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Soil respiration variability across a soil moisture and vegetation community gradient within a snow-scoured alpine meadow

John F. Knowles · Peter D. Blanken · Mark W. Williams

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Abstract The alpine tundra landscape is a patchwork of co-mingled ecosystems that vary due to mesotopographical (<100 m) landscape position, shallow subsurface heterogeneity, and subsequent soil moisture availability. This results in hotspots of biological activity, variable carbon cycling over short horizontal distances, and confounds predictions of the alpine tundra response to forecasted environmental change. To advance our understanding of carbon cycling within snow-scoured alpine meadows, we characterized the spatio-temporal variability of soil respiration (R_S) from 17 sites across a broadly representative soil moisture and vegetation gradient, within the footprint of ongoing eddy covariance measurements at Niwot Ridge, Colorado, USA. Chamber-based R_S samples were collected on a weekly to bi-weekly basis over three complete growing seasons (2011–2013), and a soil moisture threshold was used to integrate the data into dry, mesic, and wet tundra categories. In every year, measured R_S was greatest from mesic tundra, followed by wet and then dry tundra locations. Increasing soil moisture invoked a bidirectional R_S response from areas of dry and mesic tundra (directly proportional) compared to wet tundra (inversely proportional), and the optimum R_S conditions were between 0.30 and 0.45 $m^3\ m^{-3}$ soil moisture, which mainly coincided with soil temperatures below 8 °C. We also developed simple models to predict R_S from concurrent measurements of soil moisture and temperature, and from nighttime eddy covariance measurements. Both models were significant predictors of R_S in all years and for all ecosystem types (where applicable), but the models did not adequately capture the intra-seasonal R_S variability. The median cumulative growing season R_S flux ranged from 138.6 g C m^{-2} in the driest year (2013) to 221.4 g C m^{-2} in the wettest year (2011), but the cumulative growing season fluxes varied by a factor of five between sites. Our results suggest that increased or more intense precipitation in the future has the potential to increase alpine tundra R_S, although this effect will be buffered to some degree by compensatory responses from dry, mesic, and wet alpine tundra.

Keywords Alpine tundra · Soil respiration · Soil moisture · Bidirectional · Carbon cycle · Climate change

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Introduction

Soils naturally produce carbon dioxide (CO_2) as a by-product of microbial soil organic matter (SOM) decomposition and root respiration, and soil respiration (R_S) describes the collective transfer of this CO_2 from the soil matrix to the atmosphere (Ryan and Law 2005). After gross primary productivity, R_S represents the second largest surface-atmosphere terrestrial CO_2 flux, and the global R_S flux (98 ± 12 Pg CO_2 year^{-1}; Bond-Lamberty and Thomson 2010) currently exceeds anthropogenic CO_2 emissions by roughly an order of magnitude (Boden et al. 2010; Risk et al. 2012). As a result, small perturbations to the global R_S flux have the potential to significantly alter patterns of both carbon cycling and climate. For example, a 1 °C global air temperature increase could release between 11 and 30 Pg of additional soil carbon to the atmosphere (Schimel et al. 1994).

Despite its importance to ecosystem functioning and global climate, the physical dynamics of R_S are not well understood, and the global R_S flux remains poorly constrained (Bond-Lamberty and Thomson 2010; Trumbore 2006). Because R_S rates are often positively correlated with soil temperature, a warmer climate is likely to increase liberation of CO_2 from soil, mediating progressively greater rates of terrestrial carbon loss in the future (Bardgett et al. 2008; Lloyd and Taylor 1994). Major uncertainties remain, however, as to how interactions between soil temperature and moisture may affect this scenario, and the temperature sensitivity of R_S is known to decrease under very low and very high soil moisture conditions (Riveros-Iregui et al. 2007; Suseela et al. 2011). Moreover, intra-ecosystem R_S variability remains a significant source of uncertainty in regional- to global-scale projections of the response of R_S to global environmental change (Craine et al. 2010). A robust, mechanistic understanding of the physical processes governing R_S over space and time is therefore necessary to predict how carbon fluxes will respond to current and future changes in climate and vegetation (Moyano et al. 2013; Schuur and Trumbore 2006).

Alpine tundra is the only ecosystem found on every continent, comprising 3 % of the global land area and 4 % of the global plant diversity (Körner 1999). Recently, alpine tundra has also received increased attention given its role as an early warning indicator system of climate change, and its importance as a source area for nutrients and water (Williams et al. 2002; Seastedt et al. 2004; Knowles et al. 2012). Alpine ecosystems are predicted to be among the most vulnerable to climate change because air temperatures are rapidly increasing, and the flora and fauna of high-elevation ecosystems already exist near the edge of their environmental tolerance (Pepin et al. 2015; Körner 1999; Settele et al. 2014). As a result of these environmental factors working together, perturbations to climate will likely have a measurable impact on alpine areas prior to other ecosystems. Since decomposition rates are commonly less than primary productivity under low temperatures (Hirota et al. 2009; Kato et al. 2006), alpine ecosystems also contain 'hotspots' of very high soil organic carbon (e.g. moist and wet meadows), intermixed with zones of medium (dry meadow) and low (fellfield) carbon storage. The combination of these factors could act to sustain alpine R_S over a prolonged period of time, and eddy covariance (EC) measurements on Niwot Ridge show that the alpine tundra has been a net annual source of CO_2 to the atmosphere since year-round data collection began in 2008 (Knowles et al. 2014).

Previous research has shown that soil moisture variability correlates with upslope accumulated area (UAA) in mountain terrain (Riveros-Iregui and McGlynn 2009). The UAA describes the geographic area draining to a specific landscape location, and thereby serves as an estimate of the relative soil wetness potential (McGlynn and Seibert 2003). Although this is accurate at the landscape scale ($>10^3$ m) in the Colorado Rocky Mountains, meso-topographic scale ($<10^2$ m) differences in snow accumulation, driven by the interaction of snowfall, topography, and wind (Erickson et al. 2005; Freppaz et al. 2012), can also serve as ancillary controls on soil moisture, soil temperature, plant productivity, and trace gas emissions (Taylor and Seastedt 1994; Williams et al. 2009; Fisk et al. 1998; Brooks et al. 2011). Moreover, soil moisture can vary widely within individual snow-scoured alpine meadows as a result of the combination of meso-topographical hydrological focusing (Erickson et al. 2005; Litaor et al. 2008) and low-permeability layers within the shallow subsurface (Leopold et al. 2008). Accordingly, areas of ponded water and saturated sediments coincident with wet meadow vegetation within our snow-scoured study site were associated with the seasonal formation of ice lenses beneath periglacial solifluction lobes (Leopold et al.

2008), as opposed to riparian corridors, topographical low points, or deep snow accumulation. These small hotspots of relatively wet tundra have been previously identified as the most active geomorphic, hydrologic, and biologic zones within the alpine environment on Niwot Ridge (Leopold et al. 2008).

Given that labor-intensive field campaigns above alpine treeline are not often feasible due to the remote nature of alpine tundra ecosystems, our goal was to take advantage of a well-established alpine tundra study site on Niwot Ridge to: (1) investigate the seasonal, inter-annual, and spatial variability of R_S from patches of dry, mesic, and wet tundra within the measurement footprint of ongoing EC measurements over the course of three complete growing seasons; (2) correlate dry, mesic, and wet tundra R_S with concurrent soil moisture and temperature measurements in order to create a set of simple predictive models within which to describe the spatially-distributed R_S flux across a representative alpine tundra soil moisture and vegetation gradient; and (3) use these models to identify the most likely response of R_S to regionally forecasted climate change. We hypothesized that dry, mesic, and wet tundra R_S would respond to soil moisture and temperature in different ways, and that the potential for compensating responses between dry (R_S proportional to soil moisture) and wet (R_S inversely proportional to soil moisture) patches of tundra could act to ameliorate both the inter-annual R_S variability, as well as the sensitivity of alpine tundra R_S to regional and/or global environmental change.

Methods

Site description

The alpine tundra is a mosaic of vegetation communities at this snow-scoured, ridgetop location, ranging from dry fellfield to wet meadow tundra interspersed with shallow pools of standing water (Billings 1973). The study site comprised 17 sampling locations extending approximately 250 m west and northwest along the prevailing westerly/north-westerly wind direction from a site locally referred to as 'T-Van' (40°03′11″N; 105°35′11″W; 3480 m asl) (Fig. 1). The T-Van site is an alpine fellfield approximately 25–100 m above the alpine treeline (depending on which side of the ridge) on Niwot Ridge in the Colorado Rocky Mountains, USA (Knowles et al. 2012), which has been the site of ongoing EC data collection since 2007 (Blanken et al. 2009). Sampling locations were spaced approximately 50 m apart along the prevailing wind directions, forming a roughly gridded triangle that captured the major terrain and vegetation changes within the 340–381 m horizontal EC turbulent flux footprint (Blanken et al. 2009). Alpine fellfield and dry meadow vegetation communities are dominant near this location (Walker et al. 2001), and the combination of these vegetation communities represented of 11 of the 17 sampling locations (Table 1). The remaining 6 measurement locations were characterized as either moist or wet meadow, following the meso-topographic vegetation community model of Billings (1973). Thus, although the EC turbulent flux footprint contained a wide range of dry-to-wet soils and the corresponding vegetation communities, the EC data were primarily influenced by the fellfield and dry meadow vegetation adjacent to the EC towers. Soils were Inceptisols, and Dystric Cryochrepts, Pergelic Cryumbrepts, Typic Cryumbrepts, and Pergelic Cryaquepts generally coincided with fellfield, dry meadow, moist meadow, and wet meadow vegetation communities (Burns 1980; Table 1). There was an 18-m difference in elevation between the highest and lowest plots, but all measurement locations had similar full-sky exposure due to the ridgetop location. Precipitation data were collected approximately 421 m northwest of T-Van at the Saddle site (3528 m asl) and corrected for winter precipitation overcatch due to blowing snow (during clear sky conditions) following Williams et al. (1998). The long-term precipitation (1982–2013) and air temperature (1982–2012) at the Saddle were 904 mm and −2.2 °C, respectively. Air temperature was also measured at the study site using a shielded temperature/humidity probe (HMP 45C, Vaisala, Vantaa, Finland). Data collection generally spanned the 2011–2013 growing seasons, which we considered to be the 3-month period from 1 June through 31 August (Knowles 2009).

Soil respiration

The R_S was measured in triplicate at all 17 sites using a chamber (SRC-1; PP Systems, Amesbury, MA, USA) attached to an infrared gas analyzer (EGM-4; PP Systems, Amesbury, MA, USA) following the method of Pacific et al. (2008) and Riveros-Iregui and

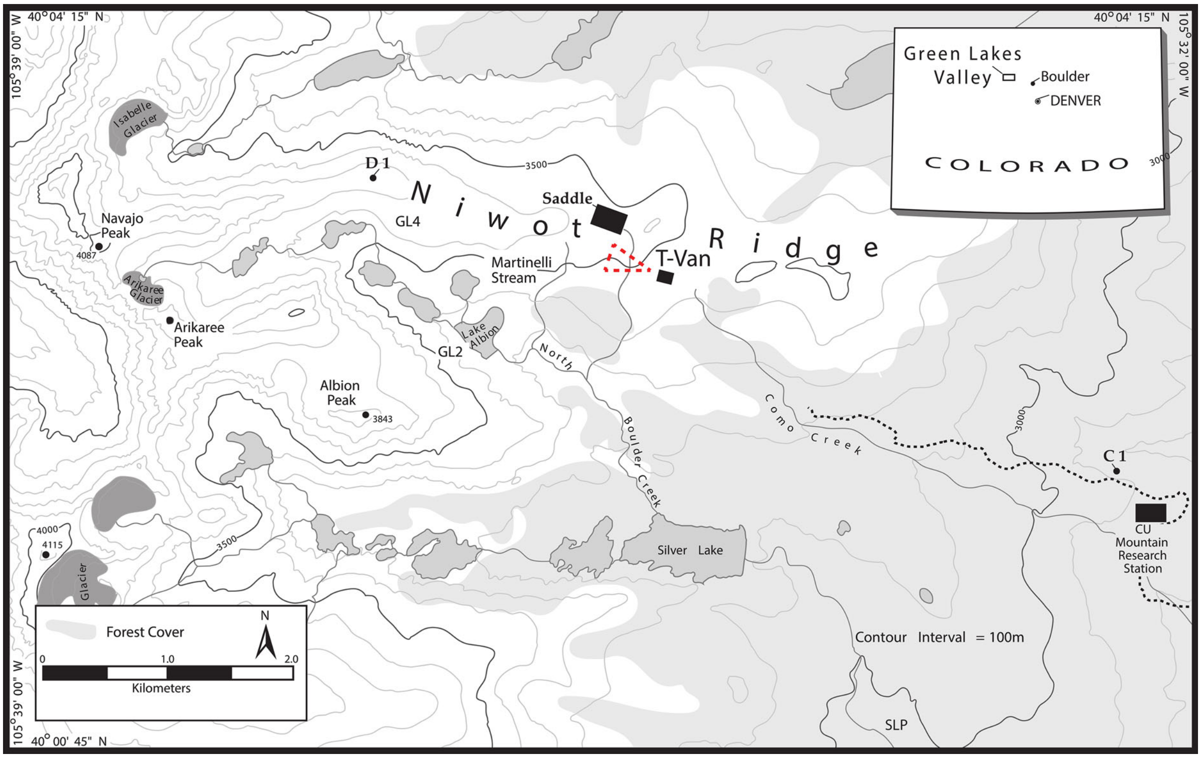


Fig. 1 Sampling locations were approximately located within the colored dashed triangle in an alpine tundra meadow between the T-Van and the Saddle on Niwot Ridge in the Colorado Rocky Mountains, USA

McGlynn (2009). The mean tundra R_S was then calculated as the average R_S from all 17 sampling locations. To measure R_S, the chamber was first flushed with ambient air for 15 s and then inserted approximately 1 cm into the soil surface to seal the soil surface from the atmosphere. Each chamber deployment lasted 90 s, or until the internal CO_2 concentration in the chamber had increased by 50 ppm. The R_S was then calculated by fitting a quadratic equation to the relationship between the increasing CO_2 concentration and elapsed time. Aboveground vegetation was clipped immediately following sample collection, but roots were left intact to minimize disturbance. All chamber measurements were collected between 08:30 and 16:30 local time to minimize sampling bias introduced by time of day (Riveros-Iregui et al. 2008). All 17 sites were sampled a total of 34 times over the course of three growing seasons; 12 times each in 2011 and 2012 and 10 times in 2013. Linear interpolation was performed between sampling events to determine the cumulative R_S of individual measurement locations (Riveros-Iregui and McGlynn 2009). We also used equations derived from multiple linear regression analysis of 2011–2012 soil moisture and temperature on R_S to predict dry, mesic, and wet tundra R_S (see below) throughout the 2013 growing season:

$$R_S = a + b(VWC) + c(T_s) \tag{1}$$

where VWC is volumetric water content ($m^3\ m^{-3}$), T_S is soil temperature (°C), and a, b, and c are regression-specific constants. Although the potential for interactions between soil moisture and temperature is well documented (Davidson et al. 1998, 2012), we did not include an interaction term ($VWC \times T_S$) since it was not significant and did not improve the overall explanatory power of this model. We used a cubic spline interpolation technique (Voltz and Webster 1990) to spatially interpolate R_S and soil moisture between sampling locations (Fig. 3).

Soil moisture and temperature

Discrete soil moisture measurements were taken concurrently with all R_S samples at a depth of 10 cm below the soil surface using a two-pronged electromagnetic impedance probe (SM 300; Delta-T,

Table 1 Growing season mean volumetric water content (*VWC*), soil temperature (T_S), C:N ratio, and soil respiration (R_S) from all 17 discrete sampling locations including mean values for dry, mesic, and wet tundra. Soil types are taken from Burns (1980)

Site number	*VWC* ($m^3 m^{-3}$)	T_S (°C)	C:N	R_S ($\mu mol\ m^{-2} s^{-1}$)	Soil type	Vegetation community	Dominant species
Dry tundra							
1	0.15	12.24	10.5	0.76	Dystric Cryochrept	Fellfield	*Silene acaulis, Carex rupestris*
2	0.15	10.32	13.1	0.92	Dystric Cryochrept	Fellfield	*Carex rupestris, Silene, Minuartia*
5	0.17	11.03	12.4	1.08	Pergelic Cryumbrept	Dry meadow	*Kobresia myosuroides, Hymnoxys*
6	0.16	11.79	11.3	1.13	Dystric Cryochrept	Fellfield	*Carex rupestris, Silene*
7	0.15	10.56	11.6	1.76	Dystric Cryochrept	Fellfield	*Geum rossii, Silene*
8	0.17	10.85	11.3	2.03	Pergelic Cryumbrept	Dry meadow	*Carex rupestris*
11	0.17	10.68	10.8	1.87	Dystric Cryochrept	Fellfield	*Geum rossii, Minuartia*
19	0.17	9.41	11.6	4.24	Pergelic Cryumbrept	Dry meadow	*Trifolium dasyphyllum*
Mean	0.16	10.86	11.6	1.72			
Mesic tundra							
9	0.20	9.76	13.7	1.48	Pergelic Cryumbrept	Dry meadow	*Silene acaulis, Kobresia*
12	0.28	8.74	13.6	2.19	Pergelic Cryumbrept	Dry meadow	*Kobresia myosuroides, Carex rupestris*
13	0.23	8.97	12.4	2.29	Pergelic Cryumbrept	Dry meadow	*Kobresia myosuroides*
14	0.42	6.94	12.6	3.07	Typic Cryumbrept	Moist meadow	*Kobresia myosuroides, Geum, Carex scopulorum*
Mean	0.28	8.60	13.1	2.26			
Wet tundra							
10	0.46	6.79	13.3	3.45	Typic Cryumbrept	Moist meadow	*Geum rossii, Artemesia*
15	0.58	5.45	16.2	1.74	Pergelic Cryaquept	Wet meadow	*Caltha leptosepala, Carex scopulorum*
16	0.64	6.38	15.3	1.18	Pergelic Cryaquept	Wet meadow	*Moss, Carex scopulorum*
17	0.45	7.38	15.7	1.41	Pergelic Cryaquept	Wet meadow	*Salix planifolia/glauca, Carex scopulorum*
18	0.59	6.15	14.8	2.39	Pergelic Cryaquept	Wet meadow	*Carex scopulorum, Gentiana*
Mean	0.54	6.43	15.1	2.03			

A qualitative assessment of the vegetation community type and the dominant vegetation species in approximate order of abundance are also shown

Burwell, Cambridge, UK) connected to a handheld readout unit (HH2; Delta-T, Burwell, Cambridge, UK). Discrete soil moisture measurements were collected in triplicate at each sampling location and then averaged to determine the representative soil moisture. Raw soil moisture data were collected as voltage measurements and then calibrated for mineral (soil carbon $< 10\ \%$) and organic (soil carbon $> 10\ \%$) soils using the sensor-specific equations developed by Vaz et al. (2013). The accuracy of these soil- and sensor-specific calibrations is approximately 0.015 $m^3\ m^{-3}$ (Vaz et al. 2013). We used the 3-year mean soil moisture to classify sites into dry ($VWC < 0.20\ m^3\ m^{-3}$), mesic ($0.20\ m^3\ m^{-3} < VWC < 0.45\ m^3\ m^{-3}$), and wet ($VWC > 0.45\ m^3\ m^{-3}$) tundra sites (Table 1).

Continuous soil moisture data were also collected using capacitance probes at representative mesic and wet sites (ECH2O; Decagon, Pullman, WA, USA) attached to Hobo Micro Station dataloggers (H21-002; Onset Computer Corp., Bourne, MA, USA), and from a representative dry site (EnviroSMART, Sentek, Stepney, Australia). Continuous soil moisture data from the wet site were adjusted to account for the high electrical conductivity of the wet soils according to Nemali et al. (2007). All continuous soil moisture data were collected from 10 cm depth below the soil surface. Soil temperature was measured concurrently with all R_S measurements at a depth of 10 cm below the soil surface using a handheld soil temperature probe (STP-1; PP Systems, Amesbury, MA, USA).

Soil physical properties

Representative soil porosity was determined as the average porosity of soil samples collected from two different dry, mesic, and wet tundra locations. Sampling locations for this analysis included sites #2 and #6 (dry tundra), #13 and #14 (mesic tundra), and #17 and #18 (wet tundra). Undisturbed soil samples were collected in soil tins (85 cm^3 volume) and then oven dried at 105 °C. The porosity was determined as the bulk soil density (oven-dry weight divided by volume) divided by the estimated particle density (2.65 $g\ cm^{-3}$). Soil samples were also collected from all 17 locations in the summer of 2013 to measure the C:N ratio. For this analysis, soils were collected from 5 to 15 cm depth within the soil profile using a standard soil sampler, then oven dried at 105 °C, passed through a 2-mm sieve, and ground using a mortar and pestle in preparation for C:N analysis. Total carbon and nitrogen were analyzed by the Colorado State University EcoCore lab on a CN analyzer (TruSpec; Leco Corp., St Joseph, MI, USA) with a typical precision (coefficient of variation) of 2.5 % at a nominal sample size. Data from these samples were also used to partition soils into mineral and organic categories for the soil moisture probe calibration.

Net ecosystem exchange

Net ecosystem exchange (*NEE*) was continuously measured using the EC technique (Baldocchi 2003) at a height of 3 m above the ground surface. Two identical EC towers were spaced 50-m apart along an east–west transect near T-Van, and we used the data from the two towers interchangeably due to their close proximity (Knowles et al. 2012). We utilized a three-dimensional sonic anemometer (CSAT 3; Campbell Scientific, Logan, UT, USA) that was co-located with an open-path infrared gas analyzer (LI-7500; LI-COR, Lincoln, NE, USA) to quantify the vertical wind fluctuations and the density of atmospheric CO_2, respectively. The *NEE* was calculated as the covariance between instantaneous (10 Hz) deviations from the 30-min mean of the vertical wind speed and the scalar density of CO_2. Post-processing of the EC data consisted of standard coordinate rotation and Webb adjustment corrections (Lee et al. 2004) and the data were gap-filled following Falge et al. (2001). Ecosystem respiration was calculated from growing season *NEE* using year-specific Arrhenius-type exponential regressions of binned nighttime (22:00–03:00 local time) soil temperature (bin size = 1 °C) versus *NEE* (Lloyd and Taylor 1994):

$$R_E = ae^{bT_S} \tag{2}$$

where T_S is soil temperature (°C), e is equal to 2.718, a and b are regression-specific constants, and a friction velocity filter of 0.15 $m\ s^{-1}$ was applied to account for periods of insufficient turbulent mixing. The median R^2 value for these regressions was 0.77. Ecosystem respiration values were then calculated from 0.5-h *NEE* and summed over the length of the R_S measurement period for comparison to measured and modeled R_S.

Results

Relative to the mean annual precipitation of 955 mm (Knowles et al. 2012), the study period encompassed a very wet year (2011; 1307 mm precipitation) followed by a dry (2012; 846 mm) and then by an average year (2013; 956 mm) (Table 2). Moreover, the 2012 growing season was uniquely characterized by a spring and early summer dry down, followed by a very wet July. This (2012) precipitation pattern was associated with both the lowest mean (averaged from discrete measurements at all 17 sites) soil moisture (0.21 $m^3\ m^{-3}$ on 20 June and 2 July) and the greatest intra-seasonal soil moisture range (0.17 $m^3\ m^{-3}$) of all 3 years. Overall, the mean soil moisture peaked at 0.39 $m^3\ m^{-3}$ on 22 June 2011. Table 1 shows the

Table 2 Total annual and growing season (*JJA*) precipitation (*P*), and mean growing season air temperature (T_a), volumetric water content (*VWC*), soil temperature (T_S), and soil respiration (R_S) for the tundra as a whole

Year	Annual *P* (mm)	*JJA P* (mm)	T_a (°C)	*VWC*	T_S (°C)	R_S (μmol $m^{-2}\ s^{-1}$)
2011	1307	313	10.04^a	0.32^a (0.18)	9.22^a (2.38)	2.30^a (1.06)
2012	846	270	10.95^b	0.30^b (0.18)	9.22^a (2.16)	1.68^b (0.84)
2013	956	177	9.99^a	0.29^b (0.17)	8.56^b (1.86)	1.83^b (0.97)

The *VWC*, T_S, and R_S values are the mean of all 17 sampling locations. Different letters denote significant differences between years. Values in parentheses are the standard deviation between sites mean growing season soil moisture, temperature, and R_S, as well as the C:N ratio, soil type, dominant plant species, and vegetation community for each site across the soil moisture gradient. In general, vegetation at the dry tundra sites was characteristic of fellfield and dry meadow vegetation communities, and principally included *Carex rupestris*, *Silene acaulis*, and *Geum rossii*. Mesic sites contained either dry or moist meadow vegetation, however, *Kobresia myosuroides* was common to all mesic sites. Wet tundra sites encompassed moist and wet meadow vegetation communities, mainly distinguished by the presence or absence of *Carex scopulorum* (Table 1). The dry, mesic, and wet tundra soil porosity was 0.37, 0.56, and 0.62, respectively.

Overall, soil moisture was a significant predictor of R_S ($p = 0.002$; Fig. 2), but soil temperature was not. Given the similar aspect, and the absence of shading vegetation, soil moisture was also significant predictor of soil temperature ($R^2 = 0.46$; $p \ll 0.001$), and there was an inverse relationship between soil moisture and temperature along the moisture gradient from dry to wet tundra (e.g. warmest soils were always dry) (Table 1). Soil temperature differences between sites on a single day (maximum difference = 14 °C) were nearly as large as the seasonal variability of soil temperature across all sites over all three growing seasons (17 °C). Over all 3 years, soil moisture was a significant predictor of R_S at 7 of 17 individual sites, while soil temperature was a significant predictor of R_S at 3 of 17 sites. The range of mean R_S fluxes from individual sites was 0.74–4.24 μmol m^{-2} s^{-1} (Table 1). Overall, the mean growing-season R_S was greatest in mesic tundra (2.26 μmol m^{-2} s^{-1}) and least in dry tundra (1.72 μmol m^{-2} s^{-1}), with wet meadow tundra values (2.03 μmol m^{-2} s^{-1}) in between (Table 1). Notwithstanding, the greatest R_S at any single site (4.24 μmol m^{-2} s^{-1}) was observed at a dry meadow site (#19) dominated by a unique nitrogen-fixing vegetation community (*Trifolium dasyphyllum*). Although the C:N ratio at site #19 was not significantly different from the dry tundra mean, the total carbon and nitrogen were 2.2 times greater, respectively. Overall, the C:N ratio decreased significantly with increasing soil moisture (Table 1).

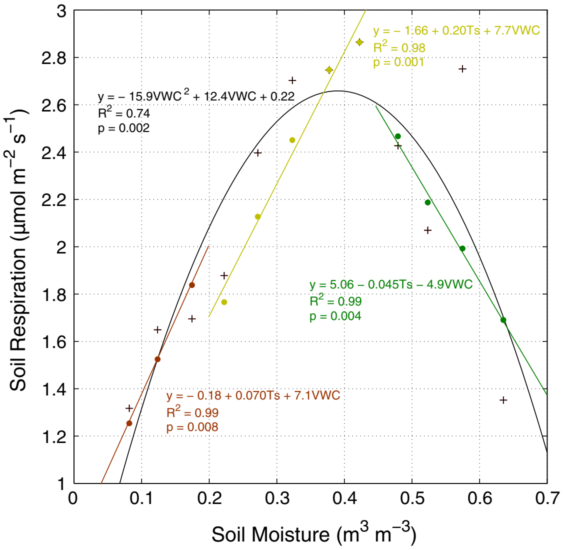


Fig. 2 Binned analysis of soil moisture (bin size = 0.05 m^3 m^{-3}) versus soil respiration over three complete growing seasons ($n = 57$) shows a bidirectional response of soil respiration to soil moisture (continuous black line and polynomial fit with error bars corresponding to the standard error). For comparison, color-coded points, lines, and text denote multiple linear regressions of soil moisture (VWC; same bins) and temperature (T_S [°C]; data not shown) on respiration from dry (*brown*), mesic (*yellow*), and wet (*green*) locations. (Color figure online)

Soil moisture, R_S, and the correlation coefficient between soil moisture and R_S were variable over short horizontal distances, and did not follow a noticeable macro-topographical pattern (Fig. 3). The driest areas of tundra were found immediately adjacent to the two EC towers at the eastern end of the study site, while wet tundra hotspots were located near the center and the western edge of the study site (Fig. 3a). The R_S was low in areas of very dry and very wet tundra, and generally highest in mesic tundra (Fig. 3b); soil moisture and R_S were positively correlated in dry areas and negatively correlated in wet areas (Fig. 3c). Intra-annually, wet meadow R_S always peaked before dry and mesic R_S, and wet meadow R_S was greater than dry and mesic R_S early in the growing season (Fig. 4). Dry and mesic tundra R_S peaked in July and generally remained higher than wet tundra R_S for the remainder of the growing season. The R_S from dry and mesic tundra, and from the tundra as a whole, reached its highest value for all three growing seasons on 19 July 2011 (Fig. 4a). Relative to 2011, the 2012 R_S fluxes were generally diminished across the entire soil moisture gradient (Fig. 4b), and discounting the end-of-season 2011 measurements, the lowest R_S of all 3 years occurred in 2012 during the early season dry down (dry, mesic, and mean of all sites) and the July

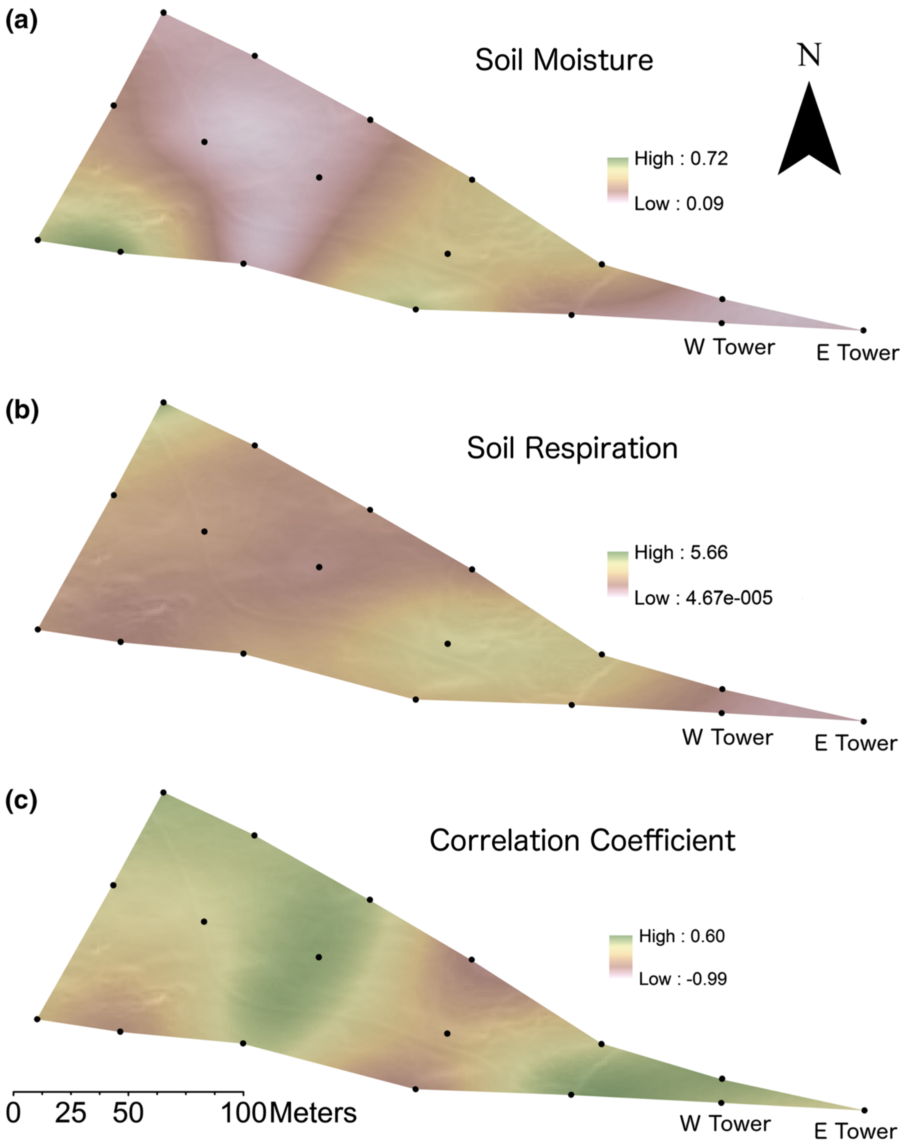
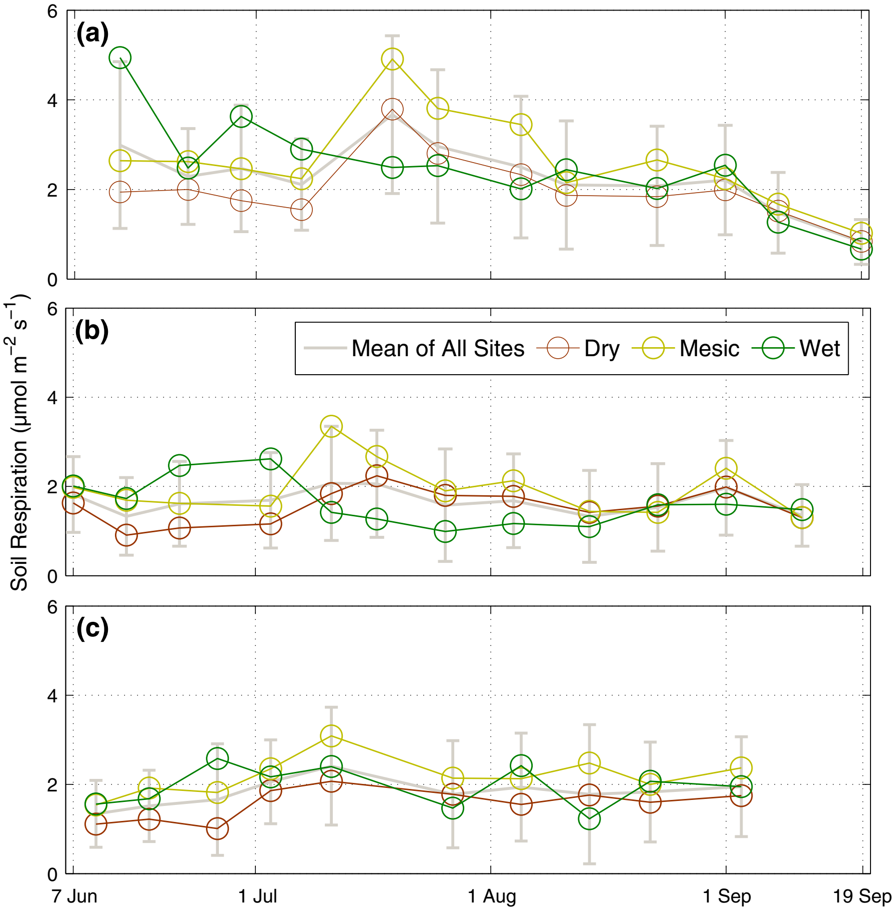


Fig. 3 Spatial variability of **a** soil moisture, **b** soil respiration, and **c** the correlation coefficient resultant from linear regression of soil moisture (independent variable) on soil respiration (dependent variable) within the statistical measurement footprint of ongoing eddy covariance measurements. Units are **a** $m^3\ m^{-3}$, **b** $\mu mol\ m^{-2}\ s^{-1}$, and **c** no units. *Dark circles* are chamber-sampling locations. Spatial interpolation was performed between sampling locations using the cubic spline technique in ArcGIS. *Dark circles* adjacent to the W and E tower labels represent the west and east eddy covariance towers near T-Van

wet period (wet tundra). The R_S fluxes were generally moderate throughout the 2013 growing season (Fig. 4c). From 2011 to 2013, the median cumulative growing season R_S flux (all 17 sites) decreased from 221.4 to 162.8, and then to 138.6 g C m^{-2} (respectively), however, the mean measured R_S fluxes were cumulatively greatest in mesic, wet, and then dry tundra in all years (Fig. 5a–c).

Multiple linear regression (MLR) and EC-based models predicted 75 and 79 % of the mean cumulative measured R_S, respectively, and both models were significant predictors of R_S in all years and for all ecosystem types (MLR only) (Table 3). The soil moisture term in the MLR model was always a significant predictor of R_S, but the soil temperature term was only significant in 2012 (Table 3). Ordinary

Fig. 4 Evolution of measured R_S during the **a** 2011, **b** 2012, and **c** 2013 growing seasons. Dry, mesic, and wet tundra values are the mean of all dry, mesic, and wet tundra locations on a particular sampling date (shown as open circles). *Error bars* correspond to the standard deviation of R_S from all sampling locations on a particular date. Values are linearly interpolated between sampling events



least squares linear regression of simultaneous measured versus modeled R_S was not significant for either model. In 2013, the MLR model under-predicted the dry, mesic, and wet R_S by 16, 34, and 24 %, respectively (Table 4; Fig. 5c, d). The coefficients for the soil moisture and temperature MLR model terms were positive for dry and mesic tundra, but negative for wet tundra. In 2011 and 2013, the soil moisture and temperature coefficients were equal, but the soil temperature coefficient was 2.5 times greater than the soil moisture coefficient for the early-melt year of 2012. Although the cumulative measured R_S fluxes from dry, mesic and wet sites were greatest in 2011, cumulative EC-modeled R_S was greatest in 2012 (Table 4), when EC-modeled R_S was greater than dry, mesic, or wet tundra measured R_S (EC model under-predicted measured R_S in all other years). In all years, there was approximately a five-fold difference in measured cumulative R_S fluxes between individual sites, despite the fact that all fluxes were greater in 2011 than in the other 2 years. The range between the mean cumulative fluxes from dry, mesic, and wet tundra was less in 2012 compared to 2011 and 2013 (Fig. 5). Although the EC-modeled R_S was much lower in 2013 than in 2011 or 2012, the *NEE* was not significantly different between growing seasons (Table 4).

Discussion

The growing season mean R_S was comparable to other reported values from alpine areas. For example, the mean R_S of 2.01 μmol m^{-2} s^{-1} was equal to that measured over high-altitude Tibetan alpine steppe (2.01 μmol m^{-2} s^{-1}; Geng et al. 2012), but less than Tibetan alpine meadow vegetation (5.49 μmol m^{-2} s^{-1}; Geng et al. 2012) and a managed (grazed and fertilized) Swiss alpine grassland (5.2–6.5 μmol m^{-2} s^{-1}; Imer et al. 2013). The range of R_S

Fig. 5 Cumulative measured or multiple linear regression (MLR)-modeled dry, mesic, and wet tundra mean R_S (*colored lines*), cumulative eddy-covariance (EC)-modeled R_S (*black line*), and cumulative measured R_S from all 17 measurement locations (*grey lines*) during **a** 2011, **b** 2012, and **c, d** 2013

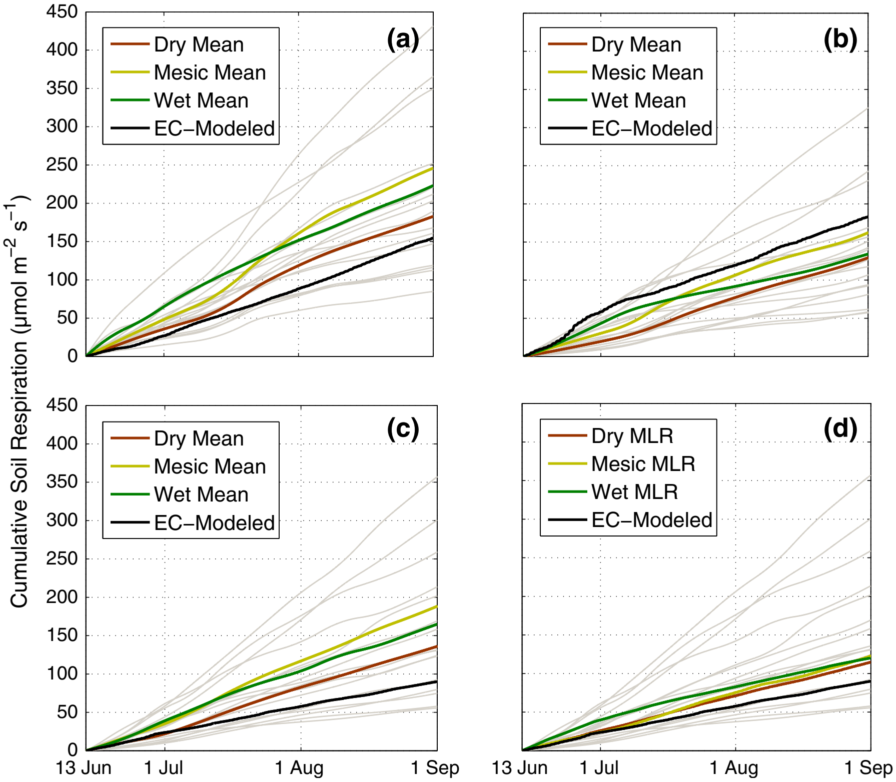


Table 3 Statistics for eddy covariance (EC)- and multiple linear regression (MLR)-based models

	Coefficient	RMSE	R^2	p value	SE
Tower footprint					
EC—T_S (2011)	n/a	n/a	0.85	0.0005	n/a
EC—T_S (2012)	n/a	n/a	0.77	0.004	n/a
EC—T_S (2013)	n/a	n/a	0.56	0.002	n/a
Dry tundra					
MLR	n/a	1.29	0.09	0.0002	n/a
T_S term	0.07	n/a	n/a	0.06	0.04
VWC term	0.07	n/a	n/a	4.2×10^{-5}	0.02
Mesic tundra					
MLR	n/a	0.97	0.38	4.3×10^{-10}	n/a
T_S term	0.20	n/a	n/a	0.0002	0.05
VWC term	0.08	n/a	n/a	7.1×10^{-11}	0.01
Wet tundra					
MLR	n/a	1.35	0.10	0.004	n/a
T_S term	−0.05	n/a	n/a	0.42	0.06
VWC term	−0.05	n/a	n/a	0.001	0.01

The RMSE is the root mean squared error and the SE is the standard error. The EC model was run for the 2011–2013 growing seasons (year in parentheses) and is representative of the land area contained within the EC tower measurement footprint. The MLR models are for 2013 only and the statistics for distinct dry, mesic, and wet MLR models are separated by soil moisture (*VWC*) and temperature (T_S) terms

Table 4 Cumulative growing season R_S fluxes for areas of dry, mesic, and wet tundra from 2011 to 2013

	2011 (98 days)	2012 (96 days)	2013 (85 days)
Measured—Dry	210.5	156.3	144.9
Measured—Mesic	277.0	194.8	200.6
Measured—Wet	249.6	163.6	176.0
MLR—Dry	n/a	n/a	122.0
MLR—Mesic	n/a	n/a	132.5
MLR—Wet	n/a	n/a	134.5
EC—T_S	162.9	198.4	96.4
EC—*NEE*	−33.2	−44.8	−37.9

Numbers in parentheses represent the number of days in each annual sampling campaign. Measured values are cumulative sums of linear interpolations between discrete sampling events. Multiple linear regression (MLR)- and eddy covariance (EC)-modeled (T_S) values and EC-measured net ecosystem exchange (*NEE*) during the same time period are also shown for comparison. Negative values denote carbon uptake by the surface. Units are g C m^{-2}

fluxes from individual sites (0.74–4.24 µmol m^{-2} s^{-1}) was also comparable to previously measured R_S fluxes from moist meadow tundra on Niwot Ridge (~2–6 µmol m^{-2} s^{-1}; Bowman et al. 2004). The similarities between these results may thus serve to constrain the upper and lower limits on the magnitude of mean growing-season alpine tundra R_S fluxes both on Niwot Ridge and around the globe.

Which environmental factors control the magnitude of cumulative and peak R_S from dry, mesic, and wet alpine tundra?

There was a significant positive relationship between soil moisture and R_S for areas of dry and mesic tundra, and a significant negative relationship between soil moisture and R_S in wet tundra. This switch occurred at a threshold soil moisture value of approximately 0.38 m^3 m^{-3} (Fig. 2). We interpret this as evidence of moisture limitation (dry and mesic tundra) versus an oxygen/diffusion limitation (wet tundra) (Orchard and Cook 1983; Skopp 1990). The resulting 'bidirectional', or opposite, relationship between soil moisture and R_S (Moyano et al. 2013) has been similarly observed at the watershed scale (Savage and Davidson 2001), particularly in complex terrain (Pacific et al. 2009; Riveros-Iregui et al. 2012), but not previously characterized within a single alpine tundra meadow. Accordingly, meso-topographical terrain complexity may have the potential to affect the alpine carbon cycle response to climate change to the same degree as the watershed-scale terrain complexity found at larger scales. Threshold values for the switch from direct to inverse proportionality in previous studies were based either on soil water matric potential (–150 kPa; Savage and Davidson 2001) or UAA (1287 m^2 in a 3.9 km^2 watershed; Riveros-Iregui et al. 2012), which are less commonly reported than soil moisture in field-based studies.

Temperature is widely considered the primary abiotic determinant of R_S (Bahn et al. 2010; Bond-Lamberty and Thomson 2010), but soil temperature and R_S were not significantly correlated within areas of dry, mesic, or wet alpine tundra. Instead, soil moisture was a significant predictor of both soil temperature and R_S; thus we infer that soil moisture acted as an overriding constraint on both soil temperature and R_S from moisture- and oxygen-limited soils in this ecosystem, which relegated soil temperature to a second-order control on R_S in the presence of adequate soil moisture (Almagro et al. 2009; Suseela et al. 2011; Mills et al. 2014). A similar pattern has been shown for dry alpine grasslands in Tibet (Geng et al. 2012) and also along a forested elevation gradient in the Colorado Rocky Mountains (Berryman et al. 2015). Given that soil moisture and temperature can also indirectly affect R_S by limiting photosynthetic rates and subsequent belowground carbon allocation available for root respiration (Irvine et al. 2005), we conclude that the R_S varied across this landscape in response to both terrain-modulated changes in soil moisture as well as the resulting feedbacks to soil temperature and vegetation.

Vegetation community composition can also affect soil nutrient cycling (Wardle et al. 2004; van der Putten et al. 2013), and the three individual dry tundra sites (#7, #11, and #19) at which soil temperature and R_S were significantly correlated represented the only three dry sites dominated by *Geum rossii*- or *Trifolium dasyphyllum* vegetation (Table 1). As such, the significant relationship between soil temperature and R_S at these sites was likely indicative of a vegetation effect (Conant et al. 2011). Previous work has shown that *Geum rossii* are known to have a higher Q_{10} than other alpine tundra vegetation (Higgins 1976), and that the temperature optimum for *Trifolium dasyphyllum* photosynthetic uptake (15 °C) was the highest among ten alpine tundra plant species (Scott and Billings 1964). Moreover, the chemical composition and diversity of plant litter are especially strong predictors of R_S on Niwot Ridge (Meier and Bowman 2008), and the phenolic compounds in *Geum rossii* are a known carbon source for soil microorganisms (Bowman et al. 2004). Since plant species diversity is greatest in dry tundra ecosystems on Niwot Ridge (Walker et al. 2001), this suggests that dry tundra R_S variability may be particularly sensitive to the interactions between vegetation and meso-topographical landscape position. In extreme cases (e.g. site #19), the additional nutrients and productivity provided by (nitrogen-fixing) vegetation may be sufficient to overcome soil moisture limitation and to create dry meadow R_S hotspots.

Antecedent soil moisture (e.g. snowmelt) may also serve as an important control on the magnitude of R_S from this ecosystem (Potts et al. 2006; Riveros-Iregui et al. 2008; Barron-Gafford et al. 2014) given that cumulative R_S fluxes followed the pattern of annual precipitation (e.g. lowest in 2012), but not growing season precipitation (lowest in 2013; Table 2). As a result, extended dry periods prior to or early in the growing season (e.g. April–June 2012) may be capable of stressing dry and mesic vegetation and/or heterotrophic microorganisms such that their ability to respond to soil rewetting is reduced (Knapp et al. 2008; Fierer and Schimel 2002). The seasonality of peak soil moisture could also factor into the discrepancy between the years that cumulative EC-modeled R_S and cumulative measured R_S peaked. For example, at the very dry sites that were co-located with the EC towers (#1 and #2), we observed the highest soil moisture and R_S of all three growing seasons in July 2012 (wettest month during this study) during a period of intense 'monsoon' precipitation. In contrast, the whole-tundra mean R_S peaked in 2011 (wettest entire growing season), when soil moisture was elevated, albeit to a lesser degree, over a longer period of time (e.g. perhaps not enough to stimulate R_S from the dry, rocky soils near the EC towers). On a larger scale, it is unlikely that the previous year's snowpack affected R_S (Blankinship and Hart 2012) since the ridgetop study site was consistently scoured snow-free throughout the winter. To account for these spatio-temporal inconsistencies, future studies should consider the frequency and/or seasonality of precipitation (the degree to which moisture and energy inputs are in phase) to further constrain alpine tundra R_S (Huxman et al. 2004; Schwinning and Sala 2004; Moyes and Bowling 2012).

Are measurements of soil moisture and temperature sufficient to predict R_S across a representative alpine tundra soil moisture and vegetation community gradient?

Our relatively simple models captured the seasonal magnitude but not the intra-seasonal variability of R_S. Specifically, the MLR model generally under-predicted measured R_S early and late in the growing season, but over-predicted R_S during the middle of the growing season. The MLR model also under-predicted mesic tundra R_S more than dry or wet tundra R_S, and MLR-modeled R_S increased monotonically with soil moisture, contrary to the bidirectional behavior of measured R_S. Taken together, we interpret this as an inability of our MLR model to account for vegetation effects (e.g. vegetation activity is greatest in mesic tundra and during the middle of the growing season). The EC model under-predicted R_S in both 2011 and 2013 but over-predicted R_S in 2012, when there was an especially intense period of monsoon precipitation during the month of July. This anomaly could be due to the particular sensitivity of the EC model to the fellfield vegetation immediately adjacent to the EC towers (requires intense precipitation to stimulate R_S), or to difficulties resolving the relationship between soil temperature and R_S when very dry and very wet periods occur within a single growing season.

The MLR model soil temperature term was only significant at mesic tundra sites, which reinforces that the effect of soil temperature on R_S was maximized when soil moisture was not strongly limiting. Based on our bidirectional framework, the optimum conditions for alpine tundra R_S were between roughly 0.30 and

0.45 m^3 m^{-3} soil moisture (Fig. 2), which corresponded to 81–100 % relative water saturation in dry tundra (porosity = 0.37), 54–80 % relative water saturation in mesic tundra (porosity = 0.56), and 48–72 % relative water saturation in wet tundra soils (porosity = 0.62) at this location. Consistent with these results, peak R_S has been shown to occur at lower relative water saturation in soils that have higher SOM fractions (Moyano et al. 2013), and the optimum relative saturation for R_S can be as low as 40 % in soils with greater than 5 % organic carbon (Moyano et al. 2013). Relative water saturation of 40 % may also coincide with a diminishing effect of soil temperature on R_S due to the development of oxygen limitation (higher microbial activity rates lead to oxygen depletion) (Rey et al. 2005). Accordingly, when interpreted with respect to soil physical processes, our modeled data provide new insights into the dominant effect of soil moisture on alpine tundra R_S, while simultaneously highlighting the need for further research into the vegetation-specific and resulting nutrient/substrate controls on alpine tundra R_S (Davidson et al. 2012).

What are the broader implications of these results in the context of regionally forecasted environmental change?

Although this study supports the idea that persistent carbon sources and sinks owe their status to the peculiar intersection of meso-topographical landscape position and vegetation community composition (Emanuel et al. 2011), we show that the relative source strength of a particular location can be modified by inter-annual meteorological variability. Environmental changes in the Rocky Mountain region are forecasted to include increased air temperature and precipitation (Baldwin et al. 2003), although individual precipitation events could become less frequent and more extreme as a result of the intensification of the hydrologic cycle (e.g. Trenberth 1999). Based on our results, we would expect increased precipitation to alleviate moisture stress from dry and mesic tundra sites, while simultaneously inhibiting oxygen (to soil microorganisms) and CO_2 (out of the soil matrix) diffusion from wet tundra soils (Moyano et al. 2013). More extreme precipitation could reduce the moisture and diffusion limitations characteristic of dry and wet tundra sites, but increase moisture stress at mesic sites (e.g. Knapp et al. 2008). Furthermore, earlier mountain snowmelt could reduce dry and mesic tundra R_S given the importance of antecedent moisture to snowmelt-dominated ecosystems (Harpold et al. 2012). Air temperature changes are only likely to affect the magnitude of R_S from this ecosystem if they result in warmer, 'stickier' spring snow events. Integrating these processes, the whole-tundra response to future hydro-climatic changes will likely be modified to some degree by the compensating nature of the soil moisture-R_S relationship between dry, mesic and wet patches of tundra. Nevertheless, our results suggest that increased precipitation (e.g. 2011) and/or more intense precipitation events (e.g. July 2012) have the potential to increase R_S carbon losses from alpine tundra ecosystems as a whole.

The controls on R_S identified by this study parallel the controls on other alpine tundra ecosystem processes, and thus contribute to a more holistic understanding of alpine tundra nutrient cycling. For example, moving from dry to wet meadow soils on Niwot Ridge, previous work has shown that total plant biomass, plant nitrogen uptake, and nitrogen use efficiency all increase, while plant allocation to belowground production, nitrogen use for production, and methane fluxes (become more negative) decrease (Fisk et al. 1998; West et al. 1999). Moreover, a growing body of work has focused on how landscape position, vegetation, and soil characteristics interact to influence soil moisture, temperature, and nutrient cycling across a wide array of ecosystem types (e.g., Cable et al. 2008; Craine and Gelderman 2011; Fisk et al. 1998; Kang et al. 2003; Lee et al. 2011; Moyano et al. 2012; Riveros-Iregui and McGlynn 2009; Stielstra et al. 2015; Wood et al. 2013), and the controls on R_S reported by this study may serve as a framework within which to explore the influence of terrain versus vegetation on R_S from other ecosystems. For example, topographic patterns of water availability are related to both productivity and decomposition in mesic grasslands (Schimel et al. 1991; Craine and Gelderman 2011), and so future amplification of the hydrologic cycle may similarly result in both positive and negative effects on the net carbon balance due to differential interactions between altered evaporative and soil moisture regimes from dry, mesic, and wet grassland ecosystems (Knapp et al. 2008). In arid and semi-arid ecosystems, soil moisture often supersedes soil temperature as the dominant control on R_S (Liu et al. 2009); thus quantifying the site-specific meso-topographical controls of aspect (Stielstra et al. 2015) and soil texture (Noy-Meir 1973) on soil moisture will be critical to predict the future carbon balance of dryland ecosystems. Although soil moisture is not generally limiting in arctic tundra ecosystems (Giblin et al. 1991), differences in nutrient availability (Nadelhoffer et al. 1991), vegetation community (Giblin et al. 1991), and surface subsidence due to permafrost thaw (Lee et al. 2011) result in meso-topographically explicit patterns of nutrient cycling. These examples highlight the need to consider the direct effects of soil moisture, temperature, texture, and vegetation on R_S as well as the potential for important bidirectional feedbacks mediated through topography, the seasonality and intensity of precipitation, and/or subsurface thaw, in order to quantify representative nutrient cycling patterns at the ecosystem level.

Conclusions

This study joins a growing body of work to suggest that moisture limitation supersedes temperature limitation to R_S in a variety of moisture-limited ecosystems. We analyzed the physical controls on dry, mesic, and wet tundra R_S to isolate a significant bidirectional response to soil moisture, similar to that which has been previously characterized in complex terrain and from forested ecosystems, but for different reasons (UAA versus subsurface permeability), and on a different spatial scale (macro- versus meso-scale topography). Overall, the R_S was greater in wet years, and in all years, the mesic tundra R_S was greater than wet tundra R_S, which was in turn, greater than dry tundra R_S. Although the R_S varied substantially within the statistical EC measurement footprint, we observed EC-modeled R_S to be most representative of the dry tundra immediately adjacent to the EC towers. Dry tundra sites were particularly sensitive to vegetation community composition, and the R_S variability was greatest between dry tundra sites, which could potentially confound R_S models that are uniquely based on abiotic factors. Notwithstanding, using MLR- and EC-based models to predict R_S from dry, mesic, and wet tundra, we were able to reproduce 75–79 % of the seasonal magnitude of direct R_S measurements. Since our study encompassed a broad range of soil moisture values commonly found throughout the Rocky Mountains, these simple models may represent an important step toward understanding the physical processes driving patterns of alpine tundra R_S throughout this region. Moreover, these results may have widespread applicability to other moisture-limited ecosystems, especially where soil moisture varies at the meso-topographical scale. Although a wetter future will likely increase alpine tundra R_S during the growing season, the ensemble response to climate change is likely to be tempered by compensatory behavior between dry, mesic, and wet patches of tundra.

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