



## Winter CO<sub>2</sub> fluxes above sagebrush-steppe ecosystems in Idaho and Oregon

Tagir G. Gilmanov<sup>a,\*</sup>, Douglas A. Johnson<sup>b</sup>, Nicanor Z. Saliendra<sup>c</sup>,  
Tony J. Svejcar<sup>d</sup>, Ray F. Angell<sup>d</sup>, Kirk L. Clawson<sup>e</sup>

<sup>a</sup> Department of Biology and Microbiology, South Dakota State University, Box 2207B, Ag. Hall 304, Brookings, SD 57007, USA

<sup>b</sup> USDA-Agricultural Research Service, Forage and Range Research Lab,  
Utah State University, Logan, UT 84322-6300, USA

<sup>c</sup> Forest, Range and Wildlife Sciences, Utah State University, Logan, UT 84322-6300, USA

<sup>d</sup> USDA-Agricultural Research Service, 67826-A Highway 205, Burns, OR 97720, USA

<sup>e</sup> Air Resources Laboratory Field Research Division, National Oceanic and Atmospheric Administration,  
1750 Foote Drive, Idaho Falls, ID 83402, USA

Received 26 October 2003; received in revised form 27 May 2004; accepted 27 May 2004

### Abstract

Sagebrush-steppe ecosystems cover more than 36 million ha in North America and represent an important economic and ecological resource. These ecosystems have a climate with an extended cold period that can last more than five months. The CO<sub>2</sub> fluxes during this protracted cold period likely play an important role in determining annual fluxes in these ecosystems; however, few studies have measured continuous CO<sub>2</sub> fluxes in sagebrush-steppe ecosystems during the winter. The objective of our study was to obtain continuous measurements of CO<sub>2</sub> fluxes during winter at representative sagebrush-steppe sites in the western USA and to study their relationships to environmental factors. Measurements of CO<sub>2</sub> fluxes were obtained using Bowen ratio/energy balance (BREB) techniques during the winter at two locations in Idaho and one location in Oregon. Average daily ecosystem respiration during the winter period (November 1–March 15) was  $1.31 \pm 0.80$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> and  $1.23 \pm 1.19$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> at the two Idaho sites and  $0.68 \pm 0.56$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> at the Oregon site. These values are well within the range of previously published results for similar ecosystems. Multivariate analyses showed that soil temperature, wind speed, and snow depth were the environmental factors most closely related to winter CO<sub>2</sub> effluxes. Based on testing of empirical flux models, additional research will be required to develop mathematical models that reliably predict winter CO<sub>2</sub> effluxes across a wide range of sagebrush-steppe sites.

© 2004 Elsevier B.V. All rights reserved.

**Keywords:** Winter CO<sub>2</sub> flux; Sagebrush steppe; Artemisia; Intermountain West; Rangeland ecosystems; Carbon cycle

### 1. Introduction

Quantification of the annual carbon cycle in terrestrial ecosystems is crucial to understanding and managing the global carbon cycle (King and O'Neill, 1989; Sommerfeld et al., 1993; Chapin et al., 1995;

\* Corresponding author. Tel.: +1 605 688 4925;  
fax: +1 605 688 6677.  
E-mail address: [tagir\\_gilmanov@sdstate.edu](mailto:tagir_gilmanov@sdstate.edu) (T.G. Gilmanov).

Ruimy et al., 1995, 1996; Oechel et al., 1997; Fahnestock et al., 1999; Frank et al., 2000; Houghton et al., 1998; Houghton, 2000; Falge et al., 2001; Frank and Dugas, 2001). Since the mid-1990s, continuous measurements of CO<sub>2</sub> exchange have been obtained in various terrestrial ecosystems (FLUXNET, 2001). These studies are helping to clarify the contributions of various ecosystems to the global carbon cycle.

Rangelands (grasslands, savannas, and shrub steppes) occupy about 50% of the world's land surface area (World Resources Institute, 1986). Because of their expansiveness, rangeland ecosystems could contribute significantly to the global carbon cycle. Continuous CO<sub>2</sub> fluxes have been quantified in various rangeland ecosystems (Kim et al., 1992; Valentini et al., 1995; Ham and Knapp, 1998; Saigusa et al., 1998; Dugas et al., 1999; Johnson et al., 1999; Frank et al., 2000; LeCain et al., 2000; Angell et al., 2001; Frank and Dugas, 2001; Meyers, 2001; Sims and Bradford, 2001; Flanagan et al., 2002; Gilmanov et al., 2003a,b). These studies documented the magnitudes of CO<sub>2</sub> fluxes above rangeland during the growing season, their dynamics, and the relationship to various environmental characteristics. Although growing season fluxes provide important information, fluxes during the non-growing season are also critical. This is especially true for some temperate rangelands, where the cold period during late autumn, winter, and early spring can represent almost half of the year. Respiratory losses during the extended cold period may offset a major portion of the carbon fixed during the growing season and could be critical in determining the annual carbon cycle of these temperate rangelands.

Some of the first data to quantify winter CO<sub>2</sub> fluxes for terrestrial ecosystems was reported by Kelley et al. (1968), who obtained year-round measurements of CO<sub>2</sub> concentrations at the soil surface and 16 m above the ground surface for a coastal arctic tundra ecosystem near Barrow, Alaska, USA. They found gradients indicating substantial rates of respiratory losses during November and December under 20–30 cm of snow. Later studies in this same ecosystem indicated respiratory losses in the winter were equivalent to mineralization of nearly 170 g m<sup>-2</sup> of organic matter (Johnson and Kelley, 1970) with the processes of soil freezing and thawing resulting in significant

respiratory losses (Coyne and Kelley, 1971). These results were confirmed by other studies in arctic tundra ecosystems. For example, Fedorov-Davydov and Gilichinsky (1993) found that winter respiratory losses for a *Vaccinium-Cetraria* community in Russia ranged from 0.0 to 0.034 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> during October (−1.4 °C) to February (−20.3 °C), resulting in an estimated total respiratory loss of 75 g CO<sub>2</sub> m<sup>-2</sup> for the seven-month winter period. Zimov et al. (1993) reported an average winter respiratory loss (December–February) of 0.55 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for arctic tundra soils in northeastern Russia. Oechel et al. (1997) found that average respiratory loss in moist tussock tundra in Alaska (October–late May) was 1.1 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. Respiratory losses were 0.25 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for the late fall/early winter period at an automorphic arctic tundra site near Kolyma in northeast Siberia with mean air temperatures of −19.3 °C, while ecosystem effluxes were 0.6 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> in a hydromorphic sedge-marsh tundra site in the same region with mean air temperature of −12.9 °C (Fedorov-Davydov, 1998). Fahnestock et al. (1999) reported an average net winter CO<sub>2</sub> efflux of 0.23 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> from soils in arctic tundra communities in Alaska with maximum efflux of 0.62 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. Mid-February measurements on a deeply frozen, snow-covered ombrotrophic bog in western Siberia showed average rates of CO<sub>2</sub> evolution of 0.07 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> (Panikov and Dedysh, 2000). These data from tundra ecosystems demonstrated that metabolic activity continues under winter conditions and suggest that respiratory losses are significant and can be important in determining annual CO<sub>2</sub> fluxes.

Similar results have been reported for montane ecosystems. For example, in a snow-covered mountain meadow at 2865 m elevation in the Wasatch Mountains in Utah, Solomon and Cerling (1987) found that winter respiration rates ranged from 0.004 to 0.075 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> during September–April. In an alpine site, at 3286 m elevation in Wyoming, Sommerfeld et al. (1993) measured respiratory losses of 0.013–0.079 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> and reported respiration rates from 0.026 to 0.246 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> in a subalpine meadow at 3182 m elevation for the snow-covered period. Mariko et al. (1994) found average winter respiration rates ranging from 0.02 to 0.07 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup> at four mountain forest sites in

Japan at elevations ranging between 1320 and 2200 m. Thus, the average daily rates of CO<sub>2</sub> evolution under snow-covered montane ecosystems are about 1.0 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> with occasional pulses to 3 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>.

Winter respiratory losses also have been reported for boreal and temperate forest communities. For example, Skogland et al. (1988) described the phenomenon of respiratory burst after freezing and thawing in soils of a Norwegian beech forest. Soil respiration in a mixed-hardwood forest in New Hampshire ranged from 0.01 to 2.8 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> during December–February when mean air temperatures were –1.8 to –4.2 °C (Crill, 1991). Studies in the Harvard Forest in central Massachusetts showed that winter respiratory losses ranged from 0.1 to 0.5 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> with soil temperatures from –5 to 0 °C (Peterjohn et al., 1994).

Only a limited number of measurements of CO<sub>2</sub> fluxes have been made during the winter for northern latitude rangelands. Low temperatures, snow, no electrical service, and accompanying logistical difficulties hamper such measurements. Existing winter flux measurements on rangelands usually involve short term, periodic determinations rather than continuous measurements. These short-term measurements typically have been used to estimate winter fluxes by calculating “mean winter flux” and multiplying this value by the length of the cold period (Fahnestock et al., 1999; Frank et al., 2000; Frank and Dugas, 2001; Sims and Bradford, 2001). Few continuous measurements of CO<sub>2</sub> fluxes have been made during the winter to evaluate if such methods accurately estimate cold-period fluxes in northern latitude rangelands.

The USDA-ARS Rangeland Carbon Dioxide Flux Network (Svejcar et al., 1997) is undertaking an effort to document CO<sub>2</sub> fluxes during the winter for several important rangeland ecosystems in the western USA. The experiments in the present paper are a part of this effort, and document winter flux measurements obtained on sagebrush-steppe ecosystems in Idaho and Oregon. We also examined the relationships of these fluxes to various environmental factors. An Idaho dataset, which was not used for model development, was used to test the generality of the derived empirical models.

## 2. Materials and methods

### 2.1. Site details

Continuous measurements of CO<sub>2</sub> exchange were obtained during the winter at three locations within the sagebrush-steppe province: (1) the Dubois site in eastern Idaho, USA, with data collection at the beginning and the end of 2000, (2) the Idaho National Engineering and Environmental Laboratory (INEEL) site in central Idaho, USA, with data collection during the winters of 1999–2000 and 2000–2001, and (3) the Burns site in southeastern Oregon, USA, with data collection during the winter of 2000–2001.

#### 2.1.1. Dubois, Idaho site description

The Dubois site is located in the northeast portion of the Snake River Plain near the foothills of the Snowcrest Range on the US Sheep Experiment Station (44°16'N, 112°08'W, 1700 m elevation) about 10 km north of Dubois, Idaho, USA. Detailed characteristics of the study area are described by Blaisdell (1958) and Laycock (1967). The study plot was protected from grazing in 1995, five years before our winter measurements were obtained. The study area has a diverse shrub-steppe community dominated by three-tipped sagebrush (*Artemisia tripartita* Rydb.; canopy cover 40%) with bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A Löve) the dominant grass and arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.) the dominant forb. The climate of the area is semiarid with moderately cold winters and warm summers, with a characteristic late-summer drought period. Mean temperature for January is –8 °C (minimum of –32 °C) and for July is 21 °C (maximum of 38 °C); mean annual temperature is 6.1 °C (Anonymous, 1993). Mean annual precipitation (78 years) for the area is 302 mm with an average snow depth of 20–30 cm. Soils at the site are represented by loamy mollisols derived from loess, residuum, or alluvium parent material of varying thickness that overlay basalt bedrock (NRCS, 1995). Major soil series ranked in order of increasing depth and degree of profile development are: Anatolian series (Typic Calcixerols), Maremma series (Pachic Haploxerolls), and Akbash series (Pachic Argixerolls). Depending on relief position, the thickness of mollic epipedon (A1, A2, and Bt horizons) varies from 0.2 to 0.9 m,

while the depth to basalt bedrock is between 0.5 and 1.5 m (Soil Survey Staff, 2004).

### 2.1.2. INEEL, Idaho site description

The INEEL site is located on the eastern portion of the Snake River Plain near the foothills of the Lost River Mountains (43°35'22"N, 112°56'23"W, 1493 m elevation) about 75 km west of Idaho Falls, Idaho, USA. The general features of the climate, vegetation, and soils at the INEEL site are similar to those at the Dubois site, but annual precipitation averages only 220 mm and soils are generally shallower. The most common shrub at the INEEL site is Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis*) with basin big sagebrush (*Artemisia tridentata* Nutt. subsp. *tridentata*) occurring as a co-dominant in areas with deep soils. Dominant grasses at the site include thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & Smith]), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), and Nevada bluegrass (*Poa secunda* Presl). Prominent forbs at the study site include: tapertip hawksbeard (*Crepis acuminata* Nutt.), hoary false yarrow (*Chaenactis douglasii* [Hook] H.&A.), and paintbrush (*Castilleja angustifolia* [Nutt.] G. Don). A comprehensive analysis of plant communities at INEEL can be found in Anderson et al. (1996). Grazing has been restricted at the INEEL site since the early 1950s.

### 2.1.3. Burns, Oregon site description

The Burns site is located on the Northern Great Basin Experimental Range (43°29'N, 119°43'W, 1380 m elevation) on an ungrazed 65-ha plot dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis*) with a canopy cover of 10%. Grasses common on the site include: Thurber's needlegrass (*Stipa thurberiana* Piper), bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve), Sandberg's bluegrass (*Poa sandbergii* Vasey), and bottlebrush squirreltail (*Elymus elymoides* [Nutt.] Smith). Forbs commonly found on the site include: prairie lupine (*Lupinus lepidus* Dougl.), hawksbeard (*Crepis occidentalis* Nutt.), and longleaf phlox (*Phlox longifolia* Nutt.). Climate at the Burns site is characterized by a mean annual precipitation (61 years) of 294 mm and a mean annual temperature of 8 °C (NOAA, 1999). The climate data for the Burns site show that 25% of annual precipitation is

received during May and June. Drought occurs during much of the growing season, but is especially pronounced during July when the mean monthly maximum of air temperature is 29.4 °C with an extreme of 40.0 °C (Sneva, 1982). Soils at the site belong to the Vil-Decantel variant of the Ratto complex with a coarse-to-fine sandy loam texture and 2–8% slopes. Thickness of the mollic epipedon is between 0.2 and 0.3 m with a depth of 0.6 m to the bedrock. Soils are underlain by basaltic parent material and classified as loamy, mixed, frigid shallow Aridic Durixerolls (Lentz and Simonson, 1986).

### 2.2. Field Bowen ratio/energy balance (BREB) measurements

Measurements were made with Bowen ratio/energy balance CO<sub>2</sub> flux systems (Model 023/CO<sub>2</sub> Bowen ratio, Campbell Scientific, Logan, Utah, USA) with insulation added around the control box for winter conditions. The theory and operation of BREB systems were described in detail by Dugas (1993) and Dugas et al. (1999). Briefly, CO<sub>2</sub> and water vapor concentrations were measured with an infrared gas analyzer (IRGA; Model LI-6262, Li-Cor Inc., Lincoln, Nebraska, USA). Air samples from two heights (0.8 and 1.8 m above the soil surface) were drawn and routed to the IRGA, which measured the concentration gradient between the two heights. A low-power pump (Model TD-3LSC, Brailsford and Co., Rye, New York, USA) aspirated the air through 1- $\mu$ m teflon filters (Model Acro 50, Gelman Sciences, Ann Arbor, Michigan, USA), which prevented dust and liquid water contamination in the air tubes and IRGA. At the beginning of each hour, the IRGA sample cell was scrubbed of CO<sub>2</sub> and water vapor, and absolute concentrations of CO<sub>2</sub> and water vapor were determined. Air temperature gradients at the two heights were simultaneously measured with fine-wire, chromel–constantan thermocouples. Gradients of CO<sub>2</sub>, water vapor, and temperature were measured every second, and the average gradients were calculated and stored every 20 min with a data logger and storage module (Models 21X and SM192, Campbell Scientific, Inc.). Fluxes of CO<sub>2</sub>, water vapor, and energy were calculated using 20 min averages. The eddy diffusivity, which was assumed equal for heat, water vapor, and CO<sub>2</sub>, was calculated from sensible heat flux and temperature

gradients. The CO<sub>2</sub> flux, corrected for vapor density gradients at the two heights (Webb et al., 1980), was calculated as the product of the eddy diffusivity and the CO<sub>2</sub> gradient. Previous work in sagebrush-steppe ecosystems showed that CO<sub>2</sub> fluxes measured by the BREB technique agreed closely with those measured with closed canopy chambers (Angell et al., 2001).

Top-soil temperature ( $T_s$ , °C) was measured at an average depth of 4 cm with an averaging soil thermocouple probe (Model TCAV, Campbell Scientific, Inc.). Wind speed ( $U$ , m s<sup>-1</sup>) was measured at a height of 2.5 m from the ground surface with a cup anemometer (Model 03101–5, R.M. Young Co., Traverse City, MI, USA). Snow depth ( $S_d$ , cm) was manually measured every day, at the same time of day, with a meter stick.

Snow on the ground surface complicates the flux measurements because of potential heat storage in the snow layer and possible subsequent errors in measurements of soil heat flux. This issue was evaluated for three sites in the USDA-ARS Rangeland Carbon Dioxide Flux Network including Burns, OR; Dubois, ID; and Mandan, ND (Dugas, W.A., personal communication). The effect of an error in soil heat flux on CO<sub>2</sub> fluxes for these three sites was estimated to be less than 10%. Because Dubois had an average snow depth of 22 cm compared to 5 cm at Burns and 3 cm at INEEL, greater uncertainties probably exist for the winter fluxes at Dubois than those at Burns and INEEL.

Three datasets were used for modeling analyses of winter CO<sub>2</sub> fluxes (Dubois, winter-spring and fall-winter 2000, Fig. 1a; INEEL, winter 1999–2000, Fig. 1b; Burns, winter 2000–2001, Fig. 2c). The fourth dataset (INEEL, winter 2000–2001) was used for model testing.

### 2.3. Modeling approach

The goal of our modeling study was to identify possible relationships between wintertime net daily CO<sub>2</sub> flux and various environmental characteristics. For this purpose, 24 h flux integrals,  $F_w(j)$ , representing net CO<sub>2</sub> exchange for calendar day,  $j$ , were calculated:

$$F_w(j) = \sum_{k=1}^{72} F_{j,k} \Delta t_k, \quad (1)$$

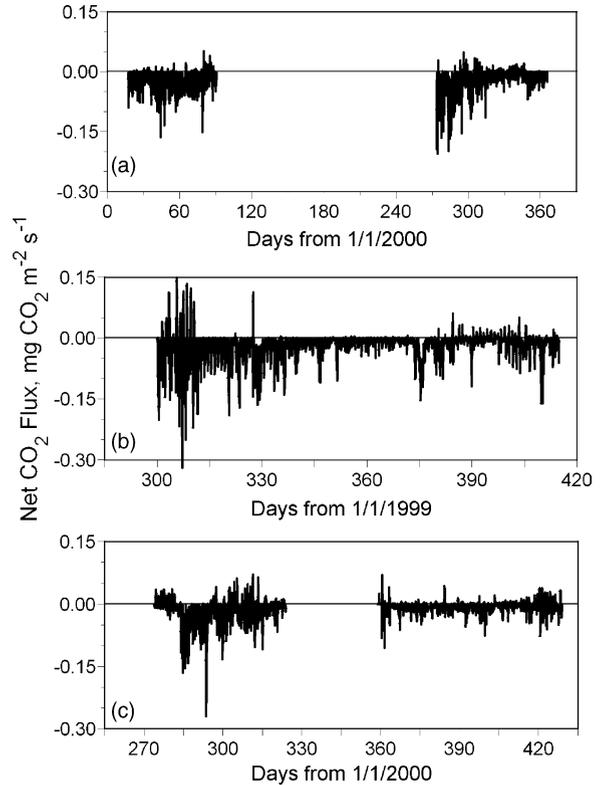


Fig. 1. Dynamics of 20 min mean net CO<sub>2</sub> fluxes during the winter at the: (a) Dubois site, (b) INEEL site, and (c) Burns site.

where  $\Delta t_k = (t_k - t_{k-1}) = \Delta t = 20$  min,  $\{t_0, t_1, t_2, \dots, t_{72}\}$  is the sequence of moments of time of 20 min field measurements across 24 h, and  $F_{j,k}$  is the average CO<sub>2</sub> flux over the interval  $(t_{k-1}, t_k)$  recorded by the flux tower. Simultaneously, for every calendar day,  $j$ , average daily characteristics of relevant environmental factors  $X_i$  (e.g., soil temperature at 4 cm depth,  $X_1 = T_s$ ; wind speed,  $X_2 = U$ ; snow depth,  $X_3 = S_d$ ; etc.) were calculated using 20 min measurements. As a result, a  $(k + 1)$  by  $n$  data array  $X = \{X_1(j), X_2(j), \dots, X_k(j), F_w(j)\}$  ( $j \in \{j_1, j_2, \dots, j_n\}$ ) was generated, where  $\{j_1, j_2, \dots, j_n\}$  is the sequence of days (may not be continuous) when measurements were obtained;  $X_i(j)$  ( $i = 1, 2, \dots, k$ ) are environmental factors for day  $j$  potentially influencing daily CO<sub>2</sub> exchange;  $k$  is the number of factors taken into consideration; and  $F_w(j)$  is the net daily CO<sub>2</sub> flux integral for day  $j$  (the dependent variable).

Though, a priori, relationships between the response variable  $F_w$  and factors  $X_1, \dots, X_k$  incorporated in the

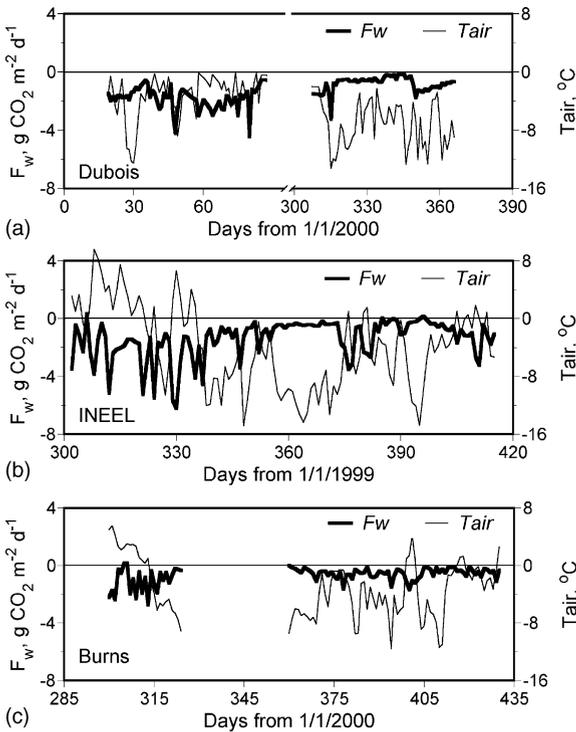


Fig. 2. Dynamics of daily integrals of net CO<sub>2</sub> flux during the winter ( $F_w$ , g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) at the (a) Dubois site, (b) INEEL site, and (c) Burns site.

multi-dimensional time series  $X$  may be quite complicated and include dependence of  $F_w(j)$  on  $X_i(t)$  and  $F_w(t)$  for  $t < j$ , we used models without time delays in our analysis:

$$F_w = f(X_1, X_2, \dots, X_k; a_1, a_2, \dots, a_p) + \varepsilon, \quad (2)$$

where factors  $X_i$  and response  $F_w$  refer to the same ( $j$ th) measurement day,  $f(\dots)$  the function to be identified,  $a_1, a_2, \dots, a_p$  are its parameters, and  $\varepsilon$  is the statistical error of measurements. The goal of the present analysis was to identify a form of the relationship  $f(\dots)$  and to estimate its parameters that minimize the difference of the sum of squares of observed and predicted daily flux integrals. Software tools available in the non-linear regression modules of Mathematica® (Wolfram Research, 2000) and Statistica™ (Statsoft, 2001) were used to implement multivariate non-linear parameter identification.

### 3. Results

#### 3.1. Winter CO<sub>2</sub> fluxes

Rates of CO<sub>2</sub> flux during the winter at the three sites ranged from  $-0.32$  to  $+0.15$  mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (Fig. 1a–c). On certain relatively rare occasions during early winter, peak respiration losses reached  $-0.3$  mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>. Uptake of CO<sub>2</sub> from the atmosphere (photosynthetic assimilation) up to  $0.05$  mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> was observed at all three sites during the winter period under conditions with relatively warm temperatures and high levels of solar radiation (positive peaks in Fig. 1).

Wintertime daily net CO<sub>2</sub> flux,  $F_w$  (g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>), was calculated by integrating 72 20-min values for each day (Eq. (1)). Dynamics of  $F_w$  integrals across the periods with winter measurements at the three sites demonstrated that the sagebrush-steppe ecosystem was a source of CO<sub>2</sub> during the winter with  $F_w$  varying from a maximum efflux of  $6$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> during pulses of respiration activity in the autumn and on certain winter days to values of less than  $1$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> during January and February (Fig. 2).

Regression analysis indicated that  $F_w$  was most closely associated with average daily soil temperature ( $T_s$ ), average wind speed ( $U$ ), and presence and/or depth of the snow cover ( $S_d$ ) at the Dubois site (Fig. 3, Dubois), and with  $T_s$  and  $U$  at the INEEL site (Fig. 3, INEEL) and the Burns site (Fig. 3, Burns). Regressions of  $F_w$  on snow depth were significant only for the Dubois site, where snow reached depths greater than  $40$  cm. At the INEEL and Burns sites, snow was not always present and snow depths were typically less than  $20$  cm, so that snow depth was not closely associated with  $F_w$  at these two sites. Nevertheless, as will be shown later, snow presence was useful as an empirical variable even at these sites.

#### 3.2. Multivariate relationships for winter CO<sub>2</sub> flux

Considerable variability was observed for  $F_w$ , even in those cases where univariate regressions were significant, indicating that other factors were important in determining  $F_w$  rates. Single-factor scatter diagrams (Fig. 3a–c) indicated that the exponential model was

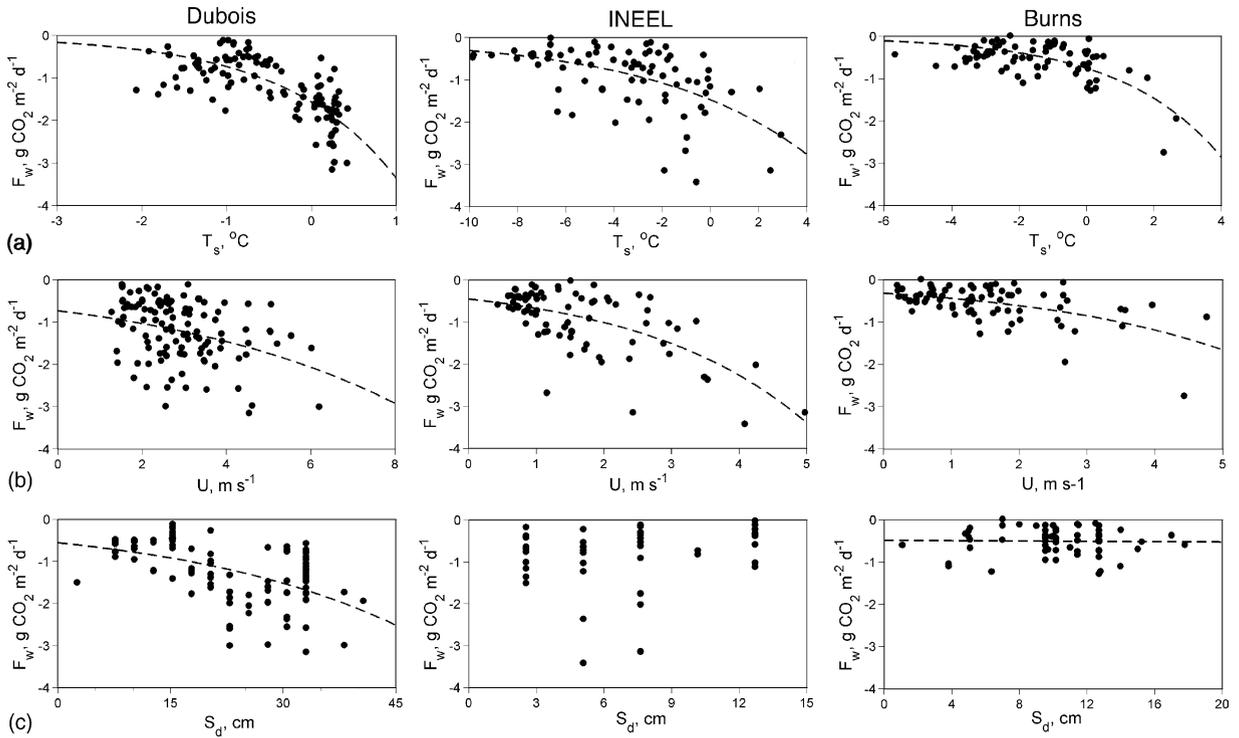


Fig. 3. Relationship between net daily CO<sub>2</sub> flux during the winter ( $F_w$ ) at the Dubois, INEEL, and Burns sites and three meteorological factors: (a) average daily top-soil temperature ( $T_s$ ), (b) average daily wind speed ( $U$ ), and (c) snow depth ( $S_d$ ). Dashed curves describing single-factorial exponential approximations are: Dubois: (a)  $F_n(T_s) = 1.56 \text{ Exp}(0.763 T_s)$ ,  $n = 113$ ,  $R^2 = 0.53$ ; (b)  $F_n(U) = 0.715 \text{ Exp}(0.178 U)$ ,  $n = 113$ ,  $R^2 = 0.13$ ; and (c)  $F_n(S_d) = 0.620 \text{ Exp}(0.298 S_d)$ ,  $n = 113$ ,  $R^2 = 0.25$ ; INEEL: (a)  $F_n(T_s) = -1.47 \text{ Exp}(0.18 T_s)$ ,  $n = 77$ ,  $R^2 = 0.29$ ; (b)  $F_n(U) = -0.443 \text{ Exp}(0.407 U)$ ,  $n = 77$ ,  $R^2 = 0.43$ ; and (c) no significant one-factor relationship was established between  $F_w$  and  $S_d$ ; Burns: (a)  $F_n(T_s) = 0.75 \text{ Exp}(0.384 T_s)$ ,  $n = 77$ ,  $R^2 = 0.38$ ; (b)  $F_n(U) = 0.309 \text{ Exp}(0.336 U)$ ,  $n = 76$ ,  $R^2 = 0.29$ ; and (c) no significant one-factor relationship was established between  $F_w$  and  $S_d$ .

a possible tool to describe factor interaction:

$$F_w = -a_0 \text{Exp}(a_T T_s + a_U U + a_S S_d) + \varepsilon, \quad (3)$$

where  $T_s$  is the soil temperature,  $U$  the wind speed,  $S_d$  the snow depth,  $\{a_i\}$  are non-linear regression parameters, and  $\varepsilon$  is the statistical error (S.E.) of the measurements. Estimates of the parameters  $\{a_i\}$  and their statistical characteristics for Eq. (3) for  $F_w$  from the Dubois site are presented in Table 1, Section 1.

With these parameters, Eq. (3) is characterized by  $R^2 = 0.64$  and a standard error (S.E.) of  $0.53 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . Comparisons of observed and predicted fluxes based on Eq. (3) on a scatter diagram (Fig. 4a) demonstrated that the regression line of observed on predicted values is statistically indistinguishable from the 1:1 line (testing the general linear hypothesis  $H_0$

= {intercept = 0 and slope = 1.0} using the  $F$  statistic indicating no reason to reject  $H_0$ ). Clustering of the points near the 1:1 line suggests that Eq. (3) is a reasonable predictor of the general pattern of  $F_w$  in relation to  $T_s$ ,  $U$ , and  $S_d$  for the 2000 wintertime flux measurements at the Dubois site.

For the Burns and INEEL sites where snow cover was not always present during the winter, parameter  $a_S$  could not be reliably estimated in Eq. (3). Nevertheless, the presence or absence of snow cover as a qualitative factor was still important for estimating  $F_w$  at these sites, as illustrated by the model:

$$F_w = \begin{cases} -a_0 \text{Exp}(a_T T_s + a_U U), & \text{when } S_d > 0 \\ -b_0 \text{Exp}(b_T T_s + b_U U), & \text{when } S_d = 0 \end{cases}, \quad (4)$$

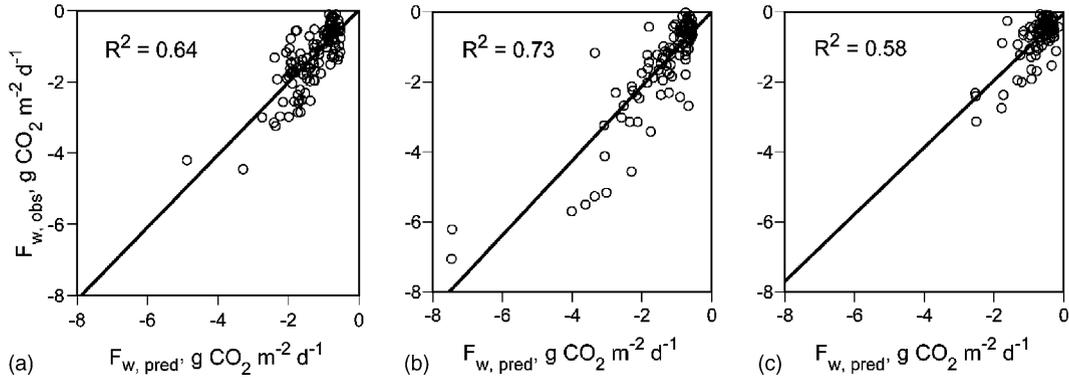


Fig. 4. Scatter diagrams of observed compared to predicted wintertime CO<sub>2</sub> fluxes ( $F_w$ ): (a) Dubois 2000;  $R^2 = 0.64$ ; (b) INEEL 1999/2000;  $R^2 = 0.73$ ; and (c) Burns 2000/2001;  $R^2 = 0.58$ . In all cases, regression lines of observed on predicted  $F_w$  values (shown) are statistically indistinguishable from 1:1 relationships.

where parameters  $\{a_i\}$  correspond to conditions with snow and parameters  $\{b_i\}$  for conditions without snow on the soil surface.

Identification of the parameters for Eq. (4) using  $F_w$  data from the Burns site for the winter of 2000 resulted in the estimates presented in Table 1, Section 2. With these parameters, Eq. (4) was characterized by  $R^2 = 0.58$  and S.E. of  $0.42 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . A comparison of observed and predicted values of  $F_w$  is shown in Fig. 4c.

For the INEEL site where the relationship between  $F_w$  and  $T_s$  was not as strong (Fig. 3, INEEL, a), a modified version of Eq. (4) was used with  $F_w$  dependent only on  $U$  when  $S_d$  was  $>0$ , which is given by:

$$F_w = \begin{cases} -a_0 \text{Exp}(a_U U), & \text{when } S_d > 0 \\ -b_0 \text{Exp}(b_T T_s + b_U U), & \text{when } S_d = 0 \end{cases} \quad (5)$$

Best fit parameters for Eq. (5) identified for the INEEL 1999/2000 dataset are presented in Table 1, Section 3. With these parameters, Eq. (5) has  $R^2 = 0.73$  and S.E. of  $0.76 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . Comparisons of observed and predicted  $F_w$  for the INEEL site using Eq. (5) and parameters from Table 1, Section 3 are shown in Fig. 4b.

Eqs. (3)–(5) were used for the Dubois, Burns, and INEEL sites, respectively, for those days when flux measurements were not available or to fill in gaps of missing flux data, providing a continuous series of

measured or estimated daily wintertime CO<sub>2</sub> fluxes. To ensure comparability between sites, integrals of  $F_w$  [ $\Sigma(F_w)$ ] were calculated for each site from November 1 to March 15, which at all three sites corresponded to predominantly winter conditions with negative average daily temperatures (though occasional warm days occurred at each site within this period). Calculations showed that  $\Sigma(F_w)$  at Dubois was  $-177.3 \text{ g CO}_2 \text{ m}^{-2}$  with a mean  $F_w$  of  $-1.31 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$  and S.E. of  $0.80 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . Corresponding values for Burns were  $\Sigma(F_w) = -92.4 \text{ g CO}_2 \text{ m}^{-2}$ , mean  $F_w = -0.68 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ , and S.E. =  $0.56 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ . For the INEEL 1999–2001 data,  $\Sigma(F_w) = -166.1 \text{ g CO}_2 \text{ m}^{-2}$ , mean  $F_w = -1.23 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ , and S.E. =  $1.19 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ .

### 3.3. Model testing

The INEEL winter 2000–2001 dataset was not used to estimate the parameters for Eqs. (3)–(5), and thus we used these data to test the performance of these models to predict  $F_w$  for the INEEL winter 2000–2001 dataset. Neither the Dubois model (Eq. (3)) nor the Burns model (Eq. (4)) accurately predicted the observed INEEL 2000–2001 data. In both cases, the  $R^2$  values were below 0.05, demonstrating site specificity of these empirical models and their lack of application to other sagebrush-steppe sites. Application of the INEEL 1999–2000 model (Eq. (5)) to the INEEL 2000–2001 dataset resulted in  $R^2 = 0.21$ , sug-

Table 1  
Numerical estimates (standard errors) of parameters of Eqs. (3)–(5) for days with  $\{a_i\}$  and without  $\{b_i\}$  snow produced by non-linear regression applied to the winter CO<sub>2</sub> fluxes at the Dubois, Burns, and INEEL sites

| $a_0$ (g CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> )                                     | $a_T$ (°C <sup>-1</sup> ) | $a_U$ (s m <sup>-1</sup> ) | $a_S$ (cm <sup>-1</sup> ) | $b_0$ (g CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> ) | $b_T$ (°C <sup>-1</sup> ) | $b_U$ (s m <sup>-1</sup> ) |
|--|---------------------------|----------------------------|---------------------------|--|---------------------------|----------------------------|
| 1. Eq. (3), Dubois site, 2000 ( $n = 121$ , $R^2 = 0.64$ )<br>0.596 (0.133)***                   | 0.399 (0.070)***          | 0.149 (0.018)**            | 0.019 (0.06)**            | –  | –                         | –                          |
| 2. Eq. (4), Burns site, 2000/2001 ( $n = 96$ , $R^2 = 0.58$ )<br>0.631 (0.129)***                | 0.170 (0.079)*            | 0.144 (0.071)*             | –                         | 0.269 (0.071)***   | 0.266 (0.051)***          | 0.318 (0.060)***           |
| 3. Eq. (5), INEEL site, 1999/2000 ( $n = 107$ , $R^2 = 0.73$ )<br>0.502 (0.076)***               | –                         | 0.332 (0.024)***           | –                         | 1.057 (0.104)***   | 0.063 (0.017)***          | 0.221 (0.022)***           |
| 4. Eq. (5), INEEL site, 1999/2000 and 2000/2001 ( $n = 228$ , $R^2 = 0.57$ )<br>0.501 (0.050)*** | –                         | 0.337 (0.017)***           | –                         | 0.811 (0.086)***   | 0.054 (0.018)**           | 0.237 (0.026)***           |

Significance levels.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

gesting that the model was also specific to individual years.

Using the combined INEEL datasets for the winters of 1999–2000 and 2000–2001, a new set of parameters was developed for Eq. (5) (Table 1, Section 4). Applying this combined model to the INEEL winter 2000–2001 dataset produced an  $R^2 = 0.39$ . Eq. (5) with the INEEL 1999/2000 parameters (Table 1, Section 3) tested against the combined INEEL 1999–2000 and 2000–2001 dataset yielded  $R^2 = 0.53$ , while Eq. (5) with parameters estimated for the combined INEEL dataset gave  $R^2 = 0.57$  (Table 1, Section 4).

#### 4. Discussion

The average daily CO<sub>2</sub> flux value for the winter period ( $F_w$ ) across the three sagebrush-steppe sites in our study was about  $-1.0$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. This corresponds to the winter respiration values that Raich and Potter (1995) proposed for ecosystems with a distinct dry season. In our study, the sagebrush-steppe sites with higher shrub cover tended to have higher respiration rates (Table 2). Raich and Tufekcioglu (2000) indicated that soil respiration was positively correlated with litterfall rates in forests and aboveground net primary production in grasslands. Although we did not make such measurements in our study, litterfall from shrubs at our study sites may also be an important factor that influences soil respiration. Interest in winter respiration rates has increased as attempts are made to quantify annual ecosystem CO<sub>2</sub> fluxes (Welker et al., 2000).

Winter respiration measurements with a BREB system for a semiarid northern mixed-grass prairie in North Dakota showed soil respiration rates of 2.3 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> in January, 0.7–1.2 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> in February and early March, and 3.0 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> in late March with an average daily efflux of 1.7 g CO<sub>2</sub> m<sup>-2</sup> for the 156-day cold season (Frank and Dugas, 2001). A three-year study of soil respiration at the same site using chamber measurements demonstrated that soil CO<sub>2</sub> fluxes decreased to near 0 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> during December, January, and February, but increased rapidly in March and April, resulting in an average dormant season  $F_w$  of 1.83 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> (Frank et al., 2002).

Table 2  
Wintertime CO<sub>2</sub> flux in different sagebrush-steppe sites in relation to shrub cover

| Site (years)      | Shrub cover (%) | Average wintertime CO <sub>2</sub> flux (g CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> ) | S.D. of the wintertime CO <sub>2</sub> flux (g CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> ) |
|-------------------|-----------------|--|--|
| Burns (2000/2001) | 10              | 0.68   | 0.56   |
| INEEL (1999–2001) | 30              | 1.23   | 1.19   |
| Dubois (2000)     | 40              | 1.31   | 0.80   |

According to the review of Raich and Potter (1995), in ecosystems with no dramatic dry season, estimates of soil respiration rates for months with mean air temperatures from  $-15$  to  $-5$  °C ranged from 0.3 to 6.2 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. In ecosystems with distinct dry seasons, respiration rates during the winter were generally below 1.0 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> (Raich and Potter, 1995). Our measurements of winter respiration rates in sagebrush-steppe ecosystems agree with those of Raich and Potter (1995).

Mielnick and Dugas (2000) presented a comprehensive study of soil CO<sub>2</sub> fluxes in tallgrass prairie near Temple, Texas, in relation to temperature and soil water content. Though their studies did not include temperatures below 6 °C, extrapolation of their model to 0 to  $-5$  °C soil temperatures with soil water contents of 0.2–0.4 m<sup>3</sup> m<sup>-3</sup> gave CO<sub>2</sub> efflux rates from 0.32 to 0.72 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>, which is comparable to rates observed on most days at the Burns site and on many days at the Dubois site. At the INEEL site, however, CO<sub>2</sub> effluxes for most days were higher than those predicted by extrapolation of the Mielnick–Dugas model.

Another study that provided a temperature-dependent model for ecosystem CO<sub>2</sub> exchange, was conducted in the tallgrass prairie of north-central Oklahoma by Suyker and Verma (2001). Their model, based on measurements with soil temperatures to  $-3$  °C, described night-time CO<sub>2</sub> efflux as a function of air temperature, soil temperature, and leaf area index (LAI). Extrapolating this model to the ranges of air and soil temperature from  $-5$  to 5 °C and assuming no live vegetation (LAI = 0), we obtained net daily fluxes in the range from  $-1.0$  to  $-2.0$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> with a mean  $F_w$  of  $-1.47$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. If we assume that some vegetation is still alive (e.g., LAI = 0.2), the fluxes ranged from  $-1.3$  to  $-2.7$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for the same temperature range with a mean  $F_w$  of  $-1.94$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. Taking into account higher general phytomass and

productivity of the tallgrass prairie compared to the sagebrush steppe, these values are consistent with results from the three sagebrush-steppe sites ( $-0.68$  to  $-1.31$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>).

The dominant paradigm in soil respiration studies, based mostly on chamber flux measurements in laboratory and field conditions, considers the process of CO<sub>2</sub> effluxes from soils as controlled by temperature and soil moisture (Lloyd and Taylor, 1994; Raich and Potter, 1995; Duiker and Lal, 2000; Mielnick and Dugas, 2000; Raich and Tufekcioglu, 2000). Applied to winter conditions, this paradigm usually leads to rather low estimates of CO<sub>2</sub> effluxes from terrestrial ecosystems. The major reason for this lies in ignoring the processes of CO<sub>2</sub> degassing during freeze–thaw events, storage of CO<sub>2</sub> in the soil porous space, and variations of its release into the atmosphere under the effects of soil surface properties and atmospheric factors. The results of measurements of wintertime CO<sub>2</sub> exchange in a number of non-forest ecosystems obtained since the late 1990s with field flux towers using both the BREB (e.g., this study; Frank, A., personal communication; Morgan, J., personal communication) and eddy covariance methods (e.g., Massman, W., personal communication; Prueger and Hatfield, 2002; Prueger, J., personal communication) demonstrated that wintertime fluxes were generally higher than those suggested by the dominant paradigm of temperature-controlled fluxes. In our study, we found that these high fluxes were typically associated with near-zero soil temperatures (Fig. 3a) and high wind velocities (Fig. 3b). Additional field studies that combine several different methods to investigate driving factors and mechanisms causing pulses in wintertime fluxes are needed.

All models developed in our study showed the temperature dependence of  $F_w$ , as indicated by the presence of  $T_s$  in all three equations and the statistical significance of the temperature coefficients

$a_T$  and  $b_T$  (Table 1). The sites, however, differed concerning the strength of this dependence, as seen in Fig. 3a, and reflected in their corresponding models (Table 1, Sections 1–4). The strongest temperature dependence, was characterized by the exponential  $k_T = 0.4\text{ }^\circ\text{C}^{-1}$ , which was observed at the Dubois site. This very high estimate may be partly due to a narrow temperature range in the Dubois dataset ( $-2$  to  $+1\text{ }^\circ\text{C}$  only, Fig. 3a). Comparable high values of  $k_T$  have been reported previously for other cold-dominated ecosystems, but occur rarely (e.g., Grogan et al., 2001; Sjögersten and Wookey, 2002). For example, Grogan et al. (2001) presented data on  $\text{CO}_2$  efflux in the sub-arctic heath tundra near Abisko, Sweden, in the soil temperature range from  $-9$  to  $-3\text{ }^\circ\text{C}$ . For control and various treatments,  $F_w$  at this site varied from  $0.3$  to  $1.8\text{ g CO}_2\text{ m}^{-2}\text{ day}^{-1}$ . Fitting an exponential model for the control site data resulted in an apparent  $k_T = 0.35\text{ }^\circ\text{C}^{-1}$ . Sjögersten and Wookey (2002) reported maximum  $Q_{10}$  values of  $15.3$  for the tundra soil in Swedish Lapland, which corresponds to  $k_T = 0.27\text{ }^\circ\text{C}^{-1}$ . In a laboratory experiment with soil from a well-drained tundra heath in NE-Greenland, Elberling and Brandt (2003) observed up to a 100-fold increase of  $Q_{10}$  of soil  $\text{CO}_2$  release at temperatures below  $0\text{ }^\circ\text{C}$  compared to temperatures above  $0\text{ }^\circ\text{C}$ . These values of temperature sensitivity coefficients are comparable to the  $k_T$  value obtained for our Dubois study site.

At our Burns study site, the temperature response coefficient was estimated as  $0.170$  and  $0.269\text{ }^\circ\text{C}^{-1}$  for days with and without snow, respectively (Table 1, Section 2). These values are also relatively high, though quite comparable with values reported in the literature for near-zero and sub-zero temperatures (e.g., Kirschbaum, 1995). Compared to Dubois,  $\text{CO}_2$  flux measurements at the Burns site covered a wider range of temperatures ( $-10$  to  $+4\text{ }^\circ\text{C}$ ). For days without snow cover, temperature coefficients at the INEEL site ( $0.063\text{ }^\circ\text{C}^{-1}$  for 1999/2000 model and  $0.054\text{ }^\circ\text{C}^{-1}$  for the combined 1999/2001 model) were within the typical range of  $k_T$  values for soil respiration previously reported (Kirschbaum, 1995; Mielnick and Dugas, 2000; Frank et al., 2002; Sjögersten and Wookey, 2002; Elberling and Brandt, 2003; Smith, 2003).

Though wind velocity and associated turbulent changes of atmospheric pressure have been recognized

as potentially important factors in determining ecosystem  $\text{CO}_2$  exchange during cold periods and under snow (Kelley et al., 1968; Massman et al., 1995), few long-term quantitative data are available. Results from our study showed a significant statistical relationship between wintertime  $\text{CO}_2$  efflux and wind velocity. As emphasized by Kelley et al. (1968),  $\text{CO}_2$  flux from the ecosystem to the atmosphere during winter is the result of a set of complex interactions of processes of production and storage of  $\text{CO}_2$  in the soil and its transport to the atmosphere through the soil and snow layer (when present). Winter measurements at our sagebrush-steppe sites confirmed that “accumulated  $\text{CO}_2$  within the snow canopy is more rapidly released under conditions of high wind speed” (Kelley et al., 1968). Models for all three of our study sites included wind speed ( $U$ ) as a significant predictor of the wintertime flux (Table 1); for days with snow cover at the INEEL site, wind speed was found to be the only statistically significant flux predictor (Eq. (5)). Most cases of significant pulses of  $\text{CO}_2$  efflux at the INEEL site were associated with high wind speed.

The phenomenon of pulses of  $\text{CO}_2$  efflux associated with freeze–thaw events (compare flux and temperature curves in Fig. 2) supports findings of other authors, who described surplus  $\text{CO}_2$  emissions (compared to what might be expected from temperature-dependence alone) from soils experiencing freeze–thaw cycles (Skogland et al., 1988; Schimel and Clein, 1996; Panikov and Dedysch, 2000; Priemé and Christensen, 2001; Elberling and Brandt, 2003; Bubier et al., 2002). Nevertheless, models (3–5) have limited ability to generate high fluxes because the simultaneous occurrence of high temperature and high wind speed are not always observed. Apparently, more detailed models explicitly describing mechanisms of  $\text{CO}_2$  degassing in the soil matrix during freeze–thaw cycles, its storage in the soil porous space, and transport to the atmosphere as controlled by soil properties and atmospheric conditions are required to further improve the models of wintertime  $\text{CO}_2$  fluxes.

Significance of snow as a factor of  $\text{CO}_2$  exchange has been investigated by several authors (Kelley et al., 1968; Massman et al., 1995; Sommerfeld et al., 1996; Welker et al., 2000; Bubier et al., 2002). Snow cover affects ecosystem  $\text{CO}_2$  exchange through at least two opposite effects. First, depending on the thickness,

porosity, and properties of the snow surface (e.g., ice crust), snow cover may significantly decrease the efflux of CO<sub>2</sub> to the atmosphere, leading to the temporary formation of pockets of high CO<sub>2</sub> concentration above the soil surface (Kelley et al., 1968). Second, snow cover through its insulation effect may significantly decrease the depth of frozen soil or even completely prevent its freezing, thereby increasing the temperature of the active soil layer during winter (Walker et al., 1999). This may allow significant CO<sub>2</sub> production through a continuation of metabolic activity of soil microorganisms with enzymatic systems efficient at low temperatures (Panikov, 1997).

The enhanced effect of snow cover on CO<sub>2</sub> efflux during the winter may be responsible for the higher rates of  $F_w$  observed at our Dubois site, which is characterized by thick snow cover throughout most of the winter. The average trend at Dubois was increasing  $F_w$  with increasing  $S_d$  (Fig. 3c, Dubois), which is reflected in the positive value of the regression coefficient  $a_S$  in Eq. (3) (Table 1, Section 1). This suggests that thicker snow cover may have better insulating effects from below-freezing air temperatures, so that more favorable soil temperatures at depth would have allowed the occurrence of below-ground respiratory processes during winter. At the Burns site (Table 1, Section 2),  $F_w$  sensitivity to temperature for days with snow ( $a_T = 0.170 \pm 0.079 \text{ } ^\circ\text{C}^{-1}$ ) was not significantly different from that for days without snow ( $b_T = 0.266 \pm 0.051 \text{ } ^\circ\text{C}^{-1}$ ). Soil temperature was also not found to be a significant factor for days with snow at the INEEL site, but was included into regression for days without snow (Table 1, Sections 3 and 4). On the effects of wind speed, the coefficient  $a_U = 0.144 \pm 0.071 \text{ s m}^{-1}$  for days with snow was not statistically different from the coefficient  $b_U = 0.318 \pm 0.060 \text{ s m}^{-1}$  for days without snow at the Burns site. Altogether, our results for the Dubois and INEEL sites demonstrate the significance of snow as a quantitative (Dubois) or qualitative (INEEL) factor of winter CO<sub>2</sub> efflux. This contradicts the results from Jones et al. (1999) who found no relationship between wintertime CO<sub>2</sub> efflux and snow depth in tundra ecosystems in northern Alaska. On the other hand, our results for the Burns site agree with the conclusions by Jones et al. (1999).

Coefficients of the empirical models for our various study sites turned out to both site-specific and year-specific, as demonstrated by poor performance of

Dubois and Burns models on the INEEL 2000–2001 validation dataset ( $R^2 < 0.05$ ). Therefore, their applicability apparently remains limited to filling of data gaps within the particular winter period. Nevertheless, we found similarity of the general functional form of the models for different sites and years, especially with respect to the multiplicative interaction of temperature and wind speed factors, as well as proximity of parameter estimates for different sites and years (Table 1). The empirical models developed in our study have provided insights on the key environmental factors influencing CO<sub>2</sub> fluxes among sagebrush-steppe ecosystems at the daily time scale.

Table 3 summarizes available data on the average rates of wintertime CO<sub>2</sub> evolution in various non-forest ecosystems. It covers a wide range of climatic conditions and ecosystem productivity, from arctic tundra to tallgrass prairie and temperate grassland, with estimates of  $F_w$  ranging from 0.2 to 4.4 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. Our estimates for sagebrush steppes (0.68–1.31 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) lie between the estimates for northern mixed prairies in Alberta, Canada, and mixed prairies in North Dakota and Montana, which have climatic conditions similar to the shrub-steppes of the US Intermountain West. Apparently, in contrast to data for European forests (Valentini et al., 2000, Table 1), which did not show close correlation of annual ecosystem respiration with annual temperature, non-forest ecosystems, especially during wintertime, are under more tight temperature control, as demonstrated by the strong latitudinal trend in Table 3. A more detailed comparative ecological analysis of a wider sample of winter respiration datasets presently available from AgriFlux, Ameriflux, GREENGRASS, and CarboMont networks will be helpful in further modeling analyses of the dependence of  $F_w$  on environmental drivers.

To evaluate the contribution of winter CO<sub>2</sub> fluxes to the annual carbon budget of sagebrush-steppe ecosystems, our estimates of winter total fluxes at the Dubois (177.3 g CO<sub>2</sub> m<sup>-2</sup> for the January 1–March 15 and November 1–December 31, 2000 period) and at the Burns site (92.4 g CO<sub>2</sub> m<sup>-2</sup> for the November 1, 2000–March 15, 2001 period) may be compared to estimates of total annual ecosystem respiration of 1453 g CO<sub>2</sub> m<sup>-2</sup> year<sup>-1</sup> at the Dubois site, 2000, and 825 g CO<sub>2</sub> m<sup>-2</sup> year<sup>-1</sup> at the Burns site (average for 1069 g CO<sub>2</sub> m<sup>-2</sup> year<sup>-1</sup> for 2000 and 581 g

Table 3  
Average rates of wintertime CO<sub>2</sub> evolution ( $F_w$ ) from various non-forest ecosystems

| Location                                    | Ecosystem                    | $F_w$ (g CO <sub>2</sub> m <sup>-2</sup> day <sup>-1</sup> ) | Method                 | Reference  |
|---|------------------------------|--|------------------------|--|
| Alaska                                      | Arctic tundra                | 0.23   | Chamber                | Fahnestock et al., 1999  |
| Kolyma, NE Siberia                          | Automorphic arctic tundra    | 0.25   | Chamber                | Fedorov-Davydov, 1998  |
| Kolyma, NE Siberia                          | Arctic tundra                | 0.55   | Chamber                | Zimov et al., 1993   |
| Kolyma, NE Siberia                          | Sedge-marsh tundra           | 0.6  | Chamber                | Fedorov-Davydov, 1998  |
| Barrington, New Hampshire                   | <i>Sphagnum</i> peatland     | 0.66   | Chamber                | Bubier et al., 2002  |
| Lethbridge, Alberta, dry years (1999, 2000) | Northern mixed prairie       | 0.56   | Tower, eddy covariance | Flanagan et al., 2002  |
| Lethbridge, Alberta, wet year (1998)        | Northern mixed prairie       | 0.77   | Tower, eddy covariance | Flanagan et al., 2002  |
| Burns, Oregon                               | Sagebrush steppe             | 0.68   | Tower, BREB            | This study   |
| Central Plains Experimental Range, Colorado | Shortgrass steppe            | 1.06   | Tower, BREB            | Morgan, J.A., personal communication   |
| INEEL, Idaho                                | Sagebrush steppe             | 1.23   | Tower, BREB            | This study   |
| Dubois, Idaho                               | Sagebrush steppe             | 1.31   | Tower, BREB            | This study   |
| Mandan, North Dakota                        | Mixed prairie                | 1.7  | Tower, BREB            | Frank and Dugas, 2001  |
| Miles City, Montana                         | Mixed prairie                | 1.83   | Tower, BREB            | Haferkamp, M.R., personal communication  |
| Woodward, Oklahoma (1999–2001)              | Mixed prairie                | 2.03   | Tower, BREB            | Sims and Bradford, 2001; Sims, P.L. and Bradford, J.A., personal communication |
| Shidler, Oklahoma, 1997/1998                | Tallgrass prairie            | 2.25   | Tower, eddy covariance | Verma, 2001; Gilmanov et al., 2003b  |
| El Reno, Oklahoma, winter 2002/2003         | Tallgrass prairie            | 2.30   | Tower, BREB            | Dugas, W.A. and Mayeux, H.S., personal communication                           |
| Iowa, February                              | Switchgrass                  | 2.8  | Chamber                | Raich and Tufekcioglu, 2000  |
| Konza Prairie, Kansas, late fall            | Tallgrass prairie            | 3.5  | Tower, eddy covariance | Ham and Knapp, 1998  |
| Switzerland, winter 1997/1998               | Lowland calcareous grassland | 4.4  | Chamber                | Volk and Niklaus, 2002   |

CO<sub>2</sub> m<sup>-2</sup> year<sup>-1</sup> for 2001) (Gilmanov et al., 2004). We estimated that wintertime respiration at Dubois constitutes 12% and at Burns 11% of the total annual ecosystem respiration in these sagebrush-steppe ecosystems.

## 5. Conclusions

Measurements of net CO<sub>2</sub> exchange at sagebrush-steppe sites in Idaho and Oregon during the winter showed that CO<sub>2</sub> efflux averaged  $1.31 \pm 0.80$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for the Dubois site,  $1.23 \pm 1.19$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for the INEEL site, and  $0.68 \pm 0.56$  g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for the Burns site. These average values agree with estimates of winter respiration from

other northern latitude ecosystems. At certain times, often associated with freeze–thaw events and high wind speed, wintertime pulses of CO<sub>2</sub> effluxes three to six times higher than average were observed at all three of our study sites. Over the annual cycle, wintertime fluxes constitute no less than 10% of the total ecosystem respiration in sagebrush-steppe ecosystems. Multivariate analysis showed that winter CO<sub>2</sub> efflux was most closely associated with soil temperature, wind speed, and snow depth, explaining 58–73% of the variability in efflux rates. Coefficients of the multivariate models for our various study sites, however, were very site-specific and year-specific, as demonstrated by poor performance of Dubois and Burns models on the INEEL 2000–2001 validation dataset. These models can be used to gap-fill values of efflux for days

with missing measurements during particular years for which they were derived. Additional studies, e.g., the use of process-based mathematical models, are needed before predictive models can be developed to describe winter CO<sub>2</sub> effluxes in sagebrush-steppe ecosystems.

## Acknowledgements

This study was supported in part by a grant from the Global Livestock Collaborative Research Support Program funded by USAID through The University of California-Davis. Special gratitude is expressed to Prof. W. Dugas for his assistance with estimating the effect of snow cover on BREB measurements. We are grateful to Drs. J. Bradford, W. Dugas, A. Frank, M. Haferkamp, J. Morgan, H. Mayeux, and P. Sims for permission to cite the unpublished results of winter flux measurements at their USDA-ARS AgriFlux Network locations, and to Drs. J. Prueger and W. Massman for discussions of wintertime CO<sub>2</sub> flux pulses.

## References

- Anderson, J.E., Ruppel, K.T., Glennon, M.M., Holte, K.E., Rope, R.C., 1996. Plant communities, ethnoecology, and flora of the Idaho National Engineering Laboratory. ESRF-005. In: Environmental Science and Research Foundation, Idaho Falls, Idaho.
- Angell, R.F., Svejcar, T., Bates, J., Saliendra, N.Z., Johnson, D.A., 2001. Bowen ratio and closed chamber carbon dioxide flux measurements over sagebrush steppe vegetation. *Agric. Forest Meteorol.* 108, 153–161.
- Anonymous, 1993. Climatological Data Annual Summary—Idaho. NOAA Report, vol. 96, No. 13.
- Blaisdell, J.P., 1958. Seasonal development and yield of native plants on the Upper Snake River Plains and their relation to certain climatic factors. *US Dept. Agric. Tech. Bull.* 1190, 68.
- Bubier, J., Crill, P., Mosedale, A., 2002. Net ecosystem CO<sub>2</sub> exchange measured by autochambers during the snow-covered season at a temperate peatland. *Hydrol. Processes* 16, 3667–3682.
- Chapin III, F.S., Shaver, G.R., Biblin, A.E., Nadelhoffer, K.J., Laundre, J.A., 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76, 694–711.
- Coyne, P.I., Kelley, J.J., 1971. Release of carbon dioxide from frozen soil to the arctic atmosphere. *Nature* 234, 407–408.
- Crill, P.M., 1991. Seasonal pattern of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochem. Cycles* 5, 319–334.
- Duiker, S.W., Lal, R., 2000. Carbon budget study using CO<sub>2</sub> flux measurements from a no till system in Central Ohio. *Soil Tillage Res.* 54, 21–30.
- Dugas, W.A., 1993. Micrometeorological and chamber measurements of CO<sub>2</sub> flux from bare soil. *Agric. Forest Meteorol.* 67, 115–128.
- Dugas, W.A., Heuer, M.L., Mayeux, H.S., 1999. Carbon dioxide fluxes over bermudagrass, native prairie, and sorghum. *Agric. Forest Meteorol.* 93, 121–139.
- Elberling, B., Brandt, K.K., 2003. Uncoupling of microbial CO<sub>2</sub> production and release in frozen soil and its implications for field studies of arctic C cycling. *Soil Biol. Biochem.* 35, 263–272.
- Fahnestock, J.T., Jones, M.H., Welker, J.M., 1999. Wintertime CO<sub>2</sub> efflux from arctic soils: implications for annual carbon budgets. *Global Biogeochem. Cycles* 13, 775–779.
- Falge, E., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.W., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., Baldocchi, D., Olson, R., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. Forest Meteorol.* 107, 43–69.
- Fedorov-Davydov, D.G., 1998. Respiration activity in tundra biocenoses and soils of the Kolyma Lowland. *Eurasian Soil Sci.* 31, 263–273.
- Fedorov-Davydov, D.G., Gilichinsky, D.A., 1993. Features of the dynamics of CO<sub>2</sub> evolution from frozen soils. [Osobennosti dinamiki vydeleniya CO<sub>2</sub> iz merzlykh pochv]. In: Zavarzin, G.A., Kudeyarov, V.N. (Eds.), *Dykhanie Pochvy* [Soil Respiration]. Institute Pochvovedeniya i Fotosinteza, Pushchino, pp. 76–100.
- Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biol.* 8, 599–615.
- FLUXNET – Integrated Worldwide CO<sub>2</sub> Flux Measurements. <http://daac.ornl.gov/FLUXNET/>.
- Frank, A.B., Dugas, W.A., 2001. Carbon dioxide fluxes over a northern, semi-arid, mixed-grass prairie. *Agric. Forest Meteorol.* 108, 317–326.
- Frank, A.B., Liebig, M.A., Hanson, J.D., 2002. Soil carbon dioxide fluxes in northern semiarid grassland. *Soil Biol. Biochem.* 34, 1235–1241.
- Frank, A.B., Sims, P.L., Bradford, J.A., Mielenick, P.C., Dugas, W.A., Mayeux, H.S., 2000. Carbon dioxide fluxes over three Great Plains grasslands. In: Follett, R.F., Kimble, J.M., Lal, R. (Eds.), *Potential of U.S. Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect*. Lewis Publishers, Boca Raton, pp. 99–115.
- Gilmanov, T.G., Johnson, D.A., Saliendra, N.Z., 2003a. Growing season CO<sub>2</sub> fluxes in a sagebrush-steppe ecosystem in Idaho: Bowen ratio/energy balance measurements and modeling. *Basic Appl. Ecol.* 4, 167–183.
- Gilmanov, T.G., Verma, S.B., Sims, P.L., Meyers, T.P., Bradford, J.A., Burba, G.G., Suyker, A.E., 2003b. Gross primary production and light response parameters of four Southern Plains ecosystems estimated using long-term CO<sub>2</sub>-flux tower

- measurements. *Global Biogeochem. Cycles* 17, 1071, doi: 10.1029/2002GB002023.
- Gilmanov, T.G., Svecjar, T., Johnson, D.A., Wylie, B.K., Angell, R.F., Saliendra, N.Z., Gross primary production, ecosystem respiration, and light-use efficiency of sagebrush ecosystems of the U.S. Intermountain West in relation to NDVI: partitioning and scaling-up of tower CO<sub>2</sub> fluxes, in preparation.
- Grogan, P., Illeris, L., Michelsen, A., Jonasson, S., 2001. Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO<sub>2</sub> production in sub-arctic heath tundra. *Climatic Change* 50, 129–142.
- Ham, J.M., Knapp, A.K., 1998. Fluxes of CO<sub>2</sub>, water vapor, and energy from a prairie ecosystem during the seasonal transition from carbon sink to carbon source. *Agric. Forest Meteorol.* 89, 1–14.
- Houghton, R.A., 2000. Interannual variability in the global carbon cycle. *J. Geophys. Res. D Atmos.* 105, 20121–20130.
- Houghton, R.A., Davidson, E.A., Woodwell, G.M., 1998. Missing sinks, feedbacks, and understanding the role of terrestrial ecosystems in the global C balance. *Global Biogeochem. Cycles* 12, 25–34.
- Johnson, D.A., Gilmanov, T.G., Saliendra, N.Z., Walker, J.W., 1999. Carbon dioxide fluxes on control and burned sites on sagebrush-steppe rangeland in the western USA. In: Eldridge, D., Freudenberger, D. (Eds.), *People and Rangelands. Building the Future. Proceedings of the VI International Rangeland Congress*, vol. 2, Organizing Committee of the VI International Rangeland Congress, Townsville, Queensland, Australia, pp. 746–747.
- Johnson, P.L., Kelley Jr., J.J., 1970. Dynamics of carbon dioxide and productivity in an arctic biosphere. *Ecology* 51, 73–80.
- Jones, M.H., Fahnestock, J.T., Welker, J.M., 1999. Early and late winter CO<sub>2</sub> efflux from arctic tundra in the Kuparuk River Watershed, Alaska, U.S.A., Arctic, Antarctic. *Alpine Res.* 31, 187–190.
- Kelley Jr., J.J., Weaver, D.F., Smith, B.P., 1968. The variation of carbon dioxide under the snow in the Arctic. *Ecology* 49, 358–361.
- Kim, J., Verma, S.B., Clement, R.J., 1992. Carbon dioxide budget in a temperate grassland ecosystem. *J. Geophys. Res.* 97 (D5), 6057–6063.
- King, A.W., O'Neill, R.V., 1989. Using ecosystem models to predict regional CO<sub>2</sub> exchange between the atmosphere and the terrestrial biosphere. *Global Biogeochem. Cycles* 3, 337–361.
- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic matter storage. *Soil Biol. Biochem.* 27, 753–760.
- Laycock, W.A., 1967. How heavy grazing and protection affect sagebrush-grass ranges. *J. Range Manage.* 20, 206–213.
- LeCain, D.R., Morgan, J.A., Schuman, G.E., Reeder, J.D., Hart, R.H., 2000. Carbon exchange rates in grazed and ungrazed pastures of Wyoming. *J. Range Manage.* 53, 199–206.
- Lentz, R.D., Simonson, G.H., 1986. Detailed soils inventory and associated vegetation of Squaw Butte Range Experiment Station. Oregon State University Agricultural Experiment Station Special Report 760.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8, 315–323.
- Mariko, S., Bekku, Y., Koizumi, H., 1994. Efflux of carbon dioxide from snow-covered forest floor. *Ecol. Res.* 9, 343–350.
- Massman, W., Hudnell, L., Rochelle, S., Sommerfield, R., Zeller, K., Hehn, T., 1995. CO<sub>2</sub> flux through a Wyoming seasonal snowpack: diffusional and pressure pumping effects. In: *Proceedings of Symposium on Biogeochemistry of Seasonally Snow-covered Catchments*, Boulder, IAHS Publication, vol. 228. pp. 71–79.
- Meyers, T.P., 2001. A comparison of summertime water and CO<sub>2</sub> fluxes over rangeland for well watered and drought conditions. *Agric. Forest Meteorol.* 106, 205–214.
- Mielnick, P.C., Dugas, W.A., 2000. Soil CO<sub>2</sub> flux in a tallgrass prairie. *Soil Biol. Biochem.* 32, 221–228.
- NOAA, 1999. Climatological data: Oregon. National Oceanic and Atmospheric Administration, 102, pp. 1–45.
- Natural Resource Conservation Service (NRCS), 1995. Soil Investigation of ARS United States Experimental Station Headquarters Range. U.S.D.A. National Resource Conservation Service, Rexburg, Idaho.
- Oechel, W.C., Vourlitis, G., Hastings, S.J., 1997. Cold season CO<sub>2</sub> emission from arctic soils. *Global Biogeochem. Cycles* 11, 163–172.
- Panikov, N.S., 1997. A kinetic approach to microbial ecology in arctic and boreal ecosystems in relation to global change. In: Oechel, W.C., Callahan, T., Gilmanov, T.G., Holten, J.I., Maxwell, B., Molau, U., Sveinbjörnsson, B. (Eds.), *Global Change and Arctic Terrestrial Ecosystems*. New York, Springer Verlag, pp. 171–188.
- Panikov, N.S., Dedysh, S.N., 2000. Cold season CH<sub>4</sub> and CO<sub>2</sub> emission from boreal peat bogs (West Siberia): winter fluxes and thaw activation dynamics. *Global Biogeochem. Cycles* 14, 1071–1080.
- Peterjohn, W.T., Melillo, J.M., Steudler, P.A., Newkirk, K.M., Bowles, F.P., Aber, J.D., 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecol. Appl.* 4, 617–625.
- Priemé, A., Christensen, S., 2001. Natural perturbations, drying-wetting and freezing-thawing cycles, and the emission of nitrous oxide, carbon dioxide and methane from farmed organic soils. *Soil Biol. Biochem.* 33, 2083–2091.
- Prueger, J.H., Hatfield, J.L., 2002. Annual patterns of carbon dioxide fluxes above corn and soybean production systems. In: *USDA Symposium on Natural Resource Management to Offset Greenhouse Gas Emissions*, Raleigh, North Carolina, November 19–21, p. 121.
- Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochem. Cycles* 9, 23–36.
- Raich, J.W., Tufekcioglu, A., 2000. Vegetation and soil respiration: correlations and controls. *Biogeochem.* 48, 71–90.
- Ruimy, A., Jarvis, P.G., Baldocchi, D.D., 1995. CO<sub>2</sub> fluxes over plant canopies and solar radiation: a review. *Adv. Ecol. Res.* 26, 1–68.
- Ruimy, A., Kergoat, L., Field, C., Saugier, B., 1996. The use of CO<sub>2</sub> flux measurements in models of the global terrestrial carbon budget. *Global Change Biol.* 2, 287–296.
- Saigusa, N., Oikawa, T., Liu, S., 1998. Seasonal variations of the exchange of CO<sub>2</sub> and H<sub>2</sub>O between a grassland and the

- atmosphere: an experimental study. *Agric. Forest Meteorol.* 89, 131–139.
- Schimel, J.P., Clein, J.S., 1996. Microbial response to freeze–thaw cycles in tundra and taiga soils. *Soil Biol. Biochem.* 28, 1061–1066.
- Sims, P.L., Bradford, J.A., 2001. Carbon dioxide fluxes in a southern plains prairie. *Agric. Forest Meteorol.* 109, 117–134.
- Sjögersten, S., Wookey, P.A., 2002. Climatic and resource quality controls on soil respiration across a forest-tundra ecotone in Swedish Lapland. *Soil Biol. Biochem.* 34, 1633–1646.
- Skogland, T., Lomel, S., Goksoyr, J., 1988. Respiratory burst after freezing and thawing of soil: experiments with soil bacteria. *Soil Biol. Biochem.* 20, 851–856.
- Smith, V.R., 2003. Soil respiration and its determinants on a sub-Antarctic island. *Soil Biol. Biochem.* 35, 77–91.
- Sneva, F.A., 1982. Relation of precipitation and temperature with yield of herbaceous plants in eastern Oregon. *Int. J. Biometeorol.* 26, 263–276.
- Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2004. Soil Series Classification Database [Online WWW]. Available URL: <http://soils.usda.gov/technical/classification/scfile/index.html>, (Accessed 13 May 2004).
- Solomon, D.K., Cerling, T.E., 1987. The annual carbon dioxide cycle in a montane soil: observations, modeling and implications for weathering. *Water Resour. Res.* 23, 2257–2265.
- Sommerfeld, R.A., Massman, W.J., Musselman, R.C., Mosier, A.R., 1996. Diffusional flux of CO<sub>2</sub> through snow: spatial and temporal variability among alpine-subalpine sites. *Global Biogeochem. Cycles* 10, 473–482.
- Sommerfeld, R.A., Mosier, A.R., Musselman, R.C., 1993. CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O flux through a Wyoming snowpack and implications for global budgets. *Nature* 361, 140–142.
- Statsoft, Inc. 2001. Statistica™, vol. III. Statistics II. StatSoft Inc., Tulsa, Oklahoma.
- Suyker, A.E., Verma, S.B., 2001. Year-round observations of the net ecosystem exchange of carbon dioxide in a native tallgrass prairie. *Global Change Biol.* 7, 279–289.
- Svejcar, T., Mayeux, H., Angell, R., 1997. The rangeland carbon dioxide flux project. *Rangelands* 19, 16–18.
- Valentini, R., Gamon, J.A., Field, C.B., 1995. Ecosystem gas exchange in a California grassland: seasonal patterns and implications for scaling. *Ecology* 76, 1940–1952.
- Valentini, R., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, U., Berbigler, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., Matteucci, G., Dolman, A.J., Schulze, E.D., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–865.
- Verma, S., 2001. Shidler site data set. <http://public.ornl.gov/ameriflux/>.
- Volk, M., Niklaus, P.A., 2002. Respiratory carbon loss of calcareous grassland in winter shows no effect of 4 years' CO<sub>2</sub> enrichment. *Funct. Ecol.* 16, 162–166.
- Walker, M.D., Bardsley, T., Brooks, P.D., Fahnestock, J.T., Jones, M.H., Losleben, M., Parsons, A.N., Seastedt, T.R., Turner, P.L., Walker, D.A., Welker, J.M., Arft, A.M., 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. *Hydrol. Process* 13, 2315–2330.
- Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurement for density effect due to heat and water vapour transfer. *Q. J. Royal Meteorol. Soc.* 106, 85–100.
- Welker, J.M., Fahnestock, J.T., Jones, M.H., 2000. Annual CO<sub>2</sub> flux in dry and moist arctic tundra: field responses to increases in summer temperatures and winter snow depth. *Climatic Change* 44, 139–150.
- Wolfram Research, 2000. Mathematica 4.0. Standard Add-on Packages. Wolfram Media.
- World Resources Institute, 1986. World Resources, 1986. Basic Books Inc., New York.
- Zimov, S.A., Zimova, G.M., Davidov, S.P., Davidova, A.I., Voropaev, Y.V., Voropaeva, Z.V., Prosiannikov, S.F., Prosiannikova, O.V., Semiletova, I.V., Semiletov, I.P., 1993. Winter biotic activity and production of CO<sub>2</sub> in Siberian soils: a factor in the greenhouse effect. *J. Geophys. Res.* 98 (D3), 5017–5023.