

Winter and early spring CO₂ efflux from tundra communities of northern Alaska

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Abstract. Carbon dioxide concentrations through snow were measured in different arctic tundra communities on the North Slope of Alaska during winter and early spring of 1996. Subnivean CO₂ concentrations were always higher than atmospheric CO₂. A steady state diffusion model was used to generate conservative estimates of CO₂ flux to the atmosphere. The magnitude of CO₂ efflux differed with tundra community type, and rates of carbon release increased from March to May. Winter CO₂ efflux was highest in riparian and snow bed communities and lowest in dry heath, upland tussock, and wet sedge communities. Snow generally accrues earlier in winter and is deeper in riparian and snow bed communities compared with other tundra communities, which are typically windswept and do not accumulate much snow during the winter. These results support the hypothesis that early and deep snow accumulation may insulate microbial populations from very cold temperatures, allowing sites with earlier snow cover to sustain higher levels of activity throughout winter compared to communities that have later developing snow cover. Extrapolating our estimates of CO₂ efflux to the entire snow-covered season indicates that total carbon flux during winter in the Arctic is 13–109 kg CO₂-C ha⁻¹, depending on the vegetation community type. Wintertime CO₂ flux is a potentially important, yet largely overlooked, part of the annual carbon cycle of tundra, and carbon release during winter should be accounted for in estimates of annual carbon balance in arctic ecosystems.

1. Introduction

Arctic tundra ecosystems have been considered sinks for atmospheric carbon dioxide during historic and recent geological times [Miller, 1981; Miller *et al.*, 1983; Billings, 1987; Gorham, 1991; Oechel and Billings, 1992]. However, recent measurements of CO₂ flux in northern ecosystems indicate that some plant communities in the Arctic may now be net sources of carbon to the atmosphere rather than sinks [Billings *et al.*, 1982; Grulke *et al.*, 1990; Oechel and Billings, 1992; Oechel *et al.*, 1993, 1995; Ciaia *et al.*, 1995]. Given the large carbon reserves in arctic soils [Michaelson *et al.*, 1996], the release of CO₂ from arctic ecosystems may exert a positive feedback on atmospheric CO₂ levels and greenhouse warming [Oechel *et al.*, 1993]. Consequently, there has been a concerted effort to quantify the current carbon balance of northern ecosystems and to assess the changes in carbon balance that may have taken place over the last few decades [e.g., Oechel *et al.*, 1995].

In arctic ecosystems, most estimations of annual carbon flux have been based primarily on measurements taken during the spring and summer months [Chapin *et al.*, 1980; Grulke *et al.*, 1990; Giblin *et al.*, 1991; Oechel *et al.*, 1993, 1994, 1995; Raich and Schlesinger, 1992], in part due to methodological limitations, but also reflecting the assumption that rates of winter

decomposition and respiratory release are minimal in frozen or snow-covered soils. However, significant microbial respiration has been measured in soils at subzero temperatures [Coxson and Parkinson, 1987; Clein and Schimel, 1995] and in snow-covered soils in several northern ecosystems [e.g., Skogland *et al.*, 1988; Taylor and Jones, 1990; Zimov *et al.*, 1993, 1996], and CO₂ concentrations are known to increase in winter under snow in the Arctic [Kelley *et al.*, 1968; Coyne and Kelley, 1974; Kling *et al.*, 1991].

Recent work in arctic and alpine regions suggests that there is considerable biological activity under snow resulting in fluxes of CO₂ from soil to the atmosphere through much of the winter [Sommerfeld *et al.*, 1993, 1996; Zimov *et al.*, 1993, 1996; Brooks *et al.*, 1995, 1996, 1997; Oechel *et al.*, 1997]. These studies also provide evidence of considerable spatial and temporal variability in the magnitude of winter CO₂ flux. Collectively, these findings suggest that nongrowing season respiration may contribute significantly to annual CO₂ flux in tundra ecosystems, especially since winter is the dominant season in the Arctic. Given the spatial extent of arctic ecosystems and of seasonal snow cover in the northern hemisphere, CO₂ fluxes during winter may represent a significant portion of the annual global carbon balance as well [Raich and Potter, 1995; Zimov *et al.*, 1996]. Moreover, since wintertime CO₂ fluxes have not been included in annual carbon budgets, current estimates of annual CO₂ loss from tundra ecosystems [e.g., Raich and Schlesinger, 1992] may be underestimated.

The purpose of our research was to obtain estimates of the magnitude of wintertime CO₂ flux through snow in the tundra of northern Alaska. We also examined the spatial and temporal heterogeneity of CO₂ production by measuring winter and early spring carbon release in a variety of different tundra plant communities in the Arctic.

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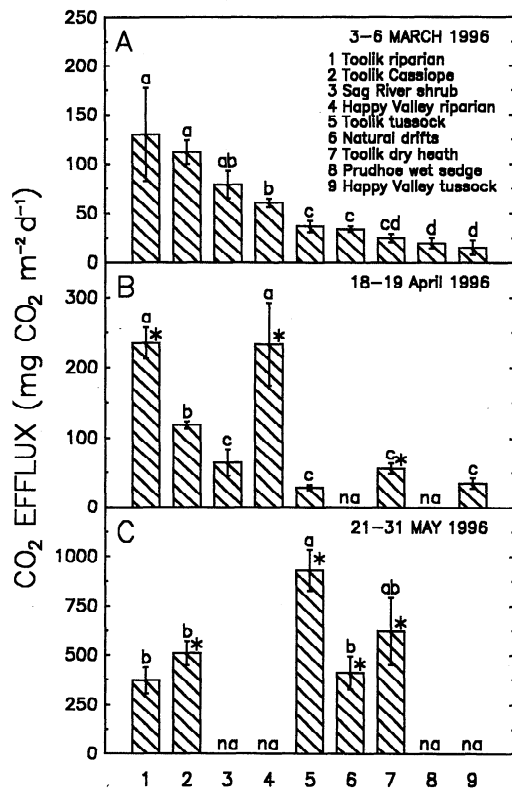


Figure 1. Mean (± 1 SE) CO₂ efflux ($\text{mg CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) for tundra vegetation communities on the North Slope of Alaska on (a) March 3–6, (b) April 18–19, and (c) May 21–31, 1996. Different letters above columns indicate significant ($P < 0.05$) differences between communities on each sampling date. Significant ($P < 0.05$) differences in flux rates between successive months are indicated by asterisks; na, data missing for some communities in April and May due to logistical constraints.

2. Materials and Methods

Carbon dioxide fluxes were measured during March 3–6, April 18–19, and May 21–31, 1996, in different Arctic tundra communities north of the Brooks Range, Alaska. Intensive measurements were made in natural snow drift and snow bed (*Cassiope tetragona*) communities, in riparian areas (*Salix* communities), and in upland tussock (moist acidic) and dry heath tundra communities around Toolik Lake ($68^{\circ}38'N$, $149^{\circ}38'W$). Additional measurements were made in upland tussock and riparian communities at Happy Valley ($69^{\circ}17'N$, $148^{\circ}82'W$), in interchannel shrub communities among braids of the Sagavanirktok River ($69^{\circ}30'N$, $148^{\circ}63'W$), and in wet sedge communities near Prudhoe Bay ($70^{\circ}23'N$, $148^{\circ}45'W$).

Carbon dioxide concentrations under snow and within snowpacks were measured using an infrared gas analyzer (PP Systems, model EGM-1) connected with 3 mm (ID) Teflon tubing to a stainless steel gas-sampling probe, which was inserted through the snowpack. Concentrations of CO₂ were measured at the snow surface and at ~ 50 cm intervals down to the ground surface. Snow depths were generally between 50 cm and 300 cm and varied with topography and vegetation. In each plant community, profiles of snow density (ρ) and texture were obtained from snow pits, and temperature within the snowpack was measured at ~ 25 cm intervals.

A steady state diffusion model [Sommerfeld *et al.*, 1993],

designed to account for changes in snowpack tortuosity and porosity associated with snow layers of different densities, was used to calculate diffusional CO₂ flux rates through snow based on our measurements along each vertical profile. Flux rates were calculated using Fick's law,

$$J_g = D_g(d[g]/dz)f$$

where J_g is the gas flux, D_g is the diffusion coefficient, g is the measured CO₂ concentration, z is the snow depth, and f is the porosity (calculated as $[1 - \rho]/\rho_{ice}$). Since most of our measurements were taken at soil temperatures between 0°C and -10°C , we used an average CO₂ diffusion coefficient of $0.129 \text{ cm}^2 \text{ s}^{-1}$. Molar volumes of CO₂ were corrected for ambient temperature and average atmospheric pressure in this region (i.e., we disregarded the potential effect of turbulent atmospheric pressure fluctuations on diffusion rates [Massman *et al.*, 1997]). More complete descriptions of this method for calculating gas fluxes through snow can be found in the works of Sommerfeld *et al.* [1996] and Brooks *et al.* [1997].

Differences ($P < 0.05$) in CO₂ efflux between communities and between sampling dates were tested using the general linear models procedure of the *Statistical Analysis System* [SAS, 1989], with community type and month as main variables. In our calculations we used the lowest porosity value for each vertical profile and reduced our final flux estimates by 35% [du Plessis and Masliyah, 1991] to account for tortuosity. Therefore our estimates of winter and spring CO₂ efflux from arctic tundra communities are conservative.

As part of this study, we calculated the net CO₂ efflux from different tundra communities of the Toolik Lake region (2078.7 ha) in order to extrapolate winter CO₂ efflux to larger areas of the North Slope of Alaska. These calculations were based on cover estimates of the different vegetation types around Toolik Lake (D. A. Walker, unpublished data, 1997) and on mean winter CO₂ efflux measurements from March and April. Efflux rates in winter appear lowest in March and April [J. T. Fahnestock, unpublished data, 1997; Oechel *et al.*, 1997]. Therefore our estimates of net ecosystem CO₂ efflux during winter are probably low. We also examined the relationship between rates of CO₂ flux in winter and soil temperature, snow depth, and sites with early or late winter snow accumulations.

3. Results and Discussion

Carbon dioxide concentrations beneath and through the snow were always higher than atmospheric CO₂ in March, April, and May 1996, resulting in net carbon flux to the atmosphere throughout the winter from all tundra plant communities (Figure 1). Mean CO₂ efflux across all plant communities around Toolik Lake, where our data are most extensive, averaged $629 \text{ g CO}_2 \text{ ha}^{-1} \text{ d}^{-1}$ in March, $1036 \text{ g CO}_2 \text{ ha}^{-1} \text{ d}^{-1}$ in April, and $5263 \text{ g CO}_2 \text{ ha}^{-1} \text{ d}^{-1}$ in May. In terms of carbon loss from soil, these fluxes are equivalent to 0.02, 0.03, and $0.14 \text{ g CO}_2\text{-C m}^{-2}$ lost daily to the atmosphere in March, April, and May, respectively.

The magnitude of CO₂ efflux differed substantially between tundra community types, and CO₂ release rates increased considerably from March to May. In March the highest fluxes were in riparian and natural snow bed (*Cassiope*) communities around Toolik Lake, with rates of 120 and $102 \text{ mg CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively (Figure 1a). Carbon efflux was also fairly high in the Sagavanirktok River shrub communities (74 mg CO_2

Table 1. Tundra Vegetation Community Types and Their Area (ha), and Winter Carbon Dioxide Efflux Estimates for the Toolik Lake Region, Alaska

	Area, ha	Relative Area	CO ₂ Efflux, kg CO ₂ ha ⁻¹ d ⁻¹	Ecosystem Flux, kg CO ₂ ha ⁻¹ d ⁻¹ * area	Percent of Total Flux
Vegetation community ^a					
rock, barren, revegetated	53.1	2.6	0 ^b	0	0
dry tundra	524.8	25.3	0.5	239	30.6
snow bed communities	93.9	4.5	1.5	140	17.9
moist nonacidic tundra	314.1	15.1	0 ^b	0	0
moist acidic tundra	620.8	29.9	0.3	203	26.0
moist dwarf shrub tundra	54.2	2.6	0 ^b	0	0
riparian shrub lands	95.3	4.6	1.8	174	22.3
wet graminoid tundra	124.1	6.0	0.2 ^c	25	3.2
water	198.5	9.6	0 ^b	0	0
Total area and flux estimates	2078.7 ha	100%		781 kg CO ₂ d ⁻¹	100%

Ecosystem CO₂ flux estimates for winter were generated by multiplying community cover area by mean CO₂ flux measurements for each community in March and April 1996 and summing community types.

^aVegetation data are from a 1:5000-scale map using hierarchical geographic information systems.

^bMeasurements were not taken in these communities, thus CO₂ efflux was conservatively estimated to be zero.

^cFlux estimates from the Prudhoe Bay wet sedge communities.

m⁻² d⁻¹) and in the Happy Valley riparian communities (56 mg CO₂ m⁻² d⁻¹). In March, CO₂ efflux was 34 and 32 mg CO₂ m⁻² d⁻¹, respectively, in upland tussock tundra and natural snow drift communities around Toolik Lake (Figure 1a). These communities had lower rates of CO₂ flux than the Toolik riparian, snow bed, and Sagavanirktok shrub communities but were higher than Prudhoe wet sedge (19 mg CO₂ m⁻² d⁻¹) and Happy Valley tussock tundra (14 mg CO₂ m⁻² d⁻¹) communities. Carbon dioxide efflux in March was 23 mg CO₂ m⁻² d⁻¹ in Toolik dry heath communities.

Rates of CO₂ efflux were 2 times greater in April than in March in Toolik (222 mg CO₂ m⁻² d⁻¹) and Happy Valley (213 mg CO₂ m⁻² d⁻¹) riparian communities and in Toolik dry heath (61 mg CO₂ m⁻² d⁻¹) communities ($P < 0.05$, Figure 1b). There were no significant changes, however, in rates of CO₂ release in the other tundra plant communities between March and April. In late May, however, CO₂ flux rates increased substantially in all plant communities. Carbon dioxide efflux in May was 342 and 379 mg CO₂ m⁻² d⁻¹, respectively, in riparian and natural snow drift communities at Toolik Lake (Figure 1c). The largest increases in CO₂ efflux in May were in moist tussock, dry heath, and *Cassiope* communities at Toolik Lake, which increased to 860, 574, and 472 mg CO₂ m⁻² d⁻¹, respectively ($P < 0.05$, Figure 1c).

The heterogeneity of CO₂ production in winter is important when examining the relative contribution of different tundra community types to total CO₂ production. For instance, moist acidic and dry heath tundra account for about 55% of the total land area around Toolik Lake and accounted for about 58% of the total CO₂ flux in March and April (Table 1). In contrast, riparian areas and snow bed communities (i.e., natural drifts and *Cassiope* sites) account for only 9% of the vegetation in the Toolik Lake region, yet together contributed over 38% of the total CO₂ released in March and April (Table 1). These latter areas generally had the highest winter fluxes (Figure 1) and typically receive earlier snow cover than other tundra plant communities.

Differences in the magnitude of winter CO₂ flux rates, both within and between plant community types and during the winter season, have been shown in other studies as well. In early studies, Kelley et al. [1968] found CO₂ concentrations under snow near Barrow, Alaska, to vary throughout the win-

ter season and to be especially high shortly after first snowfall and again as snow melted in late spring. Zimov et al. [1996] also showed a strong seasonal component to winter CO₂ production in forest tundra in northern Russia, with high rates of CO₂ efflux in September–November and May and at least some variation in CO₂ flux between different ground layer vegetation types. Similar flux patterns were found by Oechel et al. [1997] in moist tussock tundra and coastal wet sedge ecosystems in northern Alaska. Brooks et al. [1996] found no measurable CO₂ fluxes from December to February at two alpine sites in Colorado. However, at the same sites they found fluxes of 55–90 mg CO₂-C m⁻² d⁻¹ in March and over 800 mg CO₂-C m⁻² d⁻¹ in May. In contrast to the alpine sites, Brooks et al. [1996] did not detect any CO₂ production at a treeline site until May. They also found that CO₂ concentrations under snow exhibited large microsite heterogeneity, with coefficients of variation in the range of 20–25%. Similarly, Sommerfeld et al. [1993] found variation in CO₂ efflux in alpine and subalpine communities to be greater within than between communities. In a longer-term study, Sommerfeld et al. [1996] found increasing variability in CO₂ production from small (1–10 m) to large (10–100 m and 100–1000 m) scales and attributed this variability to differences in snow depth at the small scale and to differences in ecosystems and elevations at the larger scale. As these studies clearly illustrate, the spatial pattern of CO₂ production under snow is highly heterogeneous and typically increases as winter progresses into spring.

Variation in CO₂ flux between and within communities and during the winter season has generally been attributed to changes in soil temperature during the winter, leading to changes in the availability of free water in the soil and to differences in snow depth and timing of accumulation and dispersion [e.g., Kelley et al., 1968; Coyne and Kelley, 1974; Brooks et al., 1996, 1997; Sommerfeld et al., 1996; Zimov et al., 1996]. Average soil surface temperature under snow in the communities we studied increased slightly from March (−5.6°C) to April (−4.2°C) to May (−3.6°C), lending some support to the hypothesis of higher rates of subnivean respiration as soil temperatures and free water availability increase. However, snow and soil surface temperatures were not notably different between plant communities around Toolik Lake on each sampling date in this study (data not shown), suggesting

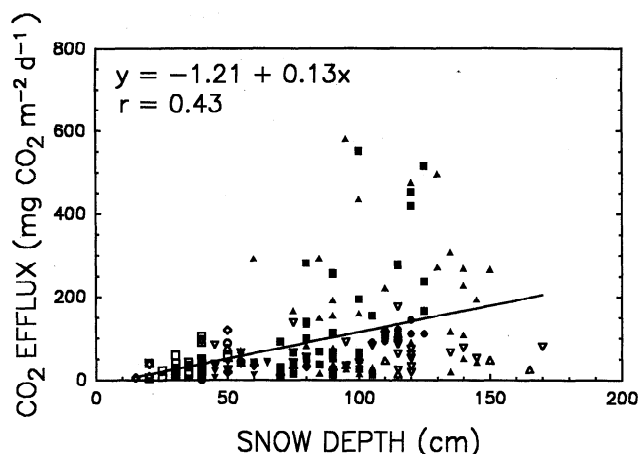


Figure 2. Relationship between CO₂ efflux (mg CO₂ m⁻² d⁻¹) in March and April 1996 and maximum snow depth (cm) for each measurement. Community types are Toolik riparian (solid triangle) and *Cassiope* (solid circle), Toolik moist tussock (inverted solid triangle) and dry heath (open diamond) tundra, Toolik natural drifts (open triangle), Sagavanirktok shrub (inverted open triangle), Happy Valley riparian (solid square) and tussock tundra (open square), and Prudhoe wet sedge (open circle). Solid line indicates regression for all sites combined. See text for additional details.

that temperature was not the primary explanation for the variance in flux between the different communities.

The relationship between maximum snow depth and rates of CO₂ efflux in March and April, when averaged across all community types, is quite weak ($R^2 = 0.19$, Figure 2), suggesting that snow depth was also not the primary cause of variance in fluxes between plant communities in our study. There was some correlation, however, between snow depth and rates of CO₂ efflux. For instance, when snow depths were less than 75 cm, rates of CO₂ efflux were generally below 200 mg CO₂ m⁻² d⁻¹ (Figure 2). The communities in this range (e.g., moist tussock and dry heath tundra) are typically windswept and rarely accumulate much snow throughout the winter. In contrast, the highest rates of CO₂ release that we measured in March and April were in riparian and natural snow bed (e.g., *Cassiope*) communities (Figure 1, Table 1). Snow accumulations in these communities are typically greater than 75 cm (Figure 2), and snow generally tends to accrue earlier in the year in these communities compared with other tundra communities. Although soil surface temperatures were not notably different between plant communities in this study, earlier snow accumulation in riparian and snow bed communities may effectively insulate microbial populations from very cold temperatures [Brooks *et al.*, 1997], especially deeper in the soil horizon, allowing these communities to sustain higher levels of microbial activity throughout the winter compared to other communities which have later developing snow cover. Because snow distribution and accumulation patterns are influenced by topography and vegetation [Evans *et al.*, 1989], future studies should focus on interactions between these two factors in controlling wintertime CO₂ effluxes in the Arctic.

Extrapolating our estimates of wintertime CO₂ efflux (Figure 1) to larger areas suggests that total CO₂ release to the atmosphere over the duration of winter ranges from 47 to 400 kg CO₂ ha⁻¹, depending on the vegetation community type (Table 1). These calculations assume that snow covers the

North Slope tundra from October to May, or about 235 days each year [Zhang *et al.*, 1996], and are based only on the mean daily CO₂ efflux measurements from March and April. In terms of respiratory carbon losses from the soil to the atmosphere, these estimates of total winter CO₂ production are equivalent to 1.3–10.9 g CO₂-C m⁻² lost over the duration of the snow-covered season.

Our estimates of wintertime CO₂ efflux are somewhat lower than those reported for the winter season by Brooks *et al.* [1995, 1996] for alpine sites in Colorado (0.3–25.7 g CO₂-C m⁻²), by Sommerfeld *et al.* [1993, 1996] for alpine and subalpine sites in Wyoming (41–232 g CO₂-C m⁻²), and by Zimov *et al.* [1996] for forest tundra in northern Russia (89 g CO₂-C m⁻²). This may reflect the unusually late accumulation of snowfall during the year of this study (February; M. Sturm, personal communication 1996), preventing significant insulation of the soil before freezing. For instance, Brooks *et al.* [1997] have found that small changes in the timing of snowpack accumulation have a large effect on the magnitude of winter CO₂ production in alpine tundra. Alternatively, our estimates of winter CO₂ production may reflect unique differences between arctic tundra ecosystems on the North Slope, such as the presence of permafrost, and other seasonally snow-covered ecosystems. However, Oechel *et al.* [1997] have also found higher rates of winter CO₂ production for tussock tundra (70 g CO₂-C m⁻²) and for wet sedge ecosystems (20 g CO₂-C m⁻²) than we found for these systems. These different estimates of cold season CO₂ efflux from northern Alaska may reflect differences in snowfall patterns and soil temperature between the years of these two studies (Oechel and colleagues took measurements in 1993 and 1994; our measurements were made in 1996), or may reflect inherent differences in the techniques used in these two studies to estimate CO₂ efflux (i.e., snow top flux chambers versus CO₂ concentration gradient and diffusion model).

Nevertheless, there is increasing evidence to suggest that wintertime CO₂ efflux to the atmosphere is a widespread and common occurrence in snow-covered systems and may be an important component of annual ecosystem CO₂ flux and of global carbon budgets. Sommerfeld *et al.* [1993] estimate that subnivean respiration during winter may oxidize more than 25% of the carbon fixed during the growing season in alpine and subalpine ecosystems in Wyoming. Similarly, Brooks *et al.* [1996] estimate that 20% of the carbon fixed annually in aboveground primary production in alpine communities of Colorado may be lost from snow-covered soils in March, April, and May. In conclusion, our study and other recent studies [Sommerfeld *et al.*, 1993, 1996; Zimov *et al.*, 1993, 1996; Brooks *et al.*, 1995, 1996, 1997; Oechel *et al.*, 1997] indicate that wintertime CO₂ flux is of considerable importance in the carbon cycling of tundra ecosystems and that winter CO₂ fluxes should be accounted for in calculations of annual carbon balance in arctic ecosystems.

Acknowledgments. National Science Foundation grants OPP9321730 and OPP9617643 provided funding for this research. We thank Bill Massman and one anonymous reviewer for comments which substantially improved this manuscript. We are grateful to the staff of the Institute of Arctic Biology, University of Alaska, Fairbanks, for logistical support and for use of the Toolik Field Station in winter.

References

Billings, W. D., Carbon balance of Alaskan tundra and taiga ecosystems: Past, present, and future, *Quat. Sci. Rev.*, 6, 165–177, 1987.

- Billings, W. D., J. O. Luken, D. A. Mortensen, and K. M. Peterson, Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment?, *Oecologia*, 53, 7–11, 1982.
- Brooks, P. D., M. W. Williams, D. A. Walker, and S. K. Schmidt, The Niwot Ridge snow fence experiment: Biogeochemical responses to changes in seasonal snowpack, in *Biogeochemistry of Seasonally Snow-Covered Catchments*, edited by K. A. Tonnessen, M. W. Williams, and M. Tranter, *IAHS Publ.* 228, pp. 293–302, Int. Assoc. of Hydrol. Sci., Gentbrugge, Belgium, 1995.
- Brooks, P. D., M. W. Williams, and S. K. Schmidt, Microbial activity under alpine snowpacks, Niwot Ridge, Colorado, *Biogeochemistry*, 32, 93–113, 1996.
- Brooks, P. D., S. K. Schmidt, and M. W. Williams, Winter production of CO₂ and N₂O from alpine tundra: Environmental controls and relationship to inter-system C and N fluxes, *Oecologia*, 110, 403–413, 1997.
- Chapin, F. S., III, P. C. Miller, W. D. Billings, and P. I. Coyne, Carbon and nutrient budgets and their control in coastal tundra, in *An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska*, edited by J. Brown, P. C. Miller, L. L. Tieszen, and F. L. Bunnell, pp. 458–482, Van Nostrand Reinhold, New York, 1980.
- Ciais, P., P. P. Tans, M. Trolier, J. W. C. White, and R. J. Francey, A large northern hemisphere terrestrial CO₂ sink indicated by the ¹³C/¹²C ratio of atmospheric CO₂, *Nature*, 269, 1098–1102, 1995.
- Clein, J. S., and J. P. Schimel, Microbial activity of tundra and taiga soils at sub-zero temperatures, *Soil Biol. Biochem.*, 27, 1231–1234, 1995.
- Coxson, D. S., and D. Parkinson, Winter respiratory activity in aspen woodland forest floor litter and soils, *Soil Biol. Biochem.*, 19, 49–59, 1987.
- Coyne, P. I., and J. J. Kelley, Variations in carbon dioxide across an arctic snowpack during winter, *J. Geophys. Res.*, 79, 799–802, 1974.
- du Plessis, J. P., and J. H. Masliyah, Flow through isotropic granular porous media, *Transp. Porous Media*, 6, 207–221, 1991.
- Evans, B. M., D. A. Walker, C. S. Benson, E. A. Nordstrand, and G. W. Petersen, Spatial interrelationships between terrain, snow distribution and vegetation patterns at an arctic foothills site in Alaska, *Holarct. Ecol.*, 12, 270–278, 1989.
- Giblin, A. E., K. J. Nadelhoffer, G. R. Shaver, J. A. Laundre, and A. J. McKerrow, Biogeochemical diversity along a riverside toposequence in arctic Alaska, *Ecol. Monogr.*, 61, 415–435, 1991.
- Gorham, E., The role of subarctic and boreal peatlands in the global carbon cycle and their probable responses to “greenhouse” climate warming, *Ecol. Appl.*, 1, 182–195, 1991.
- Grulke, N. R., G. H. Riechers, W. C. Oechel, U. Hjelm, and C. Jaeger, Carbon balance in tussock tundra under ambient and elevated atmospheric CO₂, *Oecologia*, 83, 485–494, 1990.
- Kelley, J. J., Jr., D. F. Weaver, and B. P. Smith, The variation of carbon dioxide under the snow in the Arctic, *Ecology*, 49, 358–361, 1968.
- Kling, G. W., G. W. Kipphut, and M. C. Miller, Arctic lakes and streams as conduits to the atmosphere: Implications for tundra carbon budgets, *Science*, 251, 298–301, 1991.
- Massman, W. J., R. A. Sommerfeld, A. R. Mosier, K. F. Zeller, T. J. Hehn, and S. G. Rochelle, A model investigation of turbulence-driven pressure-pumping effects on the diffusion of CO₂, N₂O, and CH₄ through layered snowpacks, *J. Geophys. Res.*, 102, 18,851–18,863, 1997.
- Michaelson, G. J., C. L. Ping, and J. M. Kimble, Carbon storage and distribution in tundra soils of Arctic Alaska, U.S.A., *Arct. Alp. Res.*, 28, 414–424, 1996.
- Miller, P. C. (Ed.), Carbon balance in northern ecosystems and the potential effect of carbon dioxide-induced climate change, *CONF-8003118*, 109 pp., Natl. Tech. Inf. Serv., Springfield, Va., 1981.
- Miller, P. C., R. Kendall, and W. C. Oechel, Simulating carbon accumulation in northern ecosystems, *Simulation*, 40, 119–131, 1983.
- Oechel, W. C., and W. D. Billings, Effects of global change on the carbon balance of arctic plants and ecosystems, in *Arctic Ecosystems in a Changing Climate*, edited by F. S. Chapin III, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, pp. 139–168, Academic, San Diego, Calif., 1992.
- Oechel, W. C., S. J. Hastings, G. L. Vourlitis, M. A. Jenkins, G. Riechers, and N. Grulke, Recent changes of arctic tundra ecosystems from a carbon sink to a source, *Nature*, 361, 520–523, 1993.
- Oechel, W. C., S. Cowles, N. Grulke, S. J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis, Transient nature of CO₂ fertilization in Arctic tundra, *Nature*, 371, 500–503, 1994.
- Oechel, W. C., G. L. Vourlitis, S. J. Hastings, and S. A. Bochkarev, Change in Arctic CO₂ flux over two decades: Effects of climate change at Barrow, Alaska, *Ecol. Appl.*, 5, 846–855, 1995.
- Oechel, W. C., G. Vourlitis, and S. J. Hastings, Cold season CO₂ emission from arctic soils, *Global Biogeochem. Cycles*, 11, 163–172, 1997.
- Raich, J. W., and C. S. Potter, Global patterns of carbon dioxide emissions from soils, *Global Biogeochem. Cycles*, 9, 23–36, 1995.
- Raich, J. W., and W. H. Schlesinger, The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate, *Tellus*, 44(B), 81–99, 1992.
- SAS Institute, *SAS/STAT User's Guide*, version 6, 4th ed., 943 pp., SAS Inst. Inc., Cary, N. C., 1989.
- Skogland, T., S. Lomeland, and J. Goksoyr, Respiratory burst after freezing and thawing of soil: Experiments with soil bacteria, *Soil Biol. Biochem.*, 20, 851–856, 1988.
- Sommerfeld, R. A., A. R. Mosier, and R. C. Musselman, CO₂, CH₄ and N₂O flux through a Wyoming snowpack and implications for global budgets, *Nature*, 361, 140–142, 1993.
- Sommerfeld, R. A., W. J. Massman, R. C. Musselman, and A. R. Mosier, Diffusional flux of CO₂ through snow: Spatial and temporal variability among alpine-subalpine sites, *Global Biogeochem. Cycles*, 10, 473–482, 1996.
- Taylor, B. R., and H. G. Jones, Litter decomposition under snow cover in a balsam fir forest, *Can. J. Bot.*, 68, 112–120, 1990.
- Zhang, T., T. E. Osterkamp, and K. Stamnes, Some characteristics of the climate in Northern Alaska, U.S.A., *Arct. Alp. Res.*, 28, 509–518, 1996.
- Zimov, S. A., G. M. Zimova, S. P. Davidov, A. I. Davidova, Y. V. Voropaev, Z. V. Voropaeva, S. F. Prosiannikov, O. V. Prosiannikova, I. V. Semiletova, and I. P. Semiletov, Winter biotic activity and production of CO₂ in Siberian soils: A factor in the greenhouse effect, *J. Geophys. Res.*, 98, 5017–5023, 1993.
- Zimov, S. A., S. P. Davidov, Y. V. Voropaev, S. F. Prosiannikov, I. P. Semiletov, M. C. Chapin, and F. S. Chapin, Siberian CO₂ efflux in winter as a CO₂ source and cause of seasonality in atmospheric CO₂, *Clim. Change*, 33, 111–120, 1996.

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(Received August 8, 1997; revised February 27, 1998; accepted March 5, 1998.)