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Final Report: Response of tundra Ecosystems to Elevated Atmospheric CO₂

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Final Report

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EXECUTIVE SUMMARY

Introduction

Atmospheric CO₂ is expected to double by the end of the next century (Bacastow and Keeling, 1973; Woodwell, *et al.*, 1983). Global mean increases in surface air temperature of 1.5-4.5°C are anticipated (Manabe and Wetherald, 1975; Allen, 1980; Manabe and Stouffer, 1980; National Research Council, 1982) with larger increases towards the poles predicted (Manabe and Stouffer, 1979). Changes in CO₂ levels and temperature could have major impacts on ecosystem functioning, including primary productivity, species composition, plant-animal interactions, and carbon storage (Oechel and Strain, 1985). Until recently, there has been little direct information on the impact of changes in CO₂ and temperature on native ecosystems.

The study described here was undertaken to evaluate the effects of a 50 and 100% increase in atmospheric CO₂, and a 100% increase in atmospheric CO₂ coupled with a 4°C summer air temperature rise on the structure and function of an arctic tussock tundra ecosystem. The arctic contains large stores of carbon as soil organic matter, much frozen in permafrost and currently not reactive or available for oxidation and release into the atmosphere (Miller, 1981; Miller, Kendall, and Oechel, 1983). About 10-27% of the world's terrestrial carbon occurs in arctic and boreal regions (Schlesinger, 1977; Armentano, 1979; Miller, 1981), and carbon is accumulating in these regions at the rate of 0.19 GT y⁻¹ (Miller, 1981; Miller, Kendall and Oechel, 1983).

Mean temperature increases of 11°C and summer temperature increases of 4°C have been suggested (Manabe and Stouffer, 1980). Mean July temperatures on the arctic coastal plain and arctic foothills regions are 4-12°C, and mean annual temperatures are -7 to -13°C (Haugen, 1982). The projected temperature increases represent a substantial elevation above current temperatures which will have major impacts on physical processes such as permafrost development and development of the active layer, and on biological and ecosystem processes such as primary productivity, carbon storage, and species composition.

Extreme nutrient and temperature limitation of this ecosystem raised questions of the responsiveness of arctic systems to elevated CO₂. Complex ecosystem interactions with the effects of increasing temperature and CO₂ and changes in the physical environment made *a priori* predictions impossible. The short stature of the vegetation, the large number of individuals and species encountered in a relatively small area, and the short growing season were advantages which were thought to increase the probability that manipulation of physical conditions would result in short- and moderate-term response. These factors were coupled with an appreciation of the important role of the arctic as a major carbon store, a carbon sink, and the unpredictability of the carbon balance under future global conditions. These factors all contributed to the selection of the arctic as the first ecosystem for *in situ* manipulation of CO₂ and temperature to determine effects on ecosystem structure and function.

Approach

The effect of atmospheric CO₂ levels of 340, 510, and 680 µl/l CO₂ and 680 µl/l CO₂ with a 4°C temperature rise above ambient on ecosystem structure and function were investigated in the tussock tundra near Toolik Lake, Alaska. Of particular

interest were responses of photosynthesis and respiration, primary production, net carbon flux, nutrient status, and tissue nutrient composition.

To control and manipulate the physical environment in the field, a unique system comprised of 12 controlled-environment greenhouses was developed to measure ecosystem carbon fluxes. This allowed experimental manipulation of CO_2 and temperature singly and in combination under the otherwise current North Slope, central Brooks Range climate. The greenhouses were established as soon after snowmelt as possible and remained in place until fall freeze-up. The longest experiment to date ran for almost three seasons, being terminated after peak season in the third year. Exposure to elevated CO_2 was not deemed necessary during the winter period when the plants and soil are frozen and the biota are largely dormant.

Results

The system developed had excellent control of both temperature and carbon dioxide concentration. Over a 24-hour period, temperatures in the chambers averaged within 1° of ambient temperatures. Despite complications involved with operating in extreme conditions and tracking a rapidly fluctuating microclimate, carbon dioxide concentration control was comparable to controlled-environment chambers at the Duke University Phytotron. Stimulation of net ecosystem carbon flux was initially large but appears to acclimate within the first growing season. Resource limitation and/or homeostatic mechanisms operate to limit the ecosystem response to elevated CO_2 .

There is a large stimulation in net carbon uptake for the first year of CO_2 addition. During the first year at $680 \mu\text{l/l}$, net ecosystem carbon uptake increases by an average of $6.0 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. The stimulation disappeared in the third year ($0.2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). The initial stimulation in net CO_2 flux was less at $510 \mu\text{l/l CO}_2$ than at $680 \mu\text{l/l CO}_2$, and the intermediate concentration of CO_2 is thought to result in a slower homeostatic adjustment to elevated CO_2 . We believe that eventually the enhancement in CO_2 uptake would also disappear at $510 \mu\text{l/l CO}_2$ as it did at $680 \mu\text{l/l CO}_2$.

Contrary to expectations, the photosynthetic rate did not necessarily increase as a result of increased ambient CO_2 concentration. In *Eriophorum vaginatum*, the most abundant species in the area, there was homeostatic adjustment in photosynthetic response at elevated CO_2 during the third year of treatment so that at the growth CO_2 concentration, photosynthetic rates of plants grown at elevated CO_2 were no higher than those of plants grown at ambient CO_2 . Certain other species showed enhanced photosynthetic rates after three years.

There was no response of plant or soil respiration to short- (minutes) or medium- (three year) term exposure to elevated CO_2 . Longer-term treatment (> three years), which might allow changes in nutrient status and species composition, could result in changes in respiration rates.

Factors such as resource limitation or physiological constraints can limit the plant and ecosystem response to elevated CO_2 . Not all species and ecosystems will respond positively to elevated CO_2 . Differences in species responses could change ecosystem structure, composition, and function.

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PREFACE

This report summarizes the results of the first CO_2 manipulation of an intact ecosystem, an arctic tussock tundra ecosystem. This is the initial step in determining the effects of an increase in atmospheric CO_2 on the structure and function of unmanaged ecosystems. Some of the results were unanticipated. Certainly the lack of a positive photosynthetic response in some species to elevated CO_2 was unexpected, as was the homeostatic adjustment of whole ecosystem response in net ecosystem CO_2 flux to a doubling of atmospheric CO_2 . However, given the diversity of environments and ecosystems worldwide, one would anticipate a variety of responses to elevated CO_2 .

The major remaining challenges include elucidation of the range of ecosystem and species response to elevated CO_2 , the interaction of elevated CO_2 in combination with other physical factors, and the formation of generalizations that will allow accurate predictions in new situations. For example, we need to determine the nature of resource availability regulations on ecosystem response, and the relationship of growth form and physiology of constituent species on ecosystem response. In general, if we understand controls on carbon and nutrient allocation, we may be in a better position to make predictions of ecosystem response to elevated CO_2 and CO_2 -induced climate changes.

THE EFFECT OF ELEVATED ATMOSPHERIC CO₂ AND TEMPERATURE ON AN ARCTIC ECOSYSTEM

INTRODUCTION

Northern ecosystems are an important component of the current and future global carbon budget. In these ecosystems, vast quantities of organic carbon are stored as peat and poorly decomposed soil organic matter. A DOE-sponsored workshop on the carbon balance of northern ecosystems (Miller, 1981) estimated that worldwide tundra and taiga contain over 200 billion metric tons of organic carbon in live biomass, peat, and soil organic matter. This amount represents 10-27% of the total terrestrial carbon in the biosphere. Despite low rates of production, tundra alone has accumulated 59 BmT of carbon, equal to nearly 12% of that in the global atmosphere. Over its circumpolar range, tundra is thought to be a net sink for carbon dioxide and to have the capacity to continue to sequester carbon from the atmosphere. The eventual fate of fixed carbon and the effect of atmospheric carbon dioxide enrichment on the rate of carbon accumulation in arctic ecosystems are crucial to an understanding of the global carbon budget. Global circulation models predict that CO₂-induced warming will be three to four times greater in polar regions than the global average (Seidel and Keyes, 1983; Manabe and Wetherald, 1980).

A priori predictions of the response of arctic ecosystems to increases in atmospheric CO₂ are difficult. Resource limitations, particularly inorganic nutrients, can restrict the ability of arctic plants and ecosystems to respond to an increase in CO₂ availability. Higher temperatures could result in deepening of the active layer to melting of the permafrost. This could result in increased drainage, which would elevate soil temperatures, soil decomposition (Billings, *et al.*, 1982), nutrient availability, and possibly result in net carbon loss from the below ground pool.

Ecosystem-level interactions can further complicate the picture (Figure 1). CO₂ availability can affect the plant patterns of carbon allocation (Oberbauer, *et al.*, 1986a; Larigauderie, *et al.*, in prep.), nutrient uptake (Norby, *et al.*, 1986a), rhizosphere activity (Norby, *et al.*, 1984, 1986b), mineralization rates, and litter quality to decomposers (Oechel and Strain, 1985; Melillo, 1983; Norby, *et al.*, 1986a) and herbivores (Lincoln, Sionit, and Strain, 1984). Many important and interesting areas confront us when we consider the response of arctic ecosystems to elevated atmospheric CO₂ including the ability to respond to increased CO₂ availability given the temperature and nutrient limitations of the system.

The most direct way of determining ecosystem response to CO₂ enrichment is to experiment at that level for a long enough period to allow interactions among its various components. For at least one ecosystem (wet tundra), representative subsamples (microcosms) have been taken into controlled-environment chambers where CO₂ enrichment was provided (Billings, *et al.*, 1983, 1984), but for most ecosystems this would not be possible. For the first time, an *in situ* system of controlled-environment chambers was used to measure the effects of elevated atmospheric carbon dioxide in tussock tundra. These chambers were analogous to a closed, null-balance, multiple-cuvette gas exchange (photosynthesis) system, and thus the long-term effects of continuously elevated carbon dioxide on instantaneous, daily, and seasonal productivity were directly measured.

Figure 1. Conceptual model showing interrelationships in photosynthesis and carbon allocation in a plant as it is affected by atmospheric CO_2 concentration. Carbon transfer following tissue death and decomposition is also shown. Control points for carbon movement are indicated by dotted lines and carbon flux is indicated by solid lines.

A general understanding of carbon dioxide effects can be facilitated through the use of simulation modeling, whether through incorporation of demonstrated effects into existing ecosystem models *e.g.* ARTUS-CO₂ (Oechel and Blake-Jacobson, in prep.), or through the eventual development of more universal models (Reynolds, *et al.*, 1985). In either case, modeling in the absence of data is not advisable, and ecosystem-level experiments will be required for parameterization and validation of the resultant models. The experiments reported here are the first of their kind for any intact ecosystem that directly address the medium- to long-term effects of carbon dioxide enrichment on ecosystem production.

Single species response to CO₂ enrichment performed in growth chambers have clearly demonstrated two facts: 1) the magnitude to which plants are able to respond varies widely among species and is not readily predictable, and 2) the species' capacity to respond is further reduced by complex interactions among other limitations to growth such as nutrient and water supplies, and how those supplies are sequestered by neighboring plants. A field study performed during the first year of CO₂ enrichment (1983) investigated the short-term response of *Eriophorum vaginatum* (Tissue and Oechel, 1987). These data show that CO₂ enrichment reduced the photosynthetic capacity of *E. vaginatum* within a growing season and suggest that growth in this species was not limited by carbohydrate supply. During the third season of CO₂ enrichment, the photosynthetic rate of *E. vaginatum* and *Ledum palustre* (see below) was remeasured. Field and phytotron experiments showed that homeostatic adjustment to elevated CO₂ is common, in many cases resulting in similar rates of photosynthesis at elevated and ambient CO₂ (Oberbauer, *et al.*, 1986a).

In natural ecosystems, limitations imposed by water, nutrients, and irradiance may moderate the impact of CO₂ enrichment, but the degree of this moderation is unknown (Oechel and Strain, 1985). We hypothesized that CO₂ enrichment should enhance the growth of these species, but the effect would decrease with lowered mineral availability because nutrient limitation would reduce the demand for the additional carbohydrate. To test this hypothesis, a controlled-environment experiment was carried out using a factorial design with two levels each of nutrition and atmospheric CO₂ concentration (Oberbauer, *et al.*, 1986a).

Computer simulations of the carbon flux from tundra soils indicate that small changes in the rates of photosynthesis or respiration as a result of elevated CO₂ and temperature increase can have a significant impact on carbon storage and the global carbon balance, as well as on local ecosystem processes (Oechel and Blake-Jacobson, in prep.). We hypothesized that enhanced photosynthesis from CO₂ enrichment would increase the carbohydrate and lignin content of litter and soil C/N ratios. Because tundra soils are already nitrogen limited (Ulrich and Gersper, 1978), we hypothesized that the net result of atmospheric CO₂ enrichment would be decreased soil respiration. To test these predictions, the effects of medium- and short-term ecosystem CO₂ enrichment on soil CO₂ efflux were investigated. The following results give insight which are not only relevant to arctic ecosystems, but also provide perspective on the response of all ecosystems.

Atmospheric CO₂ has been predicted to double to 680 $\mu\text{l/l}$ by the end of the next century (Bacastow and Keeling, 1973; Woodwell, *et al.*, 1983). Such an increase in CO₂ could result in a 1.5°-4.5°C increase in global mean temperature (Manabe and Wetherald, 1975; Allen, 1980; Manabe and Stouffer, 1980; National Research Council, 1982). Summer temperatures in the arctic have been predicted to increase by 4°C with a doubling of CO₂, more than at temperate or tropical latitudes (Manabe and Stouffer, 1979). In order to test, *in situ*, the effects of these changes on ecosystem functioning of

the tussock tundra, greenhouses were developed and maintained in the field to experimentally control CO_2 and temperature to provide treatments of 340, 510, and 680 $\mu\text{l/l}$ CO_2 at ambient temperature and 680 $\mu\text{l/l}$ CO_2 at 4°C above ambient temperature. The chambers were designed to monitor the net flux of CO_2 by arctic tussock tundra. Experiments were initiated to evaluate changes in:

- Photosynthetic rates;
- Soil and plant respiration rates;
- Growth, carbon allocation, and biomass;
- Tissue nutrient levels and C/N ratios.

Research emphasis was placed on rates and patterns of physiological and ecosystem adjustment to new conditions of temperature and CO_2 availability. The study site is located in upland tussock tundra in the northern foothills of the Brooks Range at Toolik Lake, Alaska ($68^\circ38'$ N, $149^\circ34'$ W at 760 m elevation) ≈ 225 km south of Prudhoe Bay. Mean July temperature is around 12°C , and mean annual temperature of nearby Galbraith Lake is about -9°C (Haugen, 1982). The vegetation of the tussock tundra site is ≈ 30 cm high and is dominated by *Eriophorum vaginatum*. The vegetation is dominated by nine vascular plant species and several important moss species (Chapin and Shaver, 1985). The area is similar to other circumpolar regions including those in other areas in Alaska, Canada, and the Soviet Union (Wein and Bliss, 1974; Shaver and Cutler, 1979). The ecology of the area is described in several recent publications (Fetcher and Shaver, 1985; Chapin and Shaver, 1985; Tissue and Oechel, 1987).

METHODS

FIELD GREENHOUSE DESIGN

Objectives

The field greenhouses (Figure 2) were designed to control CO_2 and air temperature while monitoring CO_2 flux of the ecosystem. They provided *in situ* treatment of tussock tundra and allowed determination of effects of variation in CO_2 and temperature on important physiological and ecosystem parameters. For the 1983-1985 field work, experimental treatments consisted of 340, 510, 680 $\mu\text{l/l}$ CO_2 and 680 $\mu\text{l/l}$ CO_2 with temperature elevated $+4^\circ\text{C}$ above ambient temperature treatment. A closed chamber design was chosen over open, ventilated chambers (Rogers, *et al.*, 1981), as the field site is remote and large quantities of CO_2 were not readily available or affordable and measurement of net ecosystem CO_2 flux was desired. Since continuous operation under highly variable field conditions was necessary, dependability with a minimum of maintenance and ruggedness of all components were considerations in the design of the system.

The measurement of CO_2 fluxes in the closed chambers was straightforward. The flux of carbon dioxide in a chamber was equal to the sum of CO_2 added (injected) and subtracted (scrubbed from the air line) to maintain its set concentration, with a correction for CO_2 leaked from the system. Mechanical refrigeration and resistance heating were used to control temperatures. Soil moisture was maintained by misting water equivalent to precipitation rates into each chamber. Although air humidity was monitored and generally tracked ambient, chamber humidity was not controlled. Some water was removed from the chamber air through condensation on the refrigeration coils. The chamber size was chosen to enclose a representative sample of the ecosystem,

Figure 2.

View of the chambers in operation at the field site in 1985 showing general construction of the chambers and the equipment housings which enclose the compressors, gas sampling equipment, and the associated electrical

and sufficient chambers were installed to provide for suitable and affordable replication of treatments.

In late July 1985, a new experimental site was established in order to investigate in more detail the short-term ecosystem responses to elevated CO_2 and to verify previous data on short-term responses to CO_2 enrichment. Due to advances implemented in system design and control during the course of the three-season experiment, cross-checking the measurements of the modified versus original system (1985 vs. 1984, 1983) was desirable.

All chambers were maintained at $340 \mu\text{l/l}$ for several days in 1985 to measure their baseline flux rate under near-ambient conditions. These data were used to test for similarity among the new chamber sites. After the baseline flux rates were measured, the chambers were set at either 340 or $680 \mu\text{l/l}$, then switched to the reverse setting on a three-day cycle. This allowed direct comparison among the chambers at each set of conditions, but it precluded analysis for effects of CO_2 concentration, since these effects were masked by the effects of day-to-day variation in weather on flux rates.

In another series of manipulations, half of the chambers were maintained at each set point on a given day. This allowed direct analysis of the effect of CO_2 concentration independently of environmental variation. Data from August 18-24, 1985 were included in these analyses (Table 7). The set points of six of the chambers were changed to $680 \mu\text{l/l}$ prior to midnight on August 18, after several days during which all of the chambers had been maintained at $340 \mu\text{l/l}$. Therefore, August 18 was the first day of treatment at $680 \mu\text{l/l}$; August 19 was the second. On August 20 and 21, all chambers were returned to $340 \mu\text{l/l}$ in preparation for the next round of short-term enrichment (August 22-24). For the second cycle of enrichment, chambers which had been maintained at $680 \mu\text{l/l}$ on August 18 and 19 were assigned to the 340 treatment and reversed. Therefore, August 22 and 24 can be considered as "first and third" days of treatment.

System Description

Physical Microenvironmental Monitoring

The experiment was composed of four treatments at 340 , 510 , and $680 \mu\text{l/l}$ CO_2 , and $680 \mu\text{l/l}$ $\text{CO}_2 + 4^\circ\text{C}$ with three replicates per treatment. A technical description of the system is available (Oechel, *et al.*, 1987; Riechers, *et al.*, in prep.). Temperatures were measured with copper-constantan (Type T) thermocouples and thermopiles, carbon dioxide concentrations with an infrared gas analyzer, and humidities with thin-film variable capacitance sensors. Photosynthetically active radiation (PAR) inside and outside the chambers was monitored with quantum sensors. The entire system was computer controlled with sensors and control devices interfacing with the computer through a single data acquisition and control unit. The capacity to scrub CO_2 from the chambers allowed a functional range ≈ 150 - $1200 \mu\text{l/l}$.

In normal operation, chambers tracked ambient temperature or were maintained at a fixed offset ($+4^\circ\text{C}$) from ambient. Depending upon radiant (solar) heat load, chambers could be cooled to 10°C or more below the outside temperature and maximum temperatures were well beyond the range of ecological interest.

Computer and Data Acquisition/Control System

The computer and data acquisition/control system (DAS) comprised the core of the monitoring and control system. A Hewlett Packard (HP) 9000, series 200 (9816) computer with 512K RAM operated the control program. An HP 15 Mbyte hard disk and 3.5 inch floppy disk were used for data storage. The HP DAS and extender provided capacity for up to 200 analog inputs and 80 digital actuator outputs. Thermocouple inputs, routed through an HP Multiplexer were referenced to an HP Thermocouple-Compensated Multiplexer. The autoranging capability of the voltmeter assembly allowed inputs from a few microvolts (as in the case of thermocouples) to 100 volts (such as the gas analyzer, 10 V full scale). Digital output boards switched a 12 V DC supply to various controlling and sampling relays.

Chambers

Chamber walls were constructed from cell-cast acrylic plastic ("Acrylite") on a frame of angle aluminum. Lids were made of 0.12 mm [5 mil] Mylar film, which reduced the heat load on the refrigeration units by providing an infrared-transparent window for heat escape. The lids were easily removable to provide access to the chambers.

Each chamber had a 1.22 m square stainless steel base and covered 1.5 m² of the experimental plot. Chamber volume was approximately 1015 l. The stainless steel bases extended 30 cm below the mean ground surface level. Back (north) walls of the chambers were 76 cm tall and front walls were 46 cm tall made from 4.76 mm thick acrylic. This provided approximately 14° of slope to the tops of the chambers and allowed for precipitation runoff. The north wall of each chamber was constructed of 6.35 mm thick acrylic to provide more support for the mounted refrigeration and air handling equipment. A rubberized gasket provided the seal between the chamber sides and a 4 cm flange on the top of the stainless steel bases.

Precipitation Collection and Distribution

The precipitation collection basin was lined with waterproof nylon tarps equal in area to the 12 chambers +20% (for anticipated losses) and were located upslope from the chamber. Precipitation which fell in the basin flowed to a holding tank and was distributed among the 12 chambers through a low-pressure pump and delivery system. Flow to each of the chambers was equalized by varying the line resistance. The delivery system was activated manually during precipitation events when sufficient water had accumulated in the holding tank, and/or when moisture conditions of the vegetation and soil indicated the need for irrigation. Precipitation volume and chemistry reflected ambient conditions.

Refrigeration

The cooling systems were completely redesigned before the 1985 season to incorporate a number of modifications of the systems used in 1983 and 1984. The original systems proved to be undersized and less dependable than desired under arctic conditions. The modified refrigeration units consisted of 1/2 horsepower, air-cooled condensing units equipped with crankcase and head pressure controls, crankcase pressure regulating valves, and refrigerant accumulators. Properly adjusted, these accessories protected the compressor units from overloading under the highly variable conditions encountered in the field. This was one of the most challenging constraints on

the design of the system. Under more predictable and stable operating conditions, much simpler systems could provide adequate, dependable cooling.

Evaporator coils, custom made for the units, were intentionally oversized relative to the condensing units. In conjunction with a high airflow rate over the evaporator coils, the large size allowed a low coil-to-air temperature gradient and reduced condensation and icing on the coil. Evaporators were equipped with thermostatic expansion valves. Flexible refrigerant lines between the condensing units and the evaporators allowed independent positioning. Resistance heaters (700 W at 120 V AC) were mounted on the evaporator coils to heat the chambers and were operated at 110 V AC. They were also used occasionally to defrost the evaporator coil.

A hot-gas bypass system was installed on each compressor to shunt hot refrigerant from the compressor through a computer-controlled solenoid valve to the evaporator without first dumping heat in the condensing coil. This turned off cooling and simultaneously provided a small amount of heat to the chamber without turning on and off the compressors. From a maintenance standpoint, continuous operation of the compressors was preferable to frequently cycling them on and off, and eliminated power surges associated with startup of compressors. Power surges of this magnitude could seriously disrupt the electronic equipment in the control system because of its limited buffering capacity. Air was circulated over the evaporator coil by two 25 cm axial flow fans with a free air capacity of 15,000 l/min air. The air turnover time in the chambers was approximately 2.0 sec.

Gas Sampling and CO₂ Control System

The gas handling and sampling system was plumbed with polyallomer thermoplastic tubing. This semi-rigid tubing had very low water and CO₂ absorptivity and was suitable for use with compression fittings and connectors which provided quick, gas-tight seals and allowed for easy assembly and disassembly of the system for transportation to the field site.

Small 1/15 horsepower carbon vane pumps continuously drew 20-30 l/min of air from each chamber. A subsample (1-2 l/min) of this air was diverted through a needle valve and sample line to a control shack for measurement of CO₂ concentration and humidity. The remainder passed to a three-way solenoid valve, where it was either sent directly back to the chamber, or first passed through two 45 cm long by 7.6 cm wide scrub tubes filled with "Soda-Sorb" indicating soda lime to remove CO₂ before being returned to the chamber.

Sample lines (0.6 cm o.d. Impolene) connecting the chambers and the shack were 15-20 m long. Lines were heated by 24 awg nichrome wires running inside the tubing to prevent condensation. Current through the resistance wires was controlled by 110 V AC triacs in the shack. Approximately 0.5 amperes (60 W) per sample line was adequate to prevent condensation even under the coldest conditions encountered. At the control shack, the sample lines entered a manifold/switching system described below.

The CO₂ injection system to each chamber consisted of a single solenoid valve and an approximately 5 cm length of capillary tubing which limited flow to 200-300 ml/min. CO₂ was provided to all chambers from a single 60 pound tank.

Gas Analysis System

At the shack each sample line was connected to a three-way solenoid valve, which was switched one at a time to an infrared CO₂ analyzer (IRGA). Initially a Liston-Edwards IRGA was employed. With this analyzer, a 2-3 μ l/l drift in the zero calibration of the analyzer per degree change in shack temperature was typical, requiring recalibration every 1/2 hr. Also, the analyzer was sensitive to vibrations. This was a significant problem on windy days, and when traffic into and out of the control shack was heavy.

The Liston-Edwards was later replaced with a Binos IRGA which had a shorter response time and more stability. Time constants were within 2-3 sec with sample flow rates of 1.0 l/min. Sample flows were vented when not under analysis to reduce pneumatic lag in the system.

Upon exiting the CO₂ analyzer, the sample stream passed to a Vaisala humidity/temperature probe. The sensor in this probe had a 0-100% relative humidity range and was not permanently damaged by condensation. The Binos IRGA replacement had dual CO₂ μ l/l and % H₂O channels.

Control Program

The control program was an HP series 200 BASIC 3.0 with full extensions. Although use of this language resulted in voluminous code for this project (30+ pg, including documentation), it was very readable and the language extensions included useful input/output enhancements. The structure of the program was hierarchical, with a relatively short (approximately 90 lines) section of code which passed control to a series of subroutines. The driver ("Control") routine is described below.

Control driver routine

The "Control" section first checked the status of a number of flags to ensure that the program was ready to begin controlling the chambers, *e.g.*, whether the clock had been set, chamber variables initialized, *etc.* Error and timers were then set (resolution of time to 0.01 sec). The length of the full measurement cycle was 100 sec, which was adequate to ensure completion of all monitoring and control operations, and to allow a short idling period before the beginning of the next cycle. During this idle period, a gas sample from one of the chambers flowed to the humidity sensor to allow for equilibrium before it was read in the subsequent cycle.

The measurement cycle consisted of passing execution sequentially to the following monitoring and controlling subroutines: "Humidity Reading"; "IRGA-Calibration" (if appropriate); "Battery Reading"; "Thermocouple Reading"; "PAR Reading"; "Control"; "Temperature Control" (turning on/off heat bypass and timing this period. The "IRGA-Calibration" was performed every 1/2 hr only on the CO₂ IRGA. The other IRGAs were calibrated manually. The second level data reduction was executed on alternate passes through the control cycle (3 mm). Control and monitoring data were summed or averaged as appropriate over two control cycles for each recording cycle (6 mm). Thus, data were recorded 10 times/hr, 240 times/day.

RECENT MODIFICATIONS

The focus of the system modifications for 1987 were made to increase the quality of the measurement of flux rates rather than to improve control. Improvements to the system included mass flow meters versus rotameters and a more stable infrared CO₂ analyzer. Precisely measuring injection and scrubbing rates was critical to calculation of carbon dioxide flux rates. In the described system, these rates were measured with rotameters. Flow rates on the rotameters were checked and recorded manually, and then the flux rates adjusted by back-calculation. Electronic mass flow meters were added to directly and instantaneously measure flow rates with the data acquisition system with much greater accuracy and precision.

Estimation of leak rates was also critical to flux measurements--carbon dioxide leaking from the chambers must be accounted for in the calculations of CO₂ flux. Therefore, a precise method of monitoring chamber leak rate was added which incorporated a low rate N₂O injection, mass flow valves, and a Liston Edwards N₂O IRGA to meter a constant, very low flow rate of N₂O into each of the chambers. Mass-balance calculations using the N₂O injection rates and steady-state concentrations directly measured the amount of N₂O leaking from the chambers, and allowed calculation of the rate of air exchange with the outside atmosphere.

FIELD PHOTOSYNTHETIC RESPONSE OF SPECIES

During the 1985 growing season, photosynthetic rates were measured on leaves of *Eriophorum vaginatum* and *Ledum palustre* in each of the four treatments at five CO₂ concentrations (680, 510, 340, 170, and 85 or 50 $\mu\text{l/l}$). Dark respiration was measured at 680, 510, and 340 $\mu\text{l/l}$ CO₂. One complete set of measurements on *Eriophorum* was made between July 4 and July 17; measurements on *Ledum* and *Eriophorum* were made between July 18 and August 5 during peak season.

Groups of leaves were placed within a temperature-controlled cuvette maintained at 15°C by a Peltier-effect cooling module and a Weather Measure temperature controller (Oechel and Lawrence, 1979). Light was supplemented with a GE Cool Beam light source to attain an irradiance of 1500 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (PAR). The CO₂ concentration in the cuvette was controlled with two Tylan mass flow controllers (Model FC-260 and FC 261) to mix pure CO₂ with CO₂-free air, and the concentration was verified with an ADC 225 infrared gas analyzer used in absolute mode. CO₂ exchange within the cuvette was measured in an open system using the ADC gas analyzer in differential mode. Transpiration rate was determined from measurements of reference and cuvette air relative humidities made with Vaisala humidity sensors. Approximately 30 min were required for the photosynthetic rate to stabilize at each new CO₂ concentration.

CO₂ response curves were developed for three plants of *Eriophorum* in each treatment during each of the two measurement periods. Several measurements were made on *Ledum* during the early period but a complete set of data was not obtained. Three *Ledum* plants in each treatment were used during the second period. After CO₂ response measurements were completed, the leaves used were harvested and the leaf area of *Ledum* was determined. The leaves were then dried at 70°C and weighed. Leaves of *Eriophorum* were dried and weighed and the leaf area was later calculated from a regression of leaf weight on manually-measured leaf area.

Analysis of variance was used to test for effects of growth CO_2 concentration on measurements of photosynthesis, respiration, transpiration, and water vapor conductance. A *posteriori* testing for differences among means was performed using Duncan's new multiple range test (Duncan, 1955).

FIELD BIOMASS AND NUTRIENT RESPONSE OF SPECIES

To evaluate the effect of the CO_2 and temperature treatments on biomass and species composition, biomass was measured in early mid-season of 1986 in six (4 cm x 4 cm) plots from each of the original (1983 to mid-1985) chamber sites. The species studied included: a sedge tussock, *E. vaginatum* and two evergreen dwarf shrubs, *L. palustre* spp. *decumbens*, and *V. vitis-idaea*. For the sedge tussock, live biomass was separated into root, green leaf, leaf base, stem base, and inflorescence. The number of tillers, flowers, and new tiller primordia were also counted in four cm^2 plots measured post-treatment in 1986. For the evergreen dwarf shrubs, ramets were separated into leaf and stem components of the current year (1986) and the previous three years of persisting live biomass (1985, 1984, and 1983).

Plant tissue from the 1983-1985 treatments was collected from tissue resprouting in July 1986 for nutrient analysis. Total Kjeldahl nitrogen were analyzed for *Eriophorum vaginatum*, *Carex*, spp. *Betula nana*, and *Aulacomnium* (Figure 3). All bars which are significantly different from one another have been marked by the same letter denoting significance at the .01 level (one-way ANOVA).

SHORT-TERM SPECIES RESPONSES

Manipulation of CO_2 levels and nutrients were conducted for *Carex bigelowii*, *Betula nana* and *Ledum palustre* in growth chambers. Whole tussocks and their associated plants were collected in September 1982 near Toolik Lake, Alaska. They were kept in the dark at 10°C for two months at which time there were separated into species, cut back to stems and rhizomes of uniform size, and planted in 8 cm diameter plastic pots in a 1:1 (v:v) mixture of gravel and vermiculite. The plants were grown in controlled-environment chambers of the Duke University Phytotron (Kramer, *et al.*, 1970) at ambient $350 \pm 10 \mu\text{l/l}$ CO_2 with day/night temperatures of $20/15^\circ\text{C}$ and a 16-hr photoperiod. Irradiance at the leaf surface was $450 \mu\text{mol m}^{-2}\text{s}^{-1}$. Plants were watered with 1/8th strength Hoagland's solution (Downs and Hellmers, 1975) in the morning and deionized water in the afternoon.

After two months of growth, plants of each of the three species were paired and divided between two growth chambers maintained at two different CO_2 concentrations. Each species was further divided into two groups in each chamber and received either 1/8th or 1/60th strength Hoagland's solution in the morning and deionized water in the afternoon. Carbon dioxide concentrations were maintained by a computer-controlled injection system (Hellmers and Giles, 1979) at 350 ± 10 and $675 \pm 20 \mu\text{l/l}$ CO_2 . After three months of growth at the above conditions, net photosynthetic rates of leaves at $450 \mu\text{mol m}^{-2}\text{s}^{-1}$ irradiance and 20°C were measured with an infrared gas analyzer (Model 225, Analytical Development Company) in an open exchange system (Oechel and Lawrence, 1979). At the completion of these measurements, plants were harvested, divided into leaves, stems, and roots, dried at 70°C for 48 hr, and weighed. Leaf tissue samples were analyzed for nitrogen and phosphorus content using an autoanalyzer and for other macro- and micronutrients using optical emission spectrometry.

Figure 3. A. Total Kjeldahl nitrogen of 1986 *Eriophorum vaginatum* leaf tissue. Similar letters denote statistically significant differences at the $p < .01$ level.

3. B. Total Kjeldahl nitrogen of 1986 *Carex*, spp. leaf tissue. Similar letters denote statistically significant differences at the $p < .01$ level.

3. C. Total Kjeldahl nitrogen of 1986 *Betula nana* leaf tissue. Similar letters denote statistically significant differences at the $p < .01$ level.

3. D. Total Kjeldahl nitrogen of 1986 *Aulacomnium turginatum* leaf tissue. Similar letters denote statistically significant differences at the $p < .01$ level.

A **B**

C

D

SOIL RESPIRATION

Soil CO₂ efflux of untreated tundra and subsamples of tundra within CO₂-controlled chambers were measured during the peak season July 17-August 1, 1985 at CO₂ concentrations of 87 ± 12 , 172 ± 7 , 344 ± 12 , 511 ± 14 , and 680 ± 17 $\mu\text{l/l}$ CO₂. Measurements were made using differential infrared gas analysis of intact tundra enclosed within an opaque, acrylic-plastic cuvette (30.8 cm deep x 13.2 cm x 9.8 cm) stirred by an 8 cm diameter fan. Chamber air temperatures were maintained at $16.2 \pm 1.3^\circ\text{C}$. Mass flow valves regulated cuvette CO₂ concentrations by mixing CO₂-free air with 5% CO₂ in air. Differential CO₂ was monitored until equilibrium was attained, usually after about 30 min. Measurements were corrected by subtracting the leak rate of the empty cuvette at each CO₂ concentration. For measurements, the open-ended cuvette was imbedded into the peat to an average depth of 9.6 cm, usually against mineral soil, until an adequate seal was made. Measurements were made on moss or litter surfaces between tussocks where vascular plants comprised a minor portion of the biomass. The 1985 growing season was unusually dry. In order to minimize the effects of drought and of unequal hydration of moss and microflora, water (0.5 to 1.0 l) was applied to all sites to be measured until they were thoroughly wet. After measurements were completed, the enclosed organic matter above the mineral soil was removed, dried at 70°C for 48 hr, and weighed. Two-way ANOVA was used to test for effects of CO₂ concentration during growth and measurement.

RESULTS

EVALUATION OF GREENHOUSE PERFORMANCE

Overview

The system provided excellent control, especially considering the adverse conditions under which it operated. The following data were used to analyze the performance of the system early in the 1985 field season.

Carbon Dioxide Concentration Control

Control of carbon dioxide concentrations in the chambers was very good. Carbon dioxide set points in the experiment were 340, 510, and 680 $\mu\text{l/l}$. Carbon dioxide concentrations measured in the chambers during June and July 1985 are summarized in Table 1. During this period, average carbon dioxide concentrations measured in the chambers set to 680 $\mu\text{l/l}$ ranged 677-685 $\mu\text{l/l}$ (standard deviations were ca. 18); those set at 510 $\mu\text{l/l}$ ranged 511-515 $\mu\text{l/l}$ (s. d. = ± 14 $\mu\text{l/l}$); and those set at 340 $\mu\text{l/l}$ ranged 343-348 $\mu\text{l/l}$ (s. d. = ± 9 $\mu\text{l/l}$). These results compare favorably to those obtained in controlled-environment growth chambers and growth chambers in the Duke University Phytotron set at 350 $\mu\text{l/l}$ varied by ± 10 $\mu\text{l/l}$ (Hellmers and Giles, 1979). Considering the fluctuating environment in which the field chambers operate and the small volume of the chambers, this represents excellent carbon dioxide control.

In 1987, the Liston-Edwards CO₂ analyzer was replaced by a Binos IRGA. The Binos provided adequate response time and greater stability than the Liston-Edwards and was a significant improvement to system performance.

TABLE 1. Control of carbon dioxide concentrations [$\mu\text{L/l}$] in each of the 12 chambers at Toolik Lake. Set point, is the mean measured CO_2 concentration, standard deviation and coefficient of variation calculated from 7636 records during June and July 1985 are presented.

CHAMBER	SET POINT [CO_2]	MEAN [CO_2]	STANDARD DEVIATION	COEFFICIENT VARIATION
1	680	681	20.0	2.94
2	510	511	15.6	3.05
3	680	685	19.0	2.77
4	340	348	9.8	2.82
5	680	683	17.9	2.63
6	680	682	17.0	2.49
7	510	514	13.4	2.62
8	680	677	20.1	2.97
9	340	343	8.8	2.57
10	680	680	18.5	2.72
11	510	515	12.9	2.50
12	340	348	8.9	2.55

Temperature Control

Evaluation of the performance of the system in controlling chamber temperatures was by t-tests for paired comparisons to determine the significance of the differences between chamber and ambient temperatures. This test was run for temperatures recorded over a five-day period in early July 1985 (Julian days 195-199). Chambers 1, 8, and 10 had average differences from ambient of +4°C since these chambers were under the elevated temperature treatment which tracked ambient +4°C. The t-tests for these chambers incorporated this 4° offset.

Average differences between chamber and ambient temperatures ranged from -0.97 to +0.87°C (Table 2, Figure 4). In general, the differences between chamber and ambient temperatures were statistically significant by the t-test ($p < 0.01$), but considering the task of tracking the often rapidly fluctuating environment, average deviations of less than 1° over the course of 24 hr represented excellent control.

The analysis also highlighted the fact that cooling the chambers was more efficient than heating. This was especially true when the radiant heat load was low. Thus, despite adjusting the control program such that during each control cycle approximately half of the chambers were cooling and half heating, undershoot of chamber temperatures following cooling cycles tended to be larger than overshoot following the heating cycles. Also, fine tuning of the temperature control scheme was complicated by the elevated temperature treatment--the same heat-timer had to be used for the elevated and ambient temperature chambers, despite the quite different requirements for heating and cooling. For this reason, temperatures of the elevated temperature chambers were slightly higher on average, while ambient chambers were slightly lower than the set points (*e.g.* Julian day 195, Table 2). This problem was minimized by a new, more frequent temperature-control scheme.

Other Environmental Measures

While only carbon dioxide and temperature were actively controlled, the system also monitored humidity and irradiance levels. During each control cycle, irradiance was measured by two quantum sensors, one inside a chamber and the other in the ambient plot (Figure 5b). Irradiance was one of the factors used to fine tune the carbon dioxide control of the chambers (Riechers, *et al.*, in prep.). Irradiance data also proved to be useful in analyzing the response of this ecosystem to the carbon dioxide treatments. Hilbert, *et al.*, (1987) used such data to analyze chamber fluxes and estimate quantum yield (light utilization efficiency), conductance, and respiration by fitting to a nonlinear model of ecosystem carbon flux. Average light intensity in the chamber was 64-76% of ambient values.

Humidity measurements inside and outside the chambers (Figure 5a) indicated that the cooling systems were capable of controlling chamber temperatures without undue desiccation of the chamber air. As described above, the refrigeration system was modified to include large evaporator coils relative to the capacity of the compressors. Also, each chamber formed a relatively closed system which reduced evaporation from the plants and soil surface. In most cases, chambers alternated between cooling and heating cycles and, as a result, the condensate collected on the coils during a cooling cycle was reintroduced to the chamber air during the subsequent heating cycle.

TABLE 2. Mean differences between chamber (ch) and ambient temperatures (deg. C) or ambient temperature +4°C (heated chambers 1, 8, and 10). No values are significantly different from target temperatures and t-tests of significance for five days during July 1985. (d = mean difference between ambient and chamber temperature; t = student's t; d.f. = > 200 for each day; significant T value at (P < .05.)

ch	1*	2	3	4	5	6	7	8*	9	10*	11	12
JULIAN DAY 195												
d	4.54	-0.24	0.61	-0.39	-0.69	-0.19	-0.30	4.23	0.10	4.50	-0.07	-0.43
t	4.04	-2.23	5.04	-4.01	-7.26	-1.89	-2.88	1.57	0.80	3.53	-0.75	-4.45
JULIAN DAY 196												
d	4.87	-0.35	0.43	-0.43	-0.63	-0.32	-0.76	4.46	0.06	4.68	-0.08	-0.74
t	6.53	-3.19	4.59	-4.71	-6.60	-3.09	-9.87	3.60	0.54	5.00	-0.79	-8.06
JULIAN DAY 197												
d	3.98	-0.68	-0.05	-0.83	-0.97	-0.73	0.07	3.97	-0.40	3.87	-0.66	-0.87
t	-0.13	-5.56	-0.46	-8.03	-10.08	-6.81	0.49	-0.19	-2.99	-0.96	-6.24	-9.15
JULIAN DAY 198												
d	3.45	-0.40	0.02	-0.65	-0.81	-0.34	-0.91	3.62	-0.25	3.46	-0.33	-0.72
t	-3.39	-2.84	0.15	-4.99	-6.11	-2.34	-6.27	-2.15	-1.68	-2.80	-2.31	-4.96
JULIAN DAY 199												
d	3.42	-0.44	0.03	-0.56	-0.64	-0.50	-0.52	3.40	-0.30	xxx	-0.30	-0.68
t	-4.78	-4.41	0.30	-7.05	-8.14	-6.41	-5.05	-4.96	-3.08	xxx	-3.58	-8.28

* These chambers controlled to 4° above ambient temperature.

xxx = data missing. Chamber 10 was removed for part of this day to allow access to plants for physiological measurements.

ARCTIC CO2 PROJECT

Toolik Lake 11AUG

Figure 4.

Typical temperature tracking of ambient air temperature (dashed line) by chamber air temperature (solid line). Six-minute measurements for August 11, 1985 are presented.

Figure 5. A. Humidity measured inside (light lines) and outside (heavy line) the chambers.

5. B. Irradiance ($\mu\text{mol m}^{-2} \text{sec}^{-2}$) measured inside (heavy line) and outside (light line) the chambers.

ARCTIC CO₂ PROJECT

Toolik Lake 6SEP

Vapor density [g water/m³ air] PAR [$\mu\text{E}/\text{m}^2/\text{sec}$]

Carbon Dioxide Flux

Measurement of the flux of carbon dioxide at ambient and elevated CO_2 and temperature was a primary function of the chambers. Fluxes measured on a representative day in June 1985 are shown in Figure 6. These plots represent a 30-min sliding mean of the sum of the inject and scrub from two averaged 3-min periods. The fluxes are converted to rates ($\text{g m}^{-2} \text{h}^{-1}$), and plotted against time of day to show the diurnal course of carbon exchange for each of the treatments.

THREE-YEAR ECOSYSTEM RESPONSE

Areas of tundra were exposed for the better part of three growing seasons to the altered regimes of carbon dioxide concentrations and temperatures described above. To determine the effects of elevated CO_2 and temperature on net ecosystem CO_2 flux, data from the three years of elevated CO_2 and temperature treatments on mean daily CO_2 flux were plotted as a function of time. Daily totals of flux for each treatment were statistically analyzed (ANOVA). In the early season in the year following the cessation of treatments (1986), subsamples were taken from the experimental plots to determine live biomass components of selected species and tiller rates of *Eriophorum vaginatum*.

Effects of Elevated CO_2 on Mean Daily Flux, 1983-1985

The differences in mean net carbon dioxide fluxes between the elevated CO_2 treatments and the control were plotted over the three years (Figure 7, Table 3). The three-year data base was prepared for plotting and analysis of variance by eliminating incomplete daily records and daily fluxes which were $>$ two standard deviations from the mean of the three replicates (Table 4). The effects of CO_2 on mean daily flux was highly significant ($F_s=37.80$). A separate ANOVA was run to test the effects of temperature on mean daily CO_2 flux between the 680 and 680 +4°C treatment. The effects of temperature on mean daily CO_2 flux was not significant (Table 4).

The 510 $\mu\text{l/l}$ treatment had higher mean daily CO_2 fluxes than the control through the three years of the experiment (Figure 7). The 680 $\mu\text{l/l}$ treatment had an even greater initial mean daily CO_2 flux relative to the control during the first and second years of treatment at elevated CO_2 . In the first year of treatment (Figure 7), daily fluxes at 680 $\mu\text{l/l}$ CO_2 were on the order of 8-10 $\text{g m}^{-2} \text{d}^{-1}$ higher than at 340 $\mu\text{l/l}$ (Prudhomme and Oechel, 1984; Riechers and Oechel, 1985). However, this response was lost by the third year of treatment (Figure 7). A decrease in CO_2 flux over a 50 to 100-year time frame had been previously predicted by Oechel and Strain (1985; Figure 8). The decrease in response to a doubled CO_2 concentration during the 1985 season indicated a remarkably fast acclimation of ecosystem-level CO_2 flux. Over the course of the three years of treatment, a factor other than CO_2 concentration had become increasingly limiting to the extent that doubling CO_2 concentration no longer had any appreciable effect on CO_2 flux. If this limitation developed more slowly at 510 $\mu\text{l/l}$ where the original effect of enrichment was smaller, it would explain the significant, although reduced, CO_2 enrichment effect in the third season of treatment.

Unfortunately, the limited number of chambers used precluded treatment of elevated temperature at ambient CO_2 . Without this treatment, it is not possible to separate the effects of elevated temperature from the interaction between temperature and CO_2 enrichment.

Figure 6.

Daily flux of carbon dioxide at 340, 510, and 680 $\mu\text{l/l}$ CO_2 , and 680 $\mu\text{l/l}$ CO_2 4°C above ambient temperature. Data presented are 30-minute sliding means of six-minute values.

MEAN DAILY CARBON DIOXIDE FLUXES

1983-1985

BARs REPRESENT MEAN DIFFERENCES BETWEEN TREATMENT AND 340 PPM FLUXES

Figure 7.

Mean net daily carbon dioxide fluxes ($\text{g m}^{-2} \text{ day}$) for the three years of study. Bars represent the differences in the mean flux rates between 510 and 340 $\mu\text{l/l}$ CO_2 and 680 and 340 $\mu\text{l/l}$ CO_2 treatments.

Figure 8. Hypothetical response of production and decomposition to a step-change in atmospheric carbon dioxide concentration. From Oechel and Strain, 1985.

TABLE 3. Mean daily flux of carbon dioxide ($\text{g m}^{-2}\text{day}$) measured *in situ* at CO_2 concentrations of 340, 510, and 680 $\mu\text{l/l}$ between June 5 and July 24, 1985.

CO_2 Concentration ($\mu\text{l/l}$)	C Flux ($\text{g m}^{-2}\text{day}$)	Statistics
340	-2.96	$F_s(\text{CO}_2) = 23.10$
510	-2.67	D.F. = 2/1262
680	-3.05	$p(f) < 0.001$
680 + 4°	-1.36	$F_s(\text{temp}) = 271.04$
		d.f. = 1/798
		$p. < 0.001$

Table 4. Effects of CO₂ and year on net daily CO₂ fluxes. Replicate chambers nested under CO₂ treatment. Level for rejection of the null hypothesis is 0.05. N.D. = No Difference.

Treatment				
Year:	340 $\mu\text{l/l}$	510 $\mu\text{l/l}$	680 $\mu\text{l/l}$	680 $\mu\text{l/l} + 4^\circ\text{C}$
1983	-3.76	-1.99	2.25	1.17
1984	-3.87	-2.16	0.17	N.D.
1985	-1.13	0.35	-0.93	2.06

Statistical test:	Fs	p(f)	D.F.
Effects of CO ₂	37.805	<0.001	2/380
Effects of Temperature	2.471	0.112	1/236

Effects of Elevated CO₂ on Mean Daily Flux, 1985 Season

The data from the original research site was collected in the third year of treatment during June to mid-July, 1985. Treatment was begun on June 5, 1985, less than ten days after the major snowmelt of the spring. Little or no thawing of the soil surface had yet occurred, and much unmelted snow remained. Deciduous species had not broken dormancy, and the evergreen species and cryptogams were probably just beginning to become physiologically active.

The daily flux rates on an area basis ($\text{g m}^{-2} \text{d}^{-1}$) for each CO₂ treatment have been plotted to show the third-year seasonal progression of net ecosystem production (June 5 to mid-July, Figure 9). Early in the season, all treatments showed positive CO₂ uptake. In midseason all treatments showed negative daily fluxes most of the time. Several factors were responsible. First, depth of thaw was increasing rapidly during this period. A portion of the CO₂ efflux probably resulted from CO₂ trapped in the soil during freeze-up the previous fall, and released during the subsequent thaw period. Second, in early spring, plants were actively producing new photosynthetic tissue and had high rates of growth and maintenance respiration relative to photosynthesis. Thirdly, the tundra was exceptionally dry due to the low amount of rainfall during this period. Desiccation and photobleaching of the moss mats were evident. This unseasonable drought presumably depressed photosynthetic rates, at least on those of some of the important non-vascular species. Lastly, actual rates of carbon sequestering in tussock tundra vegetation may be significantly lower than previously thought. Analysis of our data and that of Schell (unpubl.) indicates that there may be little or no net carbon storage under current climatic conditions. Schell's data indicate no stored peat less than 2000 years old in mesic, tussock tundra areas in the region.

An analysis of variance for the effect of carbon dioxide concentration and temperature was applied to the 1985 daily fluxes (Table 3). While the differences among the average daily flux rates were small, the effects of carbon dioxide enrichment on flux rates were highly significant statistically ($F_s=23.10$). Daily fluxes at 340 and 680 $\mu\text{l/l}$ were nearly identical, differing by less than $0.1 \text{ g m}^{-2} \text{d}^{-1}$. The effects of the elevated temperature treatment were also highly significant statistically ($F_s=271.04$). Relative to the CO₂ effect, however, the magnitude of the temperature effect was quite large. Fluxes at 4°C above ambient were, on average, more than $1.5 \text{ g m}^{-2} \text{d}^{-1}$ higher than those at 680 $\mu\text{l/l}$. This was consistent with most predictions about the effects of elevated temperature on tundra production (Chapin and Shaver, 1985) and peat accumulation (Miller, 1981). The stimulating effects of increased temperature on production and mineralization more than compensated for the effects of temperature on respiration and decomposition. Deepening of the depth of thaw associated with increased temperature did not sufficiently increase the rate of decomposition to overshadow the effects of increased productivity. Net ecosystem carbon storage was therefore increased at elevated temperature.

Effects of Elevated CO₂ on Species Biomass and Nutrient Content

In general, tissue weight was depressed in the chambers relative to the control due to mid-season freezing in 1985 following loss of temperature control. There were no obvious trends apparent in live biomass components of *Eriophorum* with regard to elevated CO₂ (340, 510, 680 $\mu\text{l/l}$) or temperature (680, 680+4°C). However, total live biomass was slightly higher in the 510 $\mu\text{l/l}$ treatment relative to the 340 and 680 $\mu\text{l/l}$ treatments supporting the possibility that a factor other than CO₂ concentration had become increasingly limiting to the

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Figure 9.

Seasonal fluxes of carbon dioxide in the third growing season of treatment, 1985.

extent that doubling the CO_2 concentration no longer had any appreciable effect. The root:shoot ratio declined appreciably from the 340 to 680 $\mu\text{l/l}$ treatment (.28, .24, .17 for 340, 510, and 680 $\mu\text{l/l}$, respectively). In the 680 $\mu\text{l/l}$ treatment, this could be accounted for by a significantly greater specific root weight ($F_s=4.099$; $p(f)=.0372$; $df=2/15$). Neither total live biomass, other biomass components (stem base, leaf), nor leaf area were significantly different as affected by CO_2 enrichment (Figure 10).

Tiller density was greater in the 510 and 680 $\mu\text{l/l}$ treatment relative to the control, but small sample size and large variance prevent a definitive conclusion on whether or not elevated CO_2 resulted in increased tillering of *Eriophorum* (Figure 11). There were no apparent trends in the number of new tiller primordia produced per tiller across CO_2 or temperature treatment. No flowers were discovered in subsamples of the 680 and 680 +4°C treatment. A greater density of tillers was found after the first season of treatment (1983; Tissue and Oechel, 1987). It remains to be seen if this increase in tillering rates is supported over a longer time period. First-year response is dependent on shoot primordia formed in previous years. Insufficient production of primordia could limit this long-term response. If this response does continue, it could have important effects on community structure and function.

Similar to the sedge tussock, no obvious trends were apparent in the live biomass components or leaf area in response to elevated CO_2 (340, 510, 680 $\mu\text{l/l}$) (Tables 5, 6). Leaf weight, leaf area, and stem weight were not significantly different in response to elevated CO_2 for *Ledum*. Stem length was significantly different in *Ledum* ($F_s=4.341$; $p(f)=.0141$; $df=2.208$) in response to elevated CO_2 . Although the low sample size and high variance preclude drawing definitive conclusions, the measured stem length of *Vaccinium vitis-idaea* grown at 680 $\mu\text{l/l}$ was greater than that in the control (Figure 12).

Although the results from the biomass and density studies are largely inconclusive, the trends support the findings from the CO_2 flux data. Slightly greater CO_2 flux, live biomass, and plant density were found at 510 $\mu\text{l/l}$ than at 680 $\mu\text{l/l}$ CO_2 which suggests some limiting factor other than CO_2 at the 680 $\mu\text{l/l}$ treatment level. Perhaps early response to the greater carbon availability at 680 $\mu\text{l/l}$ CO_2 than at 340 or 510 $\mu\text{l/l}$ led to rapid resource limitation at 680 $\mu\text{l/l}$ CO_2 by factors other than CO_2 .

SHORT-TERM ECOSYSTEM RESPONSE

In marked contrast to the flux data collected during the third year of treatment at the original site, the data from the new site established in late July 1985 and measured in mid-August 1985 show a large response to elevated CO_2 concentration under this short-term enrichment. In the third year of treatment in the first experiment, chambers maintained at 340 and 680 $\mu\text{l/l}$ had virtually identical flux rates over a 50-day period early in 1985; -2.96 and $-3.05 \text{ g m}^{-2} \text{ d}^{-1}$, respectively (Table 3). Over the short-term one to three days of manipulation, the response was much greater with fluxes on the order of $3\text{--}7 \text{ g m}^{-2} \text{ d}^{-1}$ higher at elevated CO_2 (Table 7, Figure 13). These results are similar to the first year of treatment in the three-year experiment (Figure 7).

The magnitude of the response to high CO_2 decreased throughout this period. This decrease, however, did not represent acclimation to the high CO_2 treatment, but rather reflected the effect of senescence of the vascular plants over this late-season period. The deciduous shrub species--*Salix* and *Betula*--were well past their peak productive

BIOMASS ALLOCATION

Eriophorum vaginatum

CONTROL

340

510

680

Figure 10. Biomass allocation of *Eriophorum vaginatum* for root, green leaf, leaf base, stem base, and inflorescence.

Eriophorum vaginatum

TILLER DENSITY PER 4cm² PLOT

Figure 11.

Tiller density per 4 cm² plot of *Eriophorum vaginatum*. New tillers are non-emergent primordia. Old tillers are emergent ramets.

Vaccinium vitis-idaea

Figure 12. Stem length of *Vaccinium vitis-idaea* produced in the three years of treatment.

ARCTIC CO₂ PROJECT

Toolik Lake, 1985

340 ppm 680 ppm

Figure 13.

Flux of carbon dioxide ($\text{g m}^{-2} \text{ day}$) in response to short-term enrichment (1 to 3 days) to 680 $\mu\text{l/l}$, 1985. Each bar = mean of six chambers. Chamber set-points were changed on 18 August and 22 August.

Table 5: *Ledum palustre* Subspecies *decumbens*

Tissue Type:		Leaf Area (mm)				Leaf Weight (g)				Stem Weight (g)			
Year Produced:		86	85	84	83	86	85	84	83	86	85	84	83
Treatments:													
Control	X	1.972	1.752	.321	.018	.039	.037	.007	.000	.008	.016	.016	.020
	S.E.	1.049	.919	.510	.095	.020	.022	.011	.002	.005	.008	.009	.015
	N	64	67	63	72	64	67	63	72	64	67	65	72
340	X	2.311	1.681	.267	.023	.051	.037	.006	.001	.014	.016	.017	.015
	S.E.	1.440	1.126	.582	.116	.033	.026	.013	.003	.011	.009	.009	.010
	N	74	72	69	69	74	72	69	69	74	74	70	72
510	X	1.686	.650	.176	.015	.041	.015	.004	.000	.013	.014	.014	.012
	S.E.	.850	.722	.521	.085	.024	.018	.012	.002	.010	.013	.008	.007
	N	70	71	64	67	70	71	64	67	70	71	68	67
680	X	2.075	1.007	.039	0.24	.048	.021	.001	.001	.012	.014	.013	.011
	S.E.	1.199	1.126	.143	.166	.029	.024	.003	.004	.009	.012	.014	.013
	N	68	70	63	57	68	70	62	57	68	70	67	62
680+4°C	X	1.325	.910	.196	0	0.35	.023	.005	0	.010	.015	.013	.011
	S.E.	.871	1.135	.569	0	.023	.031	.014	0	.009	.012	.013	.010
	N	44	49	47	47	44	49	47	47	44	50	52	45

Table 6: *Vaccinium vitis-idaea*

Tissue Type:		Leaf Area (mm)				Leaf Weight (g)				Stem Weight (g)							
Year Produced:		86	85	84	83	86	85	84	83	86	85	84	83	86	85	84	83
Treatments:																	
Control	X	1.060	1.144	.555	.242	.025	.028	.013	.005	.002	.004	.004	.004	9.824	12.510	12.740	11.0
	S.E.	.540	.492	.520	.194	.016	.013	.013	.004	.001	.002	.002	.002	3.666	4.394	5.433	4.14
	N	74	74	60	18	74	74	60	17	23	74	53	17	74	74	54	17
340	X	1.27	1.479	.696	.350	.028	.034	.016	.009	.003	.005	.005	.004	10.190	13.640	14.170	10.1
	S.E.	.7	.709	.530	.366	.017	.017	.013	.009	.002	.003	.003	.002	3.883	6.183	6.194	4.25
	N	69	75	68	34	69	75	68	34	68	73	63	33	69	73	63	33
510	X	1.018	1.225	0.721	.465	0.22	.027	.016	.010	.002	.004	.004	.004	8.616	12.770	12.630	.004
	S.E.	.503	.555	.453	.282	.010	.013	.011	.007	.001	.002	.002	.002	3.174	4.465	4.680	.002
	N	73	75	62	27	72	75	62	27	72	72	54	27	73	74	54	27
680	X	1.31	1.415	.694	.363	.030	.032	.015	.009	.003	.005	.006	.004	10.520	14.710	15.880	10.0
	S.E.	0.62	.721	.476	.287	.015	.018	.011	.008	.002	.003	.005	.001	4.823	7.105	8.586	2.95
	N	74	73	57	21	73	75	57	15	73	73	50	11	73	73	52	11
680+4°	X	1.001	1.166	.654	.363	.020	.024	.014	.008	.002	.004	.004	.003	9.811	15.680	13.780	7.83
	S.E.	.582	.649	.545	.287	.012	.014	.012	.007	.001	.002	.003	.001	3.91	6.586	5.872	2.85
	N	74	75	53	21	74	75	53	20	69	69	45	18	74	73	45	18

TABLE 7. Flux of CO₂ under short-term enrichment to 680 μ l/l CO₂. High CO₂ treatments were begun at midnight immediately preceding measurements on August 18 and 22 1985. High CO₂ chambers on August 22, and 24 had been at 340 μ l/l on August 18 and 19. Means of six chambers $\pm$ standard deviation and probability of significant CO₂ effect on flux rate.

p <*	Date	CO ₂ (μ l/l)	Flux (g m ⁻² d ⁻¹)	$\pm$ s. d.
.001	8-18	340	-2.36	$\pm$ 1.71
		680	+5.38	$\pm$ 3.89
.01	9-19	340	-2.55	$\pm$ 1.53
		680	+2.75	$\pm$ 3.39
.05	8-22	340	-3.09	$\pm$ 2.34
		680	+2.51	$\pm$ 4.37
n.s.	8-24	340	-3.15	$\pm$ 3.04
		680	-0.34	$\pm$ 3.87

*Probability of significance from one-way ANOVA.

period. Their leaves had lost most of their chlorophyll and were about to abscise. This accounts for both the negative daily net fluxes at 340 $\mu\text{l/l}$ throughout the period and for the decreasing effect of enrichment to 680 $\mu\text{l/l}$.

These data serve as important confirmation of the results previously obtained at the original research site. A possible criticism of the earlier data is that, because of the extensive modifications made to the system each year, it was not possible to ensure that apparent differences among flux rates measured in different years were due to homeostatic adjustment or acclimation to elevated CO_2 treatment or that the observed pattern was not simply an artifact of the changes made to the measurement system. The data from these short-term experiments performed in 1985, however, refute this argument. First, the response reported for the first year of treatment (8 to 10 $\text{g m}^{-2} \text{d}^{-1}$ higher uptake at 680 $\mu\text{l/l}$); is a reasonable estimate of the short-term response of this ecosystem to CO_2 enrichment and confirms the 3-7 $\text{g m}^{-2} \text{d}^{-1}$ found in these short-term experiments despite the fact that the latter were measured very late in the growing season. Second, these data indicate that the lack of response to high CO_2 in the third year of treatment reflected genuine homeostatic adjustment to prolonged exposure to elevated CO_2 .

FIELD MEASUREMENTS OF PHOTOSYNTHETIC RESPONSE TO ELEVATED CO_2 : *Eriophorum vaginatum* L. and *Ledum palustre* L.

While photosynthesis can be limited in the short term by CO_2 , light, and temperature, it is also limited on a longer time scale by available resources including nutrients and by sink strength. The photosynthetic response of *Eriophorum vaginatum*, the dominant plant of the tussock tundra, to elevated CO_2 was evaluated after one and three years of CO_2 treatment. In the third year, the photosynthetic response of *Ledum palustre* was also measured and compared to *Eriophorum vaginatum*.

The objective was to determine whether the photosynthetic adjustment detected earlier in *Eriophorum* (Tissue and Oechel, 1987) persisted for three years, and whether *Ledum* would also show a similar effect, as appeared to be the case in controlled-environment studies (Oberbauer, *et al.*, 1986a and below). Previous seasons' ecosystem flux results had suggested that lower respiration, rather than increased photosynthesis, accounted for greater carbon storage in the tundra blocks maintained at elevated atmospheric CO_2 (Hilbert, *et al.*, 1987). For this reason, dark respiration rates of the two species were also measured at various CO_2 concentrations.

Eriophorum vaginatum grown at elevated CO_2 adjusted very quickly to the higher CO_2 concentration so that within three weeks of the initiation of exposure, photosynthetic rates are similar to those of plants growing at ambient CO_2 levels (Tissue and Oechel, 1987, Figure 14). At their respective growth concentrations, the CO_2 uptake rates of both the plants grown at 340 and those grown at 680 $\mu\text{l/l}$ CO_2 were $\approx 17 \mu\text{mol m}^{-2} \text{s}^{-1}$. This rapid response represents a high degree of homeostasis and is consistent with the notion that many tundra species are limited less by CO_2 or carbohydrate availability than by nutrients (Tissue and Oechel, 1987; Chapin and Shaver, 1985; Oechel and Blake-Jacobson, (in prep.).

This homeostasis was quite general, and for the four sampling periods, (mid to July to mid-August), there was no significant increase in photosynthetic range at elevated CO_2 (Figure 15). However, during the last sampling period (August 20-24), the elevated CO_2 treatments did not reflect the end of the season decrease in the photosynthetic rate shown by the ambient CO_2 treatment. This indicates delayed leaf senescence of the photosynthetic machinery in the elevated CO_2 treatments.

Figure 14.

Net photosynthetic response of *Eriophorum vaginatum* that had been maintained at a CO₂ concentration of 340 μl/l or 680 μl/l when exposed to a range of CO₂ concentrations during the 5-15 July sampling period. Mean ± 1 SE, *n* = 6 plants. From Tissue and Oechel, 1987.

Figure 15.

Net photosynthetic rates for plants in the CO₂ and temperature treatments measured at their growth CO₂ concentrations at 15°C during the growing season. Except for the 4°C treatments (solid bars), temperatures tracked ambient temperatures on the dates indicated. Mean $\pm$ 1 SE, n = 4-6 plants. Within a sampling period, rates with the same letter are not significantly different ($P < .05$) as determined by the SNK test (CO₂) and Student's t test (temperature). From Tissue and Oechel, 1987.

After three years of treatment in the field at elevated CO_2 , *Eriophorum vaginatum* and *Ledum palustre* showed typical short-term responses to changes in atmospheric CO_2 concentration (Figures 16, 17, 18). Photosynthetic rates increased more or less linearly as CO_2 increased. However, the responses of plants from the various growth treatments differed among species. During the early season measurement period, *Eriophorum vaginatum* grown at $340 \mu\text{l/l}$ CO_2 consistently had the highest photosynthetic rates at each measurement CO_2 level and plants grown at $680 \mu\text{l/l}$ had the lowest rates (Figure 16). Plants grown at $680 \mu\text{l/l}$ CO_2 and elevated temperature, however, had photosynthetic rates comparable to those of plants grown at lower CO_2 . These differences were not statistically significant except at $340 \mu\text{l/l}$ CO_2 . There were no significant differences in photosynthetic rates among plants measured at their growth CO_2 concentrations (Table 8). Plants grown at $680 \mu\text{l/l}$ CO_2 and elevated temperature, however, had photosynthetic rates comparable to those of plants grown at lower CO_2 . Respiration, transpiration, and water vapor conductance did not vary significantly among plants from the different treatments at any measurement CO_2 concentration (Table 9; measurements from early and peak season did not differ and have been analyzed together).

During the second measurement period, there were no statistically significant differences in photosynthetic rates among plants from the different treatments at any measurement CO_2 level. Plants grown at $680 \mu\text{l/l}$ CO_2 tended to have lower rates than those grown at 340 and $510 \mu\text{l/l}$ (Figures 17 and 18). During this period, plants from the elevated temperature treatment had the lowest photosynthetic rates. This was probably the result of a one-night freeze which occurred in all chambers on July 17 due to a control program malfunction. Unlike the ambient temperature chambers, the elevated temperature chamber plants had not experienced subfreezing temperatures since early in the growing season, and the plants they contained were not frost hardened. Plants in the elevated temperature chambers may have been affected by freezing in such a way that photosynthetic capacity was reduced for the rest of the growing season.

There were significant differences in photosynthetic rates among plants of *Ledum* from the four treatments when measured at 170 , 340 , 510 , and $680 \mu\text{l/l}$ CO_2 (Figure 18). Plants grown at $510 \mu\text{l/l}$ CO_2 consistently had the highest rates and those grown at $680 \mu\text{l/l}$ CO_2 and elevated temperature had the lowest (data are after July 17). Among plants measured at their growth CO_2 concentrations, those from 510 and $680 \mu\text{l/l}$ CO_2 had significantly greater photosynthetic rates than those from $340 \mu\text{l/l}$ and $680 \mu\text{l/l}$ plus elevated temperature (Table 8). Therefore, unlike *Eriophorum vaginatum* photosynthesis in *Ledum palustre* was positively influenced after prolonged exposure to elevated CO_2 . However respiration, transpiration, and water vapor conductance rates did not differ significantly among plants from the four treatments (Table 10).

Specific leaf weights (SLW, g dm^{-2}) were calculated for *Eriophorum* from the leaves used to generate weight-area regressions and for *Ledum* from the leaves used in photosynthetic measurements. There were no significant differences in specific leaf weight among treatments for *Ledum* (Table 11). However, *Eriophorum* plants grown at $510 \mu\text{l/l}$ carbon dioxide had greater SLW than those from other treatments.

These two tundra species exhibit quite different photosynthetic responses to CO_2 enrichment. *Eriophorum* adjusts photosynthetic capacity so that plants growing at $680 \mu\text{l/l}$ CO_2 fix no more carbon than those growing at $350 \mu\text{l/l}$ (Table 8). These results confirm those of Tissue and Oechel, 1987; the response of *Eriophorum* to CO_2 enrichment does not change after two additional growing seasons under various CO_2 treatments at any measurement CO_2 concentration (Figures 16 and 17). Future work is

Figure 16. Photosynthesis of *Eriophorum vaginatum* grown at 340, 510, and 680 $\mu\text{l/l}$ CO_2 , and at 680 $\mu\text{l/l}$ at 4° above ambient temperature. Measurements at 85, 170, 340, 510 and 680 $\mu\text{l/l}$ during early July 1985.

Figure 17. Photosynthesis of *Eriophorum vaginatum* grown at 340, 510, and 680 $\mu\text{l/l}$ CO_2 at peak season 1985.

Figure 18. Photosynthesis of *Ledum palustre* grown at 340, 510, and 680 $\mu\text{l/l}$ at peak season 1985.

Table 8. Photosynthetic rate ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) of plants measured at their growth CO_2 concentrations. Numbers in a column not followed by the same letter are significantly different at the .05 probability level. (Numbers in parentheses are standard errors).

Growth/ Measurement CO ₂	<i>Erlophorum</i> Early Peak Season		<i>Ledum</i> Peak Season	
340/340	14.5 (2.5) A	6.8 (1.8) A	3.6 (0.1) A	
510/510	12.8 (2.6) A	10.3 (1.5) A	12.2 (0.7) B	
680/680	12.3 (0.9) A	8.8 (2.7) A	10.2 (0.7) B	
680 + 4°C/680	17.9 (2.3) A	5.5 (1.1) A	4.6 (1.5) A	

Table 9. Respiration ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), transpiration ($\mu\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and water vapor conductance ($\text{cm} \cdot \text{s}^{-1}$) rates of *Eriophorum vaginatum* at different CO_2 levels. Means combine early and peak season measurements. There were no significant differences among treatments. Numbers in parentheses are standard errors.

Treatment	Measurement $\text{CO}_2 (\mu\text{l} \cdot \text{l}^{-1})$			
	170	340	510	680
<u>Respiration</u>				
340	--	-1.8 (0.9)	-1.8 (0.6)	-2.2 (1.0)
510	--	-1.3 (0.2)	-1.3 (0.3)	-0.6 (0.5)
680	--	-0.9 (0.2)	-1.2 (0.3)	0.5 (1.2)
680 + 4°C	--	-1.0 (0.2)	-1.1 (0.2)	-1.0 (0.4)
<u>Transpiration</u>				
340	1.9 (.42)	1.9 (.28)	1.8 (.35)	1.8 (.37)
510	2.1 (.35)	2.1 (.30)	2.2 (.34)	2.2 (.49)
680	1.3 (.13)	1.8 (.49)	2.6 (.81)	3.2 (.90)
680 + 4°C	1.5 (.29)	1.9 (.58)	2.0 (.60)	2.4 (.60)
<u>Conductance</u>				
340	0.57 (.20)	0.55 (.12)	0.56 (.17)	0.53 (.22)
510	0.52 (.08)	0.51 (.07)	0.54 (.08)	0.56 (.13)
680	0.39 (.05)	0.50 (.14)	0.86 (.27)	1.54 (.35)
680 + 4°C	0.35 (.06)	0.48 (.16)	0.70 (.36)	0.77 (.30)

Table 10. Respiration ($\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), transpiration ($\mu\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and water vapor conductance ($\text{cm} \cdot \text{s}^{-1}$) rates of *Ledum palustre* at different CO_2 levels. Means combine early and peak season measurements. There were no significant differences among treatments. Numbers in parentheses are standard errors.

	Measurement CO ₂ (μl · l ⁻¹)							
Treatment	170		340		510		680	
<hr/>								
<u>Respiration</u>								
340	--		-1.0	(.32)	-0.9	(.50)	-0.2	(.60)
510	--		-1.7	(.22)	-1.6	(.28)	-1.4	(.42)
680	--		-1.1	(.16)	-.08	(.20)	-0.7	(.22)
680 + 4°C	--		-0.8	(.19)	-0.6	(.02)	-0.5	(.14)
 <u>Transpiration</u>								
340	1.2	(.17)	1.9	(.84)	1.6	(.32)	2.3	(.98)
510	1.8	(.34)	1.9	(.30)	1.8	(.34)	2.1	(.39)
680	1.2	(.13)	1.3	(.18)	1.4	(.21)	1.7	(.21)
680 + 4°C	1.0	(.22)	1.0	(.20)	1.2	(.30)	1.1	(.18)
 <u>Conductance</u>								
340	0.28	(.05)	0.51	(.28)	0.38	(.11)	0.64	(.36)
510	0.46	(.10)	0.44	(.07)	0.40	(.07)	0.50	(.07)
680	0.30	(.03)	0.32	(.05)	0.36	(.06)	0.44	(.08)
680 + 4°C	0.22	(.07)	0.22	(.07)	0.28	(.09)	0.23	(.06)

Table 11. Specific leaf weights ($\text{g d}^{-1} \text{m}^2$) of *Eriophorum vaginatum* and *Ledum palustre* grown under different CO_2 regimes. Numbers in parentheses are standard deviations. Values in a column not followed by the same letter are significantly different at the .05 level.

Growth CO_2 Concentration	<i>Eriophorum</i>			<i>Ledum</i>		
340	1.16	(.105)	A	1.81	(.464)	A
510	1.28	(.060)	B	1.79	(.287)	A
680	1.11	(.124)	A	1.85	(.091)	A
680+4°C	1.10	(.056)	A	1.68	(.371)	A

needed to learn the mechanism and controls for the lower photosynthetic capacity of high CO_2 -grown plants.

Several studies have suggested that starch accumulation in the chloroplasts of plants grown at high CO_2 concentrations may decrease photosynthetic rates (Cave, *et al.*, 1981; Wulff and Strain, 1982; DeLucia, *et al.*, 1985; Sasek, *et al.*, 1985). Tissue and Oechel, 1987 found no evidence of starch accumulation in *Eriophorum*. We found no variation in SLW or leaf starch content among treatments which would suggest that excess starch had accumulated in the leaves of the plants grown at 680 $\mu\text{l/l}$ CO_2 (Table 11). In fact, the plants with the highest measured photosynthetic rates in our short-term tests also had the highest specific leaf weights (plants grown at 510 and 340 $\mu\text{l/l}$ CO_2).

Plants of *Eriophorum vaginatum* grown at 680 $\mu\text{l/l}$ CO_2 plus 4°C over ambient temperature had photosynthetic rates comparable to those of plants grown at 340 $\mu\text{l/l}$ CO_2 during the early measurement period. This suggests that a sink-mediated limitation on photosynthetic capacity could exist in plants grown at 680 $\mu\text{l/l}$ CO_2 and ambient temperature. This limitation is not expected in the elevated temperature plants, since they presumably have higher respiration rates during growth and thereby use excess photosynthate produced. Growth of *Eriophorum* has been shown to be limited primarily by nutrient availability (Shaver and Chapin, 1980; Chapin and Shaver, 1985), suggesting further nutrient limitation was a possible mechanism for the reduction in photosynthetic capacity at elevated CO_2 .

In contrast to *Eriophorum*, plants of *Ledum* grown at high CO_2 concentrations show no loss of photosynthetic capacity (Figure 18; Table 8) with the exception of the plants grown at elevated temperature which were damaged by the freeze. Plants grown at 510 $\mu\text{l/l}$ CO_2 had the highest photosynthetic rates at all measured CO_2 concentrations, a somewhat surprising result. Apparently, sink strength does not limit photosynthetic capacity in this species. Since *Ledum* is an evergreen species, it may have better developed mechanisms for storage of excess carbohydrate. The similarity in specific leaf weights among the ambient temperature plants (Table 11) indicates a lack of starch accumulation in the leaf and supports the idea that translocation rate does not limit photosynthetic potential in *Ledum*. Our results differ from those of Oberbauer, *et al.*, (1986b), which were obtained in a controlled-environment study. This contradiction emphasizes the caution which must be taken in extrapolating laboratory studies to the field.

The varying responses of these two tundra species to growth under atmospheric CO_2 enrichment complicates the question of predicting ecosystem response to changing CO_2 concentrations. Measurements made in 1985 indicate that soil and moss-mat respiration rates did not differ among treatments (Oberbauer, *et al.*, 1986b), so any increases in carbon accumulation at higher CO_2 concentrations must be due to increased CO_2 uptake by plants. During the early part of the 1985 growing season, CO_2 uptake was greatest in the chambers maintained at 510 $\mu\text{l/l}$ CO_2 and 680 $\mu\text{l/l}$ CO_2 +4°C. Thus, it appears that tussock tundra could become a greater carbon sink in the future. Additional ecosystem experiments and investigations into the physiology of additional plant species are necessary before we can fully understand the response of tussock tundra to changing CO_2 conditions.

LABORATORY STUDIES OF SHORT-TERM SPECIES RESPONSE:

Carex bigelowii Torr., *Betula nana* L., and *Ledum palustre* L.

The ability of plants to respond to elevated CO_2 is influenced by their physiology, growth patterns, and by availability of nutrients and other resources. CO_2 enrichment might be expected to enhance the growth of arctic species less at lowered nutrition, since nutrient limitation reduces the demand for the additional carbohydrate. To test this expectation, a controlled-environment experiment was carried out using a factorial design with two levels each of nutrition and atmospheric CO_2 concentration. The species used included a representative of each of the dominant growth forms found in *Eriophorum vaginatum* L. tussock tundra: *Carex bigelowii* Torr., a sedge, *Betula nana* L., a dwarf deciduous shrub, and *Ledum palustre* L., a dwarf evergreen shrub. All three species are abundant in tussock tundra throughout arctic regions in North America.

As expected, leaf weight, root weight, and total biomass of all three species were significantly increased by nutrient enrichment at both CO_2 concentrations (Table 12). An increase in nutritional level from 1/60th to 1/8th strength Hoagland's solution resulted in a doubling of biomass for *Carex* and *Betula* and approximately a 70% increase for *Ledum*. CO_2 enrichment, however, did not increase growth of leaves, roots, or the whole plant. Total plant production at high CO_2 tended to be slightly lower than that at low CO_2 for most species-nutrition level combinations. There was no significant interaction observed between nutrient level and CO_2 concentration for leaf, root, or total plant dry weights (Table 12).

Although the effect was statistically significant only for *Ledum* and with the exception of *Carex* grown at 350 μM , root:shoot ratios decreased in response to increasing nutrient concentration. In contrast, elevated atmospheric CO_2 concentration significantly increased root:shoot ratios of *Carex* and *Ledum* at both nutrition levels. Increased root:shoot ratios of *Betula* grown under elevated CO_2 were not statistically significant. The largest root:shoot ratios were consistently found in the high CO_2 -low nutrient treatments. However, only *Carex* responded significantly to the interaction of nutrients and CO_2 level in terms of root:shoot ratio. *Carex* was also the only species which showed an effect of fertilization on LSW (gm^{-2}). CO_2 enrichment increased LSW of *Betula*, but not of *Carex* or *Ledum*. *Carex* had lower LSW with increased CO_2 during growth. None of the species had a significant interaction between nutrition and CO_2 for LSW.

Species differed substantially in the photosynthetic response to nutrient addition. Higher nutrition during growth increased leaf photosynthesis of both *Carex* and *Ledum* but decreased photosynthesis of *Betula* (Table 13). Leaf photosynthesis of all three species was significantly increased by increased CO_2 concentration during measurement (Table 13). In contrast, elevated CO_2 concentration during growth had little effect on photosynthesis for most combinations of nutrient level and CO_2 concentration at measurement. *Ledum* was the only species that showed a significant interaction between nutrition level and atmospheric CO_2 concentration during growth.

The effect of nutrition level and atmospheric CO_2 concentration during growth on macronutrient concentrations in the leaves was complex. These species demonstrated a conservative response of tissue-nutrient concentration to altered nutrient regime or CO_2 concentration. In most cases, neither nutrition nor CO_2 treatment significantly affected tissue-nutrient concentrations.

Table 12. Mean biomass allocation characteristics of three Alaskan tundra species grown at two CO₂ concentrations (350 and 675 $\mu\text{l/l}$) and two nutritional levels (1/60th and 1/8th Hoagland's solution). R/S is root:shoot ratio; LSW is leaf specific weight. Significances from two-way analysis of variance ($n = 6$) for CO₂ concentration (C) and nutritional level (N) are presented below.

Growth CO ₂ $\mu\text{l/l}$	1/60 Hoagland's					1/8 Hoagland's				
	Leaf wt., g	Root wt., g	Total wt., g	Root.wt./ shoot wt.	LSW g m ⁻²	Leaf wt., g	Root wt., g	Total wt., g	Root wt./ shoot wt.	LSW g m ⁻²
<i>Carex bigelowii</i>										
350	1.23	4.74	7.34	1.72	99.3	2.85	9.63	15.04	1.78	104.1
675	0.61	4.91	6.63	3.03	81.8	2.86	11.27	17.00	1.98	104.6
<i>Betula nana</i>										
350	1.23	1.49	6.42	0.30	70.8	2.32	2.59	12.21	0.27	76.9
675	0.92	1.14	4.44	0.36	88.2	2.08	2.51	11.03	0.30	81.5
<i>Ledum palustre</i>										
350	0.53	0.65	1.66	0.65	142.3	0.87	0.91	2.81	0.49	130.2
675	0.41	0.73	1.46	1.02	153.2	0.69	1.14	2.53	0.70	150.2

	<i>Carex</i>			<i>Betula</i>			<i>Ledum</i>		
	C	N	CXN	C	N	CXN	C	N	CXN
Leaf wt.	-	***	-	-	***	-	-	***	-
Root wt.	-	***	-	-	***	-	-	***	-
Total wt.	-	***	-	-	***	-	-	***	-
Root wt./shoot wt.	**	-	*	-	-	-	***	**	-
LSW	-	*	-	*	-	-	-	-	-

NOTE: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 13. Mean leaf photosynthetic rates ($\text{lmol m}^{-2} \text{s}^{-1}$) of three Alaskan tundra species grown at two CO_2 concentrations (350 and 675 $\mu\text{l/l}$) and two nutritional levels (1/60th and 1/8th Hoagland's solution). Significances from three-way analysis of variance for CO_2 concentration during measurement (M), CO_2 concentration during growth (G) and nutritional level (N) are presented below ($n = 3$ to 6).

Growth CO ₂ μl/l	350 μl/l ⁻¹ CO ₂		675 μl/l ⁻¹ CO ₂				
	1/60 ^a	1 / 8	1 / 60	1 / 8			
<i>Carex bigelowii</i>							
350	8.14	10.80	10.87	16.48			
675	5.96	11.42	8.37	17.46			
<i>Betula nana</i>							
350	8.03	6.17	10.94	7.36			
675	8.31	3.72	8.62	4.89			
<i>Ledum palustre</i>							
350	6.04	7.05	9.50	8.85			
675	2.42	4.98	5.24	8.25			
	Growth CO ₂	Measured CO ₂	Nutrient Concn.	G X M	G X M	M X N	G X M X N
<i>Carex</i>	.	***	***	-	-	-	-
<i>Betula</i>	*	*	*	-	-	-	-
<i>Ledum</i>	***	***	**	-	*	-	-

NOTE: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

^a Strength of Hoagland's solution

In *Betula* N and P concentrations were increased at higher nutrient availability. Of the macronutrients, only Ca in *Ledum* was affected by CO₂ treatment; it was increased at elevated CO₂. Interestingly, however *Carex* Zn and Mn showed a decrease at higher nutrient levels and an increase at higher CO₂ levels. Similar patterns were seen in *Betula* and *Ledum*.

Atmospheric CO₂ enrichment has been shown to increase biomass production for most species when tested under optimal or near-optimal nutritional levels (Kramer, 1981; Kimball, 1983). Elevated atmospheric CO₂ concentration in the present study did not enhance growth of any of the three tundra species examined at either of the two levels of nutrition used. Furthermore, no significant interaction of CO₂ enrichment with nutrition level was observed. The plant characteristic most affected by CO₂ enrichment was root:shoot ratio, which increased in all the species at elevated CO₂. We had hypothesized that CO₂ enrichment would increase biomass production in these species and the effect would increase with increased nutritional level.

Contrary to previous controlled-environment studies on crop species (Sionit, *et al.*, 1981; Sionit, 1983), the results of the present study confirm the observations of Billings, *et al.*, (1984) on tundra microcosms. These investigators discovered a positive nutrient effect on biomass production in microcosms, but did not find CO₂ enrichment or CO₂-nutrient interaction effects. They suggested that species interacting in a microcosm might behave differently than single species acting alone.

We measured biomass accumulation in different organs of individual plants grown in pots. A better indication of growth would be, of course, the total cumulative plant biomass per unit of ground surface area which is not easily approached in pot studies in growth chambers. The few existing studies of single species grown under CO₂ enrichment with nutrient limitation indicate that the relative importance of CO₂ enrichment and nutritional level is species dependent. Wheat increased production in response to CO₂ enrichment at any given nutritional level (Sionit, *et al.*, 1981), but the CO₂ effect decreased with decreasing nutritional level, indicating an interaction between CO₂ concentration and nutritional level. However, for soybean, there was no interaction between CO₂ enrichment and nutritional level, but the effect of CO₂ enrichment was large enough to overcome the effect of lowered nutrition (Sionit, 1983). Tissue-nutrient concentrations were not reported for soybean and wheat in these studies, so it is difficult to directly assess the role of nutrients in the observed interactions.

It has been postulated that growth of some tundra plants may be sink-limited for carbon and this may be a reason for repeatedly observed high levels of total nonstructural carbohydrates (TNC) (Billings and Mooney, 1968; Warren Wilson, 1966; Chapin and Shaver, 1985; Tissue and Oechel, 1987) in these plants. We did not measure TNC content of the plants in our experiment. However, the absence of large growth responses to elevated atmospheric CO₂ level may have been due to the plants' inability to enhance the use of carbohydrates for growth. The observed increase in root:shoot ratio in response to elevated CO₂ was an indication of a shift in carbon allocation rather than an increase in total biomass production.

Photosynthesis can provide important insights into the basis for observed growth responses to CO₂ enrichment. In the present study, photosynthetic rates of all three species grown and measured at 675 μ l/l CO₂ were slightly lower than those grown and measured at 350 μ l/l. This observation agreed with measurements on plant biomass production. Photosynthetic rates of low CO₂ grown plants increased when measured at 675 μ l/l CO₂. Thus, plants grown at elevated CO₂ levels had initially

higher rates of photosynthesis, but that the rates decreased with time. Similar reductions in photosynthesis have been reported for other species grown under elevated CO_2 for long periods, many of which had increased total biomass (Wulff and Strain, 1982; Peet, 1984). These reductions can be quite rapid in the case of *Gossypium hirsutum*, an agricultural species, (DeLucia, *et al.*, 1985) and *Eriophorum vaginatum*, an important tundra species, (Tissue and Oechel, 1987 and above). For *Eriophorum* growing in the field, CO_2 enrichment produced a short-term elevated photosynthetic rate for high CO_2 grown leaves that was followed by adjustment to rates similar to plants grown at ambient CO_2 (Tissue and Oechel, 1987). The adjustment was rapid enough that no biomass effects could be detected.

In this study, tissue-nutrient contents were not particularly significant in understanding the growth and photosynthetic responses to fertilization and CO_2 enrichment. For *Carex*, most macro- and micronutrients were unchanged or increased with CO_2 enrichment but decreased with fertilization (Table 14 and 15). For *Betula*, however, CO_2 enrichment decreased macronutrient concentrations in tissue while fertilization tended to increase N, P, and K content. No strong patterns in macro- or micronutrient concentrations were apparent for *Ledum*. In contrast, Shaver and Chapin (1980) reported that fertilization with N, P, and K at Eagle Creek, Alaska increased tissue-nutrient concentrations of *Carex* and *Ledum* and decreased those of *Betula*. Overall, concentrations of N, P, K, Ca, and Mg in the present study were similar to those found by Shaver and Chapin (1980) at Eagle Creek. Despite the relative differences in responses of tissue concentrations in different species in our study, their growth responses were similar. Shaver and Chapin (1980) found that large differences in tissue-nutrient contents occurred with no differences in growth rate.

Contrary to agricultural plants, tundra species which are adapted to grow under low nutrient levels may not show large growth enhancement in response to fertilization. Furthermore, the nutrient concentration which is limiting to growth of tundra plants may or may not increase with increasing growth rate (Warren Wilson, 1966). Shaver and Chapin (1980) did not find a clear relationship between changes in tissue-nutrient contents and increased growth of tundra plants with fertilization in Eagle Creek, Alaska. There was no single factor limiting tundra growth but rather a combination of additive and interactive effects of different levels of minerals and carbohydrates (Chapin and Shaver, 1985). The typically high carbohydrate contents found in tundra species have been suggested by some workers to indicate carbohydrate surplus in these plants (Billings and Mooney, 1968; Shaver and Billings, 1976). These species have intrinsically low nutrient uptake capabilities and growth rates, and therefore may be incapable of strong responses to fertilization, either with CO_2 or nutrients.

IN SITU SOIL RESPIRATION AT ELEVATED ATMOSPHERIC CARBON DIOXIDE CONCENTRATIONS

Increased CO_2 availability could increase soil respiration rates through greater carbohydrate contents in litter and the soil rhizosphere. Enhanced photosynthesis from atmospheric CO_2 enrichment over the long term would increase the carbohydrate content of litter and thus increase soil C/N ratios. Since tundra soils are already nitrogen limited (Ulrich and Gersper, 1978), soil respiration should decrease.

Long-term exposure to elevated atmospheric CO_2 concentration did not significantly affect soil CO_2 efflux on a surface area basis (Figure 19). Overall, the

Table 14. Mean tissue macronutrient concentrations (% dry weight) for three Alaskan tundra species grown at two CO₂ concentrations (350 and 675 $\mu\text{l/l}$) and two nutritional levels (1/60th and 1/8th Hoagland's solution). Significances from two-way analysis of variance for CO₂ concentration (C) and nutritional level (N) are presented below (n = 3).

Growth CO ₂ μl/l	1/60 Hoagland's					1/8 Hoagland's				
	N	P	K	Ca	Mg	N	P	K	Ca	Mg
<i>Carex bigelowii</i>										
350	0.941	0.143	0.373	0.824	0.600	0.907	0.133	1.847	1.245	0.581
675	1.307	0.189	1.553	1.264	0.644	0.924	0.157	1.313	0.932	0.414
<i>Betula nana</i>										
350	1.463	0.233	1.180	1.210	0.609	1.687	0.291	1.407	1.350	0.545
675	1.190	0.198	0.905	1.100	0.480	1.593	0.261	1.303	0.941	0.361
<i>Ledum palustre</i>										
350	1.056	0.119	1.077	0.804	0.262	1.237	0.160	1.106	0.927	0.184
675	0.905	0.138	0.948	1.277	0.225	1.178	0.176	0.922	0.992	0.237
	<i>Carex</i>			<i>Betula</i>			<i>Ledum</i>			
	C	N	CXN	C	N	CXN	C	N	CXN	
N	-	-	-	-	*	-	-	*	-	
P	-	-	-	-	-	-	-	*	-	
K	-	-	*	-	*	-	-	-	-	
Ca	-	-	-	-	-	-	**	-	*	
Mg	-	-	-	-	-	-	-	-	-	

NOTE: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$, C is CO₂ effect, N is nutrient effect, and C X N is interaction effect.

Table 15. Mean tissue micronutrient concentrations (ppm) of three Alaskan tundra species grown at two CO₂ concentrations (350 and 675 μ l/l) and two nutritional levels (1/60th and 1/8th Hoagland's solution). Significance from two-way analysis of variance for CO₂ concentration (C) and nutritional level (N) are presented below (n = 3).

Growth CO ₂ μl/l	1/60 Hoagland's					1/8 Hoagland's				
	Zn	Cu	Fe	Mn	B	Zn	Cu	Fe	Mn	B
<i>Carex bigelowii</i>										
350	34.8	7.2	541.8	583.3	57.7	11.4	7.2	141.2	251.3	32.3
675	84.2	17.4	201.5	1043.3	112.0	37.5	8.5	114.2	555.7	53.2
<i>Betula nana</i>										
350	23.9	7.7	185.7	516.0	192.3	11.3	4.8	358.7	323.7	150.7
675	34.4	6.3	193.0	569.0	152.7	13.7	3.1	151.2	260.3	142.1
<i>Ledum palustre</i>										
350	0.0	4.3	747.0	332.7	76.9	10.2	6.2	130.3	123.2	56.7
675	7.9	3.9	122.7	206.0	96.0	1.9	4.5	175.3	335.0	65.4
<hr/>										
	<i>Carex</i>			<i>Betula</i>			<i>Ledum</i>			
	C	N	CXN	C	N	CXN	C	N	CXN	
Zn	**	**	-	-	-	-	-	-	**	
Cu	-	-	-	-	-	-	-	-	-	
Fe	-	-	-	-	-	-	-	-	-	
Mn	*	*	-	-	*	-	-	-	*	
B	-	-	-	-	-	-	-	-	-	

NOTE: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

largest CO₂ efflux was found for tundra developed at 4°C above ambient and 680 µl/l CO₂, but it was not statistically different from the other treatments when all treatments were measured at the same temperature. Respiration expressed on soil dry weight basis followed the same pattern as respiration per unit area but the difference between the elevated temperature treatment and the other treatments was larger (Figure 19).

Elevated CO₂ had a similar small effect on respiration in a controlled-environment study of tundra microcosms (Billings, *et al.*, 1984). Because total system flux was not affected by CO₂ enrichment in the study, such a result is expected. Field studies of ecosystem CO₂ flux at Toolik Lake indicate a decreasing effect of CO₂ enrichment with time (see above), so the effect on soil C/N ratios may have been small.

Alternatively, soil C/N ratios may have changed but have not had the predicted effect. Fertilization of northern soils by carbohydrate and nitrogen has effected soil respiration counter to the expected in some cases. Carbohydrate addition has often increased, rather than decreased, respiration (Baath, *et al.*, 1978; Luken and Billings, 1985), and nitrogen addition has increased respiration in some (Baath, *et al.*, 1978; Billings, *et al.*, 1984; Luken and Billings, 1985), but not all studies (Stuart and Miller, 1982). CO₂ efflux from arctic soils is also controlled by the interaction of soil moisture (Billings, *et al.*, 1982; Cowling and MacLean, 1981), and temperature (Billings, *et al.*, 1982; Cowling and MacLean, 1981; Luken and Billings, 1985), which may have masked the effect of CO₂-induced changes in litter quality within the variability observed in this study.

CO₂ efflux showed a slight, but nonsignificant decrease with increased CO₂ concentration during measurement (Figure 19). Although the metabolic activity of soil microbes *in vitro* has been shown to be depressed at high CO₂ concentrations (50,000 to 900,000 µl/l (Strotsky and Coos, 1964)), the small changes in aboveground CO₂ in our study probably did not affect CO₂ concentrations in the soil atmosphere, which for tundra are on the order of 20,000 µl/l at 5 cm (Stuart and Miller, 1982).

In conclusion, the hypothesis that long-term ecosystem exposure to enriched atmospheric CO₂ decreases soil respiration is not supported. Whether this result is because the effect of CO₂ enrichment on C/N ratios is small and sufficient time had not elapsed, increased carbohydrate availability offset the otherwise depressing effects of elevated C/N ratios, or because changes in C/N ratios have otherwise not caused the predicted reduction in respiration remains to be determined.

PREDICTED RESPONSE OF ARCTIC ECOSYSTEMS TO ELEVATED CO₂

A thorough review of carbon storage in the arctic was undertaken in a workshop in 1980 (Miller, 1981). This workshop established the then current consensus of the amounts and rates of carbon storage in arctic, boreal forest, and peatland ecosystems (Table 1 from Miller, 1981). Based primarily on paleological information and records, the workshop predicted responses of northern ecosystems to elevated temperature. Subsequent to this workshop, the Northern Ecosystems Carbon Simulator (NECS) (Miller, *et al.*, 1983) was formulated and used to predict changes in carbon storage resulting from increased CO₂ and CO₂-induced changes in climate (Miller, *et al.*, 1983). This model also predicted changes in vegetation boundaries resulting from a global temperature rise.

Figure 19. Mean soil respiration per unit area (above) and per unit area (above) and per unit soil dry weight (below) for untreated tundra and for samples on chambers treated for three growing seasons at 340, 510, 680 $\mu l/l$ and at 680 $\mu l/l$ at 4°C above ambient temperature. N = 6 to 9. Measurements were made at ambient soil temperature between July 17, 1983 and August 1, 1985. Air temperatures were held at $16.2 \pm 1.3^\circ C$. Typical standard errors are shown.

These reports and simulations were accomplished in the absence of experiments or observations on the direct effects of elevated atmospheric CO_2 on arctic ecosystems. While the observations and predictions appear correct in many respects, new information has shown them to be in error in several substantive aspects. This section brings these reports up-to-date with recent research findings and explores extrapolation of recent results to the arctic region in general.

As indicated above, research on the effects of elevated CO_2 and temperature has been conducted in both the tussock tundra and in wet coastal tundra. These two types constitute the most carbon-rich systems in the arctic in terms of area and carbon density. While both are important current stores of carbon, it appears that their current carbon dynamics may be somewhat different.

WET COASTAL TUNDRA

Wet coastal tundra is accumulating carbon under current climatic and atmospheric conditions (Miller, 1981; Billings, *et al.*, 1982; Schell, pers. comm.). Rates of carbon accumulation may be about $40\text{--}120 \text{ g C m}^{-2} \text{ yr}^{-1}$ resulting in a current store of about 20 kg C m^{-2} in peat in the upper 20 cm (Billings, *et al.*, 1984). However, these rates of accumulation are not necessarily seen in recent controlled-environment studies. Phytotron experiments using microcosms of natural ecosystems indicate carbon accumulation of $78\text{--}340 \text{ g CO}_2 \text{ m}^{-2}$ per season depending on site, temperature, and water level. A doubling of CO_2 ($400\text{--}800 \mu\text{l/l}$) increased seasonal CO_2 uptake by $175 \text{ g CO}_2 \text{ m}^{-2}$ per season (Billings, *et al.*, 1984). Billings, *et al.*, (1982) feel that an increase in temperature will cause a decrease in the rate of carbon accumulation in the wet coastal tundra. Despite this effect, the authors conclude that the wet coastal tundra is not presently limited by CO_2 .

Phytotron measurements of microcosms under current ambient temperature and CO_2 conditions and a water table of -5 cm resulted in a measured seasonal loss of $49 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Billings, *et al.*, 1982). A lowered water table could result from warmer temperatures increasing the depth of the summer active layer or from increased evapotranspiration resulting from the higher summer temperatures. The depth to the water table may have a major impact on the respiration rate of the system and on the net CO_2 balance. Differences due to temperature and water table were more pronounced than those due to site. Doubled CO_2 concentration to $800 \mu\text{l/l}$ caused an increase in net CO_2 uptake from 48% with the water table at the surface to 35% with the water table at -10 cm . However, this increase was not sufficient to totally offset the increased respiration with the water table lowered from the surface to -10 cm . Increased respiration was thought to be due to higher rates of aerobic respiration by roots, rhizomes, and microorganisms in the soil and decomposing organic matter (Billings, *et al.*, 1983).

The climatic changes associated with elevated CO_2 are predicted to result in a loss of ecosystem integrity now provided by peat and permafrost in the wet coastal tundra. Billings, *et al.*, (1983) feel that increased production at doubled CO_2 will not offset increased respiration and decomposition due to increased temperatures and decreased water table. Any loss of ground ice resulting from decreased thermal insulation would result in thermokarst erosion and increased rates of decomposition. Increased decomposition would increase nutrient availability and system productivity (Billings, *et al.*, 1982). Combined effects could convert the wet coastal tundra from a CO_2 sink to a CO_2 source, thereby creating a positive feedback on the rise of global atmospheric CO_2 .

The net effect of a global rise in CO_2 is for increased carbon sequestering and productivity (Billings *et al.*, 1984). A doubling in atmospheric CO_2 raises net ecosystem carbon sequestering over the course of one simulated growing season. However, experiments longer than one growing season were not run, and it may be that homeostatic mechanisms will decrease the CO_2 effect in the second and third years as was the case in the tussock tundra described above in this report. It also appears that other factors possibly associated with a CO_2 rise will have more effect than the direct effects of CO_2 . Due to complex interactive changes involving the physical environment and ecosystem processes, the direction and magnitude of change mediated by global increases in CO_2 and temperature are difficult to predict.

No studies of longer than one growing season or field studies on the direct effects of elevated CO_2 on carbon flux and productivity have been undertaken on wet coastal tundra. The large carbon stores in wet coastal tundra, the presumed large rate of current carbon accumulation in these ecosystems, and the potential for large shifts in magnitude of carbon flux indicates that medium-term field experiments of several years should be conducted. Field studies should document current rates of carbon accumulation and the interacting effects of CO_2 , temperature, nutrients, and depth to the water table on these factors.

MESIC, TUSSOCK TUNDRA

Tussock tundra in the region of Toolik Lake, Alaska may not be currently accumulating carbon. Our work described above with environmentally-controlled greenhouses of intact tundra indicates a net loss of carbon under ambient CO_2 and temperature conditions. This work is supported by that of Schell (pers. comm.) who, using carbon-14 dating of the peat profile has found no peat younger than 2000 BP. This means either that the peat is in equilibrium near the surface, or that it is in recession. However, carbon-14 dating from material within the active zone may be unreliable because of the yearly incorporation of new carbon from current roots, as well as Cryoturbation (Billings and Peterson, 1980).

Although data comes from a single site, we can generalize from these studies at Toolik Lake to the larger arctic region. The Toolik Lake area is representative in terms of soils and vegetation of tussock tundra throughout the low arctic. Species in the tussock tundra have circumpolar distributions; soils are similar throughout much of its range and the dominating permafrost process influences much of the energy and carbon budget across the North Slope.

While it is possible to generalize our results to other similar permafrost-dominated regions, the importance of carbon stores and fluxes to understanding the current and future global carbon balance indicates the need for additional confirmatory work. Additional studies are needed to document historic and current rates of carbon accumulation in wet and mesic tundra areas throughout the circumpolar arctic.

ORIGINAL HYPOTHESES OF THE POTENTIAL EFFECT OF CARBON DIOXIDE-INDUCED CLIMATIC CHANGE ON THE CARBON BALANCE OF NORTHERN ECOSYSTEMS

The San Diego workshop on carbon balance in northern ecosystems and the potential effect of carbon dioxide-induced climatic change produced six global-level hypotheses and several corollary hypotheses that were suggested as the basis for a cooperative, multi-national research program. The focus of these hypotheses was on the indirect effects of climate change, rather than the direct effects of CO_2 , and the suggested

program was never initiated. Nevertheless, it may be worthwhile revisiting these hypotheses in light of current research and understanding. The direct effects of elevated CO_2 as well as the effects of CO_2 -induced climate change will be considered in this evaluation.

Hypothesis 1:

The net carbon accumulation rate of northern ecosystems will increase by 2.5-3.0 times as temperature increases 4°C during the period 1980 to 2030. This increase will occur by a change in the rate of carbon accumulation in the arctic (0.08 BmT/yr - 0.83 BmT/yr) in 2030 and by no change in the taiga from the current accumulation rate in 1980 of 0.41 BmT/yr . The annual rate of increase in the accumulation rate will be 0.014 - 0.018 BmT/yr in the arctic, assuming a 0.08°C/yr rise in temperature and a 100-year turnover rate. The annual rate of change in the accumulation rate in the taiga will be -0.004 - $+0.002 \text{ BmT/yr}$.

In retrospect, it was a poor choice to base predictions on percentage or factor increases or decreases in accumulation rates. These ratios have little meaning when one is dealing with possible changes in sign or division by numbers near zero. The hypothesis predicts changes by the year 2030. Therefore, to adequately attempt to falsify the hypothesis, we will have to wait until 2030 and then evaluate whether the hypothesis was correct or not. Nevertheless, short- and medium-term experiments in the wet coastal tundra and the moist tussock tundra, respectively relate to this hypothesis. Billings, *et al.*, (1982) found that within one growing season, an increase in temperature from 4 to 8°C caused a decrease in carbon accumulation in microcosms of wet coastal tundra grown at $400 \mu\text{l/l CO}_2$. Our studies indicate that there is an initial decrease in carbon accumulation in the $680 \mu\text{l/l CO}_2 + 4^\circ\text{C}$ treatment compared to $680 \mu\text{l/l CO}_2$ at ambient temperature in tussock tundra. By the third year, uptake in the $680 \mu\text{l/l CO}_2$ was positive, and 4.9 and $3.2 \text{ g m}^{-2} \text{ d}^{-1}$ were higher in the first and third years of treatment compared to the ambient treatment which showed CO_2 evolution in all years of measurement.

If we assume a universal increase of $3.2 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, a 90 d active season, and an area of tussock tundra of $0.90 \cdot 10^6 \text{ km}^2$ (Miller, 1981), then the effect of a doubling of CO_2 to $680 \mu\text{l/l}$, plus a 4°C temperature rise on CO_2 sequestering by the circumpolar tussock tundra is 0.07 BmT C , or an increase to 1.9 fold the current ambient rate estimated in the San Diego workshop for this region. If all arctic regions showed a similar increase, and if we accept the San Diego workshop estimate for current carbon accumulation in the arctic, then the net effect of a doubling CO_2 concentration and a summer temperature rise of 4° , would be to increase carbon sequestering in the arctic by 0.41 BmT C to 0.87 BmT C . While perhaps fortuitous, this is about midrange of that predicted in the above hypothesis.

The above analysis is based on results from a three-year study. Feedback and homeostatic mechanisms, including changes in nutrient status and species compositional changes which come into play over periods of years to decades, may influence the outcome of changes in concentration and climate. While the best data now available are in agreement in a general way with the above hypothesis, longer-term studies are necessary to confirm the medium-term trend observed.

Hypothesis 2:

The standing crop of live and dead carbon in northern ecosystems will increase by 10%, or 23 BmT above the current 232 BmT. This increase will occur largely by an expansion of the area extent of tussock tundra and shrub tundra onto semidesert sites and by a northward movement of the taiga. Within and south of the taiga the standing crop of carbon will remain constant although carbon in the forest floor and mineral soil will decrease while carbon in biomass increases.

There is no new information on the movement of vegetation boundaries in response to climatic effects of a change in global CO₂ beyond the analysis that led to this hypothesis and the simulation by Miller, *et al.*, (1983). Billings, *et al.*, (1984) found a statistically insignificant increase in plant area and biomass with increased CO₂ for the wet coastal tundra. To date there is no clearly demonstrable increase in standing crop with a doubling of CO₂. However, there is an increase in growth which implies an increase in standing crop with medium-term elevated CO₂ and temperature.

Hypothesis 3:

Both the estimates of net carbon flux and standing crop of carbon will be underestimated by a factor of two or more if the normal climatic warming and cooling cycles which have occurred in the past produce a natural warming in the mid-21st century as predicted, giving a synergistic effect of normal warming and "greenhouse effect" warming.

There is little new information relevant to this hypothesis. This still appears a viable possibility.

Hypothesis 4:

As temperatures rise, the increase in the production of organic carbon will be limited by available nutrients and photoperiodic control of senescence. Plant carbohydrate should rise, increasing decomposition without subsequent increase in nutrient availability. Decomposition will be limited by season length and temperature. Decomposition should increase about two times faster than production because of the different controls on the length of the respective active seasons.

The first portion of this hypothesis is supported to date. Nutrient availability strongly limits production in the wet (Billings, *et al.*, 1984; Ulrich and Gersper, 1978) and tussock tundra (Shaver and Chapin, 1980; Shaver, *et al.*, 1986) and net ecosystem CO₂ flux (Billings, *et al.*, 1984). This nutrient limitation is thought to explain the lack of response to elevated CO₂ by most tussock tundra species. The one species that showed increased growth at elevated CO₂ in the first year, *Carex bigelowii* (Oechel, *et al.*, 1984) is thought to be less nutrient limited than many other tussock tundra species (Miller, *et al.*, 1984; Oechel and Blake Jacobson, in prep.). However, increased nutrient availability did not show a statistically significant effect on the ability of wet coastal tundra to respond to elevated CO₂ (Billings, *et al.*, 1984). The lack of significance may have been due to high variability since there was a marked increase in carbon sequestering under elevated CO₂ with nutrient addition. We feel

that the ability of tussock tundra to respond to elevated CO_2 is limited by available nutrients. Recent information (Grulke, *et al.*, unpubl. data), indicates little effect of elevated CO_2 on soil solution nutrient levels.

There is some indication from non-tundra areas that even in nutrient-limited situations, some growth enhancement may occur at elevated CO_2 (Norby, *et al.*, 1986a). Although uptake of most nutrients including phosphorus was increased at elevated CO_2 , enhanced growth of white oak at elevated CO_2 in nutrient deficient soils resulted from higher nitrogen use efficiency not from increased nitrogen uptake. While larger buds were set at the end of the growing season, this dilution resulted in less available (translocatable) nitrogen for growth in the second growing season. It is unclear whether the increased growth seen in the first year could be maintained in the second and subsequent years. The greater response of white oak growth in the first growing season to elevated CO_2 compared to tundra species probably reflects the relative nutrient limitation of each. Tussock tundra species appear to be closer to their minimum nutrient concentration. The extra carbon availability at elevated CO_2 affords little opportunity for increased growth through increased nutrient use efficiency or nutrient dilution.

The second portion of this hypothesis appears less certainly true. There is little demonstrable effect of elevated CO_2 on tissue carbohydrate levels (Tissue and Oechel, 1987, unpubl. data), and it appears that the homeostatic adjustment mechanisms operate to very quickly limit photosynthetic rates before substantial build up of storage carbohydrate can occur.

Decomposition, as measured by soil CO_2 efflux, increases with temperature and would be expected to be affected by changes in season length. While increases in temperature increase decomposition rate, we found that in the first year of the elevated temperature and CO_2 treatment, decomposition increased more than primary production, and there was a net decrease in carbon accumulation. Billings, *et al.*, (1982) obtained similar results for microcosms of wet tundra growing for one season under controlled conditions. By the third year, increases in photosynthetic gain at elevated temperature surpass any increases in decomposition, so that the net effect of elevated temperature at elevated CO_2 is increased carbon sequestering. Results from the 1987 field season indicate that at elevated CO_2 , the length of period of positive carbon gain due to photosynthesis was approximately 10 d greater than at ambient CO_2 levels. The net effect will depend to a large extent on the combined effects of temperature and CO_2 on phenology, especially on end of season senescence.

Hypothesis 5:

The effect of carbon dioxide-induced climatic change on animal populations in northern ecosystems will be through disruption of the present synchrony of environmental and biological processes rather than through changes in the quantitative aspects of heat exchange or food availability. The disruption of animal populations will have little effect on carbon accumulation rates, but will have potentially large effects on the activities of persons engaged in hunting and fishing for a livelihood.

There is little new information in this area. The hypothesis is still viable with the realization that altered CO_2 and climate can change food quality and feeding rates (Lincoln, *et al.*, 1984). Results to date indicate little change in nutrient or

carbohydrate content of arctic plant tissue with elevated CO₂ or temperature treatment. Changes in other chemical characteristics which could effect feeding rate, amount, and efficiency have not been evaluated. No direct experiments with animals have been initiated.

Hypothesis 6:

The change in the carbon balance of northern ecosystems with carbon dioxide-induced climatic change is essentially unpredictable with the complexity of interacting processes and the present level of uncertainty regarding these processes.

Billings, *et al.*, (1982, 1983, 1984) and we (this report; Tissue and Oechel, 1987; Oechel and Strain, 1985) have shown specific effects of elevated CO₂ and changes in temperature and nutrient availability on important ecosystem processes including net CO₂ flux, photosynthetic rates and population dynamics. While it may not be possible to predict with confidence the actual CO₂ flux for any given date in the future, it should be possible to predict the likely effect of well-defined conditions or scenarios. Given uncertainties in global-climate models, such scenario for casting may be the most efficient method of structuring future research forecasts. There is much more uncertainty in predicting climate and vegetation changes and subsequent effects on carbon balance than there is in predicting changes in net carbon balance given future possible changes in such factors as soil and air temperatures, nutrient availability, and moisture availability. For specified likely scenarios, reasonable predictions on the sign and magnitude of the effects on ecosystem carbon flux should be possible. Use of simulation models such as ARTUS-CO₂, will likely be an important tool in this endeavor.

CONCLUSIONS

Environmental control accomplished by the greenhouse system developed in this project is very good. The ability to control temperature and CO₂ concentration and to maintain appropriate moisture status while measuring whole ecosystem diurnal, daily, and seasonal CO₂ flux was demonstrated. Ambient temperatures were accurately tracked, with control temperatures on average being within -1.0-+0.9°C of the set points. CO₂ control matched that accomplished in modern phytotrons, averaging within 18 µl/l at the set, 680 µl/l CO₂, and 9 µl/l at the set 340 µl/l CO₂ concentration.

A step increase in atmospheric CO₂ of 50 or 100% resulted in a significant initial increase in net CO₂ uptake by the ecosystem of 1.8 g CO₂ m⁻² y⁻¹ at 510 µl/l CO₂ and 6-10 g CO₂ m⁻² y⁻¹ at 680 µl/l. However, these effects may be short-term responses. A high degree of homeostasis exists such that within three years, there is complete adjustment in net ecosystem flux to a doubling in atmospheric CO₂. The 50% increase in atmospheric CO₂ concentration shows lesser adjustment within this period. Presumably, the lower stimulation of CO₂ uptake at 510 µl/l CO₂ results in slower or less complete homeostatic responses, or that less growth was stimulated and other limiting physical factors were not fully realized.

For some species such as the local dominant, *Eriophorum vaginatum*, photosynthetic rate rapidly adjusts to elevated CO₂. Homeostatic adjustment yields photosynthetic rates which are similar at growth CO₂ concentrations of 340, 510, and 680 µl/l CO₂. Reasons for this homeostasis may reflect end-product inhibition within the plant and general resource limitation in the environment. Other species show some enhancement of photosynthesis after three years. The reasons for these different response patterns are not understood and warrant further consideration.

There is no change in plant respiration or in ecosystem respiration after up to three years of treatment at elevated CO₂. However, ecosystem respiration rates may change as species composition changes or as biomass or nutrient status changes. Prolonged exposure to elevated CO₂ may result in plants with increased C/N ratios and concomitant decreases in soil decomposition.

There are species specific differences in growth and carbon allocation following exposure to elevated CO₂. These differences suggest that secondary effects on species composition, sexual and asexual reproduction, and biomass allocation may eventually affect parameters relevant to ecosystem functioning and structure. A lack of response in CO₂ flux in the moderate term of three years does not mean that there may not be effects in the longer term as species composition and vegetative structure change.

Contrary to previous expectations, this study found no evidence for carbon sequestering in the tussock tundra examined under current environmental conditions. This agrees with recent isotopic analysis which indicates little peat in the mesic tussock tundra of less than 2,000 years age, and therefore no current accumulation (Schell, pers. comm.). Original estimates of peat accumulation in mesic tussock tundra may have been in error (Miller, 1981). Areas of rapid peat accumulation may be more evident in wet coastal tundra and bogs.

The limitations on response of tussock tundra to elevated CO₂ is interesting. However, the expectation is that other ecosystems which are less limited by resource

other than CO_2 , may be more responsive to increases in atmospheric CO_2 . Additional research is required to learn which ecosystems will respond to elevated atmospheric CO_2 , how much, and in what respect. Further research will be required to determine the underlying principles so that accurate prediction of responses is possible. Manipulation studies in the arctic can be of help to uncover the interactions of temperature, nutrient availability, and growth form growth response to elevated CO_2 .

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