RESPIRATION OF RECENTLY-FIXED PLANT CARBON DOMINATES MID-WINTER ECOSYSTEM CO_2 PRODUCTION IN SUB-ARCTIC HEATH TUNDRA

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Abstract. Arctic ecosystems could provide a substantial positive feedback to global climate change if warming stimulates below-ground CO_2 release by enhancing decomposition of bulk soil organic matter reserves. Ecosystem respiration during winter is important in this context because CO_2 release from snow-covered tundra soils is a substantial component of annual net carbon (C) balance, and because global climate models predict that the most rapid rises in regional air temperature will occur in the Arctic during winter. In this manipulative field study, the relative contributions of plant and bulk soil organic matter C pools to ecosystem CO_2 production in mid-winter were investigated. We measured CO_2 efflux rates in Swedish sub-arctic heath tundra from control plots and from plots that had been clipped in the previous growing season to disrupt plant activity. Respiration derived from recently-fixed plant C (i.e., plant respiration, and respiration associated with rhizosphere exudates and decomposition of fresh litter) was the principal source of CO_2 efflux, while respiration associated with decomposition of bulk soil organic matter was low, and appeared relatively insensitive to temperature. These results suggest that warmer mid-winter temperatures in the Arctic may have a much greater impact on the cycling of recently-fixed, plant-associated C pools than on the depletion of tundra bulk soil C reserves, and consequently that there is a low potential for significant initial feedbacks from arctic ecosystems to climate change during mid-winter.

1. Introduction

The net carbon (C) balance of arctic ecosystems is of particular importance in linking terrestrial C cycling and global climate change because tundra soils contain 14% of the Earth's soil C pool (Post et al., 1982). Arctic ecosystems could provide a significant positive feedback to CO_2-induced climate change if warming stimulates decomposition of tundra soil C reserves (Lashof, 1989). To date, most models of C balance in arctic ecosystems have been focused on the net difference between C uptake and C efflux during the growing season (e.g., McKane et al., 1997). However, recent studies estimate wintertime ecosystem CO_2 releases of 89 g C m^{-2} y^{-1} in forest tundra (Zimov et al., 1996) and 2–69 g C m^{-2} y^{-1} in tussock tundra (Fahnestock et al., 1998; Oechel et al., 1997), as compared to growing season estimated gross respiratory losses of 100–200 g C m^{-2} y^{-1} (Zimov et al.,

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1996) and 162–186 g C m^{-2} y^{-1} (Vourlitis and Oechel, 1999) respectively. These results indicate that wintertime respiration can be a substantial component of annual net C balance in arctic ecosystems. Furthermore, General Circulation Models (GCMs) of global climate change predict that the most rapid increases in regional air temperature will occur at high latitudes during winter and will be accompanied by increased snowfall (Kattenberg et al., 1996). The extent of the tundra soil C pool, the magnitude of the non-growing season effluxes, and the strong winter emphasis in GCM predictions for high latitudes indicate that an understanding of the processes driving winter respiration is essential to improving future models of net C balance in the Arctic, and to evaluating potential feedbacks to climate change.

Ecosystem CO_2 release during winter is the sum of respiration derived from C recently fixed by plants (i.e., shoot, rhizome and root respiration, mycorrhizal and rhizosphere-associated microbial respiration, as well as respiration associated with the decomposition of fresh litter) and respiration of older C pools (i.e., respiration of C derived from the decomposition of the remaining 'bulk' organic matter fraction of soils). Differentiation of fluxes from plant-associated and bulk soil C pools is essential to evaluating potential arctic feedbacks to atmospheric CO_2 concentrations since it is the sheer magnitude of the tundra bulk soil C pool that makes the Arctic important in the context of global climate change. However, the controls and C source pools contributing to winter respiration in arctic ecosystems are not well understood. In general, studies demonstrating substantial CO_2 release beneath snowcover in both arctic and alpine ecosystems have attributed the observed effluxes to temperature-regulated decomposer activity by psychrophilic (cold-tolerant) microbes (Sommerfeld et al., 1993, 1996; Zimov et al., 1996; Brooks et al., 1996; Oechel et al., 1997; Fahnestock et al., 1998; Mast et al., 1998). Although technically difficult, studies in other localities are beginning to address the controls on respiration from plant and bulk soil C pools by contrasting their *relative* responses to environmental factors. For example, control and previously-trenched plots have been used to report differences in the temperature sensitivity of respiration from recent (root/rhizosphere) and old (bulk soil) below-ground C pools in a mixed hardwood forest ecosystem (Boone et al., 1998). Here, we used a similar approach to contrast relative contributions from plant and bulk soil organic matter pools to tundra ecosystem CO_2 release in mid-winter, and to compare their sensitivities to temperature. We tested the hypothesis that ecosystem CO_2 production in heath tundra at mid-winter is largely derived from respiration associated with recent plant C pools rather than from bulk soil organic matter decomposition.

2. Methods

2.1. FIELD SITE DESCRIPTION

Mid-winter CO_2 production rates were measured at a long-term experimental manipulation site within a sub-arctic heath ecosystem near Abisko (68°21′ N, 18°49′ E, elevation 450 m) in N. Sweden. The vegetation is a species-rich dwarf shrub community dominated by the evergreen *Cassiope tetragona* (L.) but also containing *Empetrum hermaphroditum* (Hagerup), *Vaccinium uliginosum* (L.), *Betula nana* (L.) and significant moss cover. The site is on an exposed, well drained slope with a soil organic layer of c. 15 cm depth. Warming (plastic tents open at the top, sealed at the base) and fertilization (addition of nitrogen, phosphorus and potassium) manipulations during each growing season were initiated in a factorial randomized block design ($n = 6$) in 1989 (Havström et al., 1993; Michelsen et al., 1996).

2.2. EXPERIMENTAL DESIGN

In mid-July 1998, aluminum frames (1056 cm^2) were placed in each of the long-term manipulated plots and all enclosed above-ground vegetation including the green moss layer was clipped and removed. Surface litter present in the moss and above-ground vegetation was also removed in this process. Afterwards, we cut narrow slots approximately 8 cm deep into the organic soil horizon (i.e., below the green moss layer) along the edges of each frame, and pressed the frames down into the soil column. At the same time, smaller frames (506 cm^2) were inserted over adjacent unclipped (control) areas in each plot. We re-visited the plots in mid-August to remove any newly emerging shoots from the clipped areas. In mid-January 1999, we returned to the site, brushed away the shallow overlying snow layer (mean depth 12 cm), and measured CO_2 efflux (i.e., ecosystem CO_2 production) from control and clipped plots. This approach to winter CO_2 flux measurements has been used previously (Alm et al., 1999), but raises several methodological issues: (a) Since some of the CO_2 respired by plants/soil during winter is accumulated within soil and the overlying snow column, our measures of ecosystem CO_2 production rates in mid-winter are not necessarily equivalent to simultaneous rates of ecosystem CO_2 release from the snow surface to the atmosphere; (b) Removal of overlying snow enhances the CO_2 concentration gradient for diffusion from vegetation/soil to the atmosphere. However, production of CO_2 by the vegetation and soils should not be directly influenced by this effect; (c) Removal of overlying snow prior to measurement could result in an over-estimate of ecosystem CO_2 production rates if soil respiration had been inhibited by high CO_2 concentration build-ups beneath the overlying snow column. However, peak CO_2 concentrations at the snow/soil interface of nearby sites with much deeper snowcover (i.e., 1 m or more) did not exceed 5000 p.p.m. (Klaus Steenberg, pers. comm.), suggesting that it is very unlikely that belowground metabolic activity would have been inhibited at our site; (d) Accumulation of CO_2 in snow-covered soils during winter results in an initial CO_2 flush following snow removal that is not representative of current CO_2 production rates. In order to validate our measurement approach, we assessed the disturbance effect of snow removal on CO_2 efflux by making a time series of respiration and soil temperature measurements on test areas from which snow had just been removed. Initial flushes due to the release of accumulated soil CO_2 resulted in transient high efflux rates for up to 15 min after snow removal (see results below). On the basis of these tests, we measured CO_2 efflux from the experimental plots 15–25 min after snow removal. However, the flux values reported here could be over-estimates of ambient ecosystem CO_2 production rates if the stored soil CO_2 pool in each experimental plot was not fully released by the end of the 15–25 min equilibration period. In any event, none of these methodological issues detract from our study's main conclusion, which is based on strong treatment differences in CO_2 efflux between clipped and control plots.

2.3. FLUX AND TEMPERATURE MEASUREMENTS

Ecosystem CO_2 production was determined with an infra-red gas analyzer (LI-COR 6200, NE, U.S.A.) attached to a perspex chamber (13.5 l) fitted with a small circulation fan. For logistical reasons, we used a single gas sampling chamber (sampling area: 506 cm^2) that fitted either directly onto the smaller frames in control plots, or onto the soil surface within the larger frames of the clipped plots. We sealed the edges of the chamber with tightly packed snow during both control and treatment measurements. Fluxes were measured over six successive 15 s intervals and averaged to calculate mean flux per sample area. The increase in CO_2 concentration inside the chamber at the end of each series of measurements did not exceed 10 $\mu l\,l^{-1}$ above ambient – a headspace CO_2 concentration increase at which effects of small chamber leaks are negligible (LI-COR, 1998). We measured efflux on two separate days: January 14 (mean air temp. –27 °C): snow removal tests and selected control areas ($n = 3$ replicates × 4 factorial long-term manipulations); January 18 (mean air temp. –12 °C): all control and clipped areas ($n = 6$ replicates × 4 factorial long-term manipulations). To test the repeatability/precision of our measurement procedure, we correlated efflux values for the same control plots on both days (Pearson $r = 0.95$; $n = 12$; Bartlett's test $p < 0.001$). To test the sensitivity of the equipment under field conditions, we placed the chamber on a plastic sheet, sealed the edges with packed snow and made successive blank measurements (mean = 0.0019 g CO_2–C m^{-2} d^{-1}; S.D. = 0.0109; $n = 11$). These results suggest that the limit of detection for each plot efflux measurement was +/–0.026 g CO_2–C m^{-2} d^{-1} (i.e., the minimum value significantly different from zero with 95% confidence). Soil temperatures at 3 cm depth in the organic soil (i.e., just above the compacted hard-frozen layer) were recorded at the time of efflux measurement by hand-held soil temperature probes and are reported as means ($n = 2$) per sample area. Soil temperatures in selected plots at the site were recorded during the entire winter season using a datalogger with thermistors (Delta-T, Cambridge, U.K.) placed at 6 cm depth in the organic horizon.

2.4. STATISTICAL ANALYSES

Effects of the clipping treatment as well as the long-term experimental manipulations (fertilization and summer warming) on plot CO_2 efflux and soil temperature were tested by separate analyses of variance (ANOVAs).

3. Results

Our test of the disturbance effect of snow removal on the time course of ecosystem CO_2 release indicated that substantial initial CO_2 flushes may occur due to localized CO_2 accumulation in snow-covered soil during winter (Figure 1). Successive respiration measurements over time indicated that these CO_2 flushes can last up to 15 mins after snow removal (Figure 1). Soil temperatures during this interval were not strongly affected by exposure to the atmosphere (Figure 1), despite the particularly cold air temperature on this day (see methods). Consequently, all CO_2 production rates for control and clipped plots reported below were measured 15–25 min. after snow removal in order to avoid initial disturbance effects of snow removal.

Ecosystem CO_2 production rates at mid-winter were dominated by respiration of recently-fixed plant C. The clipping treatment in the previous growing season resulted in a consistent decrease in ecosystem respiration across all the long-term experimental manipulations (Table I; Figure 2). Soil temperatures at the time of CO_2 efflux measurements tended to be slightly lower in the clipped plots (Table I). However, the magnitude of the difference in mean soil temperature (Control –5.6 °C; Clipped –6.1 °C) is unlikely to explain the 3-fold difference in mean CO_2 efflux because respiration from the clipped plots was relatively insensitive to soil temperature (see below). Soil temperature and snow depth were significantly correlated across the site (Spearman $r = 0.67$; $n = 24$; $p < 0.005$), suggesting that the significant variation in soil temperature between experimental blocks (Table I) may be explained by spatial heterogeneity in snowcover/local topography.

4. Discussion

Our results indicate that respiration derived from recently-fixed C in plants, fresh litter and rhizosphere exudates dominated CO_2 efflux rates in sub-arctic heath tundra at mid-winter. First, the clipping treatment removed shoot and surface litter sources of respiration from above-ground, and we assume that it also severely diminished wintertime below-ground respiration derived from rhizomes, roots and

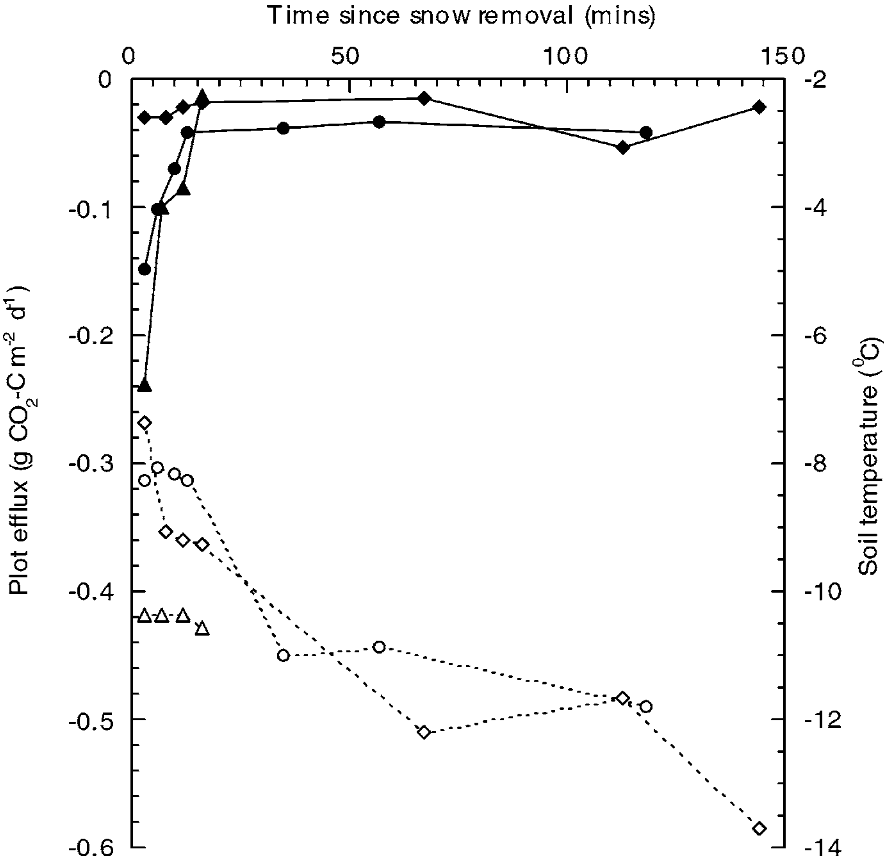

Figure 1. The effect of snow removal on the time course of CO_2 efflux and soil temperature (3 cm depth). By convention, efflux from an ecosystem to the atmosphere is represented by negative values. The solid lines with filled symbols indicate fluxes from 3 different control plots (i.e., containing plants). The dashed lines with corresponding open symbols indicate soil temperatures in the same plots. These measurements were made on January 14, 1999, when air temperature was –27 °C.

mycorrhizae as well as microbial respiration of root-exuded C into the rhizosphere. Observations of emerging shoots in the clipped plots during the summer following our winter measurements indicate that not all plants were killed by the treatment and thus that some root/rhizosphere respiration must have contributed to the winter fluxes from clipped plots. Accordingly, we interpret the fluxes from the clipped plots as representing an altered balance between recent plant C and bulk soil organic matter contributions to ecosystem respiration in which the plant-associated component had been diminished, rather than completely eliminated. Thus, the strong reduction in efflux due to the clipping treatment indicates that respiration derived from recently-fixed plant C dominated mid-winter CO_2 release in control plots. Second, the trend towards highest effluxes in the control (i.e., unclipped) plots combining long-term summer warming and fertilization manipulations (Fig-

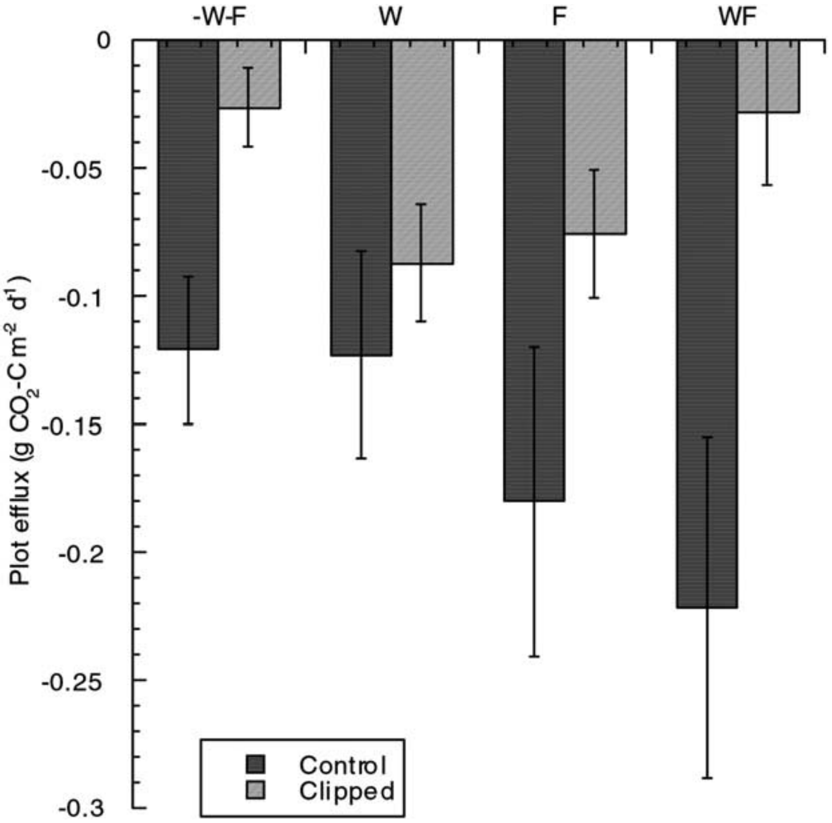

Figure 2. Ecosystem CO_2 production rates at mid-winter (1998/1999) in a sub-arctic tundra heath site in N. Sweden. Comparative flux measurements were made from control (i.e., containing intact plants) and clipped areas in plots that had undergone summer warming (W) and fertilization (F) manipulations in factorial combination since 1989 ($n = 6$, bars = SEs). These measurements were made on January 18, 1999, when air temperature was –12 °C.

ure 2) corresponds with significantly larger above-ground biomass of evergreen shrubs in these plots (Jonasson et al., 1999). Together, these results strongly suggest that respiration of recently-fixed plant C above- and below-ground was the major process governing ecosystem CO_2 production at mid-winter.

Several artifacts may have arisen due to the clipping treatment. First, the timing of seasonal below-ground C inputs arising from root mortality and exudation was altered by the treatment. There is currently considerable debate as to whether soil organic matter decomposition may be stimulated ('primed') by labile C (Cheng and Coleman, 1990, but see also Holland and Coleman, 1987; Dalenberg and Jager, 1989). In this study, we assume that if the priming process occurs during winter, the clipping treatment had no adverse effect on priming-induced release of CO_2 derived from soil organic matter. Second, enhanced labile C inputs arising from increased root mortality and exudation following clipping may have influenced

TABLE I

Statistical analyses of effects of the clipping treatment and long-term manipulations on ecosystem CO_2 production rates and plot soil temperatures ($n = 6$)

	df	Mean square	p value
Ecosystem CO_2 production:			
Clipping	1	0.128	**0.001**
Fertilization	1	0.015	0.177
Summer warming	1	0.002	0.602
Block	5	0.014	0.150
Clipping × fertilization	1	0.020	0.130
Clipping × s. warming	1	0.001	0.783
Fertilization × s. warming	1	0.003	0.528
Clip. × fert. × s. warming	1	0.015	0.180
Error	35	0.008	
Soil temperature:			
Clipping	1	3.658	0.083
Fertilization	1	1.350	0.286
Summer warming	1	3.075	0.111
Block	5	11.144	**0.001**
Clipping × fertilization	1	2.360	0.111
Clipping × s. warming	1	0.263	0.636
Fertilization × s. warming	1	1.488	0.264
Clip. × fert. × s. warming	1	0.194	0.684
Error	35	1.152	

plot efflux. Measurements of summer efflux in the days immediately before and after treatment indicated that below-ground respiration was initially enhanced by clipping (pers. obs.). We expect that most of the extra labile C inputs due to the treatment were respired during the remainder of the growing season. However, even if there were increased labile C inputs in the clipped plots at mid-winter, these should have stimulated (rather than inhibited) winter respiration, making it less likely that a significant treatment effect on winter efflux would have been observed.

The relationship between plot CO_2 efflux and soil temperature was influenced by both treatment and temperature (Figure 3). Respiratory activity was low in both sets of plots at temperatures below –5 °C, supporting previous laboratory and field studies indicating a temperature threshold for appreciable biological activity (Flanagan and Veum, 1974; Flanagan and Bunnell, 1980; Coxson and Parkinson,

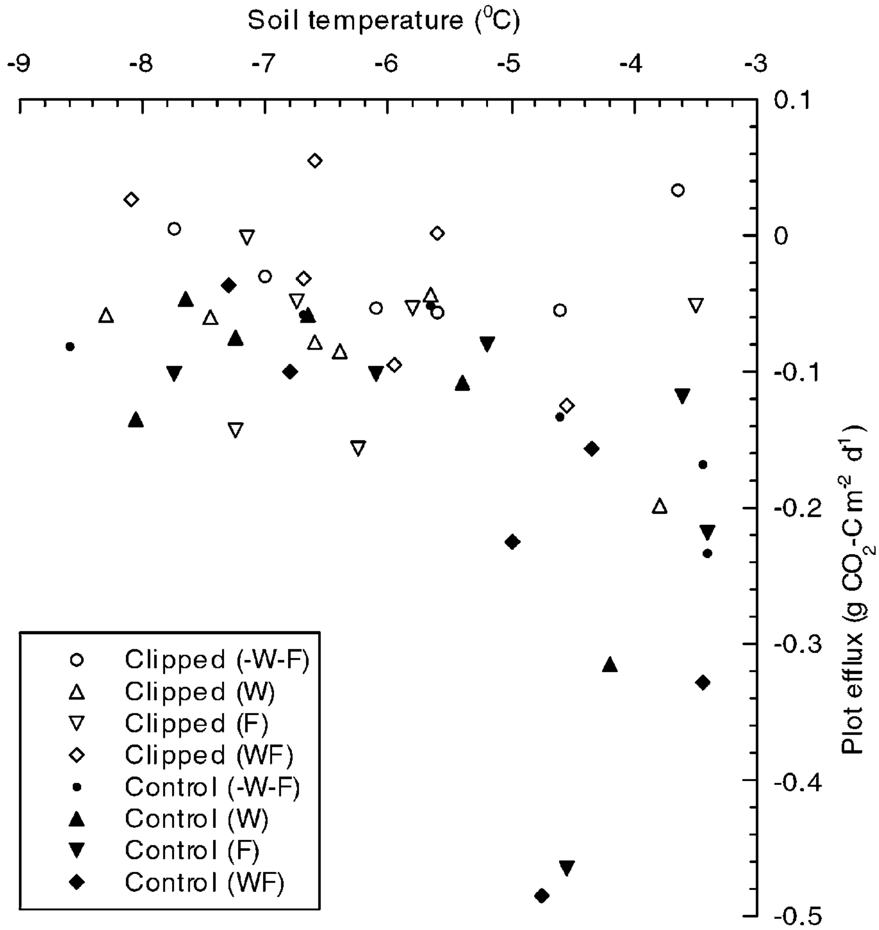

Figure 3. Ecosystem CO_2 efflux in relation to soil temperature (3 cm depth) for all plots. See Figure 2 for explanation of treatment symbols. Tests indicated that the limit of accurate detection was +/– 0.026 g CO_2–C m^{-2} d^{-1} (see Methods).

1987; Clein and Schimel, 1995). The strong treatment effect on efflux occurred at soil temperatures above –5 °C, where plots containing intact plants had substantially higher respiration rates. These plots showed considerable variation in efflux (Figure 3) that may have been caused by differences in plant biomass/leaf litter as well as by differences in soil temperature. Together, these results suggest that temperature and biomass may interact to determine ecosystem CO_2 production rates in mid-winter.

Temperature records from the site (Figure 4) indicate that mean diel soil temperature (i.e., over a 24 h cycle) was above –5 °C for 155 d in a total winter lasting 228 d (i.e., total period when mean diel soil temperature was below 0 °C), suggesting that plant-associated carbon may be an important source of respired CO_2 over a large part of winter. However, ecosystem respiration patterns may be

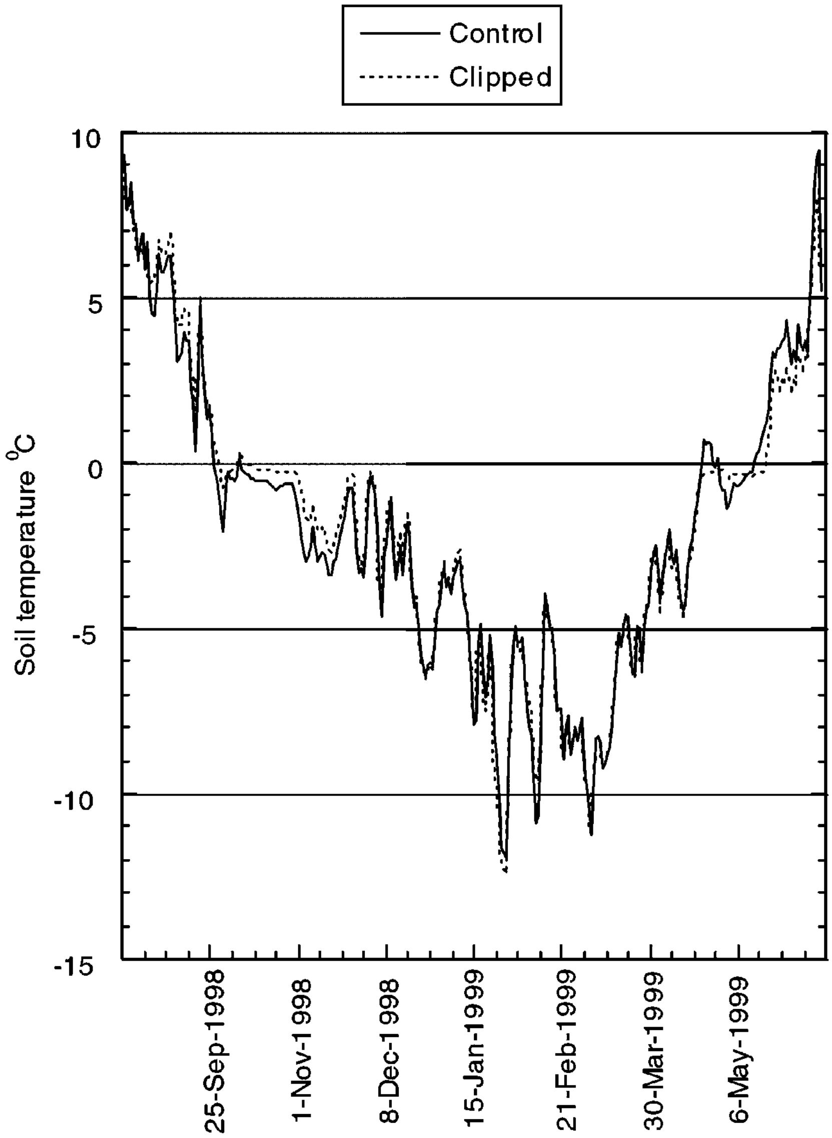

Figure 4. Mean diel soil temperatures (6 cm depth) from autumn 1998 to early summer 1999 at the site ($n = 3$–4).

strongly altered by abrupt changes in air temperature that cause freeze-thaw cycles in soils when snow cover is low/absent. Laboratory studies indicate that freeze-thaw temperature fluctuations have strong effects on microbial respiration of soil organic matter (Skogland et al., 1988; Schimel and Clein, 1996), but their effects on plant-associated respiration are not well studied. Occasional sharp fluctuations in soil temperature that may have led to thawing, occurred in both early and late winter during the year of our study (Figure 4). Further research is required to ascertain the effects of freeze-thaw on relative source pool contributions to CO_2 release in winter. Our study suggests that the recently-fixed plant C pool may dominate during the substantial periods in mid-winter when soils are above –5 °C, but below thawing temperature.

Our ecosystem CO_2 production rates for control plots are within range of many of the previously reported tundra mid-winter CO_2 efflux rates, which have been determined using a variety of different measurement approaches (Zimov et al., 1996; Brooks et al., 1996; Oechel et al., 1997; Winston et al., 1997; Mast et al., 1998). The treatment differences in CO_2 release rates reported here suggest that heterogeneity in plant biomass and/or surface litter accumulation beneath the snowpack may explain some of the spatial heterogeneity in efflux commonly observed in winter flux studies (e.g., Sommerfeld et al., 1996; Mast et al., 1998). Conversely, no significant differences were observed in integrated winter flux measurements from clipped plots across a variety of tundra vegetation-types in northern Alaska (Grogan and Chapin, 1999), suggesting that respiration in the absence of intact plants/fresh litter is relatively homogeneous. However, respiration of recent C may not dominate over bulk soil organic matter decomposition in ecosystems containing deep soil organic layers that do not freeze hard. In a recent study of three boreal forest sites (Winston et al., 1997), ^{14}C natural abundance isotopic signatures in soil CO_2 samples taken at depths of 22–92 cm were substantially lower in winter months than during summer. Soil temperatures at the gas sampling depths in each site did not descend below –5 °C. These results indicate a seasonal change in the relative contributions from ‘recent’ and ‘old’ C pools to CO_2 production at depth, and suggest that decomposition of ‘old’/bulk soil organic carbon could represent a significant portion of winter respiration in boreal forests. However, further studies will be required to ascertain whether the magnitude of bulk soil C decomposition in deep soil organic layers alters the overall balance between recent and old C sources for the entire soil column and its overlying vegetation during winter.

Characterization of the controls on winter respiration is an important component to modeling the outcome of GCM predictions of warmer winter air temperatures and increased snowfall on arctic ecosystem annual net C balance. Laboratory incubations indicate that physical processes during initial freezing can result in short pulses of CO_2 release from tundra soils (Coyne and Kelley, 1971). Recent studies indicating substantial CO_2 efflux rates beneath snowcover in arctic and alpine ecosystems have all assumed that winter respiration is due to temperature-regulated microbial respiratory activity during decomposition (Zimov et al., 1996; Sommerfeld et al., 1993, 1996; Brooks et al., 1996; Oechel et al., 1997; Mast et al., 1998; Fahnestock et al., 1998). Our study is important because it indicates that CO_2 production in sub-arctic heath at mid-winter is derived largely from respiration of recently-fixed, plant-associated C rather than from respiration of bulk soil organic matter C. This conclusion has two major implications. First, it strongly suggests that the controls and magnitude of winter CO_2 release in tundra can only be fully characterized by field measurements and/or microcosm incubations that include plants. Second, arctic ecosystems are important to global climate change models because enhanced decomposition of the extensive reserves of bulk soil C in tundra could provide a substantial positive feedback to atmospheric CO_2 concentrations, leading to enhanced global warming. Our study suggests that the warmer winter air temperatures predicted by GCMs for the Arctic are likely to have a stronger impact on the cycling of recently-fixed C pools than on the depletion of tundra bulk soil C reserves. Consequently, our results suggest that globally significant positive feedbacks from tundra to atmospheric CO_2 concentrations during mid-winter are unlikely in the initial phase of arctic ecosystem responses to climate change. Nevertheless, the enormous magnitude of the tundra bulk soil organic matter pool implies that the cumulative impact of even very small increases in its wintertime decomposition rate could provide a substantial positive feedback in the longer-term.

Recent studies indicate that ecosystem respiration in arctic wet sedge tundra vegetation during summertime is also dominated by plants and plant-associated C components (Shaver et al., 1998; Johnson et al., 2000). Considerable further research will be required to integrate summer and winter seasons in developing more advanced predictions of the overall effects of warming and lowered soil water tables on annual net C balance for each arctic vegetation-type, as well as in evaluating the implications for potential feedbacks to climate change.

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