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Abstract

Ecosystem respiration is important because it is the small imbalances between CO_2 uptake via photosynthesis and CO_2 release by ecosystem respiration that determine the effect of the biosphere on atmospheric CO_2. For subalpine grasslands with mild winters we do not know the size of under-snow respiration relative to the total annual ecosystem respiration. This study determines the contribution of respiration through snow to total annual respiration, and models annual ecosystem respiration based on relationships with soil temperature and water content. Measurements were made monthly for two years in an unmanaged subalpine grassland in the Snowy Mountains of Australia. The vegetation is sparse (aboveground mass = 355–605 g m^{-2}, belowground mass = 570–1010 g m^{-2}) and dominated by native perennial C3 grasses and sedges. Ecosystem respiration was positively related to temperature, and there was some evidence that ecosystem respiration was more temperature sensitive at temperatures between 0 and 2 °C than at warmer temperatures. Annual ecosystem respiration was 12.1 Mg C ha^{-1} yr^{-1} in 2007/2008 and 10.5 Mg C ha^{-1} yr^{-1} in 2008/2009. Maximum daily rates of ecosystem respiration of 7 µmol CO_2 m^{-2} s^{-1} occurred during summer, while minimum rates occurred under snow cover and were 0.2 to 0.9 µmol CO_2 m^{-2} s^{-1}. The duration of permanent snow cover was 60–68 days (equivalent to 16–18% of the year) and ecosystem respiration under snow was 4.1 to 4.3% of annual ecosystem respiration, which is smaller than the 10–50% commonly reported from studies in areas with longer snow-covered periods.

Introduction

Net ecosystem exchange of CO_2 is determined by the balance between carbon uptake via photosynthesis and carbon loss via ecosystem respiration. Ecosystem respiration is important because it is the small imbalances between CO_2 uptake via photosynthesis and CO_2 release by ecosystem respiration that determine the effect of the biosphere on atmospheric [CO2]. Moreover, in many ecosystems it is ecosystem respiration that determines whether an ecosystem is a net source or sink for CO_2 (Cox et al., 2000; Janssens et al., 2001). This may be because abiotic factors (temperature, rainfall, etc.) have a larger effect on ecosystem respiration than gross primary productivity (Griffis et al., 2004; Morgenstern et al., 2004), although this is not necessarily always the case (Xia et al., 2009) and there is generally a close linkage between photosynthesis and soil respiration (Ekblad and Högberg, 2001).

Cool winter temperatures and snow are characteristics of many subalpine grasslands, but for subalpine grasslands in regions with mild winters we have little idea of the significance of ecosystem respiration over winter. From measurements in ecosystems with colder and longer winters there is substantial evidence that respiration continues beneath snow and this may be a significant contributor to annual C balance (Sommerfeld et al., 1993; Monson et al., 2006a, 2006b; Larsen et al., 2007). Measured instantaneous rates of CO_2 efflux for snow-covered ecosystems have been as slow as 0.02 µmol CO_2 m^{-2} s^{-1} in an arctic tundra (Jones et al., 1999) to much faster rates of 0.71–0.86 µmol CO_2 m^{-2} s^{-1} in a subalpine meadow (Liptzin et al., 2009) and 0.77 µmol

CO_2 m^{-2} s^{-1} in a temperate conifer forest (McDowell et al., 2000). The percentage of annual flux during the snow-covered season varies among studies from as little as 10–15% in cool-temperate deciduous forests in Japan (Mariko et al., 2000; Mo et al., 2005) and coniferous subalpine forest in Austria (Schindlbacher et al., 2007), to as much as 50% in tundra forest in Russia (Zimov et al., 1996). These trends among sites in the quantitative significance of respiration beneath snow suggest that the length of the snow-covered season would appear to be one of the main determinants of the percentage of annual flux during the snow-covered season.

The primary effect of snow on ecosystem respiration over winter is an indirect effect mediated by soil temperature. This is because snow insulates the soil (and low-statured plants such as grasses) against air temperatures (Monson et al., 2006b; Schindlbacher et al., 2007). Thus during winter months, snow moderates diurnal fluctuations in soil temperature and may eliminate freeze-thaw cycles (Larsen et al., 2007) and associated fluctuations in soil respiration (Schimel and Clein, 1996). During the beginning and middle of the snow-covered season, snow tends to keep soil warmer and respiration rates faster than would otherwise be the case, whereas in spring snow may keep the soil cooler and respiration rates slower than snow-free sites (Larsen et al., 2007).

Much of the research on respiration beneath snow has focused on high-latitude and/or high-altitude ecosystems of the northern hemisphere with mean winter air temperatures that are significantly below freezing (McDowell et al., 2000). We currently have no data on ecosystem respiration under snow for temperate subalpine C3 grasslands. In temperate grasslands, mean winter air temperatures are close to zero and thus snow may not cause a

large difference, on average, between air and soil temperatures—despite the insulating effect of snow buffering soil against large diurnal fluctuations in air temperature. It is also unclear if respiration beneath snow is also a major contributor to annual respiration given the short period of snow-cover in temperate grasslands.

This study quantifies ecosystem respiration in a temperate subalpine grassland in the Snowy Mountains of Australia. The vegetation is sparse and dominated by native perennial C3 grasses and sedges. Our aims were to determine the contribution of respiration through snow to total annual respiration. To meet this aim we measured ecosystem respiration every month for two years during the snow-free season and twice a year for two years during the snow-covered season. The effect of snow and respiration at low temperatures are of particular interest in the Snowy Mountains given that climate change projections for the region are for 0.2 to 1.0 °C increases in annual temperature by 2020, accompanied by a 5–30 day decrease in the duration of snow cover (Hennessy et al., 2003, 2008).

Materials and Methods

STUDY SITE

This study was conducted in a subalpine grassland in the Snowy Mountains of Australia (36°06′S; 148°32′E) at altitudes from 1500–1650 meters above sea level. The mean annual daily maximum temperature is 13 °C, while the mean annual daily minimum is 0.5 °C. Annual precipitation is in the order of 1200 mm. Snow depth and duration have not been scientifically quantified at the field site, but long-term observations suggest the mean duration of snow cover is 2–3 months, though this varies among years (e.g. from 10 days in 2006, to 3–4 months in 2000). The vegetation in the region is a mosaic of grassland, woodland with grassy understory, and woodland with shrubby understory.

All measurements in this study were made on subalpine grassland dominated by native perennial C3 grasses and sedges. The dominant C3 grasses are *Poa costiniana* (bog snow-grass) and *Poa hiemata* (soft snow-grass), which together have a cover abundance of approximately 50%. Less abundant C3 grasses include *Austrodanthonia alpicola* (crag wallaby-grass) and *Austrostipa nivicola* (alpine spear-grass). Common C3 sedges include *Carex incomitata* (hillside sedge) and to a lesser extent *Carex breviculmis* (common sedge-grass). During spring, summer, and autumn of the 2008/2009 season we quantified aboveground mass of plant material from destructive harvests of six replicate 100-cm² temporary plots, while belowground mass was determined from replicate 5-cm-diameter soil cores taken to a depth of 30 cm. The soil is a humic umbrosol (World Reference Base) derived from Silurian Mowomba granodiorite (approximately 433 ± 1.5 million years). Additional details on the soil can be found in Warren and Taranto (2010).

A weather station was established at the field site in May 2007 (4 months after the first measurements of CO_2 efflux). Volumetric soil water content was measured at depths of 30, 10, and 5 cm with a standing wave probe (MP 406, ICT International, Armidale, Australia), and soil temperature was measured at the same depths with a type-T thermocouple. Data were stored as half-hourly averages on a data logger (Smart Logger, ICT International). Continuous and unbroken water content data were available, but there were several periods in which soil temperature data were unavailable. Where possible, data were filled based on relationships with soil temperature measured at another depth. In cases where data were unavailable for several months, they are not presented. The duration of snow cover was determined from soil temperature at 5 cm and checked by direct observation.

MEASUREMENT OF ECOSYSTEM RESPIRATION

Measurements of ecosystem respiration were made approximately every month from February 2007 to May 2009. Measurements were less frequent in winter because roads were not cleared of snow and thus vehicular access was impossible. Nevertheless, in both years there were two measurement campaigns during the snow-covered periods. Different experimental designs (and respiration systems) were used in the snow-free and snow-covered periods.

During the snow-free period, measurements were made at 6 (or in some cases 9) permanently installed collars. Collars were distributed over an area of approximately 1 km². At each of the collars we measured respiration before dawn, between 11 a.m. (11:00) and 2 p.m. (14:00), and after dusk because of the possibility of diurnal variation in respiration. In approximately one-third of cases we had to omit pre-dawn measurements due to condensation or poor weather affecting gas exchange measurements. A custom-built closed gas exchange system with an area of 3600 cm² was used during the snow-free period so as to maximize the measurement area and 'signal' due to respiration (Fig. 1). The system comprised a 600 × 600 × 600 mm Perspex box covered in double-sided reflective insulation that fitted inside stainless steel collars made of 25 × 25 mm stainless steel angle that were driven into the ground 10–20 mm. The Perspex box was sufficiently tall to completely enclose but not disturb the low-statured vegetation (height typically <30 cm). The collars caused minimal disturbance to soils, plants, and microclimate because of their small size and very low profile. To make measurements, an open-path IRGA (LI-7500, Li-Cor Inc., Lincoln, Nebraska, U.S.A.) attached to a metal spike was inserted into the center of the measurement plot and a separate metal spike with a fan was inserted midway between the LI-7500 and edge of the frame. Then the Perspex box was interfaced with the metal collar and left there for the duration of the measurement (30–90 seconds depending on rates of efflux). The metal spike that held the LI-7500 also held a type-T thermocouple, while a separate metal spike held a small computer fan to ensure adequate mixing. The metal spike with LI-7500 was always inserted into the same hole to minimize disturbance, but this was not necessary with the other metal spike because its very narrow diameter of 2.0 mm resulted in negligible disturbance. Data were collected as 1-second averages on a datalogger (CR800, Campbell Scientific, Logan, Utah, U.S.A.). The system was ventilated to avoid pressure gradients by way of a 1-cm-diameter semicircular hole at the base of the Perspex box that also served as the entry point for communication and power cables. Preliminary measurements and leak checking with elevated CO_2 showed that this ventilation hole did not permit entry of external air.

The difficulty of accessing the site over winter necessitated use of a smaller more portable system, in our case a LI-8100 (Li-Cor Inc., Lincoln, Nebraska, U.S.A.) with a 20-cm-diameter chamber and 'snowshoe' to allow measurement of CO_2 efflux directly from the snow surface (McDowell et al., 2000). The 20-cm-diameter chamber of the LI-8100 chamber has pressure vents to prevent pressure gradients. We did not use permanent collars or make diurnal measurements. Instead, measurements were made 2–3 times between 10 a.m. (10:00) and 3 p.m. (15:00) at each of 6 to 9 randomly chosen locations in the general vicinity of the permanent collars. Diurnal measurements were not made over winter due to logistic difficulties. We do not regard this as a limitation because there should be minimal diurnal variation in respiration because
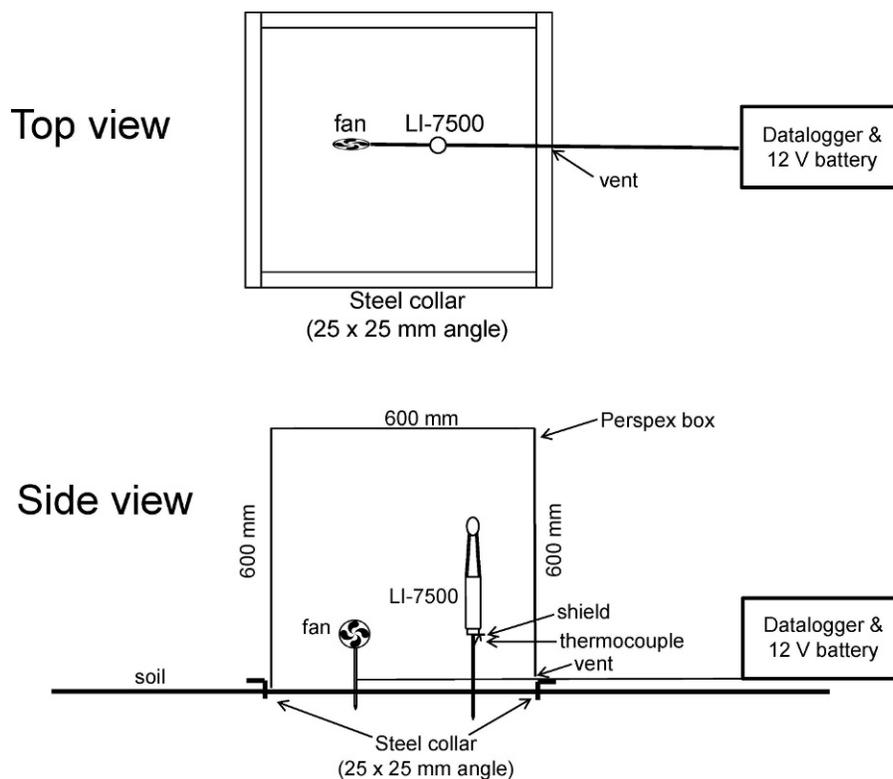
FIGURE 1. Schematic diagram of the custom-built closed gas exchange system used for measuring CO_2 efflux during the snow-free period. Diagram is not to scale and some details have been omitted for clarity.

the insulating snow cover largely eliminates diurnal variation in plant and soil temperature. To make measurements, the chamber of the LI-8100 was seated on top of a 20-cm-diameter collar of PVC pipe that was built into a 30 cm × 50 cm snowshoe of heavy plastic mesh (akin to the design of McDowell et al., 2000). The snowshoe was necessary to minimize disturbance of the snow surface and spread the LI-8100 chamber's weight over a large area. To further reduce changes in through-snow gas diffusion, human disturbance of snow was minimized by wearing cross country skis and not getting closer than 0.6 m to the chamber. Respiration measurements were made using normal protocols for the LI-8100 instrument, viz., maximum flow rate, 120-second chamber closure.

Calculations of rates of CO_2 efflux were similar for the two gas exchange systems. In both systems CO_2 efflux was corrected for dilution by water vapor, a 10–30 second "dead-band" was applied until mixing was achieved, and efflux was estimated from the *initial* rate of CO_2 increase as a function of time. Note that linear regression was not used in either system because CO_2 efflux decreases over time and there is no "linear portion." This non-linearity arises because the rise in chamber CO_2 serves to decrease the diffusional flux of CO_2 from soil (Davidson et al., 2002). Comparison of linear and *initial* (i.e. non-linear) estimates showed that linear regression underestimates CO_2 efflux by 3–6%. In the case of the LI-8100, CO_2 efflux was calculated using a 15- to 30-second dead band (determined visually) and the manufacturer's standard non-linear equations. With the custom 60 × 60 cm system, the dead band was determined visually (typically 10–20 seconds) and then second-order polynomials were fitted to CO_2 and H_2O concentrations as a function of time for 30–45 seconds (mean R^2 for CO_2 and H_2O = 0.98, n = 715). Instantaneous rates of change were calculated as derivatives of the second-order polynomial fits. The correction of CO_2 efflux for dilution by water vapor was calculated as the dry CO_2 concentration multiplied by the rate of evapotranspiration. Data from the two gas exchange systems are considered to be directly comparable given that they were calculated similarly (i.e. both were corrected for evapotrans-

piration and are based on initial rates of change). Furthermore, in both systems the increase in CO_2 concentrations inside the chamber during measurements was similarly small (generally 5–10 µmol mol^{-1} using the LI-8100 for a 2-minute measurement during winter, and 5–15 µmol mol^{-1} using the custom chamber for a 30–45 second measurement during summer). The similarity of the two systems is supported by side-by-side comparison of the two gas exchange systems in summer, when fluxes were large, and late autumn, when fluxes were small. In both tests, CO_2 efflux did not differ between systems (C. Warren, unpublished data).

EFFECT OF SNOW ON CO_2 EFFLUX AT SATELLITE SITES

Additional measurements were made at a satellite field site to investigate the effect of spatial variation in snow cover on CO_2 efflux. At the satellite sites we used the same LI-8100 system at snow-free and snow-covered sites, thereby eliminating the possibility that the effect of snow is due to use of different chambers. At the satellite site, which was 2 km from the main field site, there was large spatial variation in snow depth, and the pattern of snowmelt due to the presence of scattered trees 30–50 m upwind. This meant that during the spring snow melt it was possible to measure CO_2 efflux of sites with 30 cm of snow and contrast these with snow-free sites only 20 m away. CO_2 efflux and soil temperature were measured at 6 snow-covered and 6 snow-free locations over two days during September 2007. To measure soil temperature under snow it was necessary to dig a small hole in the snow to insert the LI-8100's thermocouple probe. This was not done until after CO_2 efflux had been measured so as to minimize possible effects on gas diffusion and efflux estimates.

STATISTICS

To enable annual modeling of CO_2 efflux we related individual measurements of CO_2 efflux to the nearest half-hour

C. R. WARREN AND M. T. TARANTO / 139

average of soil temperature and/or water content. Stepwise regression was used to find the best subset of predictors. It was necessary to natural log transform the CO_2 efflux to avoid problems with heteroscedasticity. Data were stratified according to soil temperature at 5 cm owing to different temperature responses above and below 2 °C. The 2 °C threshold approximately coincides with the presence/absence of snow, but the threshold was determined *a posteriori* based on the measured temperature response (see results). The best model was:

For $T_5 \geq 2°C$,

$$\ln(y) = -0.984 + 0.114 * T_{10} + 0.026 * water_{30}, \ R^2 = 0.78, \ n = 627 \tag{1}$$

For $T_5 < 2°C$,

$$\ln(y) = -2.015 + 1.171 * T_5, \ R^2 = 0.61, \ n = 60 \tag{2}$$

where y is daily average CO_2 efflux (µmol CO_2 m^{-2} s^{-1}), T_5 is daily average soil temperature at 5 cm (°C), T_{10} is daily average soil temperature at 10 cm (°C), $water_{30}$ is daily average volumetric water content at 30 cm. Equations (1) and (2) and the continuous records of daily average soil temperature and soil water content were used to estimate daily CO_2 efflux. Daily CO_2 efflux was summed to obtain annual CO_2 efflux.

To examine if there was diurnal variation in rates of CO_2 efflux we used an ANOVA comparing pre-dawn, mid-day, and post-dusk measurements. Temporal variation in dry mass was also examined with ANOVA. All statistics were performed with SPSS (release 16.0.1, SPSS Inc., Chicago, Illinois, U.S.A.).

Results

PLANT DRY MASS AND CLIMATE

Aboveground dry mass of plants varied from a minimum of 355 ± 70 g m^{-2} (mean ± SE, $n = 6$) in spring to a maximum of 605 ± 58 g m^{-2} in summer. Belowground dry mass of plants varied from a minimum of 570 ± 36 g m^{-2} in spring to a maximum of 1010 ± 110 g m^{-2} in summer. For both above- and belowground material, dry mass increased from spring to summer and then decreased in autumn. Dry mass was not quantified during winter, but we know from observations of grasses and sedges immediately following snowmelt that they survive underneath snow cover (i.e. there is likely substantial dry mass during winter).

Over the two seasons for which weather data were available, the absolute maximum air temperature was 31 °C while the absolute minimum was −13 °C (Fig. 2). Air temperature at the site was characterized by a distinct seasonality and large variation between days. Daily minima were below freezing for 9–10 months of the year, whereas daily maxima generally remained above zero (3 days with subzero maxima in 2007, 4 days with subzero maxima in 2008). There were 60 days of snow cover in 2007 and 68 in 2008. In both years the maximum snow depth was around 40 cm (C. Warren, personal observation).

Soil temperatures followed a similar annual pattern as air temperature (Fig. 2). During the periods of snow cover there was <0.4 °C diurnal variation in soil temperature at 5 cm, whereas in the snow-free periods soil temperature at 5 cm varied diurnally by up to 25 °C (data not shown). Soil water content was consistently 30–40% (volumetric) from April to October, whereas from early November to late March there were several periods when liquid water content was reduced to 10% or less (Fig. 2). In general
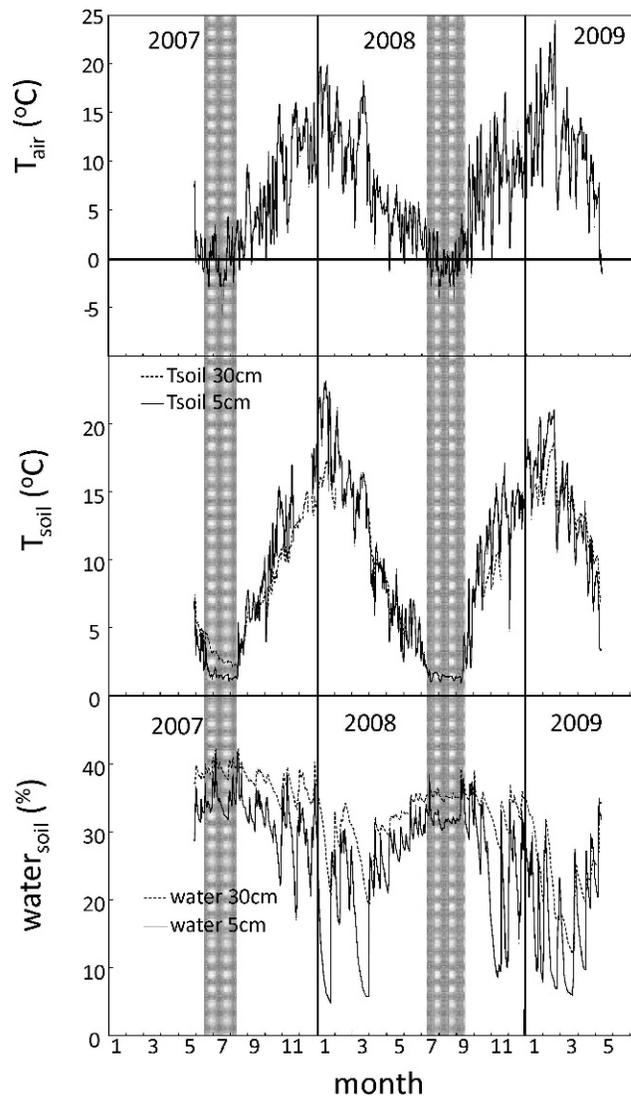

FIGURE 2. Daily average air temperature (T_{air}), soil temperature (T_{soil}), and soil water content ($water_{soil}$) measured for 2 years at a subalpine grassland in the Snowy Mountains. The shaded area denotes the period of permanent snow cover (as indicated by patterns of soil temperature and confirmed by direct observation). Data were collected as half-hourly averages. Soil temperature and water content were measured at depths of 5, 10, and 30 cm, but 10 cm has been omitted for clarity. Note that soil temperature data at 30 cm are missing for some periods.

terms, the 2007/2008 season was characterized by warmer soils with higher water content, while 2008/2009 had cooler and drier soils (Table 1).

SEASONAL VARIATION IN ECOSYSTEM RESPIRATION

There was no evidence for diurnal variation in ecosystem respiration (CO_2 efflux at pre-dawn vs. mid-day vs. post-dusk, ANOVA; $F (2, 656) = 2.52$; $P = 0.08$), and thus all data are subsequently presented as daily averages. CO_2 efflux varied seasonally in the same way as soil temperatures (compare Figs. 2 and 3). The maximum CO_2 efflux of 6–7 µmol CO_2 m^{-2} s^{-1} was measured during summer. In winter under snow cover, CO_2 efflux was 0.7 to 0.9 µmol CO_2 m^{-2} s^{-1} on three of the measurement campaigns, while on one measurement campaign CO_2 efflux was considerably slower at 0.2 µmol CO_2 m^{-2} s^{-1}. The over-winter

TABLE 1

Annual averages of soil temperature and soil water content for the 2007/2008 and 2008/2009 seasons. Soil temperature data are shown for 10 cm ($T_{soil10cm}$) and 5 cm ($T_{soil5cm}$). Data were also collected at 30 cm but averages could not be calculated due to lengthy periods of missing data. The volumetric water content of soil was measured at 30 cm (water$_{30cm}$), 10 cm (water$_{10cm}$) and 5 cm (water$_{5cm}$).

Season	$T_{soil10cm}$ (°C)	$T_{soil5cm}$ (°C)	water$_{30cm}$ (%)	water$_{10cm}$ (%)	water$_{5cm}$ (%)
May 2007–2008	9.60	9.94	34.3	30.3	27.2
May 2008–2009	9.49	9.23	30.3	28.1	24.0

campaign with slow efflux was at the end of a cold week (air temperature minima from −8 to −11 °C) and was characterized by the coldest daily mean soil temperature at 5 cm of 0.43 °C.

Stepwise regression was used to model daily average CO_2 efflux based on daily averages of soil temperature and water content. Ecosystem respiration was positively related to temperature (Fig. 4). At temperatures <2 °C, the temperature response of CO_2 efflux was steeper than the response at warmer temperatures. This is supported by the observation that models of annual ecosystem respiration with a single temperature response function overestimated ecosystem respiration at temperatures less than 2 °C (dashed line in Fig. 3). In contrast, models with separate temperature response functions ($\geq$2 °C vs. <2 °C) were closer to measured ecosystem respiration over winter (solid line in Fig. 3). Use of a model with one or two temperature response functions affected estimates of average CO_2 efflux underneath snow cover. With two temperature response functions, CO_2 efflux underneath snow cover averaged 0.069 mol CO_2 m^{-2} day^{-1} CO_2 in 2007 and 0.055 mol CO_2 m^{-2} day^{-1} in 2008 (Table 2), while with a single temperature response function estimates were 33–50% higher at 0.098 mol CO_2 m^{-2} day^{-1} CO_2 in 2007 and 0.092 mol CO_2 m^{-2} day^{-1} in 2008 (data not shown). Models that did not include water content gave poorer R^2 due to

overprediction of efflux in summer and autumn by failing to account for limitations due to dry soil (data not shown). The model with two separate temperature responses had an R^2 of 0.78 and was, on average, an accurate predictor of the measured CO_2 efflux with a 1:1 relationship between modeled and measured CO_2 efflux (Fig. 5).

Using the model with two temperature response functions, the modeled annual CO_2 efflux was around 10% greater in 2007/2008 (12.1 Mg C ha^{-1} yr^{-1}) than in 2008/2009 (10.5 Mg C ha^{-1} yr^{-1}) (Table 2). Smaller CO_2 efflux in 2008/2009 was largely due to slower efflux in February, March, and April due to water limitations (Figs. 2 and 3). Measured and modeled rates of CO_2 efflux under snow cover were roughly 20 times slower than peak rates during summer (Table 2), yet still made a significant contribution to annual CO_2 efflux. In 2007 there were 60 days of snow cover (16% of the year) and this contributed 4.1% of annual CO_2 efflux; in 2008 there were 68 days of snow cover (18% of the year) and this contributed 4.3% of annual CO_2 efflux. The model with a single temperature response function led to larger estimates of the proportion of CO_2 efflux under snow cover, but these were still a small fraction of annual efflux (5.9% in 2008, 7.1% in 2009). The sharp approximate 3 °C rise in soil temperature upon snowmelt (Fig. 2) led to a twofold increase in modeled CO_2 efflux (Fig. 3).

EFFECT OF SNOW ON CO_2 EFFLUX AT A SATELLITE FIELD SITE

Additional field measurements at a satellite site were made to investigate further the predicted sharp rise in temperature and CO_2 efflux upon snow melt. CO_2 efflux was measured at sites with 30 cm of snow and contrasted with nearby snow-free sites. To eliminate the possibility that differences between snow-free and snow-covered measurements reflect different gas exchange systems, at the satellite sites we quantified CO_2 efflux with the LI-8100 gas exchange system. Observations suggested snow at the snow-free sites had melted 5–10 days earlier. Soil at the snow-covered sites (0.83 ± 0.02 °C; mean ± SE, $n = 6$) was significantly cooler than at the snow-free sites (1.6 ± 0.2 °C; mean ± SE, $n = 6$). CO_2 efflux at the snow-covered sites (0.63 ± 0.04 μmol CO_2 m^{-2} s^{-1}; mean ± SE, $n = 6$) was approximately half the rate of CO_2 efflux at the snow-free sites (1.3 ± 0.1 μmol CO_2 m^{-2} s^{-1}; mean ± SE, $n = 6$).

Discussion

HOW DOES ECOSYSTEM RESPIRATION IN A SUBALPINE GRASSLAND COMPARE WITH OTHER ECOSYSTEMS?

Measured and modeled maximum rates of ecosystem respiration in this study were broadly similar to those reported from other temperate C3 grasslands. In this study the maximum average daily ecosystem respiration that was measured was around 7 μmol CO_2 m^{-2} s^{-1}, while the model predicted rates as high as 8 μmol CO_2 m^{-2} s^{-1} during brief warm periods with
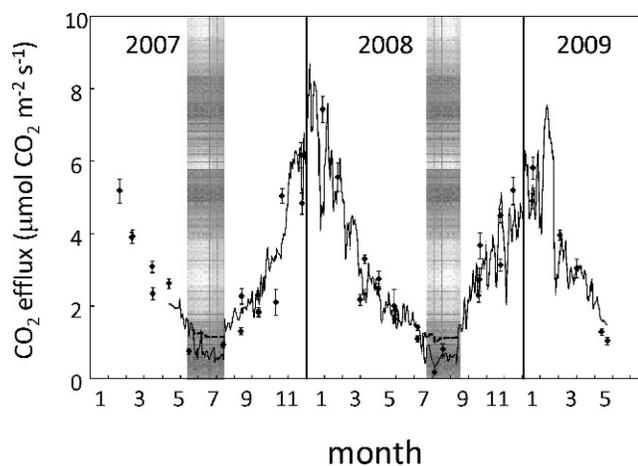

FIGURE 3. Daily average CO_2 efflux measured at a subalpine grassland. During the snow-free period, CO_2 efflux was measured at each of 6 (or 9) permanent collars on a minimum three occasions per day: before dawn, between 11 a.m. (11:00) and 2 p.m. (14:00), and after dusk ($n = 3$–6 per day). Measurements of over-snow CO_2 efflux were made 3 or 4 times between 10 a.m. (10:00) and 3 p.m. (15:00) at each of 6 randomly chosen locations in the vicinity of the permanent soil collars. Error bars are SE. The solid line is the modeled daily average of CO_2 efflux calculated from equations (1) and (2) using separate temperature responses above and below 2 °C. For comparative purposes we have shown daily average of CO_2 efflux calculated using a single temperature response for all temperatures (dashed line visible only during snow-covered period). CO_2 efflux could not be modeled between February and May 2007 because we did not have access to soil temperature or water content.
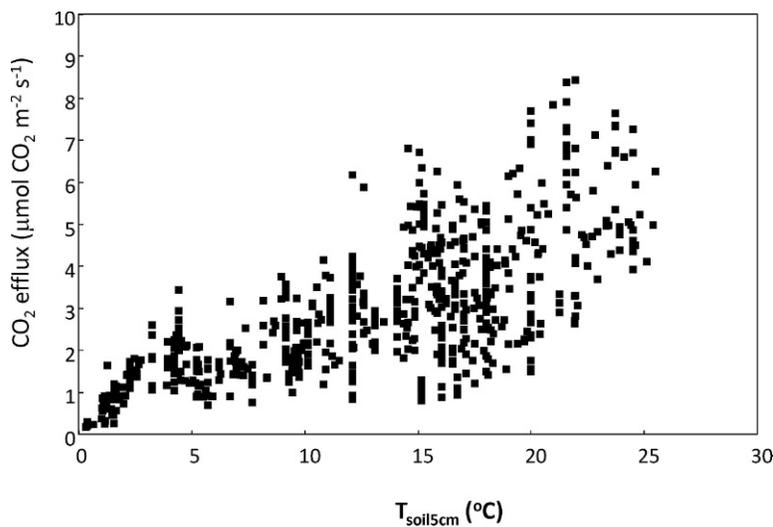
C. R. WARREN AND M. T. TARANTO / 141

FIGURE 4. The response of CO_2 efflux to temperature of soil at 5 cm. CO_2 efflux was measured approximately every month for 2 years at a subalpine grassland in the Snowy Mountains. Data are individual measurements.

adequate soil moisture (Fig. 3). This is within the range of daily maxima of 5–9~ $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for a temperate C3 grassland in Canada (Flanagan and Johnson, 2005), 7 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for a temperate steppe grassland in Mongolia (Nakano et al., 2008), 4–6 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ reported for a temperate steppe grassland in China (Xia et al., 2009), 3–14 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for a range of mountain grasslands in Europe (Wohlfahrt et al., 2008), and 2–9 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ for grasslands in Yosemite National Park (Risch and Frank, 2007). Annual ecosystem respiration in our study was in the order of 10–12 Mg C $ha^{-1}\ yr^{-1}$, which is smaller than the range of 18–60 Mg C $ha^{-1}\ yr^{-1}$ reported for 20 European grasslands (Gilmanov et al., 2007), similar to 13 Mg C $ha^{-1}\ yr^{-1}$ reported for a warm temperate C3 grassland (Novick et al., 2004), but several times greater than the 2.5–3 Mg C $ha^{-1}\ yr^{-1}$ reported for a cool temperate grassland in Canada (Flanagan et al., 2002).

An emerging trend from the literature is that ecosystem respiration is highly sensitive to interannual variability in climate (e.g. Flanagan et al., 2002; Nagy et al., 2007). For example, in a managed grassland in Hungary ecosystem respiration was 30% greater in a wet year than a dry year (Nagy et al., 2007), while ecosystem respiration was 50% greater in wet than dry years in grasslands in Canada (Flanagan et al., 2002; Flanagan and Johnson, 2005) and China (Xia et al., 2009). In the present study, ecosystem respiration was around 15% greater in the (comparatively) warm and wet 2007/2008 season than in the cooler and dryer 2008/2009 season. These large interannual differences in ecosystem respiration may have important implications for ecosystem C balance (Flanagan et al., 2002; Hunt et al., 2004). For example, variation in ecosystem respiration was at least partially responsible for a temperate grassland in New Zealand switching between being a net source of CO_2 in a dry year to a net sink in a wet year (Hunt et al., 2004), and similar results have been reported from other grasslands (Sims and Bradford, 2001; Flanagan et al., 2002) and forests (e.g. van Gorsel et al., 2008).

There was no evidence for diurnal variation in ecosystem respiration at our temperate grassland, which is at odds with results from some studies. For example, Flanagan and Johnson (2005), working in a temperate grassland, found that ecosystem respiration was approximately twice as fast in the early afternoon as at night. Such diurnal variation may be related to diurnal variation in temperature and/or photosynthate production (Craine et al., 1998). The absence of diurnal variation in our study may be because the bulk of ecosystem respiration is from soil respiration (e.g. 85% in a similarly sparse temperate grassland [Hunt et al., 2004]), and soil respiration is somewhat decoupled from air temperature due to the large thermal mass of soil and distribution of roots and microbes across a range of depths.

Ecosystem respiration was positively related to temperature (Fig. 4), as has been observed in numerous other studies (Flanagan and Johnson, 2005; Davidson and Janssens, 2006; Davidson et al., 2006). An interesting aspect of the temperature response is that ecosystem respiration was more temperature sensitive at temperatures between 0 and 2 °C than at warmer temperatures (Fig. 4). The limited range of soil temperature measurements below 2 °C and (relatively) poorer precision of measurement is problematic, yet it is doubtful that this led to the anomalously high temperature sensitivity given that similarly high temperature sensitivity has been observed in studies using different techniques and with larger temperature ranges (Mikan et al., 2002; Elberling and Brandt, 2003; Öquist et al., 2009). It seems improbable that the explanation is due to partial freezing and water limitation (Öquist et al., 2009) given that soil temperature at 5 cm was never below 0 °C. The cause may instead be related to changing patterns of substrate use and/or microbial populations

TABLE 2

Modeled CO_2 efflux on an annual basis and for the snow-covered periods. CO_2 efflux was modeled from continuous measurements of soil temperature and water content using equations (1) and (2).

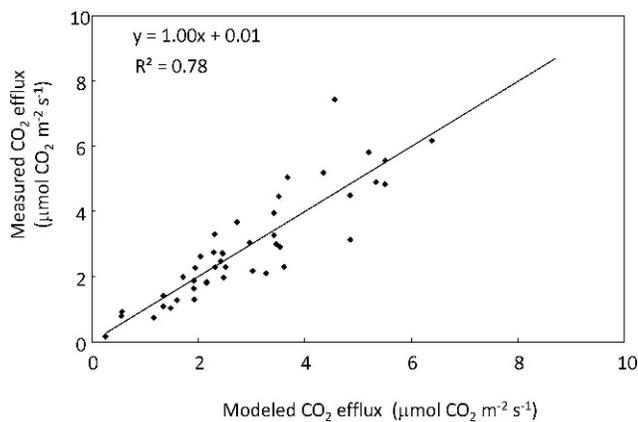| | Annual | | Snow-covered period | | |
| | Cumulative CO_2 efflux | Average CO_2 efflux | Snowcover duration | Cumulative CO_2 efflux | Average CO_2 efflux |
Season	(mol $CO_2\ m^{-2}\ yr^{-1}$)	(mol $CO_2\ m^{-2}\ day^{-1}$)	(days)	(mol $CO_2\ m^{-2}$)	(mol $CO_2\ m^{-2}\ day^{-1}$)
May 2007–2008	100.6	0.27	60	4.16	0.069
May 2008–2009	87.5	0.24	68	3.79	0.055

FIGURE 5. The relationship between daily average CO_2 efflux modeled from equations (1) and (2) and measured daily average CO_2 efflux. See Figure 3 and Materials and Methods section of the text for further details.

(e.g. Schadt et al., 2003; Schimel and Mikan, 2005; Schmidt et al., 2009), but this remains to be tested.

ECOSYSTEM RESPIRATION BENEATH SNOW

Significant ecosystem respiration was measured under snow (Table 2, Fig. 3), which is consistent with a growing body of evidence that respiration continues beneath snow (Sommerfeld et al., 1993; Zimov et al., 1996; Jones et al., 1999; Mariko et al., 2000; McDowell et al., 2000; Grogan et al., 2001; Grogan and Jonasson, 2005; Mo et al., 2005; Monson et al., 2006a, 2006b; Larsen et al., 2007; Liptzin et al., 2009). Measured rates of ecosystem respiration under snow were between 0.2 and 0.9 µmol CO_2 m^{-2} s^{-1}, which spans most of the previously reported range for *soil* respiration under snow (Jones et al., 1999; McDowell et al., 2000; Hubbard et al., 2005; Monson et al., 2006a; Liptzin et al., 2009).

While rates of respiration under snow were similar to previous reports, under-snow respiration was a smaller fraction of annual respiration than previously reported. In alpine and subalpine ecosystems of the northern hemisphere, under-snow respiration is commonly 10–20% of annual respiration (Brooks et al., 1996, 1997; Mariko et al., 2000; McDowell et al., 2000; Mo et al., 2005; Monson et al., 2006a; Schindlbacher et al., 2007), but may be as high as 30% (subalpine meadow in Colorado [Liptzin et al., 2009]), or even 50% (tundra forest in Russia [Zimov et al., 1996]). In the present study, under-snow ecosystem respiration was estimated to be 4.1–4.3% of annual ecosystem respiration using a model with two temperature response functions (Table 2) or 5.9–7.1% using one temperature response function (data not shown). Hence, under-snow respiration is a small fraction of annual respiration irrespective of how it is modeled. The primary reason that under-snow respiration is a smaller fraction of annual respiration is that the duration of snow cover (60–68 days in the two years of this study) is shorter than in previous studies.

At the temperate grassland with its mild winters the presence of snow had a modest effect on *average* soil temperatures. For example, average daily air temperatures during mid-winter were around 0 °C while soil temperature at 5 cm were somewhat warmer at 0.5–2 °C, while in the 10 days before snowmelt daily air temperature was 1.7 °C and soil temperature was 1.3 °C. By inference, the effect of snow would increase respiration over winter, but reduce it in spring. This is supported by the dramatic increases in soil temperature and ecosystem respiration when snow melts (Figs. 2 and 3), and results from the satellite site which

showed areas with delayed snowmelt had slower ecosystem respiration than snow-free sites. What is likely more important than the modest effect of snow on average soil temperatures is that snow eliminated freeze-thaw cycles (Larsen et al., 2007) and associated fluctuations in soil respiration (Schimel and Clein, 1996), which would otherwise occur almost nightly during winter.

CLIMATE CHANGE

Climate change projections for the Snowy Mountains of Australia are for increases in annual temperature by 2020 of 0.2 to 1.0 °C and a decrease in snow cover of 5 to 30 days (Hennessy et al., 2003, 2008). These climate change projections are supported by historical analyses of snow depth at four alpine sites from 1957 to 2002 that indicated we have already experienced a decline in maximum snow depths at 3 (of 4) sites and a moderate decline in mid- to late-season snow depth (August to September). These trends probably reflect mid- to late-season snow depth being determined by temperature-dependent ablation (melt and evaporation), whereas the depth of early-season snow is determined by precipitation (Hennessy et al., 2003, 2008). Irrespective of the size of changes and their cause, decreases in the duration of snow cover will affect ecosystem respiration. The presence/absence of snow will have a rather modest effect on daily *average* soil temperatures due to mild winter temperatures. The most significant effect of decreased duration of snow cover would be an increase in freeze-thaw cycles and greater day-to-day variability in temperature. Increased freeze-thaw cycles would probably increase ecosystem respiration (Schimel and Clein, 1996).

LIMITATIONS OF THE STUDY

Quantifying CO_2 efflux from snow-covered surfaces with chamber methods (e.g. this study; Mariko et al., 2000; McDowell et al., 2000; Grogan et al., 2001; Grogan and Jonasson, 2005; Mo et al., 2005; Larsen et al., 2007; Schindlbacher et al., 2007) suffers from all of the problems that afflict conventional measurements of respiration from snow-free surfaces (e.g. Davidson et al., 2002). However, these problems are compounded by slow fluxes and the complication of diffusion of CO_2 through snow. In some studies snow has been removed and respiration measured directly on the soil surface (e.g. McDowell et al., 2000; Grogan et al., 2001; Grogan and Jonasson, 2005; Larsen et al., 2007), whereas in the present study and others respiration has been measured from the snow surface with minimal disturbance of the snow profile (e.g. McDowell et al., 2000; Mo et al., 2005; Schindlbacher et al., 2007). Measurements involving snow removal tend to overestimate CO_2 efflux due to lateral diffusion of CO_2 into the excavation pit (McDowell et al., 2000), while measurements from the snow surface may underestimate CO_2 efflux if there are ice layers that impede diffusion of CO_2. Given that we made measurements from the soil surface it is possible that CO_2 efflux was underestimated, though the extent of this problem is unknown and cannot be determined without use of multiple independent methods.

We minimized the problem of CO_2 building up in the chamber headspace and affecting diffusion gradients (as discussed by Schindlbacher et al., 2007) primarily by use of a non-linear model to estimate the initial rate of efflux (see materials and methods) and also by keeping the duration of measurements short so that CO_2 concentration never increased by more than 10 µmol mol^{-1}. We also ensured accurate estimation of CO_2 efflux by quantifying the flux of H_2O vapor and correcting for its dilution of CO_2. Analyses of a subset of data showed that

C. R. WARREN AND M. T. TARANTO / 143

calculation of CO_2 efflux with a linear model underestimated true CO_2 efflux (i.e. non-linear initial efflux) by 3–6%, while CO_2 efflux was underestimated by another 2–10% if the correction for dilution by H_2O was omitted. Hence, calculated CO_2 efflux may vary by as much as 15% depending on assumptions made during calculations.

CO_2 efflux from snow-covered surfaces has been measured in other ecosystems by the largely independent method of quantifying the gradient in CO_2 concentration through the snow pack (e.g. Sommerfeld et al., 1993; Zimov et al., 1996; McDowell et al., 2000; Schindlbacher et al., 2007). We did not attempt diffusional estimates of CO_2 efflux at our field site because mild winter temperatures, frequent freeze-thaw cycles, and occasional rain result in a highly layered snow pack. As a consequence, the diffusional method would require measurements of CO_2 concentration and snow properties at higher spatial resolution than was feasible. Nevertheless, studies in other ecosystems (presumably with different snow conditions) have reported strong relationships between chamber and diffusional estimates of CO_2 efflux, which lends qualified support to the accuracy of data. Unfortunately, the precise relationship between diffusional and chamber estimates of CO_2 efflux differ among studies so it is not possible to apply a "correction factor" to convert between methods. In some studies diffusional estimates of CO_2 efflux have been higher than estimates from chambers (Mast et al., 1998; Schindlbacher et al., 2007); in another study diffusional and chamber estimates were similar (McDowell et al., 2000). This inconsistency among studies almost certainly reflects differences between studies in snow conditions, apparatus, and assumptions that bias comparisons between methods.

A major limitation of our study is the limited temporal resolution of measurements, especially over the winter months in which we had only two snow-covered measurements per year (Fig. 3). As a consequence, we have little information on the temporal pattern of CO_2 efflux over winter (e.g. Liptzin et al., 2009) and this may have biased estimates of CO_2 efflux over winter. During the snow-free months our measurements may not have captured respiration pulses that occur following rainfall (Jarvis et al., 2007). However, we do not believe respiration pulses during the snow-free months would have a large effect on estimates of annual CO_2 efflux given that an irrigation experiment at the same sites found that respiration rates were tripled by irrigation but for 24 hours only (C. Warren and M. Taranto, unpublished data).

Conclusions

Studies from cold northern hemisphere ecosystems have highlighted the role of snow in keeping soils (and low-statured plants) warm over winter and permitting relatively fast rates of respiration (Sommerfeld et al., 1993; Monson et al., 2006a, 2006b). The present study adds a useful extra dimension by showing that in a region with a mild winter there is also quantifiable ecosystem respiration underneath snow. A point of difference among ecosystems is that the contribution of under-snow respiration to total annual respiration varies enormously. At our rather mild site with a short duration of snow cover, under-snow ecosystem respiration was 4.1–4.3% of annual ecosystem respiration, which is less than the 10–50% reported for ecosystems with longer winters. These trends in the quantitative significance of under-snow respiration are consistent with the idea that under-snow respiration is more important in areas with a longer duration of snow cover.

References Cited

Brooks, P. D., Williams, M. W., and Schmidt, S. K., 1996: Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry*, 32: 93–113.

Brooks, P. D., Schmidt, S. K., and Williams, M. W., 1997: Winter production of CO_2 and N_2O from Alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia*, 110: 403–413.

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J., 2000: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, 408: 184–187.

Craine, J. M., Wedin, D. A., and Chapin, F. S., 1998: Predominance of ecophysiological controls on soil CO_2 flux in a Minnesota grassland. *Plant and Soil*, 207: 77–86.

Davidson, E. A., and Janssens, I. A., 2006: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440: 165–173.

Davidson, E. A., Savage, K., Verchot, L. V., and Navarro, R., 2002: Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology*, 113: 21–37.

Davidson, E. A., Janssens, I. A., and Luo, Y. Q., 2006: On the variability of respiration in terrestrial ecosystems: moving beyond Q(10). *Global Change Biology*, 12: 154–164.

Ekblad, A., and Högberg, P., 2001: Natural abundance of C-13 in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia*, 127: 305–308.

Elberling, B., and Brandt, K. K., 2003: Uncoupling of microbial CO_2 production and release in frozen soil and its implications for field studies of arctic C cycling. *Soil Biology & Biochemistry*, 35: 263–272.

Flanagan, L. B., and Johnson, B. G., 2005: Interacting effects of temperature, soil moisture and plant biomass production on ecosystem respiration in a northern temperate grassland. *Agricultural and Forest Meteorology*, 130: 237–253.

Flanagan, L. B., Wever, L. A., and Carlson, P. J., 2002: Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology*, 8: 599–615.

Gilmanov, T. G., Soussana, J. E., Aires, L., Allard, V., Ammann, C., Balzarolo, M., Barcza, Z., Bernhofer, C., Campbell, C. L., Cernusca, A., Cescatti, A., Clifton-Brown, J., Dirks, B. O. M., Dore, S., Eugster, W., Fuhrer, J., Gimeno, C., Gruenwald, T., Haszpra, L., Hensen, A., Ibrom, A., Jacobs, A. F. G., Jones, M. B., Lanigan, G., Laurila, T., Lohila, A., Manca, G., Marcolla, B., Nagy, Z., Pilegaard, K., Pinter, K., Pio, C., Raschi, A., Rogiers, N., Sanz, M. J., Stefani, P., Sutton, M., Tuba, Z., Valentini, R., Williams, M. L., and Wohlfahrt, G., 2007: Partitioning European grassland net ecosystem CO_2 exchange into gross primary productivity and ecosystem respiration using light response function analysis. *Agriculture Ecosystems & Environment*, 121: 93–120.

Griffis, T. J., Black, T. A., Gaumont-Guay, D., Drewitt, G. B., Nesic, Z., Barr, A. G., Morgenstern, K., and Kljun, N., 2004: Seasonal variation and partitioning of ecosystem respiration in a

southern boreal aspen forest. *Agricultural and Forest Meteorology*, 125: 207–223.

Grogan, P., and Jonasson, S., 2005: Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. *Global Change Biology*, 11: 465–475.

Grogan, P., Illeris, L., Michelsen, A., and Jonasson, S., 2001: Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO_2 production in sub-arctic heath tundra. *Climatic Change*, 50: 129–142.

Hennessy, K., Whetton, P., Smith, I., Bathols, J., Hutchinson, M., and Sharples, J., 2003: *The Impact of Climate Change on Snow Conditions in Mainland Australia*. Aspendale: CSIRO Atmospheric Research.

Hennessy, K. J., Whetton, P. H., Walsh, K., Smith, I. N., Bathols, J. M., Hutchinson, M., and Sharples, J., 2008: Climate change effects on snow conditions in mainland Australia and adaptation at ski resorts through snowmaking. *Climate Research*, 35: 255–270.

Hubbard, R. M., Ryan, M. G., Elder, K., and Rhoades, C. C., 2005: Seasonal patterns in soil surface CO_2 flux under snow cover in 50 and 300 year old subalpine forests. *Biogeochemistry*, 73: 93–107.

Hunt, J. E., Kelliher, F. M., McSeveny, T. M., Ross, D. J., and Whitehead, D., 2004: Long-term carbon exchange in a sparse, seasonally dry tussock grassland. *Global Change Biology*, 10: 1785–1800.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R., 2001: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, 7: 269–278.

Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., and Valentini, R., 2007: Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect." *Tree Physiology*, 27: 929–940.

Jones, H. G., Pomeroy, J. W., Davies, T. D., Tranter, M., and Marsh, P., 1999: CO_2 in Arctic snow cover: landscape form, in-pack gas concentration gradients, and the implications for the estimation of gaseous fluxes. *Hydrological Processes*, 13: 2977–2989.

Larsen, K. S., Grogan, P., Jonasson, S., and Michelsen, A., 2007: Dynamics and microbial dynamics in two subarctic ecosystems during winter and spring thaw: effects of increased snow depth. *Arctic, Antarctic, and Alpine Research*, 39: 268–276.

Liptzin, D., Williams, M. W., Helmig, D., Seok, B., Filippa, G., Chowanski, K., and Hueber, J., 2009: Process-level controls on CO_2 fluxes from a seasonally snow-covered subalpine meadow soil, Niwot Ridge, Colorado. *Biogeochemistry*, 95: 151–166.

Mariko, S., Nishimura, N., Mo, W. H., Matsui, Y., Kibe, T., and Koizumi, H., 2000: Winter CO_2 flux from soil and snow surfaces in a cool-temperate deciduous forest, Japan. *Ecological Research*, 15: 363–372.

Mast, M. A., Wickland, K. P., Striegl, R. T., and Clow, D. W., 1998: Winter fluxes of CO_2 and CH_4 from subalpine soils in Rocky Mountain National Park, Colorado. *Global Biogeochemical Cycles*, 12: 607–620.

McDowell, N. G., Marshall, J. D., Hooker, T. D., and Musselman, R., 2000: Estimating CO_2 flux from snowpacks at three sites in the Rocky Mountains. *Tree Physiology*, 20: 745–753.

Mikan, C. J., Schimel, J. P., and Doyle, A. P., 2002: Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology & Biochemistry*, 34: 1785–1795.

Mo, W., Nishimura, N., Mariko, S., Uchida, M., Inatomi, M., and Koizumi, H., 2005: Interannual variation in CO2 effluxes from soil and snow surfaces in a cool-temperate deciduous broad-leaved forest. *Phyton-Annales Rei Botanicae*, 45: 99–107.

Monson, R. K., Burns, S. P., Williams, M. W., Delany, A. C., Weintraub, M., and Lipson, D. A., 2006a: The contribution of beneath-snow soil respiration to total ecosystem respiration in a high-elevation, subalpine forest. *Global Biogeochemical Cycles*, 20(3): article GB3030, doi:10.1029/2005GB002684.

Monson, R. K., Lipson, D. L., Burns, S. P., Turnipseed, A. A., Delany, A. C., Williams, M. W., and Schmidt, S. K., 2006b: Winter forest soil respiration controlled by climate and microbial community composition. *Nature*, 439: 711–714.

Morgenstern, K., Black, T. A., Humphreys, E. R., Griffis, T. J., Drewitt, G. B., Cai, T., Nesic, Z., Spittlehouse, D. L., and Livingston, N. J., 2004: Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agricultural and Forest Meteorology*, 123: 201–219.

Nagy, Z., Pinter, K., Czobel, S., Balogh, J., Horvath, L., Foti, S., Barcza, Z., Weidinger, T., Csintalan, Z., Dinh, N. Q., Grosz, B., and Tuba, Z., 2007: The carbon budget of semi-arid grassland in a wet and a dry year in Hungary. *Agriculture Ecosystems & Environment*, 121: 21–29.

Nakano, T., Nemoto, M., and Shinoda, M., 2008: Environmental controls on photosynthetic production and ecosystem respiration in semi-arid grasslands of Mongolia. *Agricultural and Forest Meteorology*, 148: 1456–1466.

Novick, K. A., Stoy, P. C., Katul, G. G., Ellsworth, D. S., Siqueira, M. B. S., Juang, J., and Oren, R., 2004: Carbon dioxide and water vapor exchange in a warm temperate grassland. *Oecologia*, 138: 259–274.

Öquist, M. G., Sparrman, T., Klemedtsson, L., Drotz, S., Grip, H., Schleucher, J., and Nilsson, M. S., 2009: Water availability controls microbial temperature responses in frozen soil CO_2 production. *Global Change Biology*, 15: 2715–2722.

Risch, A. C., and Frank, D. A., 2007: Effects of increased soil water availability on grassland ecosystem carbon dioxide fluxes. *Biogeochemistry*, 86: 91–103.

Schadt, C. W., Martin, A. P., Lipson, D. A., and Schmidt, S. K., 2003: Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science*, 301: 1359–1361.

Schimel, J. P., and Clein, J. S., 1996: Microbial response to freeze-thaw cycles in tundra and taiga soils. *Soil Biology & Biochemistry*, 28: 1061–1066.

Schimel, J. P., and Mikan, C., 2005: Changing microbial substrate use in Arctic tundra soils through a freeze-thaw cycle. *Soil Biology & Biochemistry*, 37: 1411–1418.

Schindlbacher, A., Zechmeister-Boltenstern, S., Glatzel, G., and Jandl, R., 2007: Winter soil respiration from an Austrian mountain forest. *Agricultural and Forest Meteorology*, 146: 205–215.

Schmidt, S. K., Wilson, K. L., Monson, R. K., and Lipson, D. A., 2009: Exponential growth of "snow molds" at sub-zero temperatures: an explanation for high beneath-snow respiration rates and Q(10) values. *Biogeochemistry*, 95: 13–21.

Sims, P. L., and Bradford, J. A., 2001: Carbon dioxide fluxes in a southern plains prairie. *Agricultural and Forest Meteorology*, 109: 117–134.

Sommerfeld, R. A., Mosier, A. R., and Musselman, R. C., 1993: CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. *Nature*, 361: 140–142.

van Gorsel, E., Leuning, R., Cleugh, H. A., Keith, H., Kirschbaum, M. U. F., and Suni, T., 2008: Application of an alternative method to derive reliable estimates of nighttime respiration from eddy covariance measurements in moderately

complex topography. *Agricultural and Forest Meteorology*, 148: 1174–1180.

Warren, C. R., and Taranto, M. T., 2010: Temporal variation in pools of amino acids, inorganic and microbial N in a temperate grassland soil. *Soil Biology and Biochemistry*, 42: 353–359.

Wohlfahrt, G., Anderson-Dunn, M., Bahn, M., Balzarolo, M., Berninger, F., Campbell, C., Carrara, A., Cescatti, A., Christensen, T., Dore, S., Eugster, W., Friborg, T., Furger, M., Gianelle, D., Gimeno, C., Hargreaves, K., Hari, P., Haslwanter, A., Johansson, T., Marcolla, B., Milford, C., Nagy, Z., Nemitz, E., Rogiers, N., Sanz, M. J., Siegwolf, R. T. W., Susiluoto, S., Sutton, M., Tuba, Z., Ugolini, F., Valentini, R., Zorer, R., and Cernusca, A., 2008: Biotic, abiotic, and management controls on the net ecosystem CO_2 exchange of European mountain grassland ecosystems. *Ecosystems*, 11: 1338–1351.

Xia, J., Niu, S., and Wan, S., 2009: Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. *Global Change Biology*, 15: 1544–1556.

Zimov, S. A., Davidov, S. P., Voropaev, Y. V., Prosiannikov, S. F., Semiletov, I. P., Chapin, M. C., and Chapin, F. S., 1996: Siberian CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2. *Climatic Change*, 33: 111–120.

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