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# Cold-season Production of $CO_2$ in Arctic Soils: Can Laboratory and Field Estimates Be Reconciled through a Simple Modeling Approach?

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## Abstract

Microbial activity in arctic tundra soils has been evaluated through both lab incubations and field flux measurements. To determine whether these different measurement approaches can be directly linked to each other, we developed a simple model of soil microbial $CO_2$ production during the cold season in tussock tundra, moss tundra, and wet meadow tundra in the Alaskan Arctic. The model incorporated laboratory-based estimates of microbial temperature responses at sub-zero temperatures with field measurements of C stocks through the soil profile and daily temperature measurements at the sites. Estimates of total $CO_2$ production overestimated *in situ* cold season $CO_2$ fluxes for the studied sites by as much as two- to threefold, suggesting that either $CO_2$ produced *in situ* does not efflux during the cold season or that microbial respiration potentials are constrained by some other factor *in situ*. Average estimated winter $CO_2$ production was near 120 g C m$^{-2}$ in moist tundra and 60 g C m$^{-2}$ in wet meadow tundra. Production was strongly seasonal, with most of the winter $CO_2$ production happening early in the winter, before soils froze completely through. Roughly two-thirds of the total estimated $CO_2$ production was from deep soils, largely mineral soils, in contrast to growing season $CO_2$ dynamics.

## Introduction

The Arctic plays an important role in the changing global climate system through its high albedo much of the year and through the large amounts of C that are stored in arctic soils (Shaver et al., 1992). There has been concern that the large C stores may have the potential to drive a positive feedback in the climate system, in which increasing temperature increases soil organic matter decomposition rates, increasing $CO_2$ fluxes to the atmosphere (Shaver et al., 1992). While even evaluating the C balance of arctic communities during the growing season has been a challenge, (Oechel et al., 1997; Grogan and Chapin, 1999), an important development has been recognizing that microbes remain active in frozen soils (Flanagan and Bunnell, 1980; Clein and Schimel, 1995; Mikan et al., 2002) and that $CO_2$ fluxes to the atmosphere during the cold season (Olsson et al., 2003) are substantial. For example, most estimates of cold season $CO_2$ fluxes are in the broad range of 10–90 g C m$^{-2}$ (Zimov et al., 1993a; Oechel et al., 1997; Fahnestock et al., 1998; Jones, 1999; Welker et al., 2000; but see Grogan and Chapin, 1999). The bulk of litter decomposition appears to occur during the cold season as well (Hobbie and Chapin, 1996). Even accepting the lower range of cold season $CO_2$ flux estimates, they would be a substantial fraction of tundra ecosystem's annual C cycle (Clein and Schimel, 1995; Oechel et al., 1997; Grogan and Chapin, 1999), and may be enough to shift tundra ecosystems from being net sinks of $CO_2$ (in the growing season) to being net sources of $CO_2$ (for the total year). Additionally, it is clear that cold season $CO_2$ fluxes are sensitive to snow depth and the resulting change in soil temperature (McGuire et al., 2000; Schimel et al., 2004).

There are several approaches that have been used to measure efflux from frozen soils in the field, including both short-term and long-term flux chambers (Oechel et al., 1997; Grogan and Chapin, 1999; Welker et al., 2000) and snow $CO_2$ profiles (Zimov et al., 1993a, 1993b; Zimov et al., 1996; Fahnestock et al., 1999; Welker et al., 2000). However, it is difficult to match actual $CO_2$ fluxes with production rates in the soil. Frozen soil layers can trap $CO_2$ that is released in bursts when the frozen layer cracks (Kelley et al., 1968; Jones, 1999), as indicated by the 100-fold increases in short-term $CO_2$ flux when holes were drilled in the frozen soil layer (Oechel et al., 1997). A second major challenge to linking $CO_2$ production to efflux in the winter is in identifying where in the soil profile $CO_2$ is produced. Most studies in the Arctic focus on the surface soil horizons, where organic matter contents are high and summer temperatures are warm (e.g., Giblin et al., 1991; Weintraub and Schimel, 2004). However, during the winter, the deeper soils remain warmer longer, and so have a substantial potential to be major $CO_2$ sources during the cold season (Zimov et al., 1993b). Little work has been done so far to quantify how $CO_2$ production varies through the profile or how temperature interacts with changing substrate type (organic vs. mineral soils) through the profile.

Ultimately, estimating large-scale Arctic cold season $CO_2$ fluxes, and how they will change with changing climate, will require robust, process-based simulation models that go beyond these flux measurements. However, our understanding of process dynamics in cold soils is still poorly developed. Existing models either ignore winter (e.g.,

**TABLE 1**

Soil properties of study sites. % C is the soil C content of the depth interval. C stock is the total amount of C stored in the depth interval (kg m$^{-2}$) and was determined from % C and bulk density. The $\alpha$ and $\beta$ values are those that were assigned to each soil interval, based on depth and organic matter content. The units on $\alpha$ are $\mu$g C g$^{-1}$ C d$^{-1}$. $\beta$ is dimensionless.

| Soil | Depth interval | | | | |
|---|---|---|---|---|---|
| | 0–10 cm | 10–20 cm | 20–30 cm | 30–40 cm | 40–50 cm |
| Toolik tussock tundra (68°38′N, 149°38′W) | | | | | |
| % C | 35.73 | 21.58 | 4.28 | 8.93 | 6.93 |
| C stock | 4.17 | 5.26 | 4.27 | 4.37 | 2.68 |
| $\alpha$ | 75.50 | 18.55 | 52.58 | 52.58 | 52.58 |
| $\beta$ | 0.45 | 0.45 | 0.27 | 0.27 | 0.27 |
| Galbraith tussock tundra (68°29′N, 149°29′W) | | | | | |
| % C | 32.38 | 32.09 | 27.16 | 7.45 | 8.39 |
| C stock | 5.61 | 9.18 | 9.18 | 9.17 | 9.20 |
| $\alpha$ | 75.54 | 18.55 | 18.55 | 52.58 | 52.58 |
| $\beta$ | 0.45 | 0.45 | 0.45 | 0.27 | 0.27 |
| Ivotuk tussock tundra (68°29′N, 155°45′W) | | | | | |
| % C | 44.53 | 44.11 | 30.75 | 13.45 | 7.52 |
| C stock | 5.09 | 5.12 | 4.96 | 4.71 | 4.55 |
| $\alpha$ | 75.54 | 18.55 | 18.55 | 52.58 | 52.58 |
| $\beta$ | 0.45 | 0.45 | 0.45 | 0.27 | 0.27 |
| Ivotuk moss tundra (68°29′N, 155°45′W) | | | | | |
| % C | 49.46 | 47.37 | 40.06 | 17.57 | 7.50 |
| C stock | 3.15 | 7.68 | 11.05 | 8.89 | 8.17 |
| $\alpha$ | 74.70 | 42.70 | 21.66 | 52.58 | 52.58 |
| $\beta$ | 0.53 | 0.55 | 0.51 | 0.27 | 0.27 |
| Prudhoe wet meadow tundra (70°19′N, 148°42′W) | | | | | |
| % C | 44.88 | 39.03 | 43.93 | 33.48 | 32.94 |
| C stock | 1.03 | 2.61 | 7.32 | 14.36 | 12.78 |
| $\alpha$ | 74.70 | 42.70 | 21.66 | 21.66 | 21.66 |
| $\beta$ | 0.53 | 0.55 | 0.51 | 0.51 | 0.51 |

McKane et al., 1997) or simply extrapolate growing season soil dynamics down below 0°C (e.g., McGuire et al., 2000). However, recent studies suggest that processes function differently at low temperature than they do when thawed. For example, below 0°C, tundra organic soils have respiration temperature responses with $Q_{10}$ values (the proportional rate for a 10°C increase) above 60, while the values above 0°C are below 10 (Mikan et al., 2002). Further, microbes appear to shift their substrate use patterns as soils freeze, relying less on detritus and more on materials in water films and recycled microbial biomass (Michaelson and Ping, 2003; Schimel et al., 2004). Thus, it becomes clear that models of cold season processes must better incorporate the growing body of mechanistic analysis to accurately represent these phenomena.

The difficulty of Arctic cold season field work, however, means that all of the mechanistic studies have been laboratory-based (Flanagan and Bunnell, 1980; Clein and Schimel, 1995; Mikan et al., 2002). It remains unclear how best to incorporate this work into ecosystem models. Typically, laboratory measurements cannot be directly multiplied up to get accurate estimates of field process rates, though evaluating how potential rates compare to actual field rates can be useful in evaluating what the controls over field rates are and what constrains microbial potentials (Calderon et al., 2001; Billings et al., 2002; Booth et al., 2003).

To evaluate how available laboratory measurements of $CO_2$ production potentials relate to field $CO_2$ fluxes, and whether those data can be directly assimilated into existing biogeochemical models, we built a simple model that integrated laboratory-based respiration measurements, soil carbon stocks, and daily temperature estimates from *in*

*situ* temperature probes. We built a spreadsheet model that estimated daily $CO_2$ production in each 10 cm depth interval down to 50 cm depth in five tundra types and over several years. We had three specific questions to address through this modeling exercise:

(1) Can laboratory measurements of microbial respiration responses be directly scaled up using *in situ* soil C and temperature data to provide reasonable estimates of total cold season $CO_2$ production?
(2) What insights can such a model provide of the seasonal patterns of $CO_2$ production and into the relationship between production and efflux?
(3) What insights can such a model provide on where microbial activity is occurring during the cold season and on the nature of the substrates used?

## Materials and Methods

### SITES

We used data from five sites. At each we had data on soil C storage and soil temperature with depth for at least one full winter. The soil characteristics for the different sites are described in Table 1. Four of the sites were in the northern foothills of the Brooks Range, Alaska, U.S.A., and were dominated by tussock tundra (Galbraith, Toolik Lake, and Ivotuk). Tussock tundra is a mixed-plant community in which *Eriophorum vaginatum* (a sedge) tussocks are intermixed with both deciduous (*Betula nana*, *Salix* spp.) and evergreen (*Vaccinium* spp.) shrubs, and with mosses, largely feather mosses such as *Hylocomium* spp. but with some *Sphagnum* spp. We also used data on Ivotuk moss tundra. This site is close to the Ivotuk tussock tundra, but the vegetation is a mix of *E. vaginatum* tussocks surrounded by sphagnum moss. These sites are all considered moist tundra—that is, they are unsaturated upland sites. The last site is a wet meadow near Prudhoe Bay on the Alaskan coastal plain. Wet meadow tundra is saturated and accumulates thick peat layers. The vegetation is dominated by *Carex aquatalis* (a sedge) and mosses, either feather mosses or *Sphagnum*. In some areas the sedge community has *E. angustifolium* as a co-dominant, and with *E. scheuzeri* as a minor component.

### SOILS DATA

Soil C stocks for the research sites were sampled by digging soil pits and analyzing soil C stocks (Michaelson and Ping, unpublished data). All C stocks were calculated for 10 cm depth increments and were calculated from bulk density and carbon content. Soil temperature was measured constantly through the year at 11 depths between 0 and 1 m by placing thermistor probes in the ground at approximately 10 cm increments and logging the data every 5 min. These data were averaged and recorded hourly and then daily to provide daily temperatures. Volumetric liquid soil water content was also continuously measured using Vitel probes within the active layer and near-surface permafrost at three or four different depths and recorded daily. Detailed descriptions of methods of measurements and data processing have been published (Romanovsky and Osterkamp, 1995, 2000).

### MODEL CONSTRUCTION

Temperature response curves for surface organic soils and all wet meadow soils were taken from Mikan et al. (2002). Those for subsurface organic and mineral soils were taken from Michaelson and Ping (2003). Short-term incubations were done on soil samples at temperatures between 0° and −10°C. Because these were short-term lab

incubations, they measure the physiological response of soil microbes to temperature. There is little opportunity for the results to be skewed by depleting active C pools as can occur in longer incubations. The data from each study were modeled by a simple exponential temperature response function:

$$\text{Respiration rate} = \alpha e^{(\beta * T)} * C, \qquad (1)$$

where $\alpha$ is the basal respiration rate per gram of soil C per day, $\beta$ is the temperature scaler, $T$ is the temperature in degrees Celsius, and $C$ is the carbon content in a soil layer in g C m$^{-2}$. Michaelson and Ping (2003) did measurements on several surface organic soils, including some of the same soils used by Mikan et al. (2002). In those cases, the kinetic parameters were similar between the studies. We used the Mikan et al. (2002) parameters where available because the curves were developed on more separate temperatures. Rates from these studies present $CO_2$ production rates per gram.

We had soil C data for 10 cm depth intervals, and as soil C can vary substantially with depth, and can do so abruptly, it was necessary to use those intervals for the model. Therefore, we interpolated an average temperature for each depth increment. This might slightly underestimate respiration, since the respiration response is exponential and activity at the warm end of the layer will therefore be under-estimated more than the activity at the cold end of the layer will be overestimated. These errors, however, should be limited and unimportant given the nature of this exercise.

The model was implemented in Microsoft Excel. The daily $CO_2$ production rate was calculated for each 10 cm depth increment down to 50 cm by applying the lab-based temperature response models, the daily temperatures, and the C content of each layer. In tussock tundra, we used the tussock tundra parameters of Mikan et al. (2002) for surface horizons and Michaelson and Ping's (2003) parameters for the deeper Oe and mineral horizons. For Prudhoe wet meadow and Ivotuk moss samples, we used the wet meadow parameters of Mikan et al. (2002) for the organic layers and the mineral soil parameters from Michaelson and Ping (2003). For all mineral soils, we used an average value from those soils analyzed by Michaelson and Ping (2003). While the $\alpha$ values for these soils varied by a factor of 4, the $\beta$ values varied only by 25% (enough to produce a 65% difference in $Q_{10}$). Because the data came from a limited range of sites that did not overlap well with the sites we had temperature data for, we felt that applying an average to all mineral soils was likely to produce the most coherent estimate of behavior.

We modeled $CO_2$ production down to 50 cm, though permafrost was sometimes as deep as 70 cm. We modeled only to 50 cm because (1) the deeper in the soil profile, the less likely $CO_2$ would actually diffuse out and contribute to cold season $CO_2$ flux; (2) the active layer was anomalously deep relative to average over the period 1986–2000 (Romanovsky et al., 2003); and (3) more of the mineral soil temperature response data were from shallow soils, and as organic matter quality declines with depth, using the available data for deeper soils could skew the overall results.

For each year data were available, fluxes were calculated for the cold season, defined as from the day the surface soil temperature dropped below 0°C to the day it rose above it (Olsson et al., 2003). The average start date for the cold season was 26 September (ranging from 21 September to 1 October), while the average end date was 27 May (ranging from 12 May to 8 June). An obvious alternative definition of the cold season would be the snow-covered period (Schimel et al., 2004). However, we did not have adequate data for these sites to calculate those estimates, but they would generally closely match the cold season.

We did not have specific microbial parameterizations for each site and had to generalize some of them to allow them to be applied across a wide range of soils. Given the variability in the estimated param-

### TABLE 2

**Estimates of total $CO_2$ production rates. Calendar winter is defined as 1 October to 31 May. Temperature winter is defined from the day the surface soil dropped below 0°C until the day it rose above 0°C.**

| Site | Year | Cold season dates | Average temp. (°C) for 0–10 cm soil | $CO_2$ production g C m$^{-2}$ | % of C flux from 30 to 50 cm depth |
|---|---|---|---|---|---|
| | | | Cold season (0°–0°C surface temp) | | |
| Toolik tussock | 98–99 | 9/30–5/12 | −9.2 | 61.5 | 74 |
| Galbraith tussock | 97–98 | 9/21–5/14 | −8.2 | 128.2 | 82 |
| Galbraith tussock | 99–00 | 9/22–5/30 | −9.9 | 113.8 | 86 |
| Ivotuk tussock | 98–99 | 10/1–5/22 | −6.9 | 83.7 | 69 |
| Ivotuk tussock | 99–00 | 9/25–6/6 | −5.8 | 110.8 | 74 |
| Ivotuk moss | 98–99 | 9/25–5/24 | −7.8 | 137.8 | 76 |
| Ivotuk moss | 99–00 | 9/22–6/7 | −4.9 | 180.1 | 76 |
| Prudhoe wet meadow | 97–98 | 9/26–5/26 | −9.1 | 69.6 | 85 |
| Prudhoe wet meadow | 98–99 | 9/29–5/30 | −10.8 | 45.3 | 90 |
| Prudhoe wet meadow | 99–00 | 9/24–6/8 | −11.7 | 53.7 | 89 |

eters, site specific errors of up to 100% or more are probably possible, but these would likely vary randomly. However, even errors of that magnitude would allow us to evaluate whether lab-based mechanistic parameters provide an estimate of cold season $CO_2$ production that is close to field flux measurements or whether there are large directional errors that would point toward new research directions.

## Results and Discussion

### TOTAL COLD SEASON CO$_2$ PRODUCTION

For the moist tundra sites (all except Prudhoe Bay), the average estimated cold-season $CO_2$ production was 116.6 g C m$^{-2}$, while for Prudhoe Bay the average across the 3 yr of data was lower, 56.2 g C m$^{-2}$ (Table 2). In comparison, field estimates of cold-season $CO_2$ fluxes range from <1 g C m$^{-2}$ for sites near Toolik lake in a winter where snow was late and soils froze deeply early in the year to almost 200 g C m$^{-2}$ for tussock tundra in the same area (Table 3). With the exception of years where snowfall is late, most estimates, however, are on the order of 10 to 40 g C m$^{-2}$. Fahnestock et al. (unpublished) measured cold season $CO_2$ fluxes using soda lime $CO_2$ traps in a variety of tundra communities ranging from south of the Yukon river to Prudhoe Bay and repeated measurements in both 1998–1999 and 1999–2000. Their flux measures fit well within that range and had an overall average of 21.5 g C m$^{-2}$ for seasons that started in late August and lasted into June. One would therefore have expected their results to give substantially larger fluxes than our model predictions for only the cold season. Field measures can also include $CO_2$ production from any root respiration that may occur or from animals that live beneath the snowpack (Olofson et al., 2004). Thus, all these comparisons indicate that the model consistently overestimated cold season $CO_2$ efflux from Alaskan tundra sites by a factor of as much as 2–3 (Tables 2 and 3).

There are several possible reasons why the model might over-estimate field $CO_2$ fluxes. One alternative is that the model is roughly correct in predicting actual $CO_2$ production and that $CO_2$ *flux* measurements do not reflect actual $CO_2$ *production*. In frozen soils, $CO_2$ may get trapped in the ice (Oechel et al., 1997; Jones, 1999), in which case it would not be released to the atmosphere until spring, when it would either be released to the atmosphere directly or be carried off in

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## TABLE 3

### Other published estimates of wintertime $CO_2$ production or flux.

| Site | Year | Total flux (g C m$^{-2}$) | Measurement technique | Citation |
|------|------|------|------|------|
| Tussock tundra, Alaska | 1993–1994 | 68.5 | Flux chamber | Oechel et al. (1997) |
| Tussock tundra, Alaska | 1994–1995 | 1.1[a] | Base trap | Welker et al. (2000) |
| Tussock tundra, Alaska | 1995–1996 | 36[b] | Snow $CO_2$ profile | Welker et al. (2000) |
| Tussock tundra, Alaska | 1996–1997 | 20.9 | Snow $CO_2$ profile | Fahnestock et al. (1999) |
| Tussock tundra, Alaska | 1996–1997 | 190 | Base traps | Grogan and Chapin (1999) |
| Non-acid tundra, Alaska | 1996–1997 | 2.1 | Snow $CO_2$ profile | Fahnestock et al. (1999) |
| Water track, Alaska | 1996–1997 | 21.7 | Snow $CO_2$ profile | Fahnestock et al. (1999) |
| Dry heath, Alaska | 1994–1995 | 0.7[a] | Base trap | Welker et al. (2000) |
| Dry heath, Alaska | 1995–1996 | 4.5[b] | Snow $CO_2$ profile | Welker et al. (2000) |
| Forest tundra, Siberia | 1990–1992 | 89 | Snow $CO_2$ profile | Zimov et al. (1996) |
| Forest tundra, Siberia | 1989–1990 | 13.8[c] | Snow $CO_2$ profile | Zimov et al. (1993a) |
| Wet meadow tundra, Alaska | 1996–1997 | 12.2 | Snow $CO_2$ profile | Fahnestock et al. (1999) |
| Wet meadow tundra, Alaska | 1993–1994 | 19.0 | Flux chamber | Oechel et al. (1997) |

[a] Snow came late after a cold fall. Therefore soil temperatures were probably very cold.

[b] This year was closer to "normal," with snow arriving relatively early.

[c] This is only for December through February.

dissolved form into streams and lakes, where potential $CO_2$ release is substantial (Cole et al., 1994). The other alternative is that the model overestimates actual $CO_2$ production. There are several ways in which this would likely occur. First, assays on disturbed soils often produce rates that are high compared to those in undisturbed soils (Schimel et al., 1989; Sollins et al., 1996). This is more likely an issue with mineral than organic soils, because physical protection of organic matter is more likely in mineral soils; Weintraub and Schimel (2003) also observed limited evidence of a disturbance pulse in tundra organic soils. A second possibility is that the deeper mineral soils may not contribute as much to actual $CO_2$ production and flux as the model predicts. The data were least reliable for mineral soils, yet the model suggested that they should dominate cold season flux (Fig. 2). Thus, any error in estimated respiration rate for mineral soils or in the depth increments contributing to respiration would have a large impact on estimated $CO_2$ production. A third possibility is that there is a small "winter-labile" C pool that is available to be consumed by microbes. The short-term lab assays used in the model would therefore indicate the initial rates at which that pool is metabolized, but not its size, and it may be consumed over winter, limiting the amount of C respired (Clein and Schimel, 1995). Thus, whole cold season C fluxes may be constrained by the size of the available C pool rather than the kinetics of its consumption. The actual size of this pool might be quite variable with weather conditions in the fall because early freeze/thaw events could release microbial biomass into the labile substrate pool (Brooks et al., 1997). It is certainly possible that all of these mechanisms are involved in producing the model overestimates of field $CO_2$ fluxes. To be able to use the available parameters describing respiration rate vs. temperature in ecosystem- or regional-scale models, we need to evaluate these issues.

Given the poor agreement between the model and field estimates of cold season $CO_2$ production/flux dynamics, the prime value of the model is in identifying that the discrepancy exists and using it to highlight future research needs. By separating $CO_2$ production by date and depth and examining those breakdowns, the model offers insight to developing hypotheses that can help drive future research on cold season C dynamics, even if there are substantial questions about the accuracy of the model outputs.

### SEASONAL PATTERN OF $CO_2$ PRODUCTION

In all sites the model predicted a consistent pattern of total $CO_2$ production over the season (Figs. 1 and 2). Production rates were high in the early cold season while soils were still relatively warm. Early in the winter, estimated production rates in the moist tundra types were >250 mg C m$^{-2}$ d$^{-1}$, while in wet meadow tundra they were >150 mg C m$^{-2}$ d$^{-1}$. From the beginning of October into December, production rates declined slowly. During this period surface soils generally did not get much colder than −5°C. The deeper soils typically hovered at slightly below 0°C for some length of time while they froze through (Fig. 3). Bulk water freezes between −0.2 and −0.5°C in most tundra soils (Fig. 4; Romanovsky and Osterkamp, 2000). After the deep soils froze through, soil temperatures dropped rapidly and $CO_2$ production rates dropped to very low rates. In most cases, by the end of December, soil temperatures were generally fairly uniform throughout the profile with temperatures ranging from −11 to −15°C. Under these conditions, $CO_2$ production rates were generally lower than 15 mg $CO_2$-C m$^{-2}$ d$^{-1}$. The exception to this pattern was the Ivotuk sites in 1999/2000, where soils stayed relatively warm throughout the winter. Surface temperatures remained above −10°C, and deep soil temperatures remained above −8°C. In these soils, the estimated fluxes were still between 40 and 50 mg $CO_2$-C m$^{-2}$ d$^{-1}$ and only dropped toward 20 mg $CO_2$-C m$^{-2}$ d$^{-1}$ in late March when soil temperatures reached their minimum. In all soils, at the end of the season, there was a rapid increase in $CO_2$ production rates as the thaw first began and the temperature of the surface horizons increased.

The seasonality of fluxes is illustrated by the ratio of average $CO_2$ production rates in October (early winter) to those in February (mid-winter). The average ratio for moist tundra soils was 28, though in Ivotuk soils in 1999/2000 this ratio was only 6 to 7. In contrast, in the Prudhoe wet meadow soils, the ratio ranged between 900 and 1800 because of the high $Q_{10}$ values throughout the organic profile.

The seasonal pattern predicted by the model fits roughly with the pattern of measured $CO_2$ fluxes *in situ* (Oechel et al., 1997). However, the pattern generated by the model is generally more extreme than that observed in field flux measurements. Oechel et al. (1997) measured flux rates in two tussock tundra sites on the North Slope of the Brooks Range and in wet meadow tundra sites near Prudhoe Bay. In tussock tundra they found average October/March flux ratios of 7 and 17.4 in tussock tundra and wet meadow tundra, respectively. Zimov et al. (1993b) estimated a December/February flux ratio of 3.7 for forest tundra (the model generates values for this ratio in a range of 10–15). Fahnestock et al. (unpublished data) found early/mid-winter flux ratios that were generally in the range between 2 and 8 across a range of tundra communities at Toolik Lake. The only exception in their study was a tussock tundra site that had a November/late January ratio of 23.
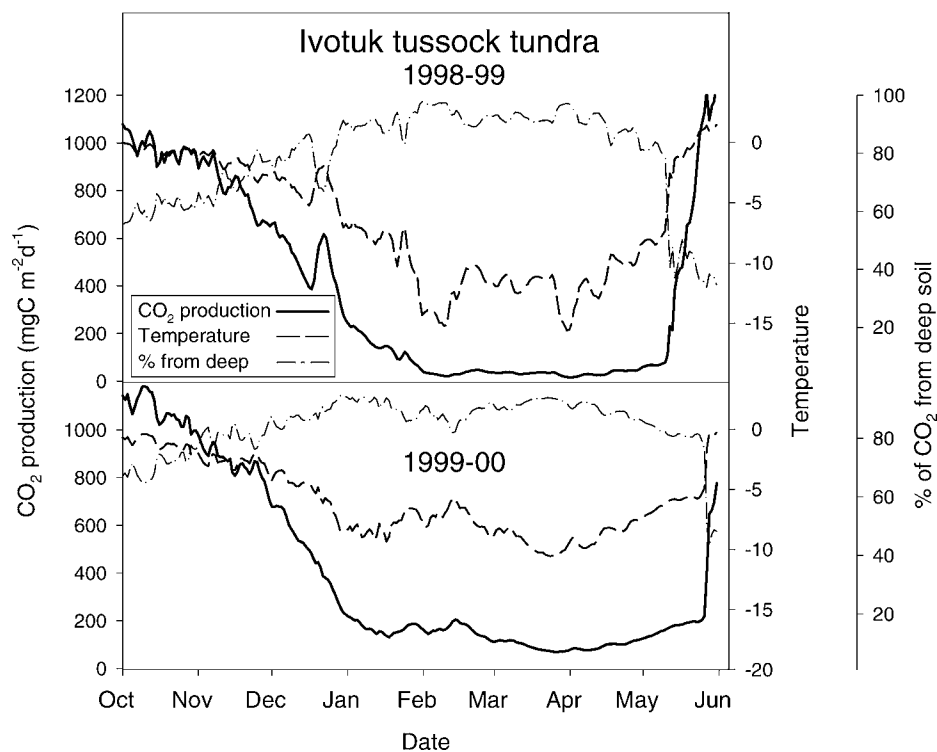
**FIGURE 1. Estimated daily $CO_2$ production, surface soil temperature, and % of produced $CO_2$ that comes from deep horizons in Ivotuk tussock tundra.**
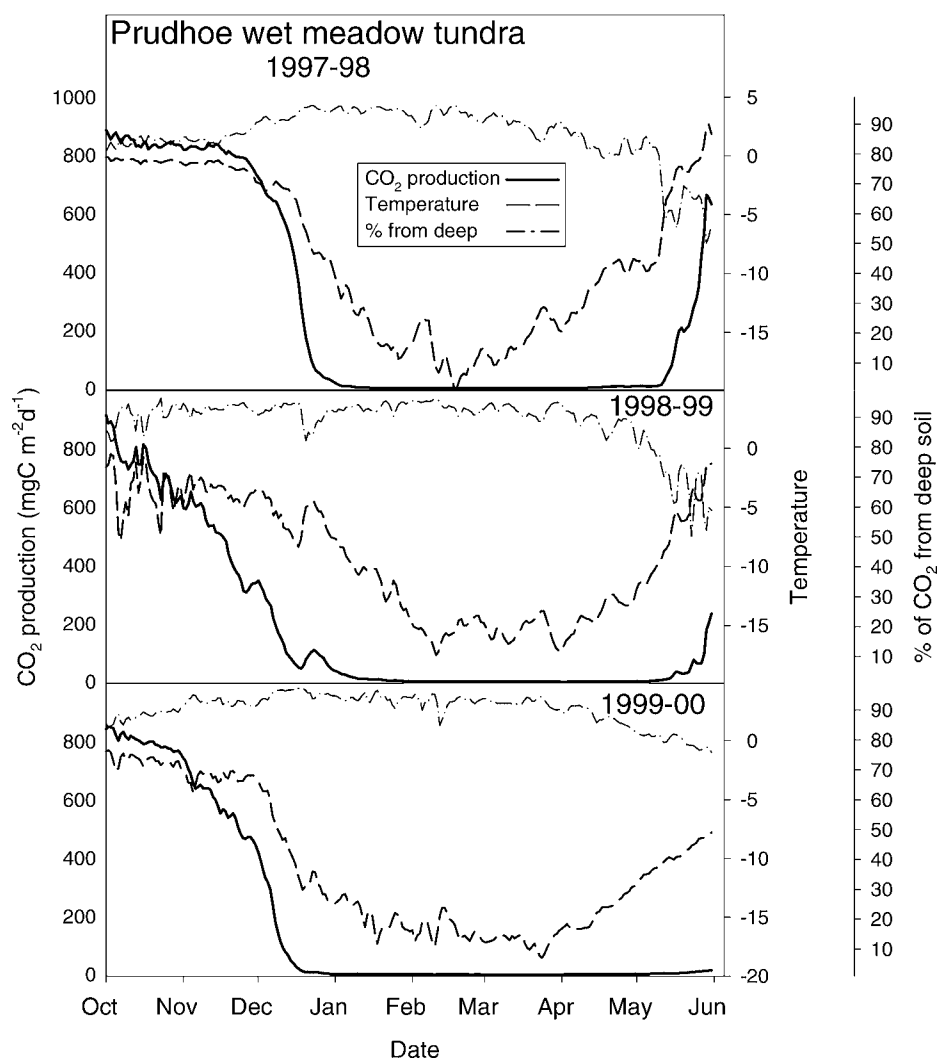


**FIGURE 2. Estimated daily $CO_2$ production, surface soil temperature, and % of produced $CO_2$ that comes from deep horizons in Prudhoe Bay wet meadow tundra.**
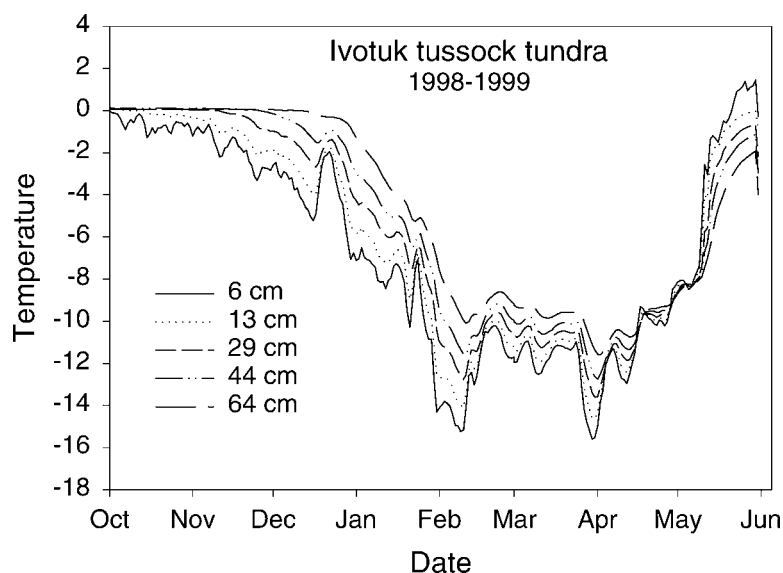
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**FIGURE 3.** Temperature at different depths in the soil profile through the winter in the Ivotuk tussock tundra in 1998–1999.

The substantially higher early/mid-winter ratios from the model than observed in the field suggest that there may be a disconnection between $CO_2$ production and $CO_2$ efflux. Because soils freeze and trap $CO_2$ (Oechel et al., 1997, Jones et al., 1999), it would be expected that late season fluxes would be higher than the actual rate of $CO_2$ production, and that much of the $CO_2$ released later in the season might well have been produced earlier in the winter.

### SOURCE OF CO₂

Across all the sites and years modeled, the model predicts that from 70 to 90% of the $CO_2$ produced comes from deep soils. This varies somewhat among sites and years, with the lowest value in Ivotuk tussock tundra in 1998–1999 (69%, Table 2), while the highest proportion (90%) was in the Prudhoe wet meadow site.

It is notable that such a substantial fraction of the modeled winter respiration comes from deep soils even though C concentrations decline with depth in moist tundra (Table 1), while quality declines with depth in wet, peat-dominated tundra (Mikan et al., 2002; Weintraub and Schimel, 2003). There are two factors that lead to such large amounts of C being respired in the deeper soils. First, deeper soils remain warm for

substantially longer than surface soils. In most of the soils, the deepest layers remained very close to 0°C until December, long after the surface soils had dropped to temperatures low enough to drastically reduce microbial activity (Figs. 1 and 2). Second, in the moss and tussock tundra sites, microbial activity in the mineral soil is important, largely because microbial activity in mineral soils is much less temperature sensitive than in organic soils. Mineral soil horizons had a β value of 0.27 compared to 0.45 for surface organic soils from moist tundra types, and up to 0.55 for wet meadow soils. These translate into $Q_{10}$ values of 15, 90, and 244, respectively. Mineral soils in these sites typically have between 5 and 10% organic matter contents (Table 1). Thus, the combination of high organic matter content, warmer temperature, and limited temperature sensitivity suggest that mineral soils should be important sources of $CO_2$ production during the cold season. In the Prudhoe Bay wet meadow soil, despite the decline in the quality of the organic matter with depth, the model predicted that between 85% and 90% of the total $CO_2$ should be produced in the deep layers. While temperature was one factor driving this pattern, the changing soil bulk density was another (Table 1). The 30–40 cm layer contained almost 15 times as much C as the surface 10 cm. In wet meadow soils, the surface 10–20 cm is often made of loosely packed dead mosses. Thus, an
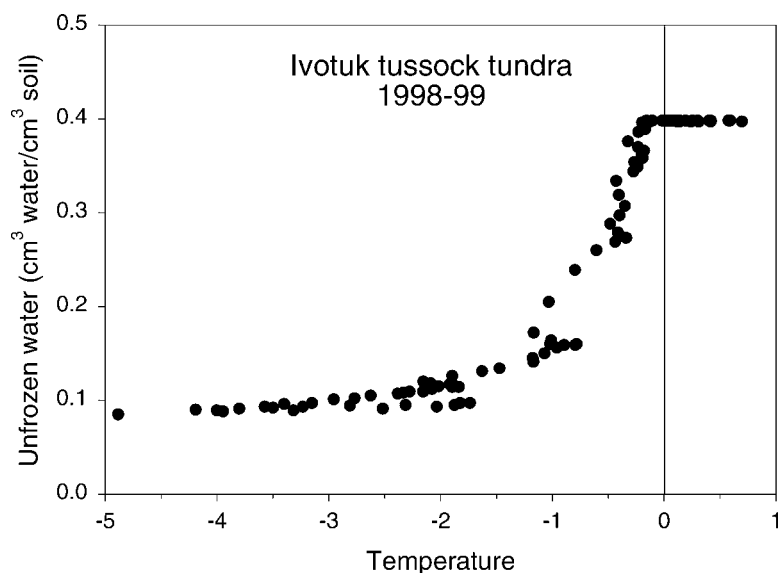


**FIGURE 4.** Relationship between soil temperature and unfrozen water content at 15 cm depth in Ivotuk tussock tundra in 1998–1999. Note that bulk freezing begins at approximately −0.3°C and that unfrozen water content declines exponentially below that.

accumulation of C at depth overcomes the reduced quality, resulting in substantial total $CO_2$ production rates. The importance of deep soil respiration was demonstrated by Zimov et al. (1993b), but not quantified in terms of the contribution to total $CO_2$ production and efflux. Otherwise, the importance of deeper soils in arctic C cycling has rarely been discussed (Ping et al., 1998).

The modeled contribution of deep soil layers to seasonal $CO_2$ production varies through the season. Early in the winter, the whole profile remains relatively close to 0°C, and deep soils contributed between 55 and 85% of the predicted total $CO_2$ production. By mid-winter, deep soils contributed between 95 and 99% of what little $CO_2$ production occurred. Finally, at the end of the cold season, the surface soils warm significantly faster than the deep soils, and the contribution of the deep soils drops to less than 50% of $CO_2$ production. During the growing season, it is likely that surface soils become progressively more important, as C stores are large, organic matter is relatively labile (Weintraub and Schimel, 2003), and surface temperatures increase substantially. During the growing season, soils at 50–60 cm rarely warm above 1 to 2°C, while surface soils may exceed 15°C. Thus, this model suggests an important pattern: microbial activity during the growing season is dominated by surface organic soils, while microbial activity in the winter should be dominated by deeper, often mineral, soils. These soil layers contain different types of soil organic matter and of different quality and this pattern therefore has important implications for modeling year-round soil C dynamics. The patterns of $CO_2$ flux predicted here are distinctly different from that found in the alpine soils of the Rocky Mountains (Brooks et al., 1997). There, the snowpack is thick and provides excellent insulation. This allows surface soils to partially thaw even if they froze during the early winter, allowing these soils to account for most of the flux, and that flux increases through the winter as soils warm (Brooks et al., 1997).

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It is likely that warming the Arctic during winter will increase wintertime $CO_2$ production. The question is, how much? That will depend on how the soil thermal regime changes. How cold the soils get depends on both the air temperature and the insulation from snow (Goodrich, 1982). If snow is late, soils will freeze deeply early in the season (Zhang et al., 1997) and $CO_2$ fluxes will be low (Brooks et al., 1997, Welker et al., 2000). Early and deep snow, on the other hand, keeps soil temperatures warm through the cold season, but could delay thaw (Schimel et al., 2004). Because of the uncertainty in how winter precipitation is likely to change and the poor match between modeled $CO_2$ production and measured field fluxes, we did not feel it appropriate to attempt to develop "warmer winter scenarios" with the model. However, there are still several inferences for future cold season fluxes that are suggested from the data synthesis. First, in any plausible scenario, soils will remain isothermal at 0°C in the early cold period, and will then fall to very cold temperatures during the mid-winter deep cold period. Because the temperature response of soil respiration is exponential, during the deep cold period $CO_2$ production rates will fall to ecologically insignificant levels (Fig. 2). Second, thaw will be relatively quick—day length increases so rapidly that there is not much variation in the date of thaw (Fig. 2). The period of the cold season where soil respiration is most sensitive to climate change is the early cold period—changes in snow cover can produce large differences in the length of the isothermal period in the surface soil and in the rate of cooling of the deeper soil (Fig. 2). That can potentially produce enormous changes in the total seasonal $CO_2$ flux. For example, a snow fence experiment in Alaska maintained winter soil temperatures above −5°C and thereby increased cold-season respiration rates by 75% over the ambient snow treatment (Schimel et al., 2004).

## Conclusions

We constructed a simple model of wintertime $CO_2$ production in several arctic tundra soils. We had two objectives: (1) evaluate how well (or poorly) the available data on microbial activity, soil thermal regimes, and soil C storage could predict measured cold season $CO_2$ fluxes, and (2) evaluate predicted seasonal patterns and specific sources of $CO_2$ to help direct future research into cold season microbial processes.

Within the limitations of the approach, this work leads to several conclusions. First, simple exponential microbial temperature responses from short-term laboratory incubations are inadequate to model cold season $CO_2$ fluxes. While such incubations may be the most powerful approach for evaluating specific physiological responses, it appears necessary to link these to better models of overall C cycling to adequately estimate *in situ* processes during the cold season. The specific reasons for the model overestimates are unclear but possibly involve disconnections between cold season $CO_2$ production and efflux, inadequate representation of deep soil processes, and the presence of a finite "winter-labile" C pool that is consumed during the cold season. These ideas need more thorough study, including both lab and field work. Second, the seasonality of soil temperatures is critical in controlling the extent of winter $CO_2$ production. Particularly important is the length of time that soils remain near 0°C at the beginning of the winter. Finally deep soil layers (particularly mineral soils) appear likely to be more important in cold season dynamics than during the growing season, when the warmer, labile-organic-matter-rich surface layers are likely to dominate C cycling processes.

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