

# Modeling the seasonality of belowground respiration along an elevation gradient in the western Chugach Mountains, Alaska

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**Abstract** Belowground respiration is typically the largest flux of carbon from terrestrial ecosystems to the atmosphere, making up >70% of total respiration in boreal forests. Recent work has shown that belowground respiration continues during the snow-covered season in boreal ecosystems, but few studies have made complementary measurements during the snow-free season and it remains uncertain what proportion of annual belowground respiration occurs during winter. Traditional models of the relationship between temperature and respiration assume fixed temperature sensitivity, but it has become clear that the apparent temperature sensitivity of belowground respiration increases as soils approach 0°C. Use of fixed temperature sensitivity to model carbon budgets of northern ecosystems may, therefore, yield misleading results. We measured belowground respiration monthly over 2 years in four ecosystems along an elevation gradient in south-central Alaska. Three models, representing different hypotheses about the

relationship between temperature and respiration, were confronted with the data. A logistic model, which allows the temperature sensitivity to vary inversely with temperature, and a variation of the  $Q_{10}$  model, which allows the temperature sensitivity to vary seasonally, performed well at all sites and produced similar estimates of seasonal and annual belowground respiration. The traditional  $Q_{10}$  model performed poorly at all sites and overestimated respiration during the snow-covered season. Annual belowground respiration was generally greater than in ecosystems of interior Alaska, where winters are colder and summers are warmer and drier. Belowground respiration during the snow-covered season made up 6–15% of the annual total—a small, but sensitive, component of annual carbon budgets.

**Keywords** AIC · Boreal · Maximum likelihood · Snow · Soil respiration · Winter

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## Introduction

Belowground respiration is made up of root and microbial respiration and it generally constitutes the largest flux of carbon (C) from ecosystems to the atmosphere (Ryan and Law 2005). In temperate and boreal forests, belowground respiration makes up more than 70% of total ecosystem respiration (Law

et al. 1999; Bolstad et al. 2004; Gaumont-Guay et al. 2006, 2009) which, in turn, may be more important than photosynthesis as a control on inter-annual variability in net ecosystem C exchange (Valentini et al. 2000). It is well-known that belowground respiration is sensitive to the direct and indirect effects of soil temperature (e.g., Flanagan and Veum 1974). More recently, it has been shown that the apparent temperature sensitivity of belowground respiration is highest when soils are near 0°C (e.g., Lloyd and Taylor 1994; Mikan et al. 2002), when indirect effects of temperature, such as substrate supply, are thought to limit respiration rates (Mikan et al. 2002; Davidson et al. 2006). Consequently, changes in climate that promote warmer soils and deeper thaw in boreal ecosystems are expected to lead to substantial losses of soil C, through increased rates of microbial respiration (Goulden et al. 1998).

A number of studies have shown that belowground respiration continues beneath the snowpack for much of the winter in boreal forests (e.g., Winston et al. 1997; Wang et al. 2002; Vogel et al. 2005; Sullivan et al. 2008). Snow insulates the soil from cold air temperatures and ecosystems with snowpacks that are deep and/or efficient insulators typically have warmer soils (Sturm et al. 2001) and exhibit greater rates of belowground respiration (Sullivan 2009). While a number of studies have estimated total belowground respiration during the snow-covered season in boreal ecosystems, few have made complementary measurements during the snow-free season (Wang et al. 2002; Vogel et al. 2005). As a result, it remains uncertain what proportion of annual belowground respiration occurs during the winter months.

Our ability to model belowground respiration lags considerably behind our ability to model other ecosystem C fluxes, such as photosynthesis (Farquhar et al. 1980). Many ecosystem process models assume that belowground respiration exhibits a fixed temperature sensitivity (e.g., McGuire et al. 2000). Given the high apparent temperature sensitivity of belowground respiration at temperatures near 0°C, the use of fixed temperature sensitivity to model annual and seasonal C budgets of high latitude ecosystems may yield misleading results.

The goals of this study were threefold. First, we set out to provide annual estimates of belowground respiration in four ecosystems of a southern boreal landscape, where studies of the terrestrial C cycle

have been rare. To this end, we selected four study sites along a 900 m elevation gradient in the western Chugach Mountains: a low elevation spruce–birch forest, a sub-alpine forest, an alder stand near the treeline and an alpine lichen–heath. Second, we aimed to estimate the proportion of annual belowground respiration that occurred during the snow-covered season in each of the four ecosystems. Third, we set out to identify an empirical model capable of providing unbiased predictions of belowground respiration across the full range of soil temperatures that occur on an annual basis at each of the study sites. Three competing models, representing different hypotheses about the temperature control of belowground respiration, were confronted with data collected on monthly intervals over a 2-year period at each of the sites. The first model is a common form of the traditional  $Q_{10}$  model (Black et al. 1996), which represents the hypothesis that belowground respiration exhibits a fixed sensitivity to temperature. The second model is a logistic model (Barr et al. 2002), which has a sigmoid shape and represents the hypothesis that the temperature sensitivity of belowground respiration varies inversely with temperature. The third model is a modified version of the  $Q_{10}$  model, where the temperature sensitivity varies as a function of the Julian day (Richardson et al. 2006). This latter model represents the hypothesis that it is not simply the seasonal cycle of temperature, but that other aspects of seasonality, such as plant phenology and substrate availability, are important controls on belowground respiration. We used likelihood methods and the information theoretic approach to identify the model with the most support in the data at each site (Burnham and Anderson 2002; Hobbs and Hilborn 2006).

## Methods

### Site descriptions

Study sites were established in four ecosystems along a 900 m elevation gradient in the western Chugach Mountains: a spruce–birch forest, a sub-alpine forest, a shrub site and an alpine site (Table 1). The low elevation spruce–birch forest site was established on the campus of the University of Alaska in Anchorage (Sullivan et al. 2008). The overstory is a near even

**Table 1** Location and soil characteristics (0–20 cm depth,  $n = 6$ ) of the study sites along an elevation gradient in the western Chugach Mountains

Site	Location	Elevation (m)	SOC (kg/m <sup>2</sup> )	Soil N (kg/m <sup>2</sup> )
Alpine	61°08'N, 149°38'W	950	6.7 (1.3) <sup>b</sup>	0.28 (0.08) <sup>b</sup>
Shrub	61°09'N, 149°40'W	650	9.1 (1.1) <sup>a</sup>	0.71 (0.09) <sup>a</sup>
Sub-alpine Forest	61°09'N, 149°42'W	310	6.0 (1.3) <sup>bc</sup>	0.24 (0.05) <sup>bc</sup>
Spruce–Birch Forest	61°12'N, 149°49'W	42	4.4 (0.6) <sup>c</sup>	0.16 (0.02) <sup>c</sup>

Standard deviations appear within parentheses. Values identified with different superscripts are significantly different at  $\alpha = 0.05$

mixture of *Picea glauca* and *Betula papyrifera*, while dominant species in the understory include *Ledum palustre*, *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Cornus canadensis*, *Lycopodium clavatum* and the mosses *Hylocomium splendens* and *Pleurozium schreberi*. Soils of the spruce–birch forest site have an organic layer that is approximately 15 cm thick. Volumetric soil water content (0–12 cm depth) during the snow-free period varied between a site-level minimum of 0.16 v/v in late July and a maximum of 0.25 v/v in October during both years of the study. The sub-alpine forest site was established at an elevation of 310 m near the northern border of Chugach State Park, approximately 250 m below the treeline. Vegetation at the site is a mosaic of forested knolls, dense thickets of *Alnus crispa* and open grasslands, dominated by *Calamagrostis canadensis*. Measurements were made on two knolls separated by approximately 1 km. The overstory of the forested knolls is primarily *P. glauca*, with lesser amounts of *B. papyrifera*. Dominant species in the understory include *Empetrum nigrum*, *Vaccinium vitis idaea*, *Lycopodium clavatum*, *Hylocomium splendens*, *Pleurozium schreberi* and the nitrogen-fixing lichen, *Peltigera aphthosa*. Soils have an organic layer that is approximately 15 cm thick. Average soil water content varied between 0.17 v/v in July and 0.30 v/v in October of both snow-free seasons. The shrub and alpine sites were established in Chugach State Park on the western slope of Wolverine Peak. The shrub site is at an elevation of 650 m, approximately 100 m above the *P. glauca* treeline and slightly above the *Tsuga mertensiana* treeline. The overstory of the shrub site is almost exclusively *Alnus crispa*, with an average height of approximately 3 m. The understory of the shrub site is dominated by three species: *Dryopteris dilatata*, *Veratrum viride* and *Heracleum lanatum*. Soils at the

shrub site have a deep organic layer >20 cm. Volumetric soil water content varied during the snow-free season between 0.22 v/v in July and 0.39 v/v in September and October. The alpine site is at an elevation of 950 m in a rich lichen heath with nearly 100% vegetation cover. Dominant species at the alpine site include *Empetrum nigrum*, *Cassiope tetragona*, *Cladina rangiferina* and *Vaccinium uliginosum*. Soils at the alpine site have an organic layer that is approximately 20 cm thick. Site-level volumetric soil water contents varied seasonally between 0.21 v/v in July and 0.34 v/v in September.

#### Microclimate monitoring

Micrometeorological stations were established at each of the four sites. The station in the spruce–birch forest consisted of a CR10 datalogger (Campbell Scientific, Logan, UT) and sensors for air temperature, relative humidity (RH) and wind speed at 3 m, as well as soil temperature and soil water content at 10 cm depth. The sub-alpine forest station also had sensors for air temperature, RH and wind speed at 2 m in addition to soil temperature and soil water content at 10 cm depth. In this case, data were logged to a CR10x datalogger (Campbell Scientific, Logan, UT). The alpine and shrub stations were equipped with Hobo Micro Station dataloggers and sensors for air temperature, RH and wind speed at 2 m, as well as soil temperature at 10 cm depth (Onset Computer Corp. Bourne, MA). Point measurements of soil temperature at 10 cm depth (Probe Model: 82021-156, VWR International, West Chester, PA) and volumetric soil water content (0–12 cm depth, HydroSense, Campbell Scientific, Logan, UT) were made adjacent to each respiration collar, when respiration measurements were made during the snow-free season.

### Summer respiration measurements

Belowground respiration was measured on approximately monthly intervals during the snow-free seasons of 2006 and 2007. Five circular PVC soil collars (20 cm in height and 30.5 cm in diameter) were installed at each of the four sites to a depth of 10 cm. Collars were installed in areas with limited above-ground vascular plant biomass. Vascular plants that were present were carefully removed at the beginning of the study. On each measurement day, the collars were checked for the presence of vascular plants, which were removed when present at least 30 min before making measurements. At both of the forest sites and shrub site, the soil surface within the collars was covered with litter and very few non-vascular plant species. At the alpine site, the soil surface within the collars was covered by a mixture of litter and live *C. rangiferina*.

Measurements were made using a LI-6200 portable photosynthesis system (LI-COR Biosciences, Lincoln, NE), plumbed to a PVC chamber. The top of the chamber was covered with reflective tape and the chamber was fitted with a small fan and a pressure vent (Davidson et al. 2002). Measurements of chamber  $[CO_2]$ , RH and temperature were logged every 2 s over a 60 s period. Chamber  $[CO_2]$  was monitored closely during the measurements for evidence of boundary layer disturbance. If there was a rapid initial increase in  $[CO_2]$ , data were discarded and the collar was re-measured. Two measurements were made from each collar and  $CO_2$  efflux was calculated following Hooper et al. (2002). The LI-6200 was calibrated against gases of known  $[CO_2]$  before each round of measurements. The LI-6200 does not have an atmospheric pressure sensor. Therefore, the pressure parameter was adjusted upon arrival at each site, according to the elevation.

### Winter respiration measurements

Subnivean  $[CO_2]$  was measured on approximately monthly intervals during early 2006, the winter of 2006–2007 and late 2007. Measurements were made using a hollow stainless steel probe equipped with a perforated tip and plumbed with 3.2 mm ID polyethylene tubing (e.g., Fahnestock et al. 1998; Sullivan 2009). The tubing was attached to a LI-800 NDIR  $CO_2$  analyzer (LI-COR Biosciences, Lincoln, NE),

which was equipped with a 5 cm optical bench, a micro-diaphragm pump downstream of the optical bench ( $850 \text{ ml min}^{-1}$ , KNF Neuberger Inc., Trenton, NJ) and a digital multimeter to measure voltage output from the LI-800 (Fluke Corporation, Everett, WA). The LI-800 was calibrated using gases of known  $[CO_2]$  the day before each measurement campaign and allowed to warm-up for 1.5 h prior to making measurements. Ten measurements of subnivean  $[CO_2]$  were made every 3.0 m along linear transects through the sites by inserting the probe to the base of the snowpack and drawing air through the analyzer until  $[CO_2]$  stabilized. Measurements of atmospheric  $[CO_2]$  above the snow surface were made before and after the series of subnivean measurements.

On each winter measurement day, snow pits were excavated for measurements of snow density and temperature at each site. Care was taken to dig snow pits in areas where the depth and density of the snowpack were representative of the area where the  $[CO_2]$  measurements were made. Two pits were always excavated at each of the forest sites, but deep snowpacks and short days necessitated the use of only one pit each at the shrub and alpine sites. Snow density and temperature measurements were made at 10 cm intervals using a stainless-steel RIP 1 density cutter and a dial stem thermometer (Snowmetrics, Fort Collins, CO).

Diffusion of  $CO_2$  from the subnivean to the atmosphere was estimated following Musselman et al. (2005):

$$J_c = \theta \tau D \frac{P_0}{RT_0} \left( \frac{T}{T_0} \right)^{0.81} \frac{\Delta C}{z}, \quad (1)$$

where  $J_c$  is  $CO_2$  efflux ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ),  $\theta$  is snowpack porosity (unitless),  $\tau$  is snowpack tortuosity (unitless),  $D$  is the diffusion coefficient for  $CO_2$  in air ( $0.1381 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ ),  $P_0/RT_0$  is the molecular density of  $CO_2$  at standard temperature and pressure ( $44.613 \text{ mol m}^{-3}$ ),  $T$  is snowpack temperature (K),  $\Delta C$  is the difference in  $[CO_2]$  between the subnivean and the atmosphere ( $\mu\text{mol mol}^{-1}$ ) and  $z$  is snow depth (m). Snowpack porosity ( $\theta$ ) was estimated using mean snowpack density ( $\rho$ ):

$$\theta = 1 - \left( \frac{\rho}{973} \right), \quad (2)$$

where  $973 \text{ g l}^{-1}$  is the density of ice. Snowpack tortuosity ( $\tau$ ) was also estimated as a function of density (Millington 1959):

$$\tau = \theta^{1/3}, \quad (3)$$

Studies that have compared this approach with chamber-based methods of estimating CO<sub>2</sub> efflux from snow-covered soils have consistently concluded that the diffusion gradient approach provides more accurate estimates of the flux (Mast et al. 1998; McDowell et al. 2000; Schindlbacher et al. 2007). Use of the diffusion gradient approach to estimate CO<sub>2</sub> efflux assumes that [CO<sub>2</sub>] increases in a linear manner with depth in the snowpack from the atmosphere to the soil surface. Two scenarios can disrupt the linear gradient. High wind speeds may disrupt the linear gradient through advection, particularly in the upper layers of the snowpack (e.g., Massman et al. 1995). In the present study, measurements were made during periods with light winds. The presence of an impermeable layer in the snowpack, such as laterally continuous ice layer may also disrupt the linear [CO<sub>2</sub>] gradient (Mast et al. 1998; Jones et al. 1999). Although the sites experienced occasional mid-winter thaws, there was no evidence of a laterally continuous ice layer when snow pits were excavated.

### Model selection

Three competing models of the relationship between soil temperature and belowground respiration were confronted with data from a wide range of soil temperatures at each of the four sites. Mean values for each sampling date at each site were used because only site-level soil temperature data were available during the snow-covered season. In all models, the units for belowground respiration ( $R$ ) are  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , while those for soil temperature are  $^{\circ}\text{C}$ . Values for  $\theta_{1-4}$  are fitted parameters that differ across the models. Model 1 is a modified version of the classic exponential  $Q_{10}$  respiration model (Black et al. 1996), which represents the hypothesis that belowground respiration exhibits a fixed sensitivity to temperature:

$$R = \theta_1 \times \theta_2^{\frac{(T-10)}{10}}. \quad (4)$$

The  $Q_{10}$  model implies that belowground respiration will increase without limit as temperatures rise and that rapid reductions in liquid water as temperatures fall below freezing will not affect the temperature

sensitivity of belowground respiration. Model 2 is a logistic model, which has a sigmoid shape that allows the temperature sensitivity of belowground respiration to decrease at high temperatures and increase as soil temperatures decline (Barr et al. 2002):

$$R = \frac{\theta_1}{1 + e^{(\theta_2 - \theta_3 T)}}. \quad (5)$$

The logistic model is similar in form to the commonly used Lloyd and Taylor model (Lloyd and Taylor 1994). Simulations have suggested that the Lloyd and Taylor model is over-parameterized, in the sense that different combinations of parameter values can fit respiration data equally well (Richardson and Hollinger 2005). Given this limitation of the Lloyd and Taylor model, we elected to use the simpler logistic model to represent the hypothesis that the temperature sensitivity of belowground respiration varies inversely with soil temperature. Model 3 is a modified version of the  $Q_{10}$  model, where the temperature sensitivity is treated as a first-order Fourier function of the Julian day (Richardson et al. 2006):

$$R = \theta_1 [\theta_2 + \theta_3 \sin(JD_{\pi}) + \theta_4 \cos(JD_{\pi})]^{\frac{(T-10)}{10}}, \quad (6)$$

where  $JD_{\pi}$  is the Julian day expressed in radians ( $=2\pi \times \text{JD}/366$ ). Model 3 represents the hypothesis that it is not simply seasonal changes in temperature that affect belowground respiration; it suggests that other attributes of the seasonal cycle affect the temperature sensitivity of belowground respiration. For instance, model 3 allows for the possibility of reduced respiration as a result of substrate depletion beneath the winter snow pack, when inputs of labile C are restricted for an extended period of time. Model 3 also allows for effects of plant phenology, such as fine root respiration and labile C exudation, which are expected to be at least partially independent of soil temperature.

Likelihood methods and the information theoretic approach were used to examine the strength of support in the data for each of the three competing models or hypotheses (Burnham and Anderson 2002; Hobbs and Hilborn 2006). Maximum likelihood estimates of parameter values and likelihood-ratio-based confidence intervals were obtained using Proc Model in SAS 9.2 (SAS Institute, Cary, NC). The Gauss–Newton method was used to minimize the

negative log-likelihood function. Examination of residual plots revealed non-normality in the distribution of the respiration data. To address this issue, all respiration data were transformed using the following equation:  $y = \log_{10}(x + 1)$ . Akaike's Information Criterion (AIC) was then calculated using the log-likelihood,

$$\text{AIC} = -2 \ln[L(\theta|Y)] + 2K, \quad (7)$$

where  $L(\theta|Y)$  is the likelihood of the model ( $\theta$ ) given the data ( $Y$ ) and  $K$  is the number of parameters in the model. AICc is a modification of AIC that includes a greater penalty for including additional parameters in the model when the sample size is small. Burnham and Anderson (2002) recommend using AICc in all cases because AIC and AICc converge with increasing sample size. AICc was calculated as follows:

$$\text{AICc} = \text{AIC} + 2 \frac{K(K+1)}{n-K-1}, \quad (8)$$

where  $n$  is the number of samples. Akaike weights ( $W_r$ ) were calculated to assess model selection uncertainty and to provide an index of the relative support in the data for a given model (Burnham and Anderson 2002; Hobbs and Hilborn 2006),

$$W_r = \frac{e^{-2\Delta_r}}{\sum_{i=1}^R e^{-2\Delta_i}}, \quad (9)$$

where  $\Delta_r$  is the difference between AICc of a given model and the best model, the numerator is the likelihood of the model in question and the denominator is the sum of the likelihoods of all three competing models.

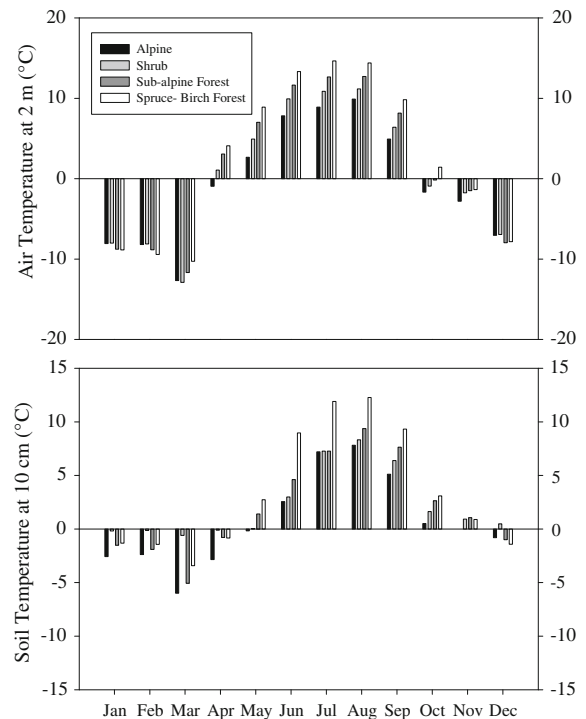
## Results

### Soil characteristics

The four study sites were evenly distributed along an elevation gradient from near sea-level to 950 m (Table 1). Soil C content in the upper 20 cm of the soil profile was lowest in the spruce–birch forest, intermediate in the sub-alpine forest and the alpine and greatest at the shrub site. Soil N content followed the same pattern, but there was more than twice the N content in the shrub soils than the other sites. Consequently, soil C:N at the shrub site was approximately half that at the other sites.

### Microclimates

During 2007, annual average air temperatures decreased with elevation from 2.5°C in the spruce–birch forest, to 1.4°C in the sub-alpine forest, to 0.5°C in the shrubs, to −0.6°C in the alpine. Similarly, average soil temperatures at 10 cm depth during 2007 decreased from 3.4°C in the spruce–birch forest, to 2.2°C in both the sub-alpine forest and the shrubs, to 0.7°C in the alpine. However, variation in air and soil temperatures with elevation depended strongly upon season (Fig. 1). Between March and November, air temperatures decreased with elevation and did so most strongly during the summer months. Average July air temperatures, for instance, were nearly 6°C cooler in the alpine than in the spruce–birch forest. In contrast, between December and February, average air temperatures were colder in the spruce–birch and sub-alpine forests than in the shrubs and alpine. Soil temperatures varied with elevation in a manner similar, in some respects, to the air temperature pattern. When all sites were free of



**Fig. 1** Monthly average air and soil temperatures at each of the study sites during 2007



snow (approximately May–October), soil temperatures decreased with elevation. During the snow-covered season, the warmest soils were generally found in the shrubs and the coldest soils were found in the alpine, while soil temperatures in the two forest sites were intermediate.

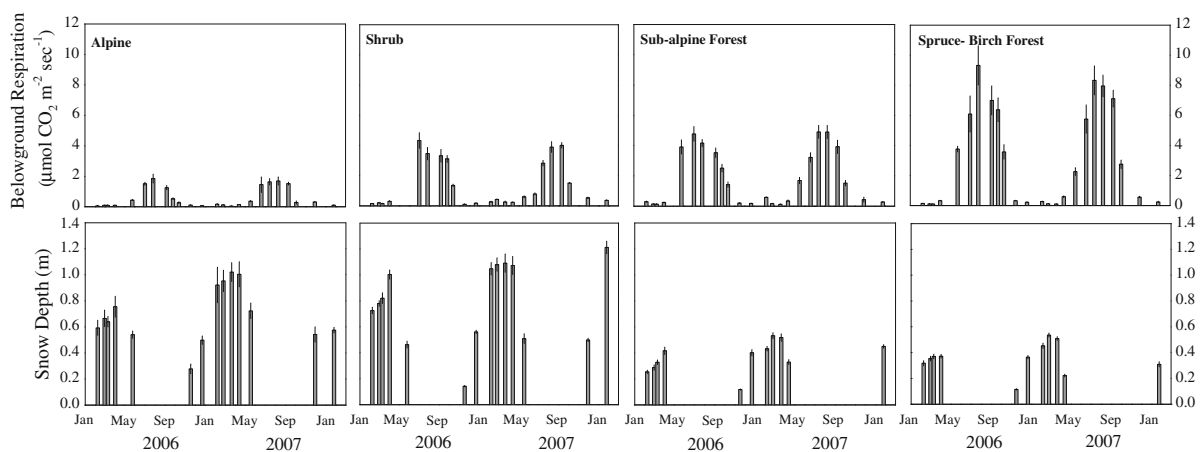
#### Seasonality of belowground respiration across sites

The highest rates of belowground respiration were observed in July and/or August at all of the study sites (Fig. 2). The magnitude of peak belowground respiration declined substantially with elevation, from approximately  $9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the spruce–birch forest to slightly less than  $2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  in the alpine. At all study sites, rates of belowground respiration were much lower during the snow-covered season than during the snow-free season. The highest rates of belowground respiration during the snow-covered season were consistently found in the shrubs, where  $\text{CO}_2$  efflux varied between 0.1 and  $0.6 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Relatively high rates of wintertime  $\text{CO}_2$  efflux and the comparatively low rates of summertime  $\text{CO}_2$  efflux led to the smallest seasonal range of belowground respiration in the shrubs. Both the shrub and alpine sites maintained relatively deep snowpacks during the mid- to late winter, but snowpack density differed strongly

between the two sites. Across all winter sampling dates, the alpine snowpack had an average density of  $372 \text{ g l}^{-1}$ , while the shrub snowpack had an average density of  $290 \text{ g l}^{-1}$ .

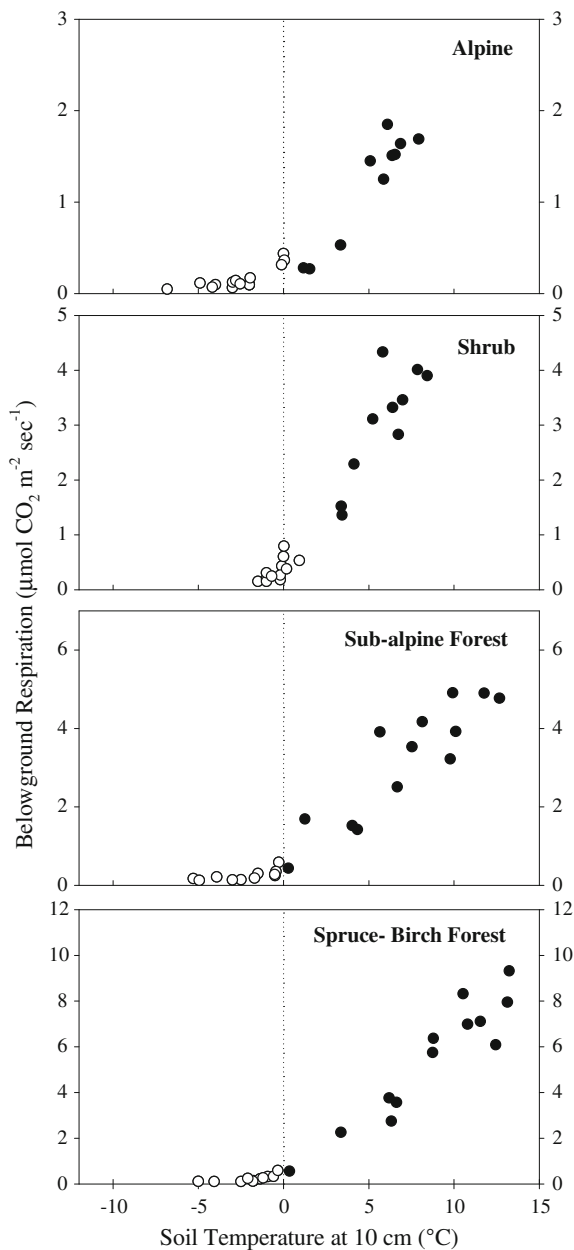
#### Competition among models

Seasonal variation in belowground respiration was very closely related to soil temperature at all study sites (Fig. 3). Belowground respiration declined strongly as soil temperatures approached and dropped below the freezing point, but the rate of decline relaxed as temperatures fell further below  $0^\circ\text{C}$ . There was some evidence that the rate of increase in belowground respiration declined as soil temperatures approached their seasonal maxima. Three models of the relationship between soil temperature and belowground respiration were confronted with the data and the model with the most support in the data was identified for each study site. The  $Q_{10}$  model performed relatively poorly at all four sites (Table 2). Even when the respiration data were log-transformed, the  $Q_{10}$  model overestimated low fluxes, when soil temperatures were near and below  $0^\circ\text{C}$ , underestimated intermediate fluxes and overestimated relatively high fluxes, when soil temperatures were near their seasonal maxima (Fig. 4). The logistic model performed well at all of the sites and was selected as the best model for the shrub and spruce–birch forest



**Fig. 2** Seasonality of belowground respiration and snow depth at each of the study sites measured between early 2006 and early 2008. Data from snow-free sampling dates are the mean

of closed chamber measurements made on five respiration collars, while those from the snow-covered season are the mean of 10  $[\text{CO}_2]$  gradient measurements. Bars are S.E



**Fig. 3** Belowground respiration as a function of soil temperature at each of the study sites between early 2006 and early 2008. *Open symbols* are estimates made using the  $[CO_2]$  gradient approach during the snow-covered season, while *closed symbols* are measurements made using a closed chamber during the snow-free season. *Open symbols* are the mean of 10 estimates, while closed symbols are the mean of 5 estimates. The dotted line indicates a soil temperature of 0°C

sites. There was no evidence in the residual plots of a bias in the predictions of the logistic model across the range of soil temperatures. The time-varying  $Q_{10}$

model also performed well at all of the sites and was selected as the best model for the alpine and sub-alpine forest sites. The time-varying  $Q_{10}$  model predicted a seasonal hysteresis in the response of belowground respiration to soil temperature for the alpine and sub-alpine forest sites, where it was selected as the best model, but not for the shrub and spruce–birch forest sites, where the logistic model had the most support in the data (Fig. 5). In both the alpine and sub-alpine forest, belowground respiration at a given temperature was predicted to be greater early in the snow-free season than late in the snow-free season.

#### Estimates of annual and seasonal C efflux

Hourly soil temperature data from each of the sites were used with each model to predict the total C efflux attributable to belowground respiration on an annual and seasonal basis (winter vs. summer). The three models generally produced similar estimates of annual C efflux for the alpine, shrub and spruce–birch forest sites (Table 3). For the sub-alpine forest, the  $Q_{10}$  model produced the lowest estimate ( $467 \text{ g C m}^{-2}$ ), the logistic model yielded an intermediate estimate ( $543 \text{ g C m}^{-2}$ ) and the time-varying  $Q_{10}$  model produced the highest estimate ( $656 \text{ g C m}^{-2}$ ). In contrast with the annual estimates, the seasonality of C efflux depended strongly upon the model used to predict belowground respiration. The  $Q_{10}$  model consistently generated estimates of winter C efflux that were approximately 50% greater than the other two models. For the alpine and shrub sites, the  $Q_{10}$  model produced estimates of summer C efflux that were generally similar to those from the other two models. In the two forest sites, however, the  $Q_{10}$  predictions were considerably lower than the estimates generated using the logistic and time-varying  $Q_{10}$  models.

## Discussion

### Microclimates

Variation in air and soil temperatures with elevation depended strongly upon season. Between March and November, air temperatures decreased with

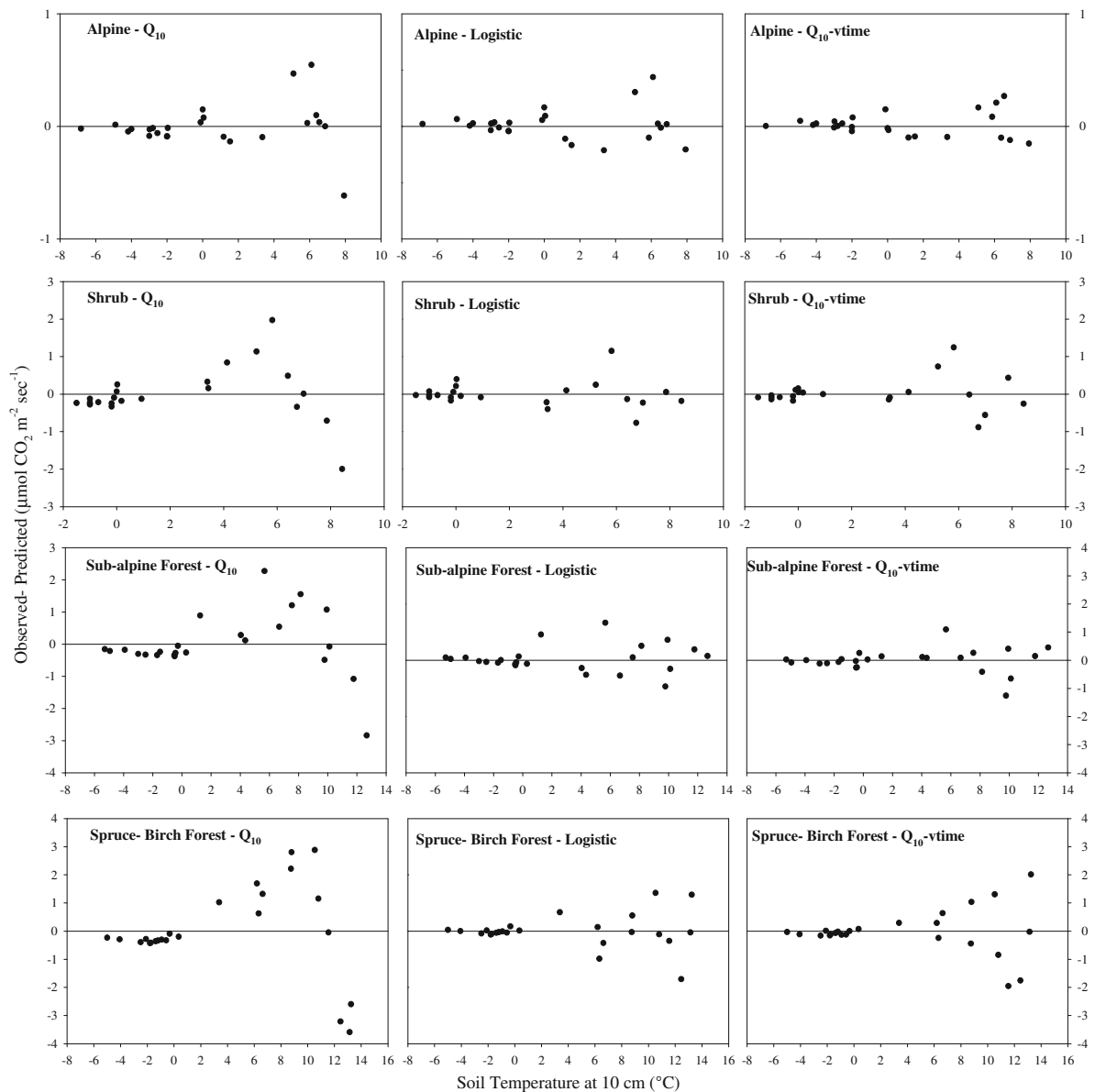


**Table 2** The weight of support in the data for each of the alternative models, along with maximum likelihood estimates of model parameters and likelihood-ratio-based estimates of parameter confidence intervals

Site	<i>n</i>	Model	$\ln[L(\theta Y)]$	AICc	$\Delta_r$	$W_r$	$\theta_1$	95% CI	$\theta_2$	95% CI	$\theta_3$	95% CI	$\theta_4$	95% CI
Alpine	24	Q <sub>10</sub>	43.79	-83.01	18.47	0.00	0.78	0.68–0.90	7.14	5.49–9.66				
	24	Logistic	49.18	-91.17	10.32	0.00	0.60	0.47–1.05	1.57	1.17–2.20	0.35	0.26–0.47		
	24	Q <sub>10</sub> -vtime	55.79	-101.48	0.00	1.00	0.52	0.42–0.64	5.34	4.19–6.82	1.07	0.18–1.72	3.50	2.62–4.50
Shrub	21	Q <sub>10</sub>	22.60	-40.53	24.43	0.00	1.11	0.94–1.30	5.97	4.35–8.52				
	21	Logistic	36.19	-64.97	0.00	0.99	0.74	0.67–0.84	1.43	1.16–1.71	0.53	0.41–0.66		
	21	Q <sub>10</sub> -vtime	36.42	-62.34	2.63	0.01	0.72	0.59–0.86	3.49	2.68–4.52	1.36	0.89–1.88	2.01	1.56–2.60
Sub-alpine	24	Q <sub>10</sub>	19.05	-33.53	33.43	0.00	0.69	0.62–0.76	3.12	2.51–4.00				
	24	Logistic	32.66	-58.12	8.84	0.00	0.77	0.69–0.89	1.21	0.89–1.55	0.38	0.29–0.51		
	24	Q <sub>10</sub> -vtime	38.53	-66.96	0.00	1.00	0.74	0.70–0.77	3.42	2.94–4.04	0.49	0.08–0.92	2.49	1.89–3.23
Spruce– Birch	24	Q <sub>10</sub>	15.83	-33.53	33.43	0.00	0.76	0.69–0.83	3.23	2.64–4.07				
	24	Logistic	40.47	-73.74	0.00	1.00	0.99	0.93–1.06	1.58	1.37–1.82	0.37	0.32–0.43		
	24	Q <sub>10</sub> -vtime	37.85	-65.60	8.15	0.00	0.90	0.86–0.94	3.85	3.35–4.49	0.96	0.47–1.50	2.62	1.99–3.37

At each site, the model with the lowest AICc (most negative) and the highest  $W_r$  had the greatest support in the data. Parameter values predict the log-transformed CO<sub>2</sub> flux

increasing elevation. In contrast, between December and February, average air temperatures were colder in the two lower elevation sites, reflecting the development of a strong temperature inversion. The development of a temperature inversion is a consequence of negative radiation balance at the lower elevation land surface throughout most of the diurnal cycle during the darkest months of the year. The temperature inversion is enhanced by occasional warm air advection over the mountains from Prince William Sound and cold air drainage downward along the slopes of the western Chugach Mountains (P. Olsson pers. comm.). During the snow-free season, soil temperatures declined with increasing elevation, much like the pattern observed for air temperatures. During the snow-covered season, soil temperatures varied across sites in response to the depth and insulative properties of the snowpack, much like observations across vegetation types on the North Slope of Alaska (Sturm et al. 2001). The alpine and shrub sites maintained much deeper snowpacks than the two forest sites during the winter months. While some of this difference can likely be attributed to an orographic effect on snowfall, our study sites were established in leeward areas and most of the difference is probably attributable to redistribution of snow by wind in the two higher elevation sites. Comparison of soil temperatures in the alpine and shrub sites illustrates the importance of the insulative properties of the snowpack, because snow depths were generally similar across the two sites. The alpine snowpack was composed almost entirely of wind slab, as reflected in its very high average density (372 g/l), while the shrub snowpack was generally composed of large faceted snow crystals that develop under steep temperature gradients (e.g., Akitaya 1974). Sturm et al. (2001) showed that snowpacks dominated by large faceted crystals have a much higher thermal resistance than those dominated by wind slab, explaining the much warmer soils at our shrub site during the snow-covered season. The snowpacks of the two forest sites were shallow in comparison with those in the alpine and shrubs, but also dominated by large faceted crystals. The forest snowpacks were likely better insulators per unit thickness than the alpine snowpack, and this explains why soil temperatures tended to be warmer in the forest sites than in the alpine, despite the development of air temperature inversions during much of the winter.

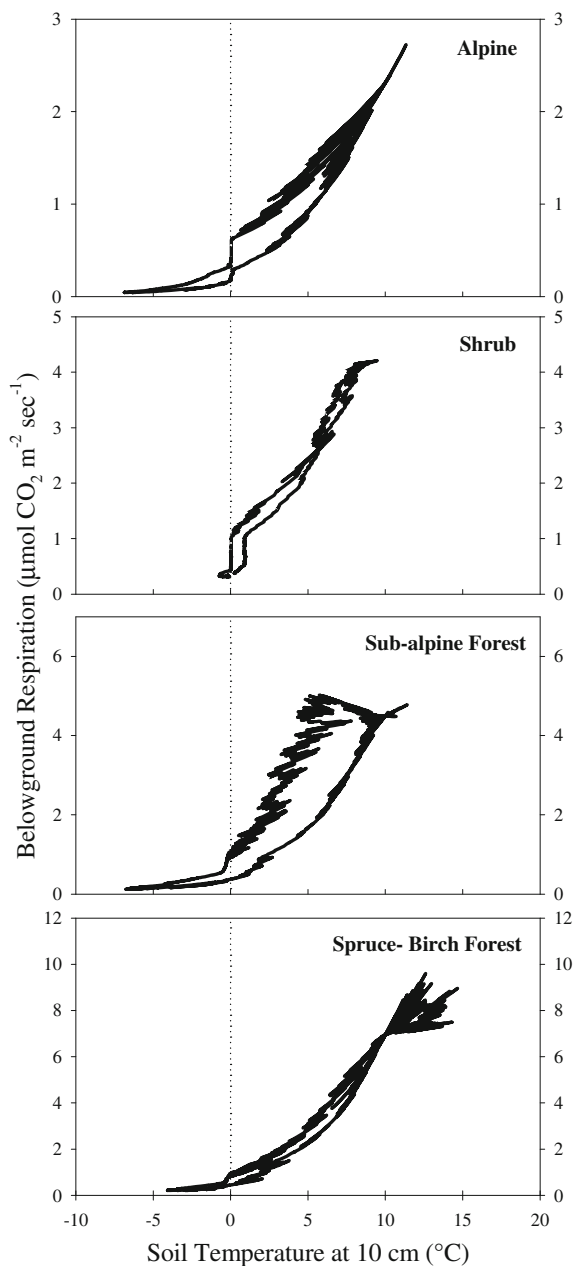


**Fig. 4** Residual plots for each of the three competing models at the four study sites along an elevation gradient in the western Chugach Mountains

### Model comparison

The Q<sub>10</sub> model performed poorly at all four sites, as it overestimated low fluxes when soils were near and below 0°C, underestimated intermediate fluxes and overestimated relatively high fluxes when soil temperatures were near their seasonal maxima. These biases in the fit of the Q<sub>10</sub> model to the data led to very different estimates of seasonal C fluxes. The Q<sub>10</sub>

model severely overestimated C efflux from November through April (+50%), compared with the logistic and time-varying Q<sub>10</sub> models, which generally produced similar results. C efflux during the snow-covered season was, however, small relative to that during the snow-free season and annual estimates of C efflux obtained using the Q<sub>10</sub> model were not consistently biased compared with those obtained using the other two models. Estimates of C efflux



**Fig. 5** Hourly estimates of belowground respiration during 2007 made using the time-varying  $Q_{10}$  model and plotted against measurements of soil temperature. Maximum likelihood estimates of the model parameters are shown in Table 2

obtained using the  $Q_{10}$  model for the snow-free season were generally similar to those obtained using the other two models. However, residual plots indicate the  $Q_{10}$  model tended to overestimate fluxes at intermediate soil temperatures and underestimate fluxes when soil temperatures were near their

seasonal maxima. It is likely that these two errors cancelled at the scale of the entire snow-free season and produced C efflux estimates that were approximately correct, but for the wrong reason. Given the generally poor performance of the  $Q_{10}$  model, we concur with the conclusions of many recent studies, that use of the  $Q_{10}$  model in ecosystem process models and as a tool to interpolate among measured fluxes should be phased-out (e.g., Lloyd and Taylor 1994; Davidson et al. 2006; Richardson et al. 2006). Fitting the  $Q_{10}$  model to respiration data may, however, serve as a useful tool to identify changes in the temperature sensitivity of respiration in response to environmental stress. In the case of our study, residual plots for the  $Q_{10}$  model clearly show a decline in the temperature sensitivity of belowground respiration when soil temperatures were near their seasonal maxima at all sites—a response that was not readily apparent in plots of belowground respiration against soil temperature.

The logistic and time-varying  $Q_{10}$  models generally performed well at all sites. The former was selected as the best model at the shrub and spruce–birch forest sites, where there was very little indication of a seasonal hysteresis. The latter was identified as the best model in the alpine and sub-alpine forest sites, where the model predicted higher rates of belowground respiration at a given temperature in the spring and early summer than in the late summer and fall. The seasonal hysteresis was predicted at soil temperatures between 0 and 10°C in the sub-alpine forest and between 0 and 6°C in the alpine. There are several possible explanations for this pattern. One possibility is that soil moisture was more favorable in early summer than in late summer. This is likely not the case, however, because the seasonality of precipitation in Anchorage is such that soil water contents are generally higher at our study sites in the late summer and fall (0.25–0.39 v/v) than in the early and mid-summer (0.16–0.32 v/v), when there is some evidence that low soil water contents may slightly restrict belowground respiration. Furthermore, measurements of volumetric soil moisture, made adjacent to each respiration collar on all snow-free measurement dates, showed that the spruce–birch forest consistently had drier soils than the sub-alpine forest. If the hysteresis was driven by the seasonality of soil water availability, we would expect it to be more apparent at the drier

**Table 3** Estimates of annual, summer (May 1 to Oct 31, 2007) and winter (Jan 1 to April 30 and Nov 1 to Dec 31, 2007) carbon efflux ( $\text{g C m}^{-2}$ ) from each of the study sites made using hourly measurements of soil temperature at 10 cm depth and each of the three competing models

Site	$Q_{10}$			Logistic			$Q_{10}\text{-vtime}$		
	Annual	Summer	Winter	Annual	Summer	Winter	Annual	Summer	Winter
Alpine	249.9	215.4	34.4	217.5	190.7	26.9	218.5	197.1	21.4
Shrub	595.7	493.3	102.5	530.0	452.2	77.8	541.6	463.9	77.7
Sub-alpine Forest	467.3	362.5	104.7	542.8	474.9	67.8	655.5	588.3	67.2
Spruce–Birch Forest	1019.1	904.5	114.5	1025.3	961.5	63.9	1051.3	979.0	72.3

Maximum likelihood estimates of model parameters are shown in Table 2

spruce–birch forest than at the sub-alpine forest site. At the alpine site, several measurements of belowground respiration were made when soil temperatures were at  $0^{\circ}\text{C}$  and these measurements show higher fluxes than would be expected, based on fluxes measured slightly above and slightly below  $0^{\circ}\text{C}$ . Physical processes in the soil may decouple the production and efflux of  $\text{CO}_2$  as soils begin to freeze and as they begin to thaw. As soils begin to freeze, ice expands into previously air-filled pore spaces and this may physically force trace gases out of the soil (Mastepanov et al. 2008). It is well-known that belowground respiration continues at soil temperatures below freezing. Some of the winter-produced  $\text{CO}_2$  may become trapped within the soil and subsequently released when soils thaw (Oechel et al. 1997). We think it is possible that  $\text{CO}_2$  efflux in response to physical processes may have “trained” the time-varying  $Q_{10}$  model to predict a seasonal hysteresis at our alpine site, when there was very little biological evidence of hysteresis in the data. In the sub-alpine forest, data from two measurement dates during the first-half of the snow-free season lie slightly ( $\sim 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) above what would be expected based on surrounding data. We think these two measurement dates may have led to the prediction of a seasonal hysteresis and we suggest that future studies use caution when fitting the time-varying  $Q_{10}$  model to small data sets. It is possible that the seasonal hysteresis is not an artifact of fitting a relatively complex model to a small data set, as previous work with sub-hourly respiration data have also predicted a seasonal hysteresis (Richardson et al. 2006). We suggest that future work with near continuous

respiration data in similar ecosystems may be warranted. Given our lack of a satisfactory biological explanation for the seasonal hysteresis and the likelihood that it was predicted based on very few measurement dates, we restrict our discussion from this point forward to the seasonal and annual C efflux estimates made using the logistic model.

The logistic model was able to explain more than 95% of the variance in site-level belowground respiration using soil temperature alone at all of our study sites. Variation in soil water content (e.g., Cable et al. 2010), fine root biomass (e.g., Boone et al. 1998) and substrate availability (e.g., Gershenson et al. 2009) are also known to be important controls on the temperature response of belowground respiration in unmanaged ecosystems. Soils at our study sites are well-drained and volumetric soil water contents generally vary between 0.2 and 0.4 v/v. We believe that during most of the snow-free season, soil water contents are favorable for microbial respiration, with the possible exception of mid-summer in the spruce–birch forest, when soil water contents may reach levels low enough to slightly restrict respiration rates. It is very likely that soil temperature was such a good predictor of belowground respiration at our study sites because secondary controls on belowground respiration, such as fine root biomass and substrate availability, may be positively correlated with soil temperature. Although there was considerable overlap in the confidence intervals for our parameter estimates across the study sites, we feel that the most accurate estimates of seasonal and annual belowground respiration in future studies of different ecosystems will be obtained when the logistic model is first fit to direct measurements of respiration.

### Estimates of annual and seasonal C efflux

Our estimates of annual C efflux attributable to belowground respiration at the alpine ( $218 \text{ g C m}^{-2}$ ) and shrub ( $530 \text{ g C m}^{-2}$ ) sites are the only estimates we are aware of for these ecosystem types in Alaska. Our estimate of annual belowground respiration for the shrub site is very similar to our estimate for the sub-alpine forest site ( $543 \text{ g C m}^{-2}$ ) which, in turn, is within the range of estimates for evergreen and deciduous forests in interior Alaska ( $370\text{--}625 \text{ g C m}^{-2}$ ) (Schlentner and Van Cleve 1985; Gordon et al. 1985; Ruess et al. 2003; Vogel et al. 2005). Our estimate of annual belowground respiration for the spruce–birch forest ( $1,025 \text{ g C m}^{-2}$ ) is much higher than that for boreal forests in interior Alaska and is consistent with annual efflux from many temperate forests (Raich and Schlesinger 1992). Greater rates of belowground respiration in our forest sites than in forests of interior Alaska likely reflect differences in forest productivity and climate. Soil temperatures in interior Alaska may fall near or below the threshold for microbial activity at times during the winter while, in summer, belowground respiration may become limited by water availability, as observed for white spruce in the interior (Barber et al. 2000). The temperature regime of south-central Alaska is moderate in comparison with interior Alaska. Belowground respiration occurs at measurable levels throughout the snow-covered season in the spruce–birch forest (Sullivan et al. 2008) and moisture availability may be an important constraint only when soil temperatures are near their annual maxima.

In recent years, the winter C cycle of boreal ecosystems has received considerable attention (e.g., Winston et al. 1997; Wang et al. 2002; Vogel et al. 2005) and estimates of total belowground respiration during the snow-covered season range from  $22 \text{ g C m}^{-2}$  at the treeline in northwest Alaska (Sullivan 2009) to approximately  $60 \text{ g C m}^{-2}$  in black spruce forests of interior Alaska (Vogel et al. 2005) and a white spruce forest in northwest Alaska (Sullivan 2009). Our estimates for the shrub and forest sites are slightly greater than estimates for more continental boreal forest sites—an observation that is not surprising given the moderate winter climate of the Anchorage area, which is near the southern limit of the boreal forest in Alaska.

Although estimates of total belowground respiration during the snow-covered season in boreal ecosystems are increasingly available, few studies have made complementary measurements during the snow-free season. Wang et al. (2002) estimated that belowground respiration during the snow-covered season accounted for between 8 and 14% of annual belowground respiration in black spruce forests of Manitoba, while Vogel et al. (2005) reported very similar estimates of 7–15% for black spruce forests of interior Alaska. Our estimates agree very closely with these previous studies and range from 6% in the spruce–birch forest to 15% at the shrub site. Taken together, these estimates from a wide range of boreal ecosystems suggest that belowground respiration during the snow-covered season constitutes a small, but sensitive and potentially important, component of annual C budgets.

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