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A B S T R A C T

Atmospheric warming is expected to cause shifts in arctic tundra vegetation composition, especially in the abundance and distribution of shrub species. Greater shrub abundance will impact the carbon exchanges between tundra ecosystems and the atmosphere, including ecosystem respiration. Here, total respiration under the shrub canopy (R_T) and its components soil respiration (R_S) and respiration from the ground cover vegetation (R_G) were investigated at three tundra sites in the Canadian Low Arctic with varying shrub coverage. Seasonal R_T and R_S mean values were significantly greater ($P < 0.05$) at the site with greatest shrub abundance; mean values were 3.70 and 3.22 μmol m^{-2} s^{-1}, respectively. Mean R_G did not differ among sites; mean values ranged from 0.45 to 0.52 μmol m^{-2} s^{-1}. Soil temperature exerted a stronger control on R_T and R_S compared to soil moisture. Differences in R_T and R_S among sites were attributed to differences in soil properties, such as soil total N content and bulk density. These findings suggest that belowground sources of respired carbon dioxide in Low Arctic tundra may vary with long-term shrub expansion as soil microclimate conditions and physiochemical properties adjust to changes in shrub coverage.

INTRODUCTION

Warming in the Arctic is projected to alter tundra vegetation communities, including an increase in the relative abundance and cover of deciduous shrub species (Walker et al., 2003; Tape et al., 2006; Pearson et al., 2013). Such changes will ultimately result in feedbacks on carbon cycling in the Arctic. In recent decades, satellite observations of greening trends in the Arctic, which suggest increased productivity and photosynthetic uptake of carbon dioxide (CO_2), have been linked to increasing temperatures (Bunn et al., 2005; Beck and Goetz, 2011). However, broad-scale changes in ecosystem respiration (ER) are more difficult to detect, and ER response to changing arctic climate and vegetation cover remains uncertain. To understand these

impacts, it is necessary to separate ER into its component sources. Different sources of ER may respond differently to environmental controls (Yan et al., 2009; Subke et al., 2011) and, therefore, may be influenced differently by increasing shrub cover and density. Although tundra ER can be partitioned in various ways in terms of changing shrub cover effects, a useful approach is to divide ER into two main streams: (1) autotrophic respiration from the shrub canopy, and (2) respiration from below the canopy. The latter includes the ground cover vegetation respiration (R_G) and soil respiration (R_S) representing the combined respiration from roots and microbial communities. While it is expected that autotrophic respiration from the shrub canopy and root-derived R_S should increase with greater plant biomass and root productivity (Hobbie and Chapin, 1998), the expected

variations in R_S and R_G with increasing shrub cover are relatively unexplored.

There are large and potentially labile carbon (C) pools stored in arctic soils (Ping et al., 2008; Tarnocai et al., 2009; Hugelius et al., 2014) and microbe-derived R_S is the major pathway for this stored C to enter the atmosphere. In most models, respiration from soil sources is determined by soil microclimate and other properties, including soil temperature, soil moisture, and aeration (Raich and Potter, 1995; Shaver et al., 2007, 2013), substrate supply (Ryan and Law, 2005), and substrate lability (Buckeridge et al., 2010). Thus, how these variables change with increased shrub cover and density will determine future trends in R_S of arctic tundra.

Climate warming generally favors growth of deciduous shrubs at the expense of forbs, graminoids, bryophytes, and lichens in arctic tundra ecosystems (Walker et al., 2006) because of the interspecific competition for light and nutrients (Totland and Esaete, 2002; Fargione et al., 2003). Differences in ground cover and overstory vegetation could affect R_S through changes in rhizosphere conditions, soil temperature, moisture, and substrate quantity and quality. Changes in aboveground vegetation could also influence root respiration through changes in root biomass, productivity, and turnover (Parker et al., 2015). Ground cover, such as lichens, increase surface albedo, and mosses tend to insulate the soil from summer heat, resulting in cooler soil temperatures (Gornall et al., 2007; Blok et al., 2011). In winter, taller shrubs can trap blowing snow, resulting in greater snow depth, which insulates the soil, leading to warmer winter soil temperatures (Sturm et al., 2001; Bewley et al., 2010). Conversely, by experimentally removing *Betula nana* canopies, Blok et al. (2010) found that soils were warmer and thaw depths were deeper in summer, which suggests that shading from shrubs in summer resulted in cooler soil temperatures and less thawing within the active layer. However, model studies of the impacts of increasing shrub abundance suggest that when climate feedbacks such as surface albedo changes are considered, large-scale expansion of shrubs could lead to warmer soil temperature and deeper permafrost thaw (Lawrence and Swenson, 2011; Bonfils et al., 2012).

While there is uncertainty about the impact of shrub expansion in regulating soil temperatures, there is also continued uncertainty regarding the temperature sensitivity of soil C decomposition (Davidson and Janssens, 2006; Karhu et al., 2014). Short-term experiments have demonstrated that the rate of soil respiration increases with temperature (Friedlingstein et al., 2006; Kirschbaum, 2006); however, long-term responses are not well known (Bradford, 2013). For instance, acclimation of plant respiration to temperature could greatly reduce the sensitivity of respiration to changes in environmental temperature resulting from climate warming (Atkin and Tjoelker, 2003). Warming-induced changes in the soil microbial community have also been observed to amplify the instantaneous increase in the rates of CO_2 production in arctic soils (Hartley et al., 2008) and in other ecosystems (Hartley et al., 2007; Nie et al., 2013).

Apart from temperature, soil moisture may also change with long-term shrub expansion. The accumulation of wind-blown snow in tall shrubs can lead to greater soil moisture content in spring (Sturm et al., 2005). Conversely, some authors suggest that greater deciduous shrub cover may increase evapotranspiration rates and lead to soil drying in summer (Pearson et al., 2013). It is well established that soil respiration can vary significantly among tundra ecosystems of different hydrological regimes (Oberbauer et al., 1996; Grogan and Jonasson, 2005). Soil incubation studies have demonstrated that respiration responds positively to moisture at low levels, but negatively at saturating levels because of oxygen limitation (Johnson et al., 1996).

Besides its influences on soil temperature and moisture, expansion of shrubs will lead to more deciduous litter production, which decomposes 60% faster than evergreen species litter (Cornwell et al., 2008). Buckeridge et al. (2010) also found soil nitrogen cycling rates were ~3 times faster in tall deciduous birch tundra compared to surrounding dwarf birch hummock vegetation. In contrast, other studies have suggested deciduous shrub litter is more recalcitrant relative to herbaceous litter resulting in slower decomposition rates (Hobbie, 1996; Baptist et al., 2010) because woody plants store more C as lignin (De Deyn et al., 2008). Thus, the net effect of shrub expansion on R_S will likely depend on the vegetation that was replaced.

The objectives of this study were to quantify R_S and R_G across three tundra sites with varying levels of shrub cover and to examine the importance of soil temperature, moisture, and soil physiochemical properties in governing differences in respiration rates among the three sites. We hypothesized that (1) soil respiration would increase with increases in shrub cover, (2) respiration from ground cover vegetation would decrease with greater shrub cover, and (3) soil temperature and moisture would drive temporal variations in R_S and R_G. In testing these hypotheses, our aim was to develop a better understanding of the potential changes in respiration rates that may result through climate-induced changes in arctic tundra ecosystem vegetation.

Methods

Study Site

The study area was located in the Low Arctic near the Tundra Ecosystem Research Station (TERS) at Dar-

ing Lake in Canada's Northwest Territories (64°52′N, 111°34′W). It is approximately 70 km north of treeline. The area is underlain by continuous permafrost with the maximum active layer depth typically ranging from 0.3 m to 1.0 m. Local elevation ranges from 414 to 470 m above sea level. Soils in the region typically have a thin surface organic horizon in drier areas (less than 0.1 m) and a thicker organic horizon in wetter areas (up to 0.7 m), overlying coarse mineral soil (Humphreys and Lafleur, 2011). Climate in this region is characterized by long cold winters with a short growing season (mid-June to early September). The mean annual temperature is −9 °C and mean annual precipitation ranges between 200 and 300 mm (Lafleur et al., 2012).

Three research sites, located within 3 km of each other and where the vegetation varied in percent cover and height of the dominant birch shrub, *Betula glandulosa* (Michx.), were selected. Sites were described and named according to the Circumpolar Arctic Vegetation Map classification (CAVM; Walker et al., 2005). The mixed tundra site (CAVM designations S1 and G4) included 10- to 30-cm-tall *B. glandulosa* shrubs with coverage of ~17%. The dwarf shrub site (S1) was located approximately 1 km northeast of the mixed tundra site, had 40- to 60-cm-tall *B. glandulosa* shrubs covering ~45% percent of the site. The low shrub site (S2), located approximately 2.5 km southwest of the mixed tundra site, had ~60% coverage of taller (50 to 100 cm) *B. glandulosa* shrubs. The other common species at all three sites included *Vaccinium uliginosum* (L.), *Rhododendron* subsect. *Ledum*, *Empetrum nigrum* (L.), *Vaccinium vitis-idaea* (L.), *Andromeda polifolia* (L.), *Rubus chamaemorus* (L.), some graminoids, and various mosses and lichens. All three sites were located on slightly sloping terrain (<1°) with generally coarse textured mineral soils varying from sand to silt loam with a trend toward more silt

at the dwarf and low shrub sites. All sites were characterized by a large range of near-surface soil moisture conditions with no significant difference among sites (see Results section below).

Experimental Design

At each site, six plots (1 m × 1 m) were randomly selected that contained at least one *B. glandulosa* shrub. In each plot, three replicate locations (~15 cm in diameter) were established for the measurement of R_T, including respiration from ground cover species such as mosses, lichen, and small stature vascular plants, and R_S only. To achieve this, two collars constructed of opaque PVC tubing with an inner diameter of 11 cm and a height of 8 cm, were installed in each replicate location (Fig. 1). The collars were inserted into the soil to a depth of 5 cm, leaving approximately 3 cm above the surface. In the R_T collars (labeled A, B, and C in Fig. 1, part a) surface vegetation and litter were left undisturbed (Fig. 1, part b). The second set of collars was a plant removal treatment (labeled a, b, and c in Fig. 1, part a) designed to measure R_S. After installation, all green moss and aboveground vascular vegetation with associated surface roots (top ~1–2 cm) were removed within these collars (Fig. 1, part b). Any senesced leaf litter was replaced on the soil surface. This treatment reduced the total root biomass in the collars to some extent such that R_S represented respiration from roots below ~2 cm and from soil microbial communities. The difference between R_T and R_S was designated as ground cover vegetation respiration (R_G), which also included contributions from surface roots. We realize the potential for spatial variability and disturbance confounding results in this type of manipulation. To reduce these impacts, we set the paired collars as close together as possible and were careful to minimize the disturbance. This approach is similar to that used in past experiments
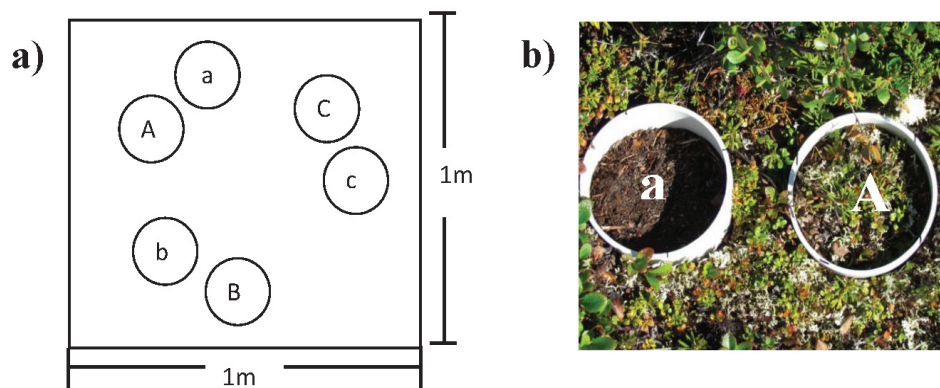
FIGURE 1. (a) Layout of chamber flux collars at each plot and (b) photo of one pair of soil collars for respiration measurement. Upper-case letters indicate respiration measurements collars with no removal of ground cover vegetation. Lower-case letters indicate soil respiration measurements with ground cover species and near-surface roots removed.

(Blok et al., 2011; Nobrega and Grogan, 2008). Using this design of six plots and three replications, each respiration variable had an *n* of 18 for each site. Respiration measurements began 1 week after establishment of the treatments to eliminate any disturbance effects from inserting the collars (Nobrega and Grogan, 2008).

Respiration Measurements

Respiration measurements were conducted weekly during the growing season (27 June–25 August 2014) at all sites. Respiration rates for each collar location were measured using a LI-COR 6400-09 soil respiration chamber linked to the 6400XT Portable Photosynthesis System (LI-COR, Lincoln, Nebraska, U.S.A.). All measurements took place between 10:00 a.m. and 4:00 p.m. local time, and selection of the site, plots, and collars was randomized for each week of measurements. Measurements were performed according to the protocol suggested by LI-COR (2003). Every measurement cycle automatically repeated three times at each collar and final soil CO_2 flux for each soil collar was calculated as the average of the three measurement cycles. During the measurement of each set of paired collars, R_T was measured first, then the chamber was lifted for approximately 20 s to restore ambient conditions, and then it was placed on the vegetation removal collar to measure R_S.

Soil Microclimate Measurements

Soil temperature was measured at 5 cm depth (Thermo Recorder TR-51, T & D Co. Ltd., Japan) adjacent to the three paired collars and at the center of each plot (*n* = 4 for each plot). Soil moisture was assessed as volumetric water content (VWC) measured using a Hydrosense probe (Campbell Scientific Inc., Logan, Utah, U.S.A.) outfitted with a 12 cm probe inserted vertically into the soil beside the paired collars and at the center of each plot (*n* = 4). Because of the vegetation manipulation in the R_S collars, near surface soil moisture and temperature may have differed from the surroundings and the R_T collars. Whereas this disturbance was not assessed, we assumed the effects would be minimal.

Thaw depth beside each collar pair and at the center of each plot (*n* = 4) was measured by inserting a steel rod into the soil. Thaw depth was defined as the distance between the top of the moss layer and the permafrost table. These data were collected every week immediately after the respiration measurements in each plot.

Soil Properties Measurements

Surface soils were sampled for carbon and nitrogen content analysis from the edge of each plot at a weekly interval in 2014. Soil samples were taken with an open-sided soil auger (5 cm in diameter) at weekly intervals. The auger was inserted to a depth of ~15 cm at least 50 cm from the central shrub to minimize disturbance to the shrub. Loose leaf litter, living vegetation including mosses (and up to ~5 cm of moss stems where *Sphagnum* moss was present) and large roots were removed from the samples in an attempt to characterize the near-surface rooting medium of the shrubs. After collection, samples were dried at 70 °C for 48 h, and samples from each site were mixed together in sealed plastic bags and stored in a dry environment for later analysis. At the end of the field season, surface litter and soil samples were transported to Trent University, prepared, and analyzed for total carbon and nitrogen content (Elementar CNS analyzer, Hanau, Germany).

In 2014, soil bulk density for surface soil (below the litter) was determined by collecting a soil core with a metal ring (2.5 cm in radius and 7.3 cm in length = volume 143.3 cm³) at the edge of each semi–permanent plot. The soil sample was dried at 60 °C for 48 h and weighed to determine the dry mass.

Vegetation

Ten vegetation survey plots had already been randomly established at each site, where the point quadrat method (PQM) (Groeneveld, 1997) was used to provide estimates of species leaf area index (LAI). A vegetation survey was conducted three times during late July through early August of 2014. The PQM was performed using a frame (0.5 m × 0.5 m) with evenly strung fishing line creating 25 intersects within the grid. At each survey plot, the frame was positioned above the vegetation and a long, thin metal pin was inserted vertically through the grid at each intersect (*n* = 25). The number of pin contacts with a green leaf for each species was recorded. The LAI for a given species was computed as the total number of contacts for all intersections divided by the number of grid intersects. As well, at each intersect the ground cover (moss, lichen, or bare soil) was recorded and used to estimate percent cover of moss and lichen in each plot. LAI at the ten vegetation survey plots was also measured using a plant canopy analyzer (LAI-2000, LI-COR Inc.) (LAI$_{optical}$) four times from mid-July to mid–August in 2014. This method is unable to represent the leaf area associated with prostrate vegetation and other ground cover plant species and, as a result, is a measure of the leaf (and stem) area of the overstory vegetation only.

Statistical Analyses

A mixed effects model was used to test for differences in respiration rates and their relationships with soil microclimate variables among the three sites. Plots and collars were treated as random effects, site as a fixed effect,

and soil temperature and soil moisture measured directly beside each collar (n = 3/plot) as covariates. All soil microclimate measurements at each plot (n = 4/plot) were also tested separately for differences among sites with plots and collars treated as random effects, weeks as a repeated effect, and site as a fixed effect. Differences in soil properties and vegetation among the three sites were determined using one-way ANOVA. When a site was found to be a significant model effect, a least significant difference (LSD) test was then used to identify differences between the sites. Relationships between respiration rates and various soil properties for a given site (n = 8 for soil nitrogen, n = 48 for soil temperature and soil moisture) were also tested using simple linear regression and non-linear regression. However, given the narrow range of soil temperature variation (4 to 10 °C) and the poorer fit for the non-linear regressions, such as exponential regression of R_s on soil temperature, only linear regression analyses are presented in this paper. Prior to statistical analyses all data were checked for normality. Respiration rates at the low shrub site were non-normal, and these data were log-transformed for all sites to achieve normality for the statistical testing. We used P = 0.05 for significance level for all tests. All statistical analyses were conducted using SPSS version 16.0 software (SPSS, Chicago, Illinois, U.S.A.).

RESULTS

Air Temperature and Precipitation

The 10-year average (2005–2014) air temperature and rainfall at Daring Lake for July and August was 12.0 ± 1.1 °C and 89 ± 27 mm (±1 SD). In comparison, the 2014 study period (26 June–28 August) was relatively warm (13.7 °C). The distribution of precipitation during the period was extremely uneven. Two heavy rain events occurred on 16 July (57.5 mm) and 16 August (16.0 mm) (Fig. 2), which together accounted for 74% of the total precipitation (99.3 mm) during the two-month period.

Soil Temperature, Moisture, and Thaw Depth

There were significant effects of site, weeks, and their interaction on soil temperature at 5 cm depth among the three sites (Table1). Soil temperature at the low shrub site was significantly lower than at the other two sites. Soil temperature varied over the growing season, and despite a significant effect of site ´ weeks (Table 1), the seasonal patterns were somewhat similar for all sites (Fig. 3). However, there was no significant difference in soil moisture among the three sites where seasonal mean
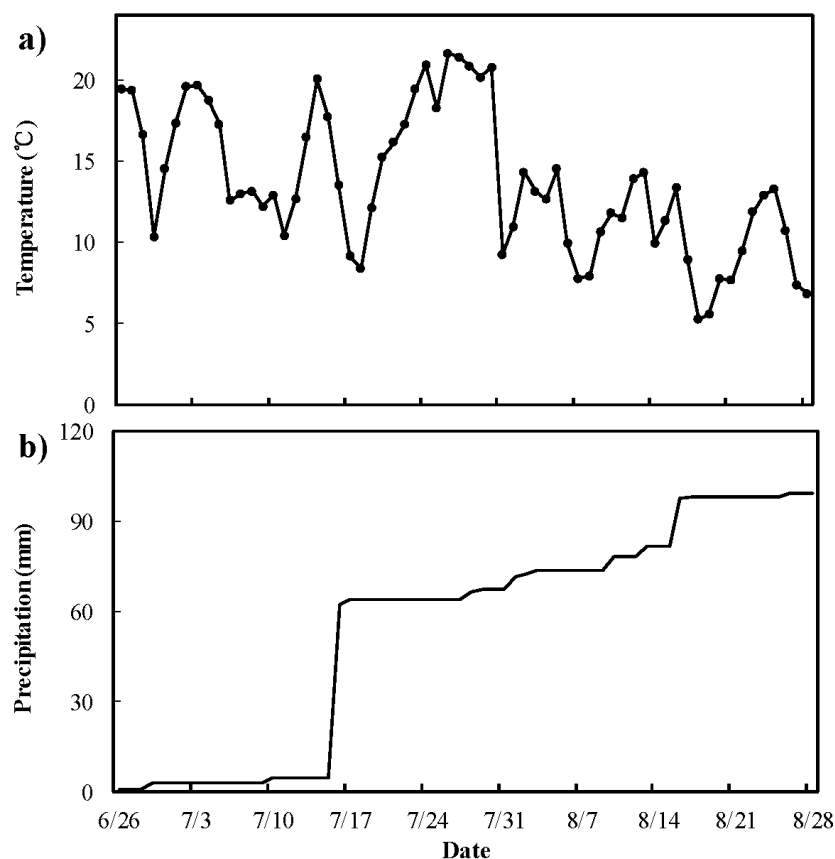
FIGURE 2. (a) Daily mean air temperature (°C) and (b) cumulative precipitation (mm) during 2014 summer at Daring Lake, NWT. Dates are given as m/dd.

TABLE 1

Mean 5 cm soil temperature (T), volumetric water content (VWC) in the upper 12 cm of the soil and thaw depth in 2014. Values in parentheses are standard errors. Different letters indicate a significant difference based on one-way ANOVA followed by the LSD test.

	Soil T (°C)	Soil VWC (m^3 m^{-3})	Thaw depth (cm)
Mixed tundra	7.13[a] (0.24)	0.47[a] (0.03)	56.93[a] (2.87)
Dwarf shrub	7.16[a] (0.23)	0.42[a] (0.01)	59.80[a] (2.36)
Low shrub	5.80[b] (0.23)	0.59[a] (0.03)	44.62[b] (2.59)

Sources of variation	*P* values		
Site	0.001	0.251	0.031
Weeks	<0.001	<0.001	<0.001
Site × weeks	<0.001	<0.001	<0.001

values ranged from 0.42 to 0.59 m^3 m^{-3}. Thaw depth increased over the growing season at all sites and was significantly shallower at the low shrub site compared to the mixed tundra and dwarf shrub sites (Table 1, Fig. 3).

Soil Properties

The 0–7.3 cm soil dry bulk density ranged from 0.21 g cm^{-3} to 0.50 g cm^{-3} with significantly lower bulk density at low shrub site compared to the other sites. Bulk density at all three sites indicated the presence of substantial organic matter in the near-surface soils with values well below the root growth limiting bulk density of 1.6 g cm^{-3} in sandy soils. Average soil C and N were similar at the mixed tundra and dwarf shrub sites, but greater soil C and significantly greater soil total N content were found at the low shrub site (Table 2). Soil C/N also differed significantly among three sites, with greatest C/N at the mixed tundra and lowest C/N at the low shrub site.

Vegetation

The leaf area index ($LAI_{optical}$) of overstory shrubs was significantly greater at the low shrub site; however, ground cover vascular LAI was not significantly different among sites (Table 3). The low shrub site also had the greatest moss cover (55.5%) and the lowest lichen cover (9.5%) among the three sites.

Respiration Fluxes and Controls

R_T, R_S, and R_G varied over the growing season (Fig. 4) with the highest values at all sites measured in the first week of the study (29 June—5 July). After the heavy rain event on 16 July and accompanying cool temper-
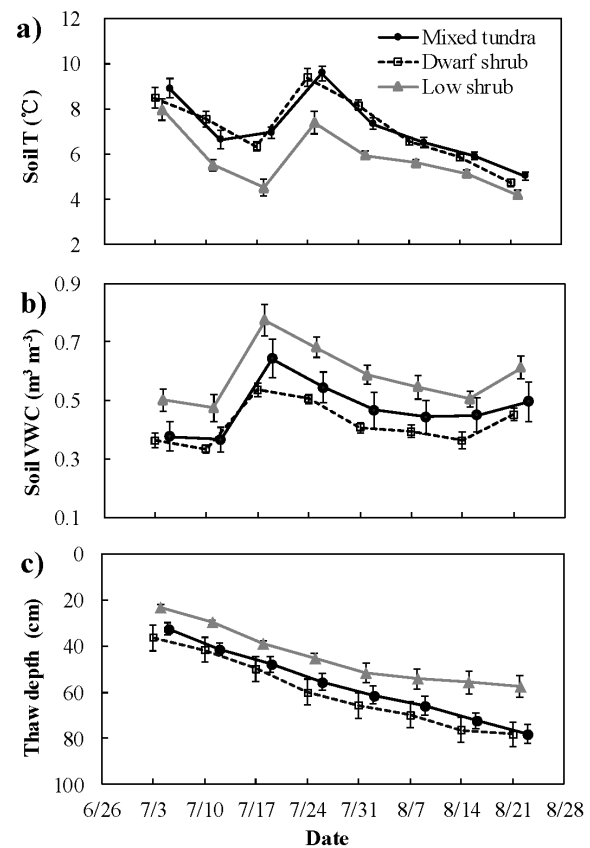

FIGURE 3. Variation of (a) soil temperatures at 5 cm depth (T, °C), (b) 0–12 cm soil volumetric water content (VWC, m^3 m^{-3}), and (c) thaw depth (cm) at the three sites in 2014. Points are site mean and error bars indicate standard errors of the mean for each measurement date.

atures (Fig. 2), respiration rates decreased and did not recover entirely by 24 July when soil and air temperatures reached their highest values of the season and were coincident with peak leaf area. Following this period,

TABLE 2

Mean surface soil dry bulk density (BD) ($n = 6$), soil total N and C content ($n = 8$) and soil C/N ($n = 8$) at the three sites. Parentheses indicate standard errors of the mean. Values within a column with different superscript letters were significantly different (One-way ANOVA followed by LSD test).

	Soil BD (g cm⁻³)	Soil N (%)	Soil C (%)	Soil C/N
Mixed tundra	0.50[a] (0.04)	1.04[a] (0.12)	26.8[a] (2.72)	26.5[a] (0.58)
Dwarf shrub	0.47[a] (0.04)	1.24[a] (0.10)	25.1[a] (1.69)	21.0[b] (0.28)
Low shrub	0.21[b] (0.01)	1.69[b] (0.08)	30.4[a] (1.55)	18.0[c] (0.46)

TABLE 3

Mean total shrub leaf area index as measured using a plant canopy analyzer (LAI$_{optical}$) ($n = 10$), other ground cover vegetation LAI, and percent cover of moss and lichen as measured using the PQM ($n = 10$) at the three sites. Parentheses indicate standard errors of the mean. Values within a column with different superscript letters were significantly different (one-way ANOVA followed by LSD test).

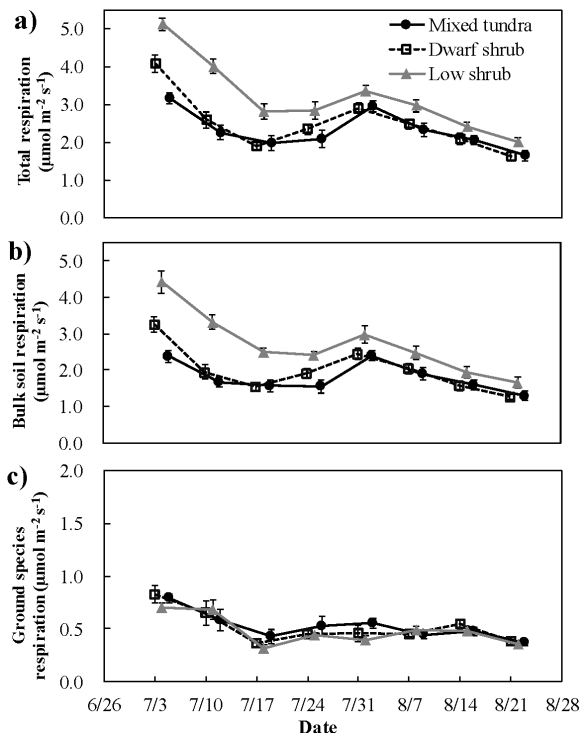|	Total LAI$_{optical}$ ($m^2\,m^{-2}$)	Other groundcover vegetation LAI ($m^2\,m^{-2}$)	Moss cover (%)	Lichen cover (%)
Mixed tundra	0.62[a] (0.08)	1.24[a] (0.10)	26.1[a] (5.1)	46.0[a] (5.6)
Dwarf shrub	0.73[a] (0.07)	0.97[b] (0.08)	40.5[b] (4.2)	39.6[a] (4.6)
Low shrub	1.16[b] (0.09)	1.17[ab] (0.09)	55.5[c] (4.4)	9.5[b] (2.0)

FIGURE 4. Mean daytime respiration rates of (a) total soil surface, (b) bulk soil, and (c) ground cover vegetation at mixed tundra, dwarf shrub, and low shrub sites. Bars show standard errors of the mean ($n = 18$). Note the y-axis for (c) is different from the y-axis in (a) and (b).

respiration rates declined as soil and air temperatures decreased.

R_T and R_S differed among the three sites with significantly greater respiration rates at the low shrub site and no differences between the other two sites (Table 4). There was no significant difference in mean R_G among the three sites. All respiration rates were significantly related to soil temperature whereas only R_T and R_S were significantly related to soil moisture (Table 4). The significant interactions between site and these variables indicated the relationships between R_T and R_S and soil temperature and/or soil moisture differed among sites (Table 4). Again, R_G did not relate to soil moisture and there were no significant site interactions with this environmental variable.

In general, our results show that respiration rates increased with increasing soil temperature and decreased with increasing soil moisture. Respiration rates showed stronger relationships with soil temperature than with soil moisture at all sites (Fig. 5). However, the proportion of variation in respiration explained by temperature was always less than 30% (Table 5). Using both soil moisture and soil temperature to explain variations in respiration produced modest improvements in the coefficient of determination, especially at the dwarf shrub and low shrub sites. R_T and R_S variations were significantly related to soil temperature at all three sites, and the response

TABLE 4

Mixed effects model results for respiration rates (µmol m⁻² s⁻¹) of total understory (R_T), bulk soil (R_S), and ground cover respiration (R_G) with the covariates of soil temperature (T) and soil volumetric water content (VWC) at mixed tundra, dwarf shrub, and low shrub sites. Different superscript letters indicate a significant difference among the three sites based on LSD test.

	R_T	R_S	R_G
Mixed tundra	2.27[a] (0.11)	1.74[a](0.10)	0.52[a](0.03)
Dwarf shrub	2.16[a](0.13)	1.71[a](0.12)	0.45[a](0.04)
Low shrub	3.70[b](0.13)	3.22[b](0.11)	0.48[a](0.03)

Sources of variation	*P* values		
Site	0.026	0.027	0.139
Soil T	<0.001	<0.001	0.002
VWC	0.001	0.001	0.160
Soil T ×VWC	<0.001	<0.001	<0.001
Site × soil T	<0.001	<0.001	0.007
Site ×VWC	0.001	<0.001	0.452
Site × soil T ×VWC	0.002	0.005	0.193

(slope) tended to increase with increasing shrub cover (Fig. 5). R_T and R_S were significantly negatively related to soil moisture at dwarf shrub and low shrub sites but not at the mixed tundra site. There was no significant relationship between soil temperature or moisture and R_G at the low shrub site.

To analyze the controls on spatial variations in respiration rates across the three sites, we regressed average respiration rates from each plot during the peak growing week, 24 July–26 July, against soil temperature, moisture, and bulk density for that same period. Spatial variations in soil temperature (Fig. 6, part a) and soil volumetric water content (Fig. 6, part b) did not relate well to spatial variations in respiration rates among the three sites. However, 61% and 66% of the variation in R_T and R_S, respectively, could be explained by variations in surface soil bulk density with respiration rates increasing with decreasing bulk density (Fig. 6, part c). Among the three sites, the mixed tundra site had the highest bulk density and lowest R_T and R_S rates, whereas the low shrub site has the lowest soil bulk density and highest R_T and R_S rates.

Seasonal mean R_T and R_S rates had similar trends as soil total N content across the three sites (Fig. 6, part d). Greater R_T and R_S rates at the low shrub site were associated with relatively high soil total N content, and lower R_T and R_S rates at the mixed tundra site were associated with relatively low soil total N content. However, with only three values it is uncertain how well

these relationships may explain spatial variations in respiration at Daring Lake.

Discussion

Respiration from Soil

We hypothesized that greater R_S would be associated with greater shrub coverage. This is supported by the evidence that the low shrub site had significantly greater R_S compared to the other sites. There was little difference in R_S at the dwarf shrub and mixed tundra sites where there was also no significant difference in most vegetation, soil, and soil microclimate characteristics. Only at the low shrub site, with its taller and denser shrub cover, did soil conditions differ substantially. Although not assessed directly, the near-surface soil contained greater organic matter content (inferred from the significantly lower soil bulk density) at the low shrub site. The low shrub site also had significantly lower litter C/N compared with the other two sites (29.8 at low shrub site, 35.8 at the dwarf shrub site, and 39.7 at low shrub site). The low litter C/N generally represents relatively easily decomposable (high quality) substrate matter (Quested et al., 2003; Cornwell et al., 2008). The lowest soil C/N at the low shrub site (Table 2) may reflect highly decomposed soil organic material, high turnover rates, and/or less recalcitrant substrates (Gundersen et al., 1998; Ollinger et al., 2002; Björk et al., 2007). In contrast to our results, previ-
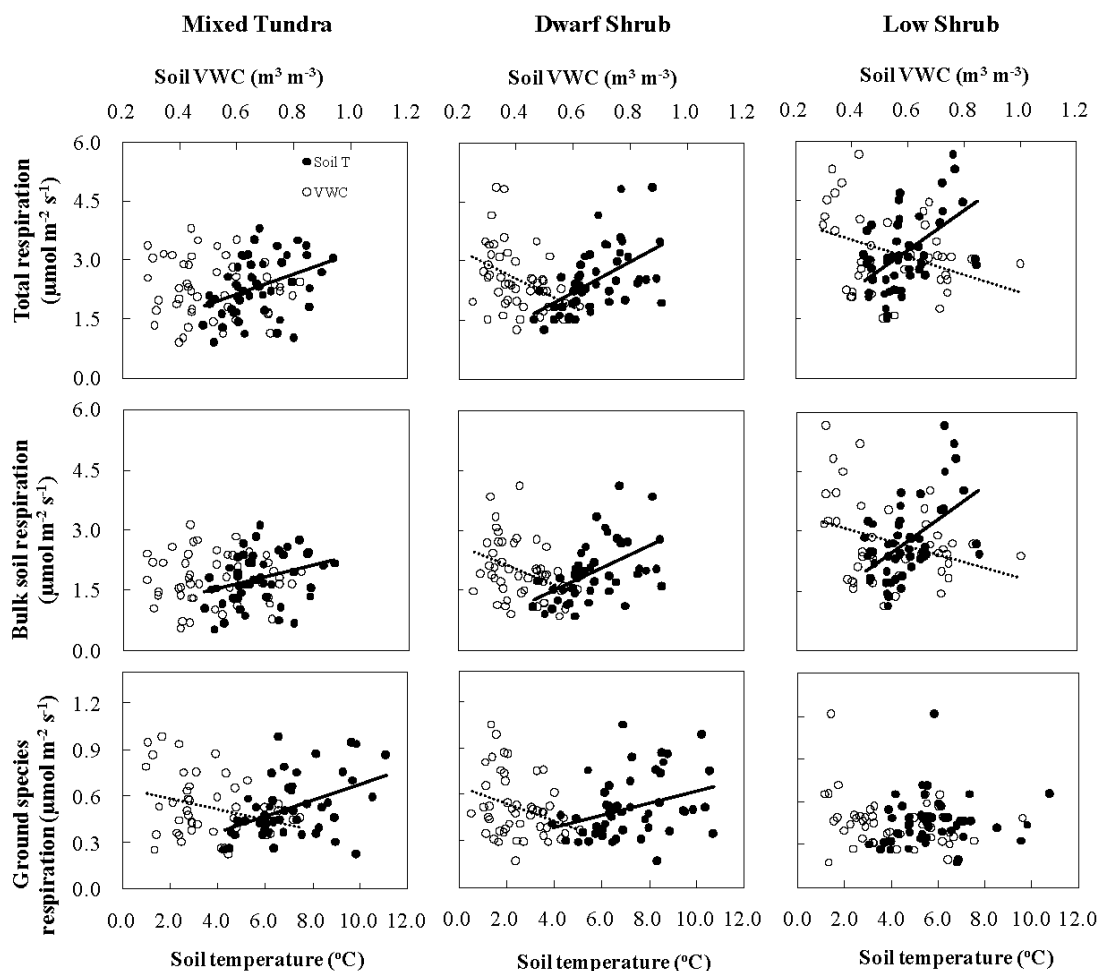
Mixed Tundra **Dwarf Shrub** **Low Shrub**

Soil VWC (m³ m⁻³)

FIGURE 5. Relationship between respiration rates and soil temperature (°C) at 5 cm depth (filled circles) and soil moisture (m³ m⁻³) at 0–12 cm depth (open circles) at mixed tundra (left column), dwarf shrub (middle column), and low shrub (right column) sites. Black lines indicate significant ($P < 0.05$) linear regressions of respiration rates to soil temperature. Gray lines indicate the linear significant regressions of respiration rates to soil moisture.

TABLE 5

Coefficient of determination (R^2) for soil temperature (T), soil volumetric water content (VWC), and T × VWC in least squares linear regression analysis to predict variation in total understory (R_T), soil (R_S), and ground cover respiration (R_G). Levels of significance were represented as "*" $P < 0.05$, "**" $P < 0.001$, and "***" $P < 0.0001$.

	Mixed tundra			Dwarf shrub			Low shrub		
	T	VWC	T × VWC	T	VWC	T × VWC	T	VWC	T × VWC
R_T	0.144**	0.004	0.112*	0.296***	0.156**	0.435***	0.258***	0.120*	0.339***
R_S	0.099*	0.000	0.059	0.272***	0.132*	0.384***	0.284*	0.108**	0.354***
R_G	0.195**	0.098*	0.274***	0.112*	0.092*	0.435***	0.045	0.001	0.007

ous studies have shown that soil decomposition rates decreased with increasing shrubs due to a more recalcitrant substrate supply (Hobbie, 1996; Cornelissen et al., 2007; Baptist et al., 2010). However, this is likely to depend on the nature of the vegetation replaced, with the previous studies finding deciduous shrub litter to be more recalcitrant compared to herbaceous litter (De Deyn et al., 2008). At the Daring Lake sites, ericaceous and evergreen dwarf shrubs such as *E. nigrum* and *R. decumbens* are common and decrease in abundance in areas where *B. glandulosa* dominates. As a result, a shift to deciduous over evergreen litter may be driv-
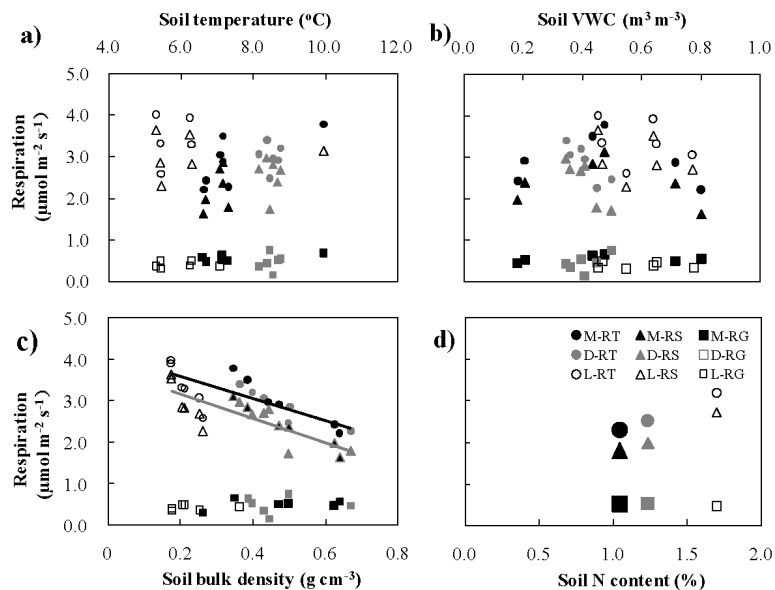
FIGURE 6. Relationship between peak season respiration rates and (a) soil temperature, (b) soil volumetric water content, (c) soil bulk density, where black lines indicate significant ($P < 0.05$) linear regressions of total respiration rates (R_T) to soil bulk density; gray lines indicate the linear significant regressions of bulk soil respiration rates (R_S) to soil bulk density and (d) seasonal mean soil total N (the size of symbol scaled to soil C/N [i.e., larger symbols represent higher C/N]). "M" represents mixed tundra site; "D" represents dwarf shrub site, and "L" represents low shrub site.

ing faster decomposition and greater soil respiration rates. Parker et al. (2015) also found greater soil respiration rates for higher productivity deciduous shrub vegetation than for lower productivity tundra heath, and this might be caused by the increased growth rates of fungal hyphae across the transition from heath to shrub. Although we cannot conclude that soil total N or C/N are the dominating controls on soil respiration rates with our limited sample size, these observations at least highlight the importance of substrate characteristics in controlling soil respired CO_2 with increased shrub cover and density.

Although not assessed directly, contributions from root respiration might also differ among sites. The variation in root respiration may vary in response to aboveground plant phenology and the differences in community composition among sites (Rey et al., 2002; Yuste et al., 2004). The low shrub site likely had greater root productivity because of the greater shrub biomass, thereby resulting in greater root respiration. Significantly higher shrub photosynthetic capacity at the low shrub site (data not shown) also suggests stronger root respiration at this site because root respiration has been observed to be tightly coupled with allocation of photosynthate to the rhizosphere and aboveground productivity (Kuzyakov and Cheng, 2001; Vargas et al., 2011).

Respiration from Ground Cover Vegetation

Increased shrub cover in arctic tundra ecosystems might reduce the abundance of lichens and mosses and other ground cover plants (forbs and graminoids) be-

cause of the dominating role of taller deciduous shrubs in obtaining light and nutrients (Walker et al., 2006; Dahlgren et al., 2006). In this study, we found relatively low respiration rates from ground cover vegetation at the three sites (Fig. 4). The contribution of R_G to R_T varied from 23% at the mixed tundra site, and 21% at the dwarf shrub site, to 15% at the low shrub site. This might be caused by the low rates of respiration from mosses and lichens, as observed in a previous study (Sveinbjörnsson and Sonesson, 1997). We also found no significant differences in R_G among sites (Table 4) despite an inverse trend of moss cover and lichen cover across the sites, as the site with more moss cover had less lichen cover (Table 3). Thus, an increase in the contribution of respired CO_2 from more mosses might be offset by a decrease in respired CO_2 from fewer lichens, resulting in little net effect on total R_G. In addition, the lack of a major difference in the understory vascular plant LAI between the low shrub site and the other two sites may have also been a reason for why R_G was similar among sites.

Spatial and Temporal Variation of Respiration

Instantaneous R_S rates measured at our sites ranged from 1.67 to 4.45 µmol m^{-2} s^{-1} over the growing seasons and were comparable with soil respiration values reported for other arctic ecosystems (Elberling, 2007; Nobrega and Grogan, 2008; Cahoon et al., 2016). Soil temperature is the dominant factor regulating temporal variations in CO_2 effluxes in the Arctic (Kim et al., 2013; Jensen et al., 2014) and other terrestrial ecosystems (Davidson et al., 1998; Davidson and Janssens, 2006). In general, the

role of soil moisture in controlling soil respiration has not been as clearly distinguished as soil temperature. Incubation studies in tundra ecosystems (Johnson et al., 1996) and temperate ecosystems (Davidson et al., 1998) indicate that soil respiration positively correlates with soil moisture at low levels (<0.2 m^3 m^{-3}), but negatively correlates with soil moisture at high levels (>0.2 m^3 m^{-3}) due to oxygen limitation. We found weak negative relationships between R_S and soil moisture at the dwarf shrub and low shrub sites where soil moisture content exceeded 0.2 m^3 m^{-3} during the growing season (Fig. 5, Table 5). Jensen et al. (2014) reported variations in annual CO_2 effluxes in a tundra ecosystem as a result of changes in soil moisture because of severe rainfall events. A substantial input of rainwater can inhibit soil production of CO_2 and limit diffusion rates to the atmosphere. We observed a decline in R_S and R_T at all three sites immediately following a heavy precipitation event (and cool air and soil temperatures) on 16 July 2014. Respiration rates did not fully recover despite a return to warm conditions in the following week. This may have been because the soils remained relatively wet; limiting both CO_2 production and transport rates (Oechel et al., 2000; Oberbauer et al., 2007). These findings highlight the importance of unusually large rain events in controlling respired CO_2 rates, which could be important considering expected increases in precipitation in the Arctic associated with climate change (Macdonald et al., 2005; Koenigk et al., 2013).

Although our hypothesis that soil temperature and moisture would be the main drivers of respiration variability was supported by the temporal variations in these variables, spatial variations in R_T and R_S were better correlated with soil physiochemical properties as noted above. The low shrub site with the coldest soil had the highest R_S and R_T, therefore soil temperature was clearly not the primary control on respiration differences among sites. Nobrega and Grogan (2008) found soil moisture to be the dominating factor controlling patterns of R_S among tundra ecosystems across a moisture gradient, where summer soil respiration was greatest at moderate soil moisture conditions (~0.3 m^3 m^{-3}). There was no relationship between peak season respiration and soil moisture across the three sites (Fig. 6b). Instead, we also found R_S and R_T increased with increasing soil moisture content up to ~0.45 m^3 m^{-3} and decreased with wetter conditions. It is notable, however, that there was large variability in respiration rates across the range of soil moisture values.

The three sites examined in this study experience the same climate conditions, yet have developed differences in shrub cover due to other differences in habitat characteristics. Although we recognize this fact tempers possible interpretations from our study, if we consider the three sites to reflect the impact of long-term shrub expansion in similar tundra of the Low Arctic, there are important implications arising from this study. No significant differences in mean R_T, R_S, and R_G rates between the mixed tundra and dwarf shrub sites suggests a weak response of respiration rates in the early stages of shrub expansion (i.e., as invading shrubs start to become dominant on herbaceous tundra). As shrub expansion approaches a relative mature phase (i.e., similar to our low shrub site) continued inputs of larger amounts and relatively higher quality litter may substantially improve the decomposability of soil organic matter, to support increased R_S and R_T. Our results suggest that total understory respiration in Low Arctic tundra may not be fixed with long-term shrub expansion. Presently, these notions are untested, but ecosystem models could be used to disentangle the linkages between shrub expansion, soil nutrients, and ecosystem respiration.

CONCLUSIONS

This study documented the temporal and spatial variations in soil and ground cover vegetation respiration at three Low Arctic sites with varying birch shrub cover. Despite colder soils, increased soil–respired CO_2 at the taller and denser deciduous shrub site was likely caused by greater plant productivity and higher soil nitrogen content. This highlights the importance of shifts in litter input and soil nitrogen content in driving the future soil respiration trend during long-term shrub expansion. Future shrub expansion in arctic tundra will alter the exchanges of energy and carbon that can impact the trajectory of future atmospheric warming. Hence, accurately predicting these changes is important, and our study shows that the amount and nature of shrub cover change combined with direct and indirect effects on soil climate, vegetation structure, and biogeochemistry are all important factors that should be considered when predicting the response of tundra ecosystem respiration to continued climate warming.

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