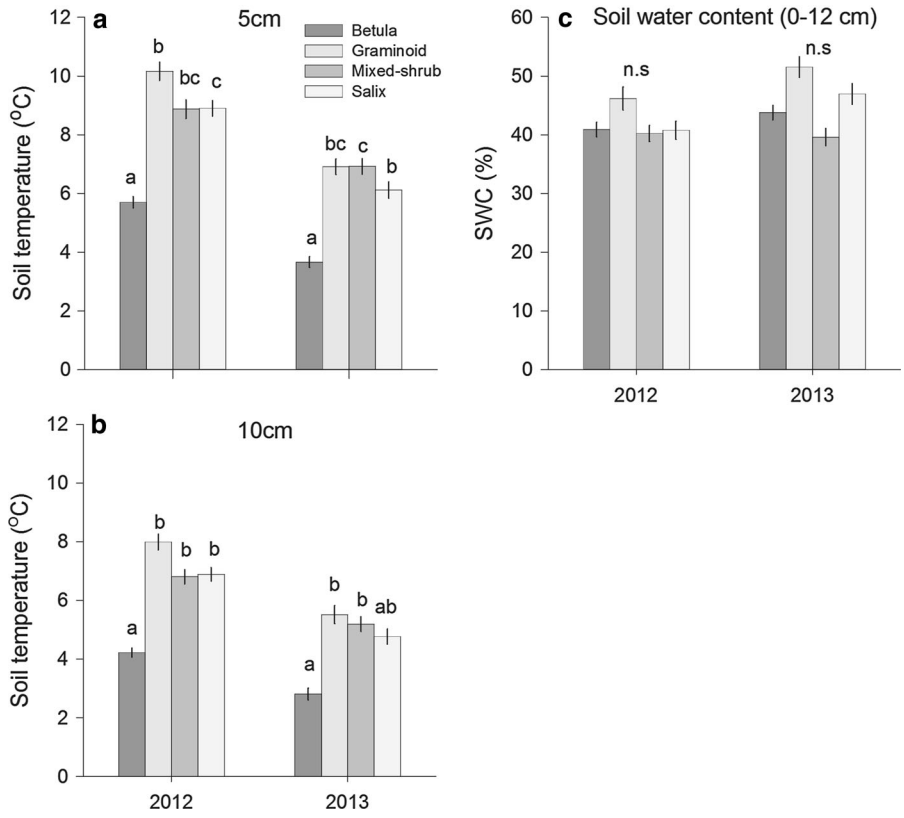

Fig. 1 Average midday soil temperature at 5 cm (**a**) and 10 cm depth (**b**) and soil water content (SWC, 0–12 cm depth, **c**). *Bars* represent the mean and error bars are ±1 standard error ($n = 9$). Sites that share a letter did not differ significantly ($P < 0.05$) from one another

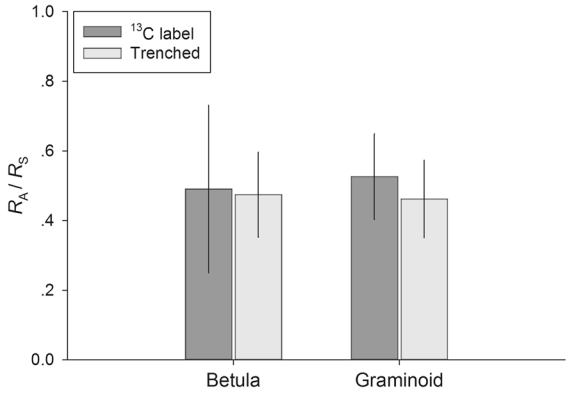

Fig. 2 Autotrophic proportion of soil respiration estimated from ^{13}C pulse-chase in 2014 and the trenching method in 2012 and 2013. *Bars* represent the mean of all plots across all dates for each species in the labeling experiment (^{13}C, $n = 4$) and during a similar time period in the 2012 growing season (June 25–July 17) in the trenched plots ($n = 9$). Error bars were generated using Eq. 1 and 3 for the trenched and ^{13}C techniques, respectively

Discussion

Our estimates of R_A from the trenching experiment were corroborated by ^{13}C labeling in the *Betula* and graminoid sites. Limitations to the trenching technique have been discussed thoroughly in previous reviews (Hanson et al. 2000; Kuzyakov 2006; Subke et al. 2006), however we have accounted for several of these biases. First, flux measurements were collected at least 1 year following trenching to allow for the rapid decomposition of labile root biomass. Figure A1 (Online Resource) provides evidence that the effect of disturbance is relatively short-lived and stabilizes within just a few weeks. Second, we corrected R_H for an increase in temperature in the trenched plots where vegetation was removed. Although trenching can lead to higher soil water content due to the lack of transpiration (Epron et al. 1999; Ngao et al. 2007), the difference in soil moisture at our site was small relative to the larger differences in soil temperature and we found less support for a model that included soil water content. Finally, the strong agreement between the two methods increases our confidence that the trenching experiment provided an accurate representation of R_H and R_A dynamics.

Our measurements of R_S are consistent with those from other arctic ecosystems (Christensen et al. 1998;

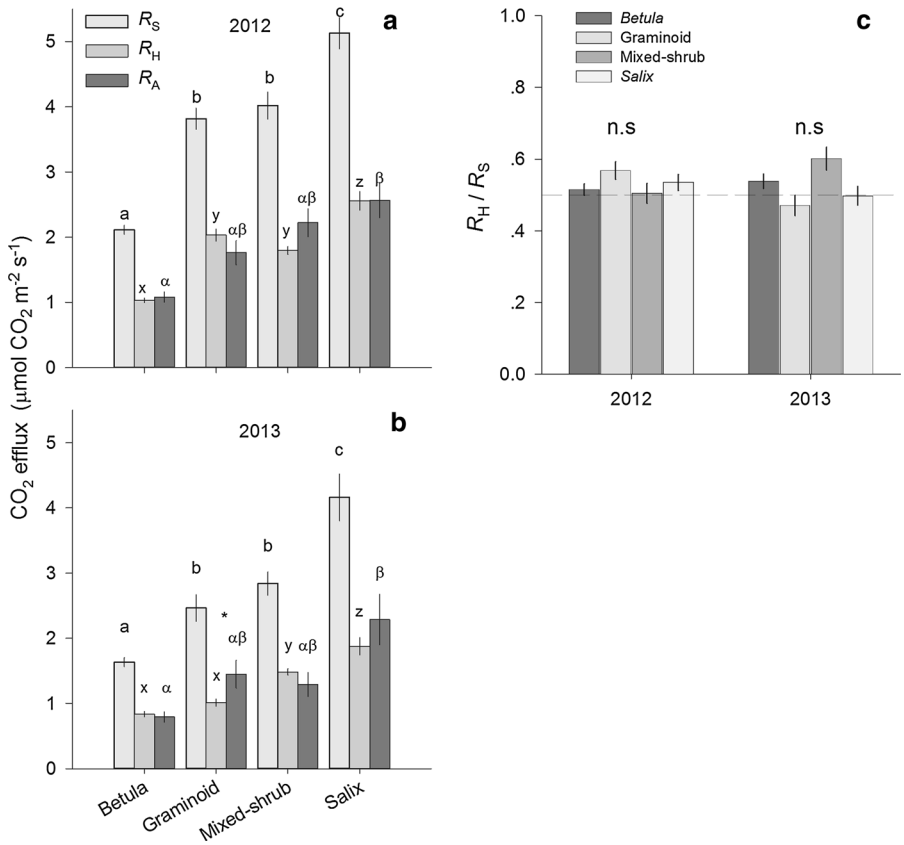

Fig. 3 Midday rates of total soil respiration (R_S), heterotrophic respiration (R_H) and autotrophic respiration (R_A) averaged over all dates in 2012 (**a**) and 2013 (**b**). The proportion of heterotrophic respiration (R_H/R_S) averaged over all dates in 2012 and 2013 is displayed in panel **c**. *Bars* represent the mean and error bars are ±1 standard error ($n = 9$). Significance difference ($P < 0.05$) between R_H and R_A within each site are noted with *asterisk* above the bars. Differences between sites are represented separately for R_S (a–c), R_H (x–z) and R_A (α–β). Sites that share a character did not significantly differ from one another. Sites that were not significantly different are represented by *n.s*

Rustad et al. 2001; Elberling 2007; Björkman et al. 2010). There were, however, major differences between vegetation types. In particular, there was a stark difference in R_S between the two dominant woody shrubs in the region; *Betula nana* and *Salix glauca* (Fig. 3a, b). Soil temperatures were much cooler beneath *Betula*, which likely played a major role in reducing soil microbial activity and root production. However, the major difference in soil temperature between *Betula* and *Salix* suggests that differences in shrub species may elicit divergent effects on soil thermal properties and soil CO_2 efflux (e.g. Blok et al. 2010). For instance, although soil temperature was intermediate at the *Salix* vegetation type, R_S was consistently greater than all other vegetation types (Fig. 3a, b). This discrepancy may be due to more labile leaf litter in *Salix* (C:N = 22.1) compared with *Betula* (C:N = 26.1; Cahoon, unpublished data). Recent work in the Arctic has indicated that litter quality (Myers-Smith and Hik 2013) and quantity (DeMarco et al. 2014) effects on decomposition were relatively more important than the effect of soil temperature. A similar process may have been occurring at our site, contributing to the contrasting patterns in R_S between the co-dominant woody shrub species.

At our Low Arctic location, the proportion of R_A accounted for 40–48 % of R_S when averaged across all vegetation types, which is a much narrower range than early partitioning studies from the Arctic (Billings et al. 1977; Chapin et al. 1980; Nakatsubo et al. 1998), but similar to a recent study that attributed 40–60 % of ecosystem respiration to R_A in a sub-Arctic boreal rich fen (McConnell et al. 2013). We were surprised to find such limited variation in the partitioning of R_S (R_H/R_S; Fig. 3c) among vegetation types, as we hypothesized the prolific graminoid root systems would result in higher R_A and R_A/R_S compared with the other vegetation types. Despite dramatic differences in growing-season microclimate (Table 1; Fig. 1) and soil CO_2 efflux (Fig. 3a, b), we did not detect a significant difference in the relative contribution from

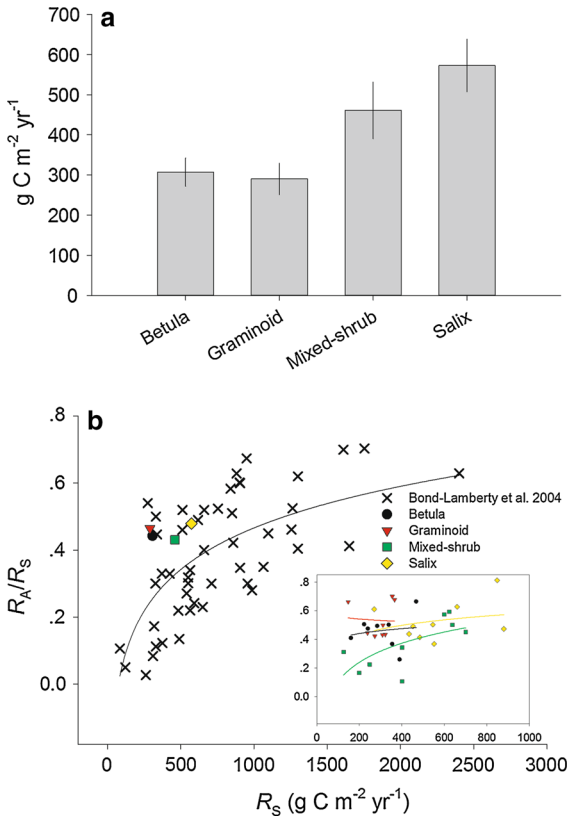

Fig. 4 Annual CO_2 efflux (R_S) estimated over the 2013 calendar year (**a**). *Bars* represent the mean and error bars are ± 1 standard error ($n = 9$). Annual R_S was estimated using the logistic model parameterized for each vegetation type. Panel **b** shows the global relationship between autotrophic contribution (R_A/R_S) and annual soil CO_2 efflux as compiled by Bond-Lamberty and Thomson (2010) and displayed in Bond-Lamberty et al. (2004). Note that R_A/R_S is the same as root contribution (RC) from Bond-Lamberty et al. (2004). Data from our sites are shown in *color*. The *inset* shows the relationship at the plot-level within the vegetation types at our site. The autotrophic contribution was averaged over all dates in 2013

R_H between growing seasons and among vegetation types (Fig. 3c).

Our results suggest that, when averaged across all vegetation types and seasons, R_H contributes approximately 53 % to total belowground efflux, which is identical to the value estimated by Segal and Sullivan (2014) for tussock tundra near Toolik Lake, Alaska. The similarity in the proportion of R_H, despite strong variation in R_S and widely different vegetation structural and functional attributes, is suggestive of an intimate link between vegetation production and soil microbial activity. This relationship may simply be attributable to the fact that both roots and soil microbes ultimately depend on photosynthate as a substrate for respiration. While our data do fall within the range of global estimates of the relationship between annual R_S and R_A/R_S, they are not supportive of a strong decline in R_A/R_S at low R_S (Bond-Lamberty et al. 2004). In fact, the global model underestimates the autotrophic proportion by 0.19, 0.21, 0.11 and 0.12 in the *Betula*, graminoid, mixed-shrub and *Salix* vegetation types at our site, respectively. We argue that more partitioning studies are needed in systems with low R_S to ensure that this end of the spectrum is not dominated by few sites or confounded by the partitioning method and/or the stage of soil development.

Partitioning R_S into auto- and heterotrophic proportions may serve as a useful diagnostic for ecosystems that have fallen out of C exchange equilibrium with the atmosphere. Systems that show a decline in R_A/R_S may be susceptible to losses of soil C stocks, as R_A may be closely correlated with C inputs, while R_H reflects C outputs. An excellent example is the case of permafrost degradation in arctic ecosystems, where the mineralization of old C at depth could increase R_H (Dorrepaal et al. 2009), dilute the root contribution and lead to a decline in R_A/R_S (Hicks Pries et al. 2013, 2015). Meanwhile, ecosystems that show an increase in R_A/R_S may be rapidly aggrading soil C. An arctic example could be a case where shrub encroachment into graminoid ecosystems and the associated increase in leaf area leads to shading and cooling of the soil (Blok et al. 2010), thereby restricting R_H (Cahoon et al. 2012) and leading to an increase in R_A/R_S.

Conclusions

Despite the challenges of partitioning R_S, our more limited ^{13}C labeling study confirmed that our more extensive trenching approach provided reliable estimates of R_A and R_H. Our study benefited from two contrasting growing seasons, which led to different magnitudes of soil CO_2 efflux, yet we detected minimal differences in the relative contributions from R_H and R_A over time and across widely different vegetation types. Our results, and those from Toolik Lake, Alaska (Segal and Sullivan 2014), suggest that the contribution of R_A to R_S may be more consistent over time and across vegetation types with low R_S than

previously thought. The potential benefit of using soil respiration partitioning as an indicator of systems that have fallen out of equilibrium is that change may be detectable long before a measureable shift in the soil C stock. As such, examining the breakdown of R_S into its auto- and heterotrophic components may be a useful tool in forecasting the fate of the large pool of SOC in the Arctic and associated feedbacks to the global climate.

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