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Final Report

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Response of a Tundra Ecosystem to Elevated
Atmospheric Carbon Dioxide and CO₂-Induced
Climate Change

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ABSTRACT

The overall objective of this research was to document current patterns of CO₂ flux in selected locations of the circumpolar arctic, and to develop the information necessary to predict how these fluxes may be affected by climate change. In fulfillment of these objectives, net CO₂ flux was measured at several sites on the North Slope of Alaska during the 1990-94 growing season (June-August) to determine the local and regional patterns of seasonal CO₂ exchange. In addition, net CO₂ flux was measured in the Russian and Icelandic Arctic to determine if the patterns of CO₂ exchange observed in Arctic Alaska were representative of the circumpolar arctic, while cold-season CO₂ flux measurements were carried out during the 1993-94 winter season to determine the magnitude of CO₂ efflux not accounted for by the growing season measurements. Manipulations of soil water table depth and surface temperature, which were identified from the extensive measurements as being the most important variables in determining the magnitude and direction of net CO₂ exchange, were carried out during the 1993-94 growing seasons in tussock and wet sedge tundra ecosystems. Finally, measurements of CH₄ flux were also measured at several of the North Slope study sites during the 1990-91 growing seasons.

Measurements were made on small (e.g. 0.5 m²) plots using a portable gas-exchange system and cuvette. The sample design allowed frequent measurements of net CO₂ exchange and respiration over diurnal and seasonal cycles, and a large spatial extent that incorporated both locally and regionally diverse tundra surface types. Measurements both within and between ecosystem types typically extended over soil water table depth and temperature gradients, allowing for the indirect analysis of the effects of anticipated climate change scenarios on net CO₂ exchange. *In situ* experiments provided a direct means for testing hypotheses.

The most striking result from this 3-year research campaign is that many arctic tundra ecosystems are currently net sources of CO₂ to the atmosphere over the growing season. This loss is apparently widespread, and was both qualitatively and quantitatively characterized in the Russian and Icelandic Arctic. Furthermore, taking into account the seasonally large net loss of CO₂ during the cold-season indicates that the annual net efflux of CO₂ from arctic ecosystems is substantially higher than growing season losses observed by this study. Field observations and *in situ* experiments indicate that net CO₂ flux is controlled primarily by soil moisture, and secondarily by temperature, indicating that warmer and drier climate change scenarios are likely to result in initially significant net losses of C as CO₂ from arctic ecosystems.

Whether the arctic will represent a positive or negative feed back to global climate change is largely a function of how drastic the temperature and hydrologic change is, the response of vegetation and soils to the changes in hydrology associated with an increase in temperature, and the time scales required for each level of biological organization to respond to such changes. Over the short term, it appears that soil respiration has increased relative to GPP due to more favorable soil aeration due to soil surface warming and drying. Although this change is thought to be transient, due to increases in nutrient availability from organic matter decomposition, there is currently no evidence of increased plant productivity in response to the recent soil warming and drying. Over the long term, this increase in soil decomposition should lead to greater nutrient mineralization and concomitant plant productivity, and arctic ecosystems may once again become sinks for atmospheric CO₂. Changes in the species composition of high-latitude ecosystems due to the northward migration of vegetation is expected, however, the time scale for this migration is extremely long compared to the relatively instantaneous response of soil microorganisms and the extant vegetation.

INTRODUCTION

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The Arctic represents a model biome to study the effects of climate change on ecosystem function, due to the sensitivity of arctic ecosystems to global warming and climate change (Schlesinger and Mitchell, 1987), the recently reported high latitude warming (Lachenbruch and Marshall, 1986; Chapman and Walsh, 1993), and the recently reported change in net ecosystem CO₂ flux (Grulke *et al.*, 1990; Oechel *et al.*, 1993). In addition, because of the presence of permafrost and the large C stores in arctic soils (Miller *et al.*, 1983), the arctic could represent a significant positive feedback to global atmospheric CO₂ concentration in response to high latitude warming and climate change (Billings *et al.*, 1982; Post, 1990; Oechel *et al.*, 1993). Therefore, knowledge of the magnitude of, and controls on, carbon storage in arctic ecosystems is of considerable importance to understanding current dynamics of atmospheric CO₂ concentration, and to predicting future changes in atmospheric CO₂ and associated greenhouse warming.

Arctic ecosystems are estimated to contain approximately 173 Gt of soil C (1 Gt = 10¹⁵ g) (Schlesinger, 1991; Post *et al.*, 1982), and an additional 5.8 Gt C in plant biomass (Miller *et al.*, 1983). Tussock tundra is estimated to contain 29.1 Gt of C worldwide, while wet sedge tundra is estimated to contain 14.4 Gt of C (Miller *et al.*, 1983). Approximately 95 % of this C is located below ground, and a majority of this below ground C is dead organic matter (Miller *et al.*, 1983). These soil C stores are substantial, and although the arctic makes up only about 6 % of the total world terrestrial ecosystem area (Miller *et al.*, 1983; Schlesinger, 1991), they contain roughly 11 % of the total soil C pool (Post *et al.*, 1982; Miller *et al.*, 1983; Schlesinger, 1991)

Although growth of arctic plants is relatively slow, the arctic has been a sink for atmospheric CO₂ in the recent and historic past (Coyne and Kelley, 1975; Chapin *et al.*, 1980; Miller *et al.*, 1983; Post, 1990). Low soil temperatures and permafrost, which impedes drainage leading to poor soil aeration, have resulted in low rates of soil decomposition (Oechel and Billings, 1992). Recent estimates of C accumulation vary widely, and are predominately a function of the method or integration time used (Oechel and Billings, 1992). Tussock tundra was estimated by harvest and flux techniques to be accumulating roughly 23 gC m⁻² yr⁻¹ (Miller *et al.*, 1983). Using similar methods, wet sedge tundra was estimated to be accumulating between 27 and 109 gC m⁻² yr⁻¹ (Coyne and Kelley, 1975; Chapin *et al.*, 1980; Miller *et al.*, 1983). Analysis of peat cores using ¹⁴C profiling information, however, estimate C accumulation rates to be between 2 to 3.5 gC m⁻² yr⁻¹ for tussock tundra, and 1.3 gC m⁻² yr⁻¹ for wet sedge tundra over the last 4000 years (Marion and Oechel, 1993).

Tussock tundra ecosystems presently are net sources of CO₂ to the atmosphere, while wet sedge ecosystems are approximately in balance (Grulke *et al.*, 1990; Oechel *et al.*, 1993; Oechel and Vourlitis, 1994 and 1995). This change has apparently occurred over the last 2 decades (Oechel and Vourlitis, 1994 and 1995; Oechel *et al.*, 1995), and coincides with a trend of increasing high latitude surface temperatures (Lachenbruch and Marshall, 1986; Beltrami and Mareschal, 1991; Chapman and Walsh, 1993; Oechel *et al.*, 1993). The recent change in CO₂ flux is attributed to an increase in ecosystem respiration following a change in soil moisture status in response to elevated surface temperatures (Oechel *et al.*, 1993; Oechel *et al.*, 1995). Over the short-term, net CO₂ loss is expected to continue, and arctic ecosystems will represent a positive feedback to atmospheric CO₂ concentration and associated climate change (Oechel *et al.*, 1993; Oechel and Vourlitis, 1994 and 1995). Over the long term, increases in mineralization are expected to enhance plant productivity (Shaver *et al.*, 1992). However, denitrification, immobilization, or losses of mineralized N to streams, lakes, and oceans could act to limit the fertilization effects (Nadelhoffer *et al.*, 1992; Moorehead and Reynolds, 1993). Migration of boreal forest species into arctic regions should act to increase the potential productivity and above-ground C storage as well (Smith and Shugart, 1993; Landhäusser and Wein, 1993). If C gain from plant productivity eventually exceeds C loss from decomposition, arctic ecosystems will become a sink for atmospheric CO₂, and represent a negative feedback to atmospheric CO₂ concentration (Oechel and Billings, 1992; Shaver *et al.*, 1992).

RESEARCH OBJECTIVES AND HYPOTHESES

Objectives

The overall objective of this proposed research was "to document current patterns of CO₂ flux in selected locations of the circumpolar arctic and to develop the information necessary to predict how these fluxes may be affected by climate change". The research proposed comprised three principal areas:

- A) Circumpolar patterns of net ecosystem CO₂ flux.
- B) *In situ* controls by temperature and moisture on net ecosystem CO₂ flux.
- C) Scaling of CO₂ flux from plot, to landscape, to regional scales (in conjunction with research proposed for NSF support).

All areas build on our past research and contribute to answering the overall objectives above. These objectives build on particular windows of opportunity (research in Russia and Iceland) and/or cooperation with other agencies (e.g. with NSF on scaling and site manipulations).

Hypotheses

The following hypotheses were investigated over the course of this research.

Hypothesis 1: The tundra in the Russian arctic and western Iceland is currently a source of CO₂ to the atmosphere.

Explanation. The tundra of the eastern central north slope of Alaska has been a sink for carbon with respect to the atmosphere in the historic and recent geologic past. This area is now a source of CO₂ to the atmosphere. This change appears to be due to a combination of increased temperature followed by a lowering of the soil moisture. Since warming has been reported for much of the circumpolar arctic, we anticipate that other arctic regions, including those in Iceland and Russia, have experienced a reduction in net ecosystem carbon uptake, or even a net loss to the atmosphere as is the case in central Alaska.

Hypothesis 2: Increased soil temperature will increase net ecosystem CO₂ flux to the atmosphere in well-drained habitats and decrease net ecosystem flux to the atmosphere in flooded habitats.

Explanation. Decomposition of dead organic matter is primarily a function of temperature and the reduction-oxidation (redox) potential of the substrate. In arctic tundra ecosystems, soil temperatures are often too low for significant respiratory activity by soil microorganisms. Increases in soil temperature will directly increase microbial activity, decomposition rates, and CO₂ efflux. In addition, higher soil temperatures will also increase thaw depth which will increase soil aeration and the total amount of carbon available for decomposition. Decomposition will be stimulated more than net primary productivity. However, since the C:N ratio of arctic plants is higher than arctic soils (Oechel and Billings, 1992), increased decomposition with elevated temperatures could result in more carbon accumulated above-ground than is released below-ground, and the sink strength of the arctic could be increased. In flooded habitats, the increase in temperature and thaw depth will not significantly affect the water balance of the site. Soil decomposition will continue to be limited by redox potential, and net primary productivity will be increased more than soil decomposition. As a result, the site will be a greater net CO₂ sink with respect to the atmosphere.

Hypothesis 3: Increased soil drainage will increase CO₂ flux to the atmosphere, especially in habitats of poor drainage and water-logged soil conditions.

Explanation. Poor drainage (often due to or exacerbated by the presence of permafrost) creates water-logged conditions which reduce rates of aerobic respiration and decomposition. Increased drainage will result in better soil aeration, higher rates of decomposition, and higher rates of CO₂ flux to the atmosphere. Plant productivity may increase due to greater nutrient availability and greater nutrient uptake capacity, but the increase in net primary productivity will be less than the increase in soil decomposition.

Hypothesis 4: Higher soil moisture will increase CH₄ flux to the atmosphere and will increase carbon sequestering by the ecosystem, especially in habitats which have better drainage.

Explanation. CH₄ production is an anaerobic process. Factors which reduce soil aeration tend to increase CH₄ production. In habitats that have well-drained soils, CH₄ production is low. If the drainage characteristics are altered enough to encourage anaerobiosis, CH₄ production will increase. The opposite tends to be true for soil decomposition and CO₂ production. Adding water in well-drained soils should decrease decomposition and increase net CO₂ sequestering. In habitats that already have poor drainage, adding water should not significantly further reduce soil aeration and decomposition.

Hypothesis 5: The tundra of the eastern-central North Slope of Alaska is currently a source of CO₂ to the atmosphere, the rate of which is accurately predicted by the additive fluxes observed at the plot scale. Incorporating all vegetation terrain units present will not alter the qualitative conclusions drawn from measurements of the dominant vegetation types at the plot scale (however, the magnitude of the fluxes may be refined).

Explanation. Arctic landscapes are a heterogeneous collection of vegetation terrain units with differing community composition, soil types, water balances, and thaw depths. Each of these variables affect carbon balance, resulting in a mosaic of CO₂ flux within a region that differ not only in rate but also potentially in direction. For example, the extensive chamber measurements made in a variety of habitat types during the 1990-91 sampling years indicate that the measurement sites were losing carbon to the atmosphere. Some habitats, however, were stronger sources than others, while others were, at times, slight sinks. The additive fluxes of these habitat types will determine the regional flux. More of the habitats measured were sources than were sinks, indicating that the tundra on a regional scale is a net source of carbon to the atmosphere. However, minor vegetation terrain units have not been measured, and consideration of these types may affect the calculation of the regional fluxes.

RESEARCH APPROACH

North Slope

Site Descriptions

Net ecosystem CO₂ flux and respiration were sampled on the North Slope of Alaska during the summer of 1990-1994 at several sites along a 200 km latitudinal gradient extending from Prudhoe Bay near the arctic coast south to Toolik Lake (Fig. 1). Interior sites are classified as *Eriophorum vaginatum* dominated moist-tussock, dwarf shrub tundra ecosystems (Walker *et al.*, 1989). Tussock tundra occupies nearly 0.9 x 10⁶ km² (i.e. 16 %) of circumpolar tundra and comprises roughly 47% of the total arctic soil C stores (Miller *et al.*, 1983). In Alaska, tussock tundra covers approximately 80 % of the arctic region (Oechel 1989). Sites on the arctic coastal plain and adjacent to the arctic ocean (APL-133, West Dock, and Barrow; see Fig. 1) are classified as *Eriophorum angustifolium*, *Carex aquatilis*, and *C. bigelowii* dominated wet sedge tundra (Walker *et al.*, 1989). These ecosystems comprise approximately 1 x 10⁶ km², or 17.5 % of the circumpolar tundra (Miller *et al.*,

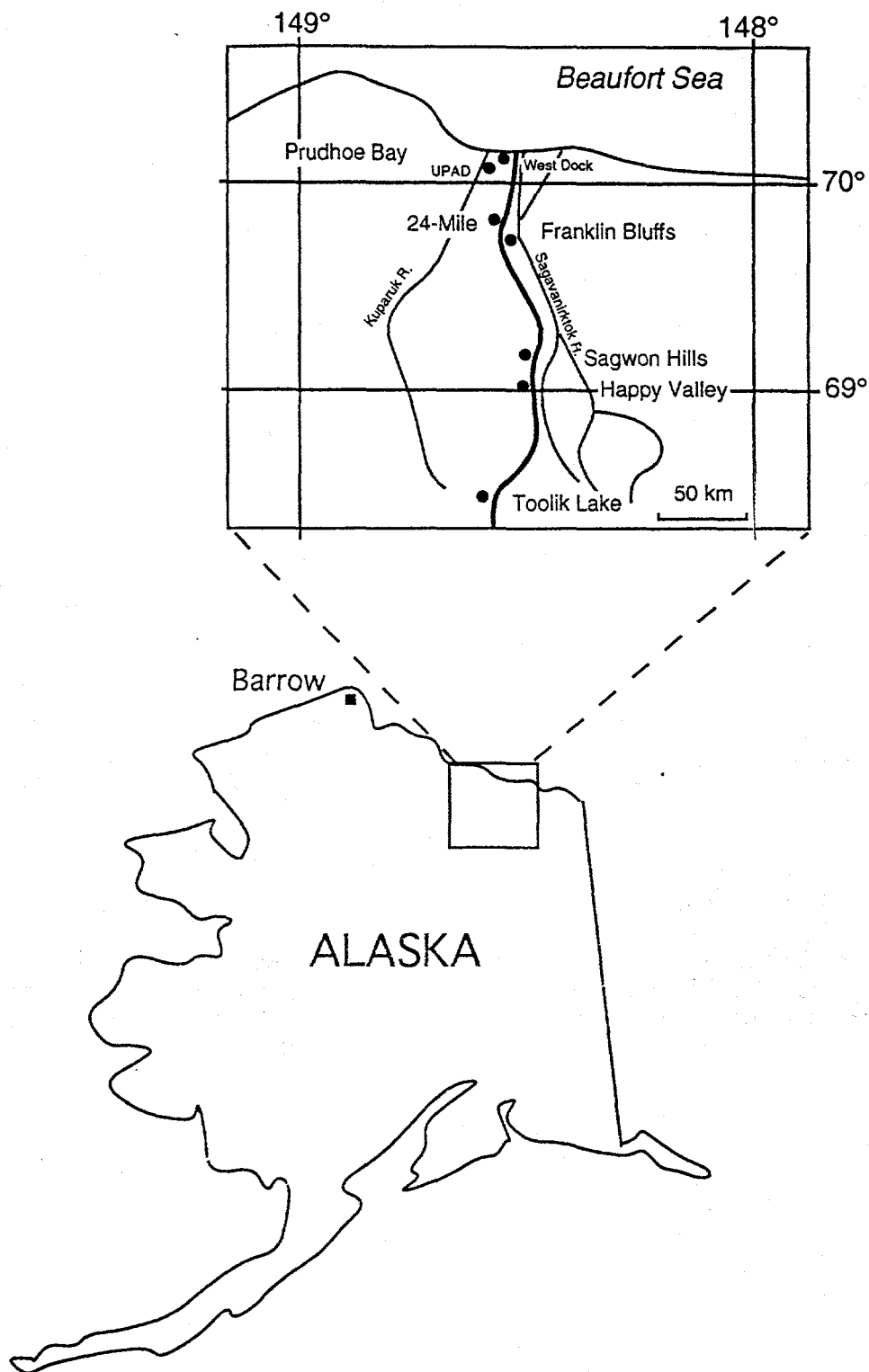


Fig. 1. Study sites along the North-South transect on the North Slope of Alaska. Net CO₂ flux measurements were carried out at Toolik Lake, Happy Valley, and West Dock (1990-91, 1993-94), APL 133-3 (1990-91), Sagwon Hills (1991), and U-Pad (1993-94). In situ experiments (1993-94) were carried out at Toolik Lake and West Dock. Cold season net CO₂ flux measurements (1993-94) were carried out at Toolik Lake, Happy Valley, West Dock and U-Pad. Barrow sites (1992) are not shown.

1983), while in the Beechey Point region on Alaska's North Slope, these ecosystems comprise nearly 30% of wet sedge tundra (Walker and Acevedo, 1987).

Soils along the latitudinal gradient are classified as Histic Pergelic Cryaquepts (Rieger *et al.*, 1979) with a 15-30 cm organic layer overlying mineral soil (Marion and Oechel, 1993). Soils can be nearly saturated throughout the growing season in the wet sedge tundra along the arctic coast, and water table depth may frequently be at, or near, the soil surface (Gersper *et al.*, 1980). Organic surface soils in the inland tussock tundra, however, may not be saturated throughout the growing season (Kane *et al.*, 1989), and water table depth may be well below the soil surface.

Mean annual temperature ranges between -11.1 to -6.7 °C near the foothills of the Brooks Range to between -12.8 to -10.3 °C along the arctic coastal plain (Oechel, 1989), while mean annual summer temperature (June - August) ranges between 4 °C on the arctic coast to 11 °C in the interior. Interior annual precipitation is on average between 225 - 325 mm, while coastal precipitation is generally between 180 - 210 mm (Alaska Cooperative Snow Survey Data, 1992). The majority of this precipitation (60 - 80 %) falls as snow during the winter and spring seasons (Kane *et al.*, 1992). Date of snow melt is between early-May to early-June for interior regions and between mid- to late-June for the coastal high arctic areas (Kane *et al.*, 1992). As a result, growing season length, expressed as the number of degree days (the summed daily mean air temperatures greater than zero between May and September), is substantially longer in the interior regions than near the arctic coast (Shaver *et al.*, 1986).

Net CO₂ Flux Sampling

Flux and respiration measurements were made on 0.5 m² plots using a closed gas exchange system and a 257 L ecosystem cuvette (Vourlitis *et al.*, 1993). Sample plots were affixed with a 0.5 m² polycarbonate chamber base to allow an air-tight seal between the ecosystem and cuvette. Chamber bases were installed to a depth of 10-20 cm into the permafrost at the beginning of the growing season using a chainsaw. Plants were still dormant at this time, thus minimizing damage to roots and rhizomes. The chamber bases were found to effect the substrate, and hence, ecosystem CO₂ flux, minimally (Vourlitis *et al.*, 1993).

Flux measurements were repeated every 1-1.5 hours over a 24 hour cycle, and were repeated every 5-7 days throughout both growing seasons. Respiration measurements were made following each flux measurement by covering the chamber with an opaque blanket (Vourlitis *et al.*, 1993). Growing season sampling at all sites during each year typically began in late-May, early-June and ended in mid-September. In 1993 and 1994, field sampling at Toolik Lake and Prudhoe Bay occurred in conjunction with *in situ* soil moisture and temperature manipulations (see below). Six to twelve plots per site were sampled during each growing season. Diurnal CO₂ flux was calculated by integrating hourly measurements over the 24 hour cycle. Gross primary productivity (GPP) was calculated as the difference between net flux and respiration measurements. Seasonal flux, ecosystem respiration, and GPP were calculated by integrating daily totals over the period of snow melt to the first significant snowfall, which is assumed to correlate with soil freezing. Thus, the estimated length of the growing season was 127, 147, 93, and 130 days for the 1990, 1991, 1992, and 1993 field seasons, respectively. Flux measurements were not made on the beginning and end of season dates, and CO₂ flux was assumed to equal zero on these dates.

Measurements of net ecosystem CO₂ flux and whole ecosystem respiration were measured using the static chamber described above (Vourlitis *et al.*, 1993) in Barrow, Alaska during the 1991-92 growing seasons (Oechel *et al.*, 1995). Preliminary measurements in 1991 were made over three, 24-hour periods (17 and 27 July, 17 August) at the IBP-II intensive site. One 0.5 m² plot in each replicate habitat was sampled every hour over a 24-hour period. Intensive measurements of whole ecosystem CO₂ flux and respiration were carried out during the 1992 sampling season at the Coyne and Kelley (1975) aerodynamic tower site, in polygonized tundra habitats at the IBP intensive site II,

and at the Central Marsh wet meadow site (Oechel *et al.*, 1995). Three replicate high and low centered polygons ranging from extremely wet (standing water or saturated soils) to dry (no visible standing water and non-saturated soils) were selected for study at IBP-II, while two replicate ice wedges were selected in close proximity to the high and low centered polygons. In the moist meadow habitat adjacent to the Coyne and Kelley aerodynamic tower site at IBP-II, three patch types were selected to encompass the dominant vegetation types observed. Sites at Central Marsh were selected on the basis of plant species composition, which is indicative of site water balance (Walker and Acevedo 1987). The wettest site was dominated by *Arctophila fulva*, while the dryer site was dominated by *Eriophorum angustifolium* and *Dupontia fisheri*.

Two sample plots in each habitat replicate were selected between 15-18 June at IBP-II. Each sample plot was affixed with a 0.5 m² polycarbonate chamber base as described above. Plots at Central Marsh were selected on 20 June. Four plots were selected within each habitat, however, polycarbonate chamber bases were not required in this area due to the evenness of the terrain and the presence of standing water which provides an air-tight seal between the chamber and the ecosystem. Flux and whole ecosystem respiration measurements were repeated every 1-1.5 hours over a 48 hour cycle at the polygonized IBP-II sites. At the moist meadow sites, measurements were repeated every hour over a 24 hour cycle until 16 July, and over a 48 hour cycle thereafter. Diurnal flux measurements were repeated every 5-7 days between 25 June and 30 August. Flux measurements at Central Marsh were made every hour over a 24 hour cycle every 2 weeks. Diurnal CO₂ flux was calculated by integrating hourly measurements over the 24 or 48 hour cycle.

CH₄ Flux Sampling

Whole ecosystem CH₄ flux was sampled 3-5 times during the 1990-91 growing seasons on 2-0.5 m² bases at Happy Valley, Toolik Lake, West Dock, and APL 133 (Franklin Bluffs) (Fig. 1). Samples were taken by sealing a 257 liter chamber onto a 0.56 m² polypropylene base previously cut into the permafrost (Vourlitis *et al.*, 1993, 1994). The chamber consisted of an aluminum frame with Acrylic sides and top, six-10 cm radial fans to ensure mixing of the chamber atmosphere, and a rubber septum for gas sample extraction. The chamber was affixed to the base using rubber "bungee" chords, while the chamber/base interface was sealed using a closed cell foam tape.

During each sampling event, the chamber was sealed to the permanent base for up to 20 minutes, and covered with an opaque tarp to inhibit soil heating. Gas samples were taken at 0 (immediately after the chamber was affixed to the base), and at 5, 10, and either 15 or 20 minutes following chamber installation by withdrawing approximately 10 cc of gas using B-D Glaspak™ syringes affixed with B-D 21 gauge needles. Gas samples were taken every 6-8 hours over a 24 hour period during each sampling event, and immediately returned to our lab located in Prudhoe Bay for analysis. The concentration of CH₄ in each gas sample was determined using a Shimadzu GC Mini-2™ gas chromatograph affixed with a flame ionization detector, and a MS 5A 80/100 column. The column temperature was 90 °C, with a carrier gas (N₂) flow rate of 0.5 L min⁻¹. Sample CH₄ concentration was calculated from a standard curve using 10.3 and 9.03 ppmv standards (Scott Specialty Gases). Methane flux was calculated as the rate of concentration change over the 15 or 20 minute sampling duration.

Cold Season Net CO₂ Flux Measurements

Cold-season (fall-spring) net CO₂ flux was measured at the Toolik Lake, Happy Valley, West-Dock, and U-Pad sites on the North Slope of Alaska (Fig. 1) between October, 1993 and May, 1994. At each site, 3 to 6-0.5m² plots were measured 4 times during the cold-season (October, November, March, and Late-May) using the 257 L cuvette and portable gas-analyzer described earlier (Vourlitis *et al.*, 1993). Measurements in October and late-May were conducted on hourly intervals over the diurnal cycle. Measurements in November and March were taken over a 2-3 hour period during the day, because little diurnal pattern in flux was apparent from the October data. Due to

equipment failure, November measurements from Happy Valley were not obtained, however, there was good correlation between efflux measured at Toolik Lake and Happy Valley for the remaining dates ($y = 1.152x + 0.053$, $R^2 = 0.999$, $p = 0.02$, $n = 3$), so November emissions for Happy Valley, were estimated from the Toolik Lake data.

Each instantaneous flux measurement consisted of 3-20 second observations taken over a 1 minute interval (Vourlitis *et al.*, 1993). These 20 second observations were subsequently averaged for each instantaneous flux measurement. Average daily flux was calculated by either integrating hourly flux estimates (October and May), or by assuming that the average flux determined during the 2-3 hour sampling event was indicative of the diurnal average (November and March). Cold-season flux was calculated by integrating the diurnal flux measurements taken in October, November, March, and May, which corresponds to a 229 day season.

Soil Moisture and Temperature Manipulations

In situ experiments were initiated the 1993 field season at Toolik Lake and Prudhoe Bay to determine the effects of soil moisture and elevated temperature on tussock and wet sedge tundra ecosystems, respectively. At the Toolik Lake tussock tundra site, a polypropylene dam was installed to a depth of 50 cm perpendicular to a gentle slope at the end of the 1992 field season. At the end of the 1992 field season, 4-0.5 m² polypropylene chamber bases were installed approximately 1 m upslope of the dam, while 4 bases were installed 1 m downslope of the dam to determine the effect of elevated and reduced soil moisture, respectively. With this configuration, water moving downslope was impounded upslope of the dam and diverted downslope. In addition to the manipulated plots, 4 control plots were installed approximately 10 m away from the dam so they would not be affected by the diverted subsurface water flow.

At Prudhoe Bay, there was very little slope which precluded the use of the dam to either divert or impound subsurface water flow. Instead, 4 plots were enclosed in 60 cm deep polypropylene enclosures with one plot per enclosure. Battery operated, float activated bilge pumps were installed to a maximum depth of 60 cm within each polypropylene enclosure to reduce the water table. Hence at Prudhoe Bay, only the effect of reduced water table and soil moisture on flux was analyzed. In addition to the enclosed plots, 4 "cut-control" plots and 4 control plots were also installed. For the cut-control plots, a 60 cm deep cut surrounding each chamber base was made through the soil active layer and permafrost to determine the effect that the cut, made during the installation of the enclosures, had on net CO₂ flux.

Soil surface temperature was elevated using open-top Plexiglas cones (Sun-Lite HP, Solar Components Corporation) which were fit over each randomly assigned chamber base (Marion *et al.*, 1993). The cones have an open-top diameter of 1.02 m, and are made of 2 mm thick Lexan Plexiglas which transmits 90 % of visible wavelengths and approximately 5 % of infra-red wavelengths (Marion *et al.*, 1993). In addition, the cones have inwardly inclined sides (60° from horizontal) which improves transmittance of solar radiation and heat trapping efficiency (Marion *et al.*, 1993). The cones were installed at both sites between 9-15 July, 1993 when the material became available. At Toolik Lake, 2 cones were randomly assigned to each experimental group (e.g. 2 in the control group, 2 in the impounded group, and 2 in the drained group). At Prudhoe Bay, 2 cones were randomly assigned to each drained, cut-control and control group.

Surface soil temperatures (0-2 cm depth) were monitored in each plot using type-t thermocouples and a Campbell Scientific 21-X Micrologger. Three thermocouples were averaged within each plot to account for intra-plot variability in surface temperature. Temperature differences between cone and control plots were analyzed using paired t-tests ($n = 39$ at Prudhoe Bay and $n = 248$ at Toolik Lake). Water table depth and depth to permafrost was determined following each diurnal flux measurement period within each enclosure, and adjacent to the control plots as described in the previous section.

Ancillary Measurements

Percent soil moisture was measured gravimetrically in conjunction with CO₂ flux measurements. Approximately 5-7 soil samples were obtained at each site after each diurnal flux measurement period. Samples were taken at a depth of 10 cm, weighed immediately following the diurnal flux measurements for the determination of wet weight, dried in an oven at a temperature of 105 °C for 4-5 days, and re-weighed for the determination of water loss. Water table depth was determined each day flux was measured from 6, 1 m long x 1.9 cm diameter perforated PVC tubes at each site. The tubes were installed to an approximate depth of 90 cm using a hammer drill (Hilti Corp., Tulsa, OK). The tubes quickly froze into the permafrost, and remained frozen throughout the sampling season. Water table depth relative to the soil surface was measured by placing a clear sampling tube into the PVC water well, plugging the exposed end of the tube to trap its contents, withdrawing the sampling tube, and measuring the height of its contents. Active layer depth was measured at every plot (5-10 subsamples per plot) at each site after each diurnal measurement period between 1990 and 1994 by driving a steel rod into the soil until permafrost was reached. The portion of the rod between the permafrost layer and the soil surface, which corresponds to the active layer depth, was measured using a meter stick.

Weather conditions at each site were monitored on a hourly basis throughout each growing season using a semi-portable weather station and a Campbell Scientific CR 21X Micrologger. Weather stations contained a LI-COR LI-190S quantum sensor (Lambda Instruments Inc., Lincoln, NE) for measurements of photosynthetically active radiation (PAR), a Campbell Scientific 207 relative humidity and temperature sensor (Campbell Scientific Inc., Logan, Utah), type-T thermocouples for soil temperature at a depth of 10 cm, a wind direction sensor and a cup anemometer (Met-One Inc., Sunnyvale, CA), and a tipping bucket rain gauge (Sierra-Misco Inc., Berkeley, CA). Weather data for Sagwon Hills and APL 133-3 in 1991 was provided by D. Kane of the University of Alaska, Fairbanks, while weather data for Toolik Lake during 1991 was provided by J. Laundre of The Ecosystems Center at Woods Hole, MA.

Iceland

Site Description

Net CO₂ flux measurements were conducted adjacent to a cold, naturally emitting CO₂ spring located in *Nardus stricta* dominated grassland on the Snaefellness Peninsula of Western Iceland. The vegetation is of low-stature and typical of most high latitude grasslands. The spring emits approximately 99% pure CO₂ into the atmosphere, creating a CO₂ concentration gradient that decreases with distance from the spring. CO₂ concentrations vary from approximately 1200 ppm immediately adjacent to the spring to the ambient CO₂ concentration of 355 ppm in control areas approximately 100m away from the spring.

Plots (28 x 38 cm) were installed at an intermediate distance from the spring, where the average CO₂ concentration was approximately 500 ppm, while control plots were installed in the adjacent grassland which was exposed to ambient CO₂. Each plot was centered around a *Nardus stricta* tussock, but included many other grass and shrub species. To insure that the main difference between the spring and control plots was CO₂ concentration, great care was taken to match the spring and control plots with respect to species composition, soil type, and water table depth. Spring and control plots were all located within 50 meter of each other on the same hillside, and the depth to the water table was similar for both sites.

Net CO₂ Flux Sampling

A passive, closed system chamber sampling technique (Vourlitis *et al.* 1993) was used to measure the carbon balance of intact, multi-species, grassland ecosystem plots. Diurnal measurements were conducted once a week throughout the approximately 90 day growing season on

6 plots located near the CO₂ spring and 4 plots located in the adjacent grassland. Net ecosystem productivity was measured in the ambient light using a LiCor 6200 portable photosynthesis system (Lincoln, Nebraska, USA) which was fitted with a custom-made 28 x 38 x 40 cm (L x W x H) cuvette with acrylic sides and a mylar top. The ecosystem cuvette was made completely dark with an opaque cloth cover to measure total ecosystem respiration. These measurements were repeated throughout the 24 hour sampling period at approximately 2 hour intervals.

A computer program "CO₂ Exchange" (Nosov 1994) was used to estimate the daily and seasonal dynamics of GPP, whole ecosystem respiration, and net ecosystem CO₂ exchange from field gas exchange measurements and weather station data. Predictive relationships were built between PAR, GPP, temperature, and ecosystem respiration so that the carbon dynamics of the ecosystem could be interpolated for periods when measurements were not taken.

Russian Arctic

Site Descriptions

Net CO₂ flux measurements were made in July, 1993 to determine the circumpolar extent of mid-season net CO₂ efflux previously observed from research conducted in Arctic Alaska (Grulke *et al.*, 1990; Oechel *et al.*, 1993). Field sites were situated along a 550 km latitudinal transect in the western portion of the Taymyr Peninsula. The main study site was located on the Taymyr Peninsula at the Taymyr Biological Research Station located near the confluence of Pyasina and Tareya rivers (73°15'N, 90°36'E). This site comprises one of the former International Biological Program (IBP) intensive sites, and therefore, has a long history of ecosystems research. The climate of the region is typical of high-arctic environments, with an average January temperature of -31.4 °C, while the average July temperature is 10.5 °C (Romanova, 1971).

Carbon flux measurements were carried out in two ecosystem types: (I) mossy Dryas-sedge hummocky tundra, and (II) polygonal wetland complex. The mossy Dryas-sedge hummocky tundra (*Hylocomium splendens*, *Aulacomnium turgidum*, *Tomenthypnum nitens*, *Carex ensifolia*, and *Dryas punctata*) is characteristic of upland watershed areas formed on loamy soils. Hummocks comprise nearly 60% of the surface area in this region, and are typically 10-12 cm high and 15-30 cm in diameter, forming various patterns of branched, chain-like structures. The polygonal-wetland complex is dissected by frost-boil cracks forming polygons with 7-10 m sides. The complex is a combination of the dwarf shrub-herbaceous-moss associations (*Drepanocladus revolvens*, *Meesia trietra*, *Carex stans*, *Carex chordorrhiza*, *Salix reptans*) in the central part of polygons (60%). The shrub stratum is dominated by *Betula nana* found on the sides of the weekly expressed polygon rims (30% in area) and the sedge-*Eriophorum*-moss association in the bog within the cracks (10% in area).

The southernmost site, Kresty (70°51'N, 89°54'E), also has a long history of complex ecosystem studies, and is located near the confluence of the Dudypa and Pyasina rivers. Mean annual temperature is approximately -12.3 °C, but due to the more southern location compared to the Taymyr study sites, the growing season is longer, with positive average daily temperatures observed from the beginning of June to the mid of October. Mean July temperature is 11.4 °C, while mean January temperature is -30.6 °C. The annual precipitation is 344 mm. The vegetation was characteristic of a dwarf shrub, shrub-moss-sedge (e.g. tussock tundra) complex dominated by *Eriophorum vaginatum*, *Sphagnum aongstroemi*, *Aulacomnium turgidum*, *Vaccinium vitis-idea*, and *Betula nana* (Matveeva, 1977). This ecosystem occupies the upper parts of the low round-top hills and ridges, and the most characteristic feature of this community is the specific microrelief of phytogenic origin formed by *E. vaginatum* tussocks. The intertussock areas are typically covered by a blanket of moss with occasional spots of bare ground.

Net CO₂ Flux Sampling

Net CO₂ measurements were carried out using the portable gas exchange measurement

apparatus described previously (Oechel *et al.*, 1993, Vourlitis *et al.*, 1993). We used a cylindrical acrylic chamber (40 cm in diameter, 70 cm in height), permanently connected to a stainless steel base with a serrated edge on the bottom. At the completion of a measurement, both base and chamber were moved to the next plot to be measured. Changes in the CO₂ concentration in the chamber were recorded using an infra-red gas analyzer (IRGA) LiCor-6200.

Eight sample plots per subsite were measured every 1-1.5 hours over 1-2, 24 hour measurement cycles in July, 1993. Respiration measurements were made following each flux measurement by covering the chamber with an opaque blanket (Vourlitis *et al.*, 1993). The duration of a measurement was 1 minute to minimize large deviations in CO₂ concentration and temperature between the chamber and the ambient environment. In addition to CO₂ concentration, chamber temperature, chamber relative humidity and ambient photosynthetically available radiation were recorded. Daily carbon flux values were calculated by integrating the instantaneous flux measurements for each sample plot over the 24 hour measurement period, and weighted to reflect the actual cover of the various communities over the whole landscape.

Ancillary Measurements

Additional meteorological information was collected at the sampling sites in conjunction with the flux measurements. Temperature of the ambient air, soil temperature at the soil surface, 1 cm, 5 cm and 10 cm were determined using type-T thermocouples just prior to making an individual flux measurement so that a complete daily pattern could be obtained. Depth of thaw was determined using a steel rod inserted through the unfrozen soil till the underlying permafrost was reached at 20 randomly chosen points at each site. In some sampling plots, aboveground components of phytomass (green and woody part of shrubs, grasses, mosses, lichens) were cut, dried and weighted.

RESULTS

Ecosystem CO₂ Flux on the North Slope of Alaska

The magnitude of net CO₂ efflux on the North Slope of Alaska during the 1990-92 growing seasons increased from north to south, primarily due to the temperature and soil water content gradient which is superimposed on the latitudinal transect (Fig. 2). Sites with lower soil water content and higher temperature, such as the tussock tundra sites to the south were greater sources of CO₂ to the atmosphere, but weaker sources of CH₄ (Fig. 2). In contrast, sites with greater soil water content, such as the wet sedge tundra to the north, were weaker sources of CO₂ (or approximately in balance) but were greater sources of CH₄ to the atmosphere (Fig. 2).

The seasonal CO₂ flux pattern is strikingly similar for the years examined. For example, source activity of tussock tundra at Toolik Lake increased into late June (Fig. 3). Peak sink activity was observed during mid-July, followed by a second, and generally higher, period of source activity (Fig. 3). Early season CO₂ loss was observed in wet sedge ecosystems at Prudhoe Bay as well, however, there are 2 peaks of sink activity observed, one in late-June and early-July and another in late-July and early-August (Fig. 3). This may be due to differences in the timing of monocotyledon and dicotyledon productivity and chlorophyll concentration (Tieszen, 1973), or to differing seasonal time scales for peak non-vascular and vascular plant activity (Oechel and Sveinbjornsson, 1978). Sink activity decreases rapidly at the end of the growing season (late-August), while net CO₂ efflux peaks through September when plants are dormant, and water table and active layer depth are at a seasonal maximum (Fig. 3).

These results indicate that net loss of CO₂ is substantial from moist tussock tundra ecosystems in the foothills of the Brooks Range, while net CO₂ flux of the moist and wet sedge ecosystems of the arctic coastal plain is roughly in balance (Oechel *et al.*, 1993; Oechel and Vourlitis, 1994 and 1995). This change is attributed to the recently reported high-latitude warming (Lachenbruch and Marshall, 1986; Chapman and Walsh, 1993) and an associated decrease in surface (0-10 cm) soil water content

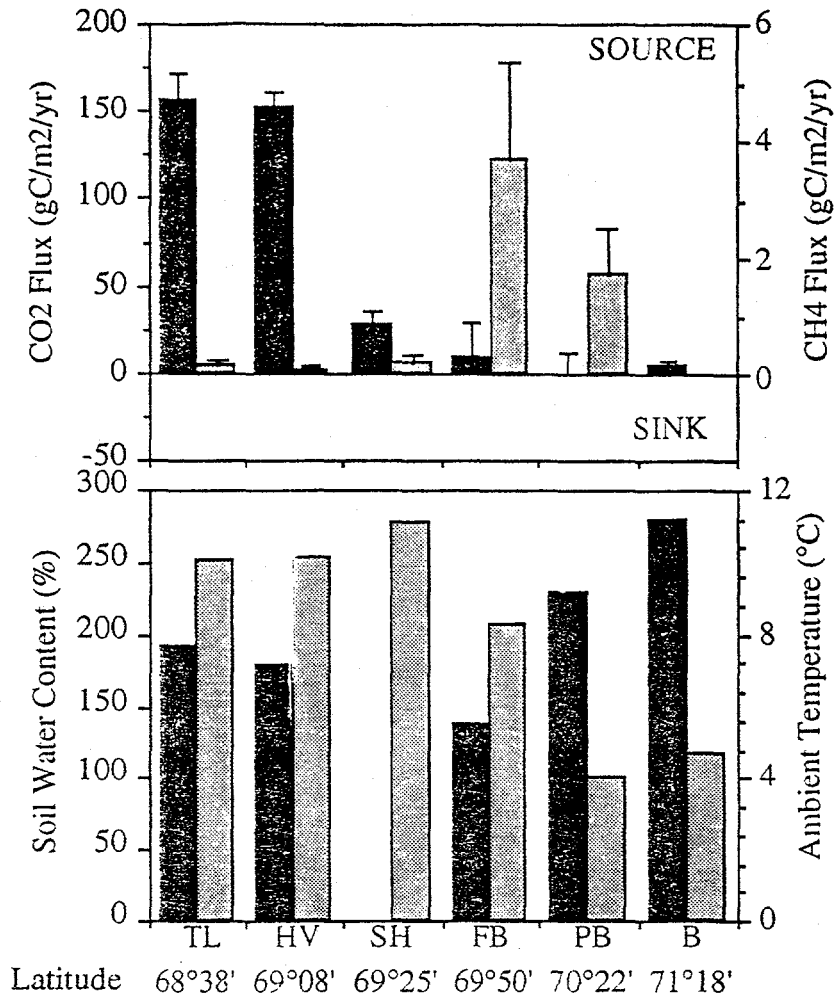


Fig. 2. Net ecosystem CO₂ (closed bars) and CH₄ (stippled bars) flux (top panel), and (bottom panel) percent soil moisture (closed bars) and temperature (stippled bars) along a latitudinal gradient on the North Slope of Alaska between 1990-1992. Data are means \pm 1 SE, n (corresponding to the number of plots measured at each site) = 4-6 for TL (Toolik Lake) and HV (Happy Valley), n = 12-18 for FB (Franklin Bluffs), n = 8-12 for PB (Prudhoe Bay), n = 4 at SH (Sagwon Hills), and n = 30 for B (Barrow). Positive flux values indicate net efflux to the atmosphere. CH₄ flux and soil moisture were not determined at Barrow and Sagwon Hills, respectively. Data from Oechel and Vourlitis (1995).

(Oechel *et al.*, 1993; Oechel and Vourlitis, 1994 and 1995). To assess the magnitude of the potential change in net CO₂ flux over the last three decades, measurements of net CO₂ flux were performed at the Barrow, Alaska IBP site II where direct comparisons between contemporary and past CO₂ exchange (Coyne and Kelley, 1975) can be made.

Carbon efflux was greatest during the early and late season periods when rates of primary productivity were low (Fig. 4). Ecosystem CO₂ uptake was at a maximum during the month of July, as plants neared their seasonal potential photosynthetic peak and environmental conditions became more suitable for plant growth (Fig. 4). As the season progressed, the magnitude of GPP decreased relatively more than respiration, and each habitat became more of a source of CO₂ to the atmosphere (e.g. early August, Fig. 4). The decrease in GPP was due to the decrease in mean daily PAR and the onset of senescence. Whole ecosystem respiration remained high through August (Fig. 4), as average

daily temperature remained adequate and water table depth reached its lowest point. This combination of phenological and environmental conditions in the latter part of the growing season should act to reduce ecosystem sink strength relative to respiration, and promote greater rates of net ecosystem C loss. Seasonal C loss was highest in high center polygon habitats, which lost approximately 14 ± 5 $\text{gC m}^{-2} \text{yr}^{-1}$ during the 1992 growing season. Moist and wet meadows and low center polygons were on average slight sources during 1992, while ice wedges were slight sinks. Incomplete seasonal data collected during the 1991 mid-season peak in ecosystem productivity indicates a similar trend to that observed in 1992 (dashed lines, Fig. 4, top panel) and 1993 (Y. Harazono and W. Oechel, unpublished data).

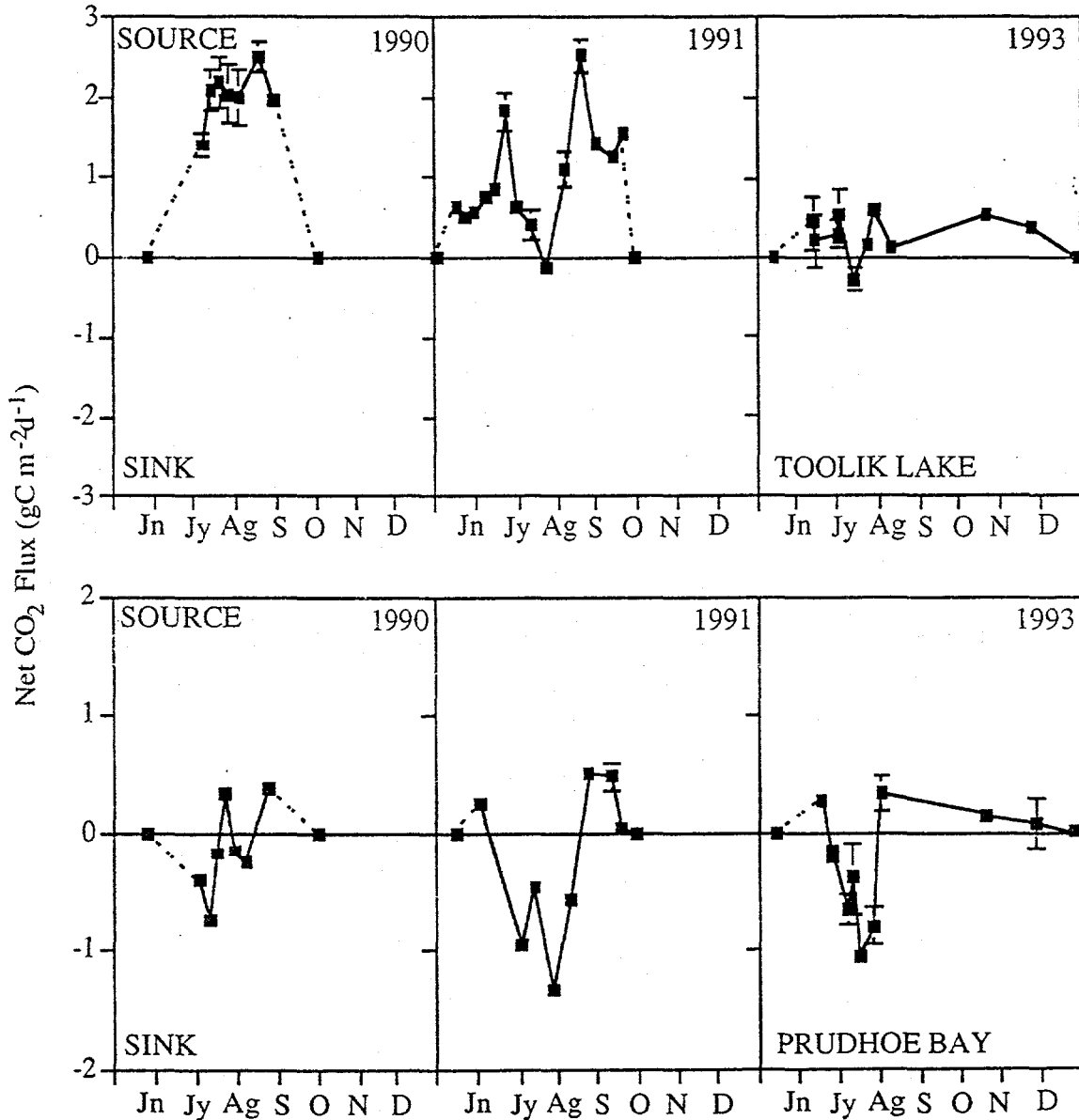


Fig. 3. Seasonal pattern of net CO₂ flux at the Toolik Lake tussock tundra site (top panels) and at the saturated wet sedge tundra site at Prudhoe Bay (bottom panels) during the 1990, 1991, and 1993 growing seasons. Data are means \pm 1 SE, $n = 6$ for 1990, $n = 4$ for 1991, and $n = 2$ for 1993.

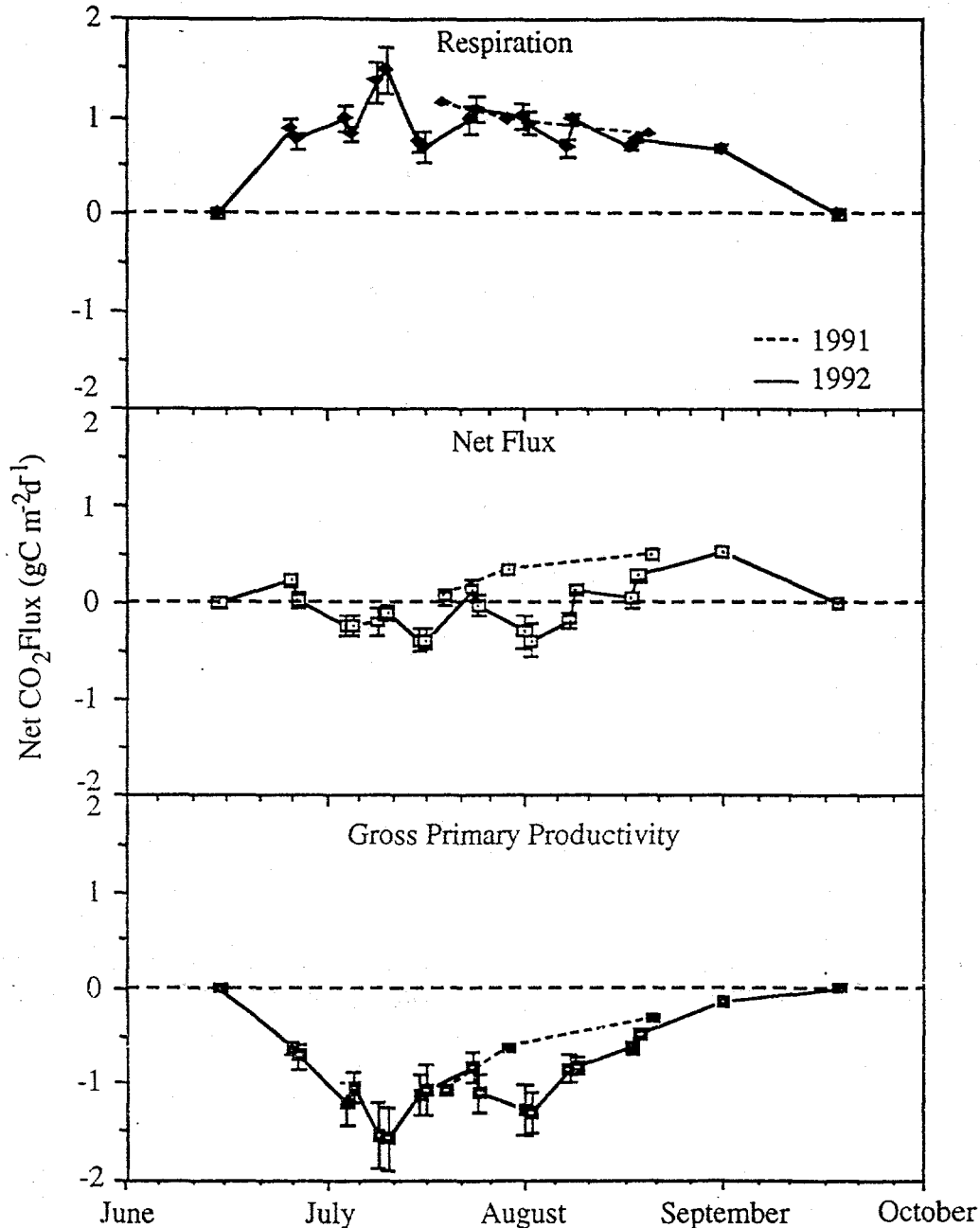


Fig. 4. Seasonal net ecosystem CO₂ flux (◻), respiration (♦), and gross primary productivity (◻), in polygonized habitats at the IBP-II site during the 1991 (dashed lines) and 1992 (solid lines) growing seasons. Positive values indicate net CO₂ efflux to the atmosphere, while negative values indicate net accumulation of CO₂ by the ecosystem. Data for flux, respiration, and GPP are means ± 1 SE, n = 3 habitat types. From Oechel *et al.* (1995)

Comparisons between the plot level measurements reported here and aerodynamic measurements made by Coyne and Kelley (1975) over a comparable growing season indicate that the sink activity of these ecosystems has diminished significantly over the past 20 years (Fig. 5). Wet meadow ecosystems were reported to accumulate approximately 25 gC m⁻² yr⁻¹ in 1971 (Coyne and Kelley, 1975), while the current ecosystems are now sources of about 1.3 gC m⁻² yr⁻¹ (Fig. 5). Net flux during the early season thaw period was similar in 1971 and 1992 (Fig. 5). However, peak season sink activity ceased, and these ecosystems were a slight source of CO₂ during 1991-92

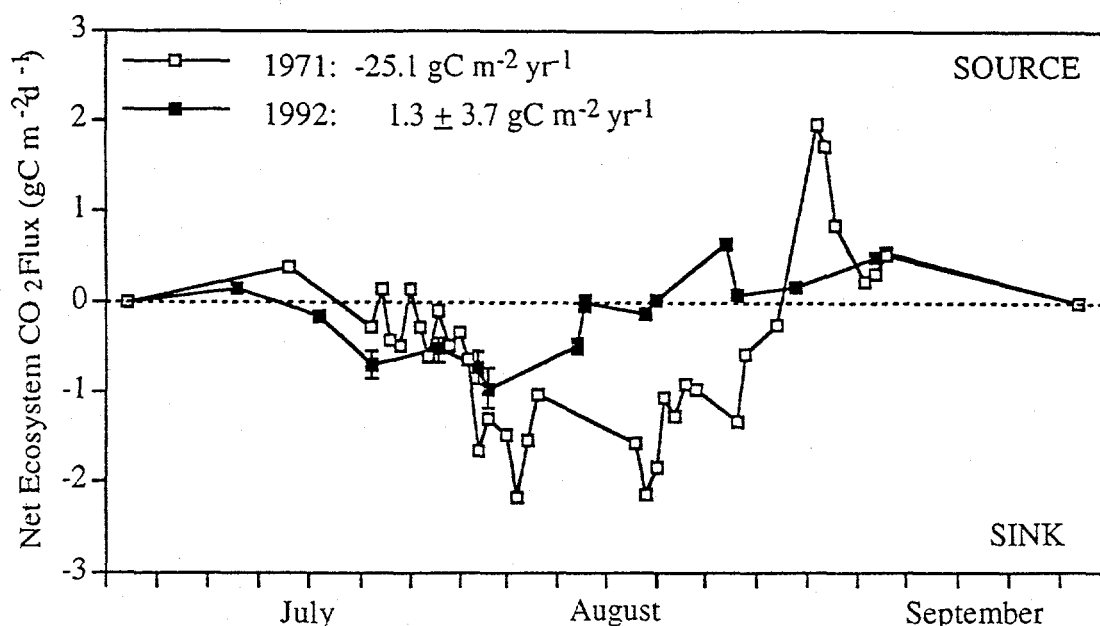


Fig. 5. Seasonal net CO₂ flux measured during the 1971 (Coyne and Kelley 1973, 1975) and 1992 growing seasons at IBP-II. Data are daily CO₂ flux totals calculated over a 24 hour period. Positive values indicate net CO₂ efflux, while negative values indicate net accumulation of atmospheric CO₂. From Oechel *et al.* (1995).

(Fig. 5). Coyne and Kelley (1975) reported an average accumulation of 1.5 gC m⁻² day⁻¹ during late July of 1971, while net ecosystem CO₂ accumulation in 1991 and 1992 was on average only about 0.3 and 0.5 gC m⁻² day⁻¹, respectively. These results indicate a significant reduction in sink strength during the mid-season peak in ecosystem productivity, and an overall change from sink to source activity for the entire growing season (Fig. 5). Coyne and Kelley (1975) reported a large late season efflux which was absent in 1991-92. During 1971, however, there was a significant snowfall which completely covered the vegetation, thus resulting in reduced ecosystem GPP (Coyne and Kelley 1975).

The change in net CO₂ exchange was due primarily to a change in soil water content (Oechel *et al.*, 1995). Differences in summer temperatures between 1971 and 1992 are modest in June and July (Fig. 6a). In August, however, 1992 temperatures were approximately 4-times higher compared to August 1971 (Fig. 6a). More importantly, summer air temperatures have increased by approximately 1.5 °C since 1970 (Fig. 6b). This temperature rise may lead to significant changes in soil water content and water table depth (Kane *et al.* 1992, Waelbroeck 1993). Although there are no data available on the water table depth of these ecosystems in 1971, the IBP sites during the 1991 and 1992 sampling years were significantly drier compared to conditions experienced during the early 1970's, as soil water content was 2-3 times higher in 1971 compared to 1992 (Fig. 7).

It is possible that the recent change in ecosystem carbon balance that we are reporting is due more to methodological differences (i.e. chamber vs. aerodynamic tower measurements), however, this does not appear to be the case (Oechel *et al.*, 1995). Preliminary analysis during the 1993 mid-season photosynthetic peak indicates that good agreement between micrometeorological (eddy correlation) and static chamber methods exists (Fig. 8). The chamber measurements yield greater estimates of peak sink and peak source activity than do the eddy correlation estimates (Fig. 8). These differences maybe due to differences in sampling location and spatial averaging (Hope *et al.*, 1995). For example, eddy correlation flux measurements were taken from a height of 2.5 m, which, depending on the wind speed and temperature profile, corresponds to sampling area that is at least 4 orders of magnitude greater than the chamber sampling area (Schuepp *et al.* 1990). In addition, the

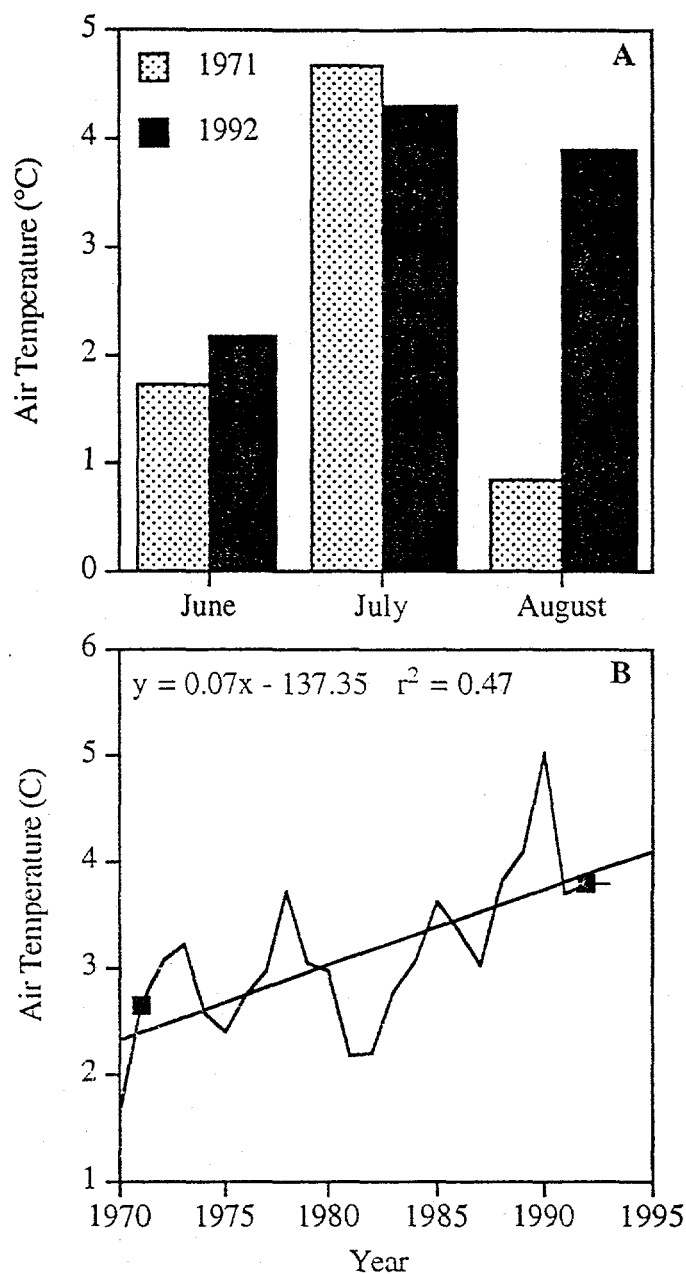


Fig. 6. A. Mean monthly air temperature during the summer months in 1971 (stippled bars) and 1992 (closed bars). Data are from the National Weather Service, Barrow, Alaska. B. Average summer temperatures (June through August) between 1970 and 1993 in Barrow, Alaska. Data are 3-bar running averages, and the regression line corresponds to the temperature trend over the last 2 decades. Closed boxes indicate the average summer temperature in 1971 and 1992. Data courtesy of the National Weather Service, Barrow, Alaska. From Oechel *et al.* (1995).

tower footprint changes as a function of wind direction, so the tower may at times be sampling a habitat that is much different compared to the chamber sampling location. Even with these possible sources of variance, the chamber measurements appear to be in generally good agreement with the aerodynamic measurements, and the change in ecosystem carbon balance appears to be due to a change in the magnitude and sign of ecosystem CO₂ flux rather than differences in methodology.

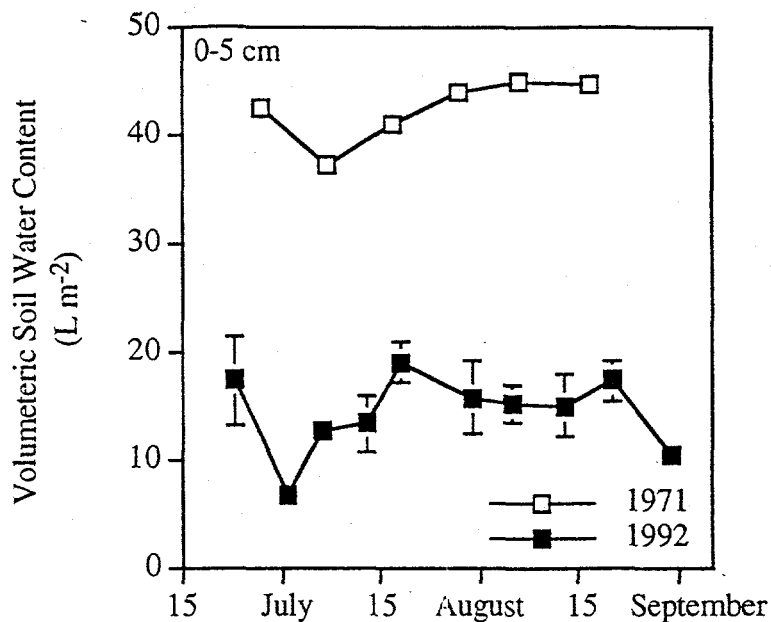


Fig. 7. Soil water content in 1971 (open boxes) and 1992 (closed boxes) in the upper 5 cm of soil at the IBP-II site. Volumetric soil water content was calculated assuming a bulk density of 0.27 g cm^{-3} (Gersper *et al.* 1974). Data for 1971 are from Gersper *et al.* (1974), while data from 1992 are mean ± 1 SE from 3 sites. From Oechel *et al.* (1995).

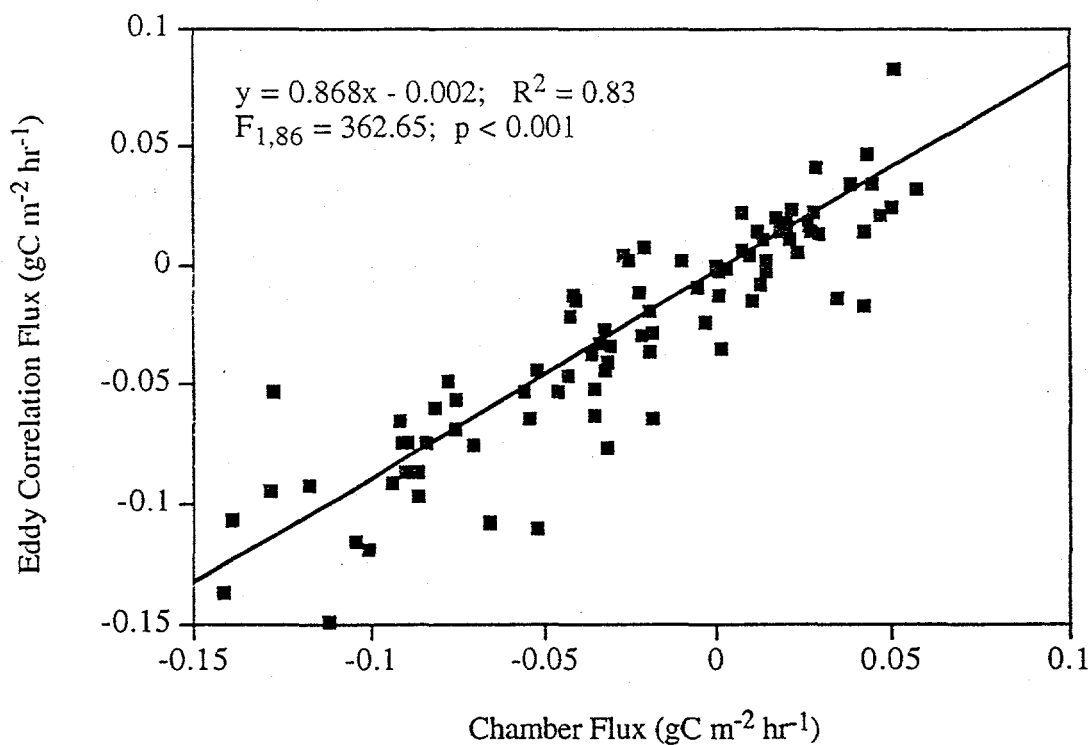


Fig. 8. The relationship between net CO_2 flux measured using a static chamber (Vourlitis *et al.* 1993) and by eddy correlation at Central Marsh between 10 and 30 July, 1993. Chamber data are means of four subsamples. From Oechel *et al.* (1995).

Circumpolar Estimates of Net CO₂ Exchange

Estimates of net CO₂ flux for Siberian subarctic and arctic tundra in mid-July, 1993 are qualitatively similar to those reported for Alaskan Arctic tundra ecosystems (Oechel *et al.*, 1993 and 1995; Oechel and Vourlitis, 1993 and 1995). Hummock ecosystems at the former IBP Tareya site on the Taymyr Peninsula were small net sources of approximately 0.25 gC m⁻² d⁻¹, while wetter polygonal ecosystems were slight sinks of 0.13 gC m⁻² d⁻¹. Tussock tundra sites near Kresty were net sources of approximately 0.3 gC m⁻² d⁻¹. Although these estimates correspond to only 1-2 diurnal measurement periods per site, they qualitatively support the hypothesis that the recently reported change in net CO₂ exchange may be widespread.

Results from Iceland offer quantitative support for the hypothesis that net CO₂ loss is widespread. When considered over the course of the entire 83 day measurement period, there was a greater net loss of carbon to the atmosphere from the CO₂ spring ecosystem (-60 gC m⁻²) than from the adjacent grassland (-25 gC m⁻²). The component process most responsible for the difference in whole ecosystem carbon flux appears to be gross ecosystem productivity. The CO₂ spring ecosystem exhibited 13% less gross ecosystem productivity than the adjacent grassland, fixing at total of 182 gC m⁻² while the adjacent ecosystem fixed 210 gC m⁻². The CO₂ spring and adjacent ecosystem exhibited slightly different patterns of carbon uptake over the course of the growing season, with the rates being similar during the first half of the growing season but lower near the CO₂ spring during the second half of the growing season.

Both ecosystems lost about the same amount of carbon to the atmosphere through respiration processes, with the CO₂ spring ecosystem losing at total of 242 gC m⁻² during the measurement period and adjacent grassland losing 236 gC m⁻². The pattern of carbon loss differed for the sites as well, with CO₂ spring ecosystem losing more carbon to the atmosphere relative to the adjacent ecosystem during the first half of the growing season and less during the second half of the growing season.

Cold Season Estimates of Net CO₂ Exchange

How long CO₂ loss extends beyond the growing season is still a question of debate. Net efflux of CO₂ from both moist tussock and coastal wet sedge ecosystems was observed throughout the 1993-94 cold-season (Fig. 9). At Toolik Lake, emission rates were on average 0.6 and 0.5 gC m⁻² d⁻¹ in October and November, respectively (Fig. 9). Net CO₂ emission rates late in the cold-season were approximately 20 % of the early season rates (Fig. 9), and were on average 0.1 gC m⁻² d⁻¹. The same trend is apparent at the Happy Valley moist tussock tundra site, as early season net emission rates were nearly 0.8 and 0.6 gC m⁻² d⁻¹ for October and November, respectively, while late season emissions were on average 0.2 gC m⁻² d⁻¹ (Fig. 9). Wet sedge ecosystems were comparable sources of CO₂ in October and late-May. Efflux rates decreased approximately exponentially at both West Dock and U-PAD from a maximum of 0.2 gC m⁻² d⁻¹ in October to a cold-season minimum of 0.01-0.02 gC m⁻² d⁻¹ in March (Fig. 9). Late-season loss rates, however, were as high as 0.25 gC m⁻² d⁻¹ at U-PAD, or nearly one order of magnitude greater than the efflux measured 2 months earlier.

Average daily CO₂ emission (respiration) rates increased significantly with temperature, with the highest rates of efflux occurring in October and late-May when temperatures were generally greater than -3 °C (Fig. 10). Efflux from wet sedge ecosystems (circles) followed soil surface temperature closely, and increased exponentially as soil surface temperature increased, while efflux from tussock tundra ecosystems (squares) followed soil surface temperature nearly logarithmically (Fig. 10). These data, although collected during the arctic cold season, are not qualitatively different than temperature response curves of microbial populations reported during the warm season, and suggest that a biogenic source is responsible for the cold-season CO₂ emissions (Kelley *et al.*, 1968;

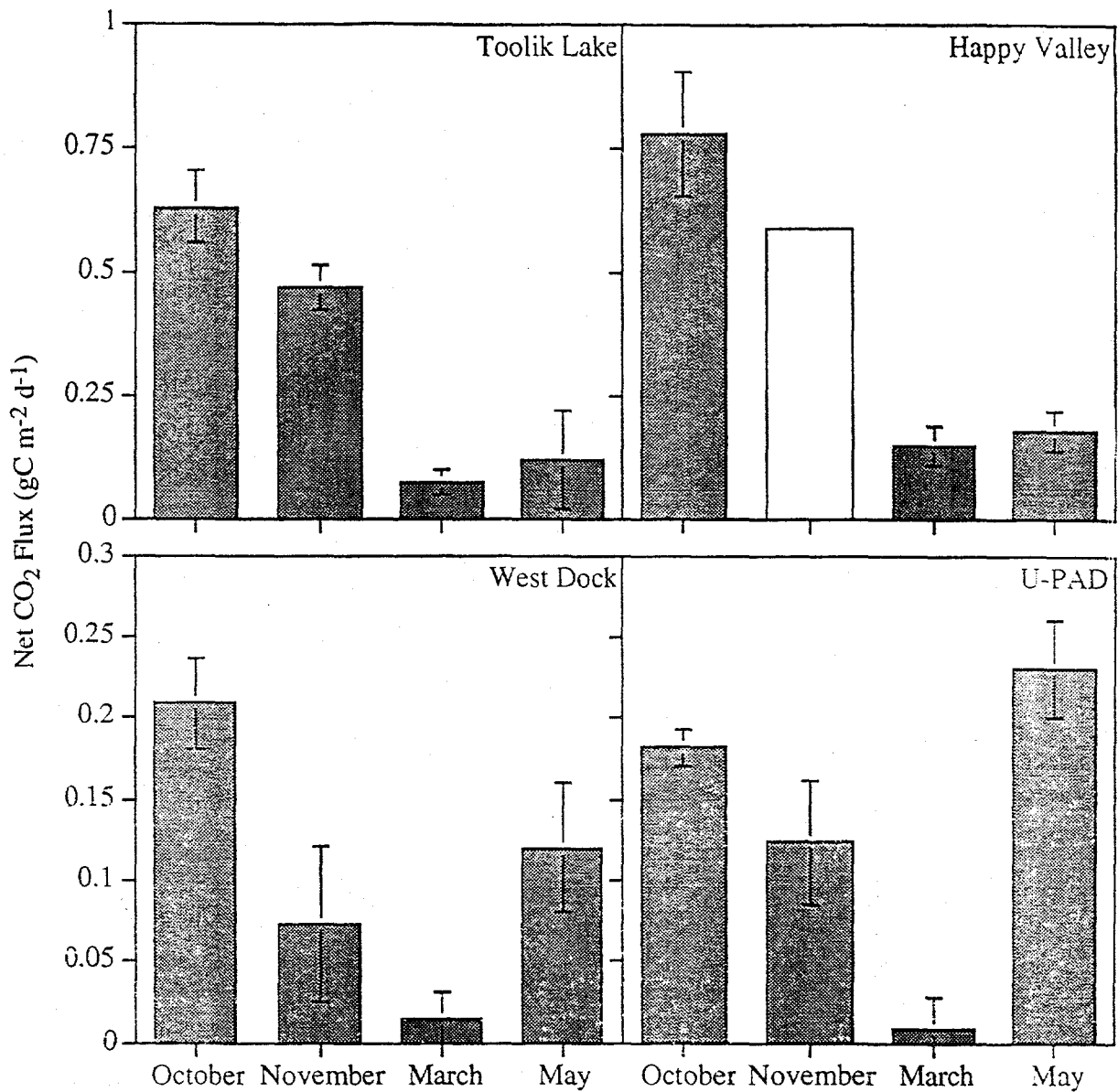


Fig. 9. Mean daily net CO₂ flux in October and November, 1993 and March and late-May through Early June, 1994 at Toolik Lake, Happy Valley, West Dock and U-PAD. Data are means \pm 1 SE, n (number of plots sampled) for October, November, March, and May-June are as follows: Toolik Lake (2,3,6,2); Happy Valley (3,NA,6,2); West Dock (3,3,6,2); and U-PAD (3,3,6,2). The open bar for the Happy Valley November flux estimate was estimated from the Toolik Lake data (see Methods). From Oechel *et al.* (*In press A*).

Zimov *et al.*, 1993). However, although there appears to be a correspondence between soil surface temperature and ecosystem respiration, it is unknown whether the emission observed during November and March was due to biological activity, as soil temperature measurements indicate that temperatures in the upper 80 cm of soil were below the presumed minimum threshold for biological activity (e.g. -6 to -8 °C; Flanagan and Bunnell, 1980).

Integrated flux over the cold-season is significant compared to warm season flux estimates. For example, cold-season flux estimates integrated over a 229 day period (15 October-30 May) were (mean \pm 1 SE, n = 2) 68.5 ± 12.9 gC m⁻² for the moist tussock tundra ecosystems measured and

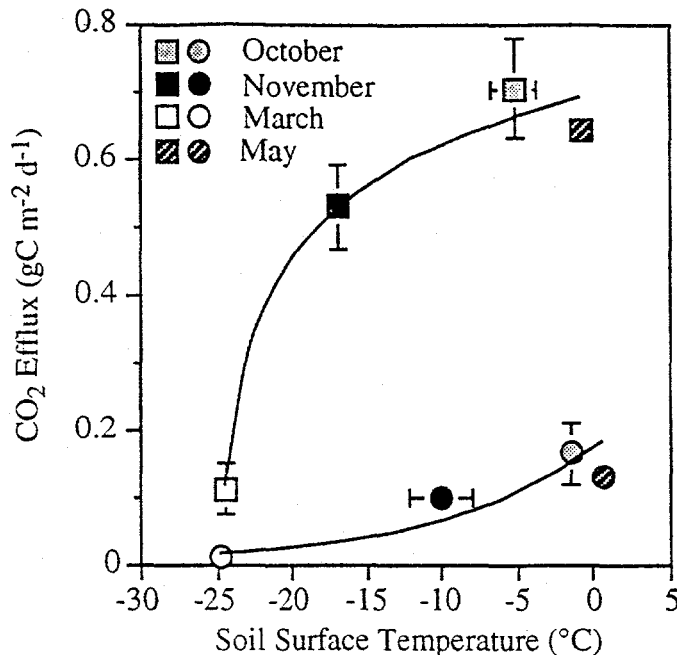


Fig. 10. Net daily efflux (respiration) as a function average daily soil surface temperature for moist tussock (boxes) and wet sedge tundra ecosystems (circles) in October, November, March, and late-May-early June. Data are means \pm 1 se, n = 2 sites per month.

19.0 ± 4.3 gC m⁻² for the coastal wet sedge ecosystems. In contrast, warm season flux estimates for the 1993 growing season (136 days) were approximately 44.0 and 4.4 gC m⁻² for moist tussock and wet sedge ecosystems, respectively. Incorporating the cold-season efflux estimates, moist tussock tundra ecosystems were net sources of approximately 112 gC m⁻² during the 1993-94 calendar year. Similarly, wet coastal sedge ecosystems were sources of nearly 25 gC m⁻² during the 1993-94 calendar year. Failure to account for the significant cold-season C loss would have, therefore, resulted in an underestimation in net seasonal C loss of nearly 60 % for moist tussock tundra, and 81 % for wet sedge (Oechel *et al.*, *in press A*).

Controls on CO₂ Flux

Flux along the latitudinal transect is influenced by annual soil moisture and temperature (Fig. 11). Net efflux is negatively correlated to soil moisture and positively correlated to temperature (Fig. 11). A multiple regression equation with both soil moisture and temperature as independent variables was a good predictor of seasonal flux (flux = $0.472 + (0.094 \cdot T^\circ) - (0.002 \cdot \% \text{ H}_2\text{O})$; $R^2 = 0.852$; $F_{2,5} = 14.431$; $p < 0.01$), however, the best predictor of seasonal flux was soil moisture and distance from the arctic coast (flux = $0.749 - (0.002 \cdot \% \text{ H}_2\text{O}) + (0.004 \cdot \text{Distance})$; $R^2 = 0.930$; $F_{2,5} = 31.483$; $p < 0.002$). Although there is a soil moisture and temperature gradient superimposed along the latitudinal gradient, the variable "distance" may also reflect the effects of continentality on temperature ranges and differences in plant species composition. Within a given ecosystem type, differences in soil moisture and water table depth can be dramatic over small spatial scales. At APL 133 (Franklin Bluffs), net CO₂ efflux increases logarithmically with soil surface drying, however, CH₄ efflux increases as soil water content increases (Fig. 12).

The *in situ* manipulations conducted at Toolik Lake and Prudhoe Bay, West Dock were designed to directly assess the hypothesis that net CO₂ flux is controlled by a complex interaction between soil moisture and surface temperature. The performance of the water table depth and soil surface temperature manipulations was impressive (Oechel *et al.*, *in press B*). Water table depth in the enclosed plots at Prudhoe Bay was on average 10 cm lower than the control plots throughout the

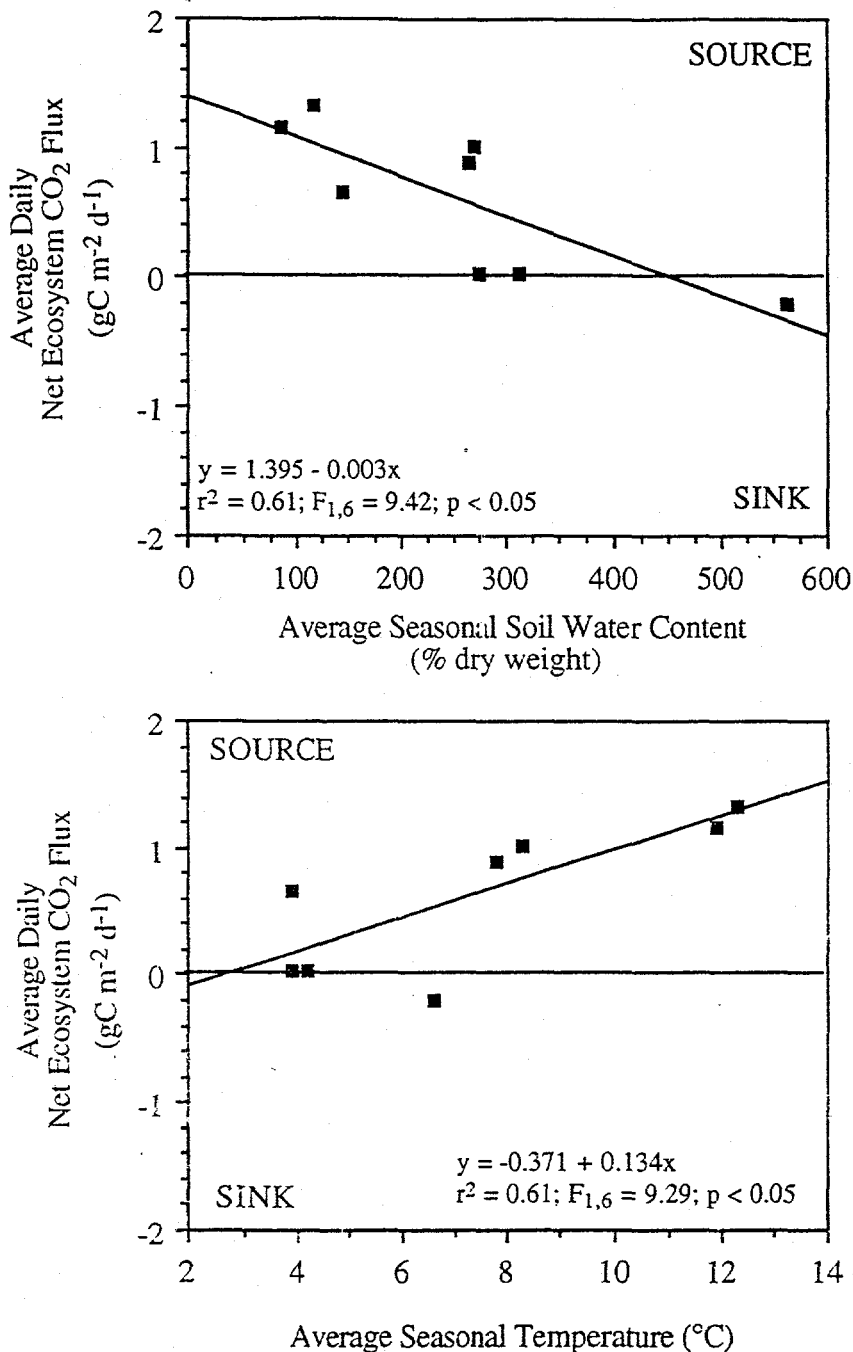


Fig. 11. The relationship between average net CO₂ flux and average seasonal soil moisture (top panel) and average seasonal air temperature (bottom panel) during the 1990 and 1991 growing seasons. Sites analyzed are the wet and moist sites at Prudhoe Bay, Happy Valley, and Toolik Lake, $n = 8$.

1993-94 growing seasons. In contrast, the inundated plot at Toolik Lake had a higher water table immediately after the spring thaw, while water table depth in the drained and control plots was comparable throughout the growing season. It is assumed that surface soil moisture (0 - 20 cm) was lower in drained plots, due not only to greater water table depth (such as at Prudhoe Bay), but to diversion of run-off during snow melt. At Toolik Lake, diversion of run-off during snow melt should significantly reduce surface soil moisture during the subsequent growing season. For

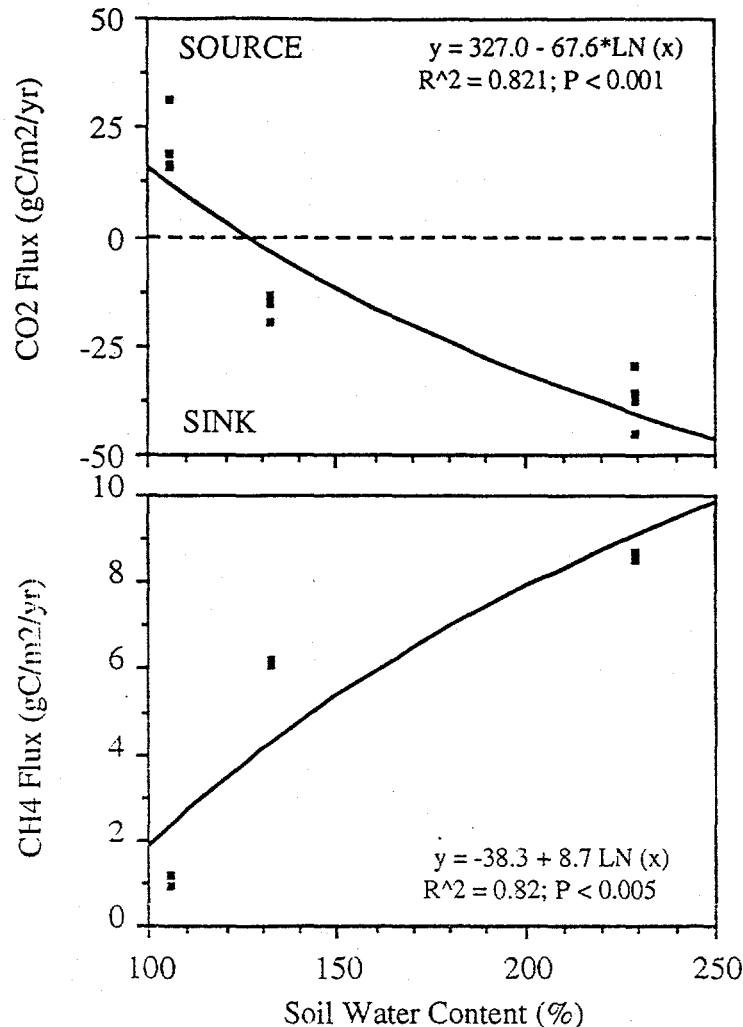


Fig. 12. Net annual CO₂ (top panel) and CH₄ flux (bottom panel) as a function of soil moisture at Franklin Bluffs during the 1991 growing season. Positive values indicate net loss of C to the atmosphere. n (corresponding to the number of plots repeatedly measured throughout the growing season) = 12 for CO₂ and 6 for CH₄ flux, df for ≥ 10 for CO₂ and 4 for CH₄. From Oechel and Vourlitis (1995).

example, during the summer, the surface organic layer dries due to evapotranspiration of water stored during snow melt (Kane *et al.*, 1989). If this water is diverted, soil moisture in the plot must be recharged during summer precipitation events, which occur primarily during July and August (Kane *et al.*, 1989). Water storage in the subsurface is, however, very limited, and rainfall events in excess of 15 mm nearly always produce runoff (Kane *et al.*, 1989). Hence, re-wetting of the dry surface soil may be difficult, even if summer precipitation is adequate.

Soil surface temperature in the Prudhoe Bay manipulation plots was only increased by approximately 0.5 C, due to the addition of the open-top, fiberglass cones, during the nighttime hours. At Toolik Lake, soil surface temperature was on average 1.9 °C higher in the manipulated plots during the midday hours (1200-1500 hours), while nighttime temperature differences were much lower (e.g. 0.3 °C). Although small, the differences in average and maximum daily temperatures observed between ambient and elevated plots are similar in magnitude to the observed decadal-scale increase in high latitude spring and summer temperatures (e.g. 0.75-1.25 °C decade⁻¹, respectively; Chapman and Walsh, 1993).

Seasonal CO₂ flux at Prudhoe Bay was significantly affected by water table depth, and only

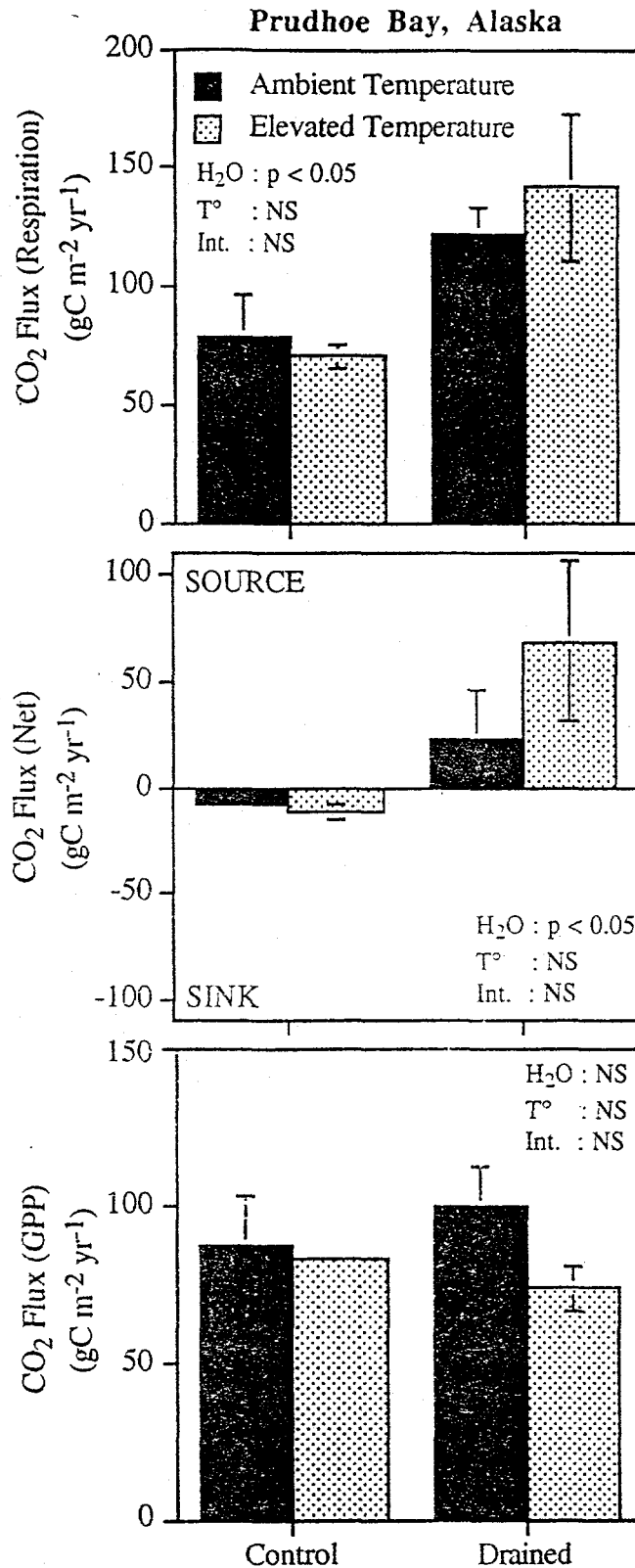


Fig. 13. Mean (± 1 SE, $n=2$) respiration (top panel), net CO₂ flux (middle panel) and gross primary productivity (bottom panel) of control and drained plots exposed to ambient (closed bars) and elevated soil surface temperature (stippled bars) at West Dock during the 1993 growing season (130 days).

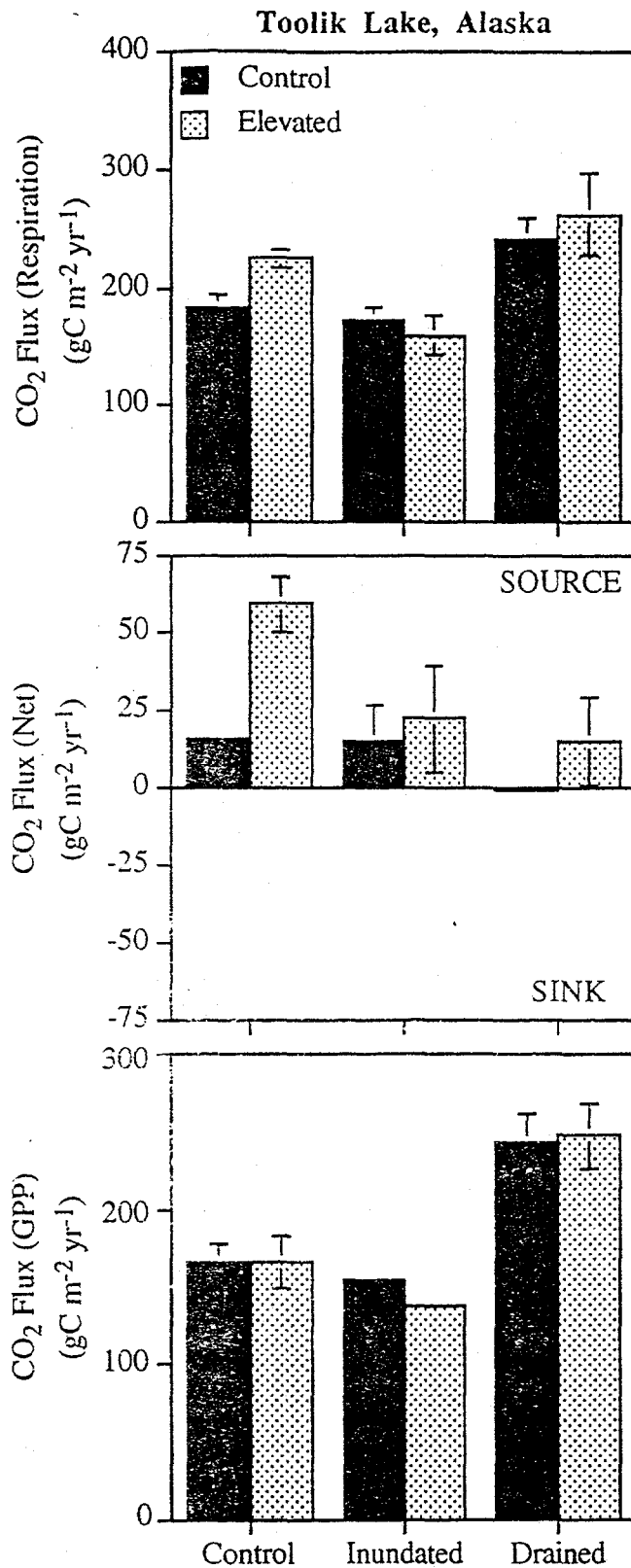


Fig. 14. Mean (± 1 SE, $n=2$) respiration (top panel), net CO₂ flux (middle panel) and gross primary productivity (bottom panel) of control, inundated, and drained plots exposed to ambient (closed bars) and elevated soil surface temperature (stippled bars) at West Dock during the 1993 growing season (130 days).

minimally affected by elevated temperature during both the 1993-94 growing seasons (Fig. 13). During the 1993 growing season, control plots net sinks of approximately $15 \text{ gC m}^{-2} \text{ yr}^{-1}$, while drained plots were on average sources of between $25 \text{ gC m}^{-2} \text{ yr}^{-1}$ (drained + ambient temperature) and $75 \text{ gC m}^{-2} \text{ yr}^{-1}$ (drained + elevated temperature; Fig. 13, middle panel). These results are both quantitatively and qualitatively similar to those observed in 1994 (Oechel *et al.*, *in press B*). The greater efflux was due to the significantly greater respiration in the drained plots (Fig. 13, top panel). For example, respiration in drained plots was approximately 1.5 times higher than control plots, while whole ecosystem GPP was unaffected by either the water table depth or temperature manipulations (Fig. 13, bottom panel).

Drained plots exposed to ambient temperature at Toolik Lake were approximately in balance, while the control and inundated plots were sources of nearly $16 \text{ gC m}^{-2} \text{ yr}^{-1}$ (Fig. 14, middle panel). Under elevated temperature, all plots were net sources of CO_2 , however, net loss from the drained plots was lower than either the inundated or control plots (Fig. 14). Respiration and GPP were greater in the drained plots exposed to ambient temperatures, suggesting that nutrient availability via enhanced decomposition may have been greater in the drained plots (Fig. 14). Elevated temperature stimulated respiration in control and drained plots, but had little effect on GPP (Fig. 14).

DISCUSSION AND CONCLUSIONS

The DOE supported research conducted over the last three years allowed for the testing of our previously stated hypotheses, and the fulfillment of our research objectives. Measurement and observations allow us to first characterize the diurnal, seasonal, and interannual patterns of net CO_2 and CH_4 exchange in Arctic Alaska. Extensive measurements in Siberian and Icelandic Arctic ecosystems further allowed us to determine if the patterns observed in Alaska were characteristic of circumpolar tundra. Measurements in Barrow allowed for a retrospective analysis of the recent change in net CO_2 flux through the comparison of contemporary and historical measurements of trace-gas flux, winter measurements allowed for the analysis of annual CO_2 emissions. Finally, *in situ* experiments allowed us to directly assess the controls of CO_2 balance through the manipulation of the hypothesized driving variables.

Hypothesis 1: The tundra in the Russian arctic and western Iceland is currently a source of CO_2 to the atmosphere.

Preliminary measurements made on the Taymyr Peninsula in July, 1993, which corresponds to the peak in ecosystem productivity, support the hypothesis that tundra in the Russian arctic is currently a source of CO_2 to the atmosphere. Subsequent measurements of the Taymyr sites, and other sites in the eastern-Siberian arctic during the 1994 growing season, exhibit similar patterns of CO_2 balance observed on the North Slope of Alaska. Upland, more well-drained tundra types tended to be small net sources of CO_2 , while wetter vegetation types tended to be slight sinks for atmospheric CO_2 (Zamolodchikov *et al.*, *submitted*). Measurements in Iceland indicate that *Nardus stricta* dominated tundra grasslands exposed to ambient and elevated levels of CO_2 are net sources of CO_2 over the growing season of approximately $30\text{-}50 \text{ gC m}^{-2} \text{ season}^{-1}$. Therefore, the hypothesis that the both Russian and Icelandic Arctic ecosystems are currently sources of CO_2 to the atmosphere is supported.

Hypothesis 2: Increased soil temperature will increase net ecosystem CO_2 flux to the atmosphere in well-drained habitats and decrease net ecosystem flux to the atmosphere in flooded habitats.

Observations of net CO_2 flux across the Haul Road transect suggest that elevated temperature leads to an increase in net CO_2 efflux. In laboratory incubations of wet sedge microcosms, a 4°C increase in temperature was found to result in a significant decrease in net C storage (Billings *et al.*, 1982). However, results from *in situ* manipulations carried out at Prudhoe Bay between 1993-94

indicate that the effects of temperature alone are minimal. Rather, elevated temperature appeared to interact with soil moisture drainage, resulting in greater net loss of CO₂. Flooded plots exposed to elevated temperature, in contrast, exhibited greater net sequestration in both 1993 and 1994 (Oechel *et al.*, *in press B*). Although this interaction was not statistically significant in 1993, it was in 1994 (Oechel *et al.*, *in press B*), lending support to the above hypothesis. In the Toolik Lake manipulation, elevated temperature lead to greater net efflux, regardless to the water table manipulation. Therefore, in the more well drained tussock tundra, elevated temperature lead to an increase in net efflux, as predicted by this hypothesis. Therefore, this hypothesis was supported by both the observational and experimental data.

Hypothesis 3: Increased soil drainage will increase CO₂ flux to the atmosphere, especially in habitats of poor drainage and water-logged soil conditions.

As with the prior hypothesis, observational data both within and between tundra ecosystems indicate that net CO₂ efflux increases in more well drained soils. Data from the *in situ* manipulations at Prudhoe Bay dramatically demonstrated that soil drainage results in increased net CO₂ efflux due primarily to more rapid rates of soil respiration. Similar results have been previously demonstrated using laboratory soil incubations (Billings *et al.*, 1982; Freeman *et al.*, 1993; Funk *et al.*, 1994) and in drained peatlands (Silvola, 1986; Hogg *et al.*, 1992). In the Toolik Lake manipulations, however, draining (or diverting) soil water lead to reduced rates of net CO₂ efflux, due primarily to enhanced GPP of drained plots. Presumably, draining lead to greater rates of soil organic matter decomposition, as evidenced by the more rapid rates of ecosystem respiration (see Fig. 14), and as a result, greater soil nutrient availability (Nadelhoffer *et al.*, 1992). Since arctic plant growth is known to be limited by low nutrient availability (Shaver and Chapin, 1980; Chapin and Shaver, 1985; Shaver *et al.*, 1992), the presumed increase in nutrient availability apparently lead to relatively greater rates of GPP. In addition, because plant C:N ratios (30:1) are much greater than are soil C:N ratios (16:1), more C can be sequestered in plant material than was liberated from the soil from decomposition (Oechel and Billings, 1992; Rastetter *et al.*, 1992). Therefore, the hypothesis is supported in the more typically saturated tundra ecosystems (as stated), but is not supported in the more well drained ecosystems.

Hypothesis 4: Higher soil moisture will increase CH₄ flux to the atmosphere and will increase carbon sequestering by the ecosystem, especially in habitats which have better drainage.

Measurements of CH₄ efflux both within and between tundra ecosystems support this hypothesis. Methane efflux within wet sedge ecosystems increased linearly as soil moisture increased (Vourlitis *et al.*, 1994), and CH₄ emission from more saturated wet sedge ecosystems was typically orders of magnitude higher than emissions measured from more well drained tussock tundra ecosystems (Oechel and Vourlitis, 1995; Vourlitis and Oechel, *in press*). Similarly, tundra ecosystems with higher water table depth and soil water content tended to have either greater CO₂ sequestration or lower net emission. However, this pattern was only weakly demonstrated in the *in situ* manipulations, as both "inundated" and control plots were comparable net sources of CO₂ over the 1993-94 growing seasons.

Hypothesis 5: The tundra of the eastern-central North Slope of Alaska is currently a source of CO₂ to the atmosphere, the rate of which is accurately predicted by the additive fluxes observed at the plot scale. Incorporating all vegetation terrain units present will not alter the qualitative conclusions drawn from measurements of the dominant vegetation types at the plot scale (however, the magnitude of the fluxes may be refined).

Comparisons made between the eddy correlation tower and chamber measurements (e.g. see Fig. 8) support this hypothesis. These comparisons were made in more detail during the 1994-95 growing seasons as part of the NSF-ARCSS LAII flux study with quantitatively similar results

(Vourlitis and Oechel, submitted). Therefore, incorporation of other net CO₂ flux data measured from other terrain units do not qualitatively alter the conclusions drawn from measurements derived from the dominant vegetation types.

Conclusions

The most striking conclusion from this 3-year research campaign is that many arctic tundra ecosystems are currently net sources of CO₂ to the atmosphere during the growing season. This loss is apparently widespread, and was both qualitatively and quantitatively characterized in the Russian and Icelandic Arctic. Furthermore, taking into account the seasonally large net loss of CO₂ during the cold-season indicates that the annual net efflux of CO₂ from arctic ecosystems is substantially higher than growing season estimates reported by Grulke *et al.* (1990) and Oechel *et al.* (1993). Field observations and *in situ* experiments indicate that net CO₂ flux is controlled primarily by soil moisture, and secondarily by temperature (Billings *et al.*, 1983; Oechel *et al.*, 1993; Oechel and Vourlitis, 1994 and 1995; Nadelhoffer *et al.*, 1992; Oechel *et al.*, *in press A*). Prolonged exposure to elevated CO₂ apparently lead to a decrease in gross primary production (GPP), and an increase in net CO₂ loss relative to ambient CO₂ exposed plots.

Whether the arctic will represent a positive or negative feed back to global climate change is largely a function of how drastic the temperature and hydrologic change is, the response of vegetation and soils to the changes in hydrology associated with an increase in temperature, and the time scales required for each level of biological organization to respond to such changes (Oechel and Billings, 1992; Shaver *et al.*, 1992; Oechel *et al.*, 1993; Smith and Shugart, 1993; Oechel and Vourlitis, 1994). Over the short term, it appears that soil respiration has increased relative to gross ecosystem uptake due to more favorable soil aeration due to soil surface warming and drying. Although this change is thought to be transient (Oechel *et al.*, 1993; Marion and Oechel, 1993; Smith and Shugart, 1993; Oechel and Vourlitis, 1994), there is currently no evidence that this situation will end in the near future, as plant productivity appears to be relatively unresponsive to the observed warming.

Over the long term, this increase in soil decomposition should lead to greater nutrient mineralization and concomitant plant productivity (Shaver *et al.*, 1992), and arctic ecosystems may once again become sinks for atmospheric CO₂ (Oechel and Vourlitis, 1994 and 1995). Changes in the species composition of high-latitude ecosystems due to the northward migration of vegetation is expected (Neilson, 1993; Landhäusser and Wein, 1993). However, the time scale for this migration is extremely long compared to the relatively instantaneous response of soil microorganisms and the extant vegetation (Smith and Shugart, 1993).

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