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Response of Tundra Ecosystems to Elevated Atmospheric Carbon Dioxide

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ABSTRACT

Our past research shows that arctic tussock tundra responds to elevated atmospheric CO_2 with marked increases in net ecosystem carbon flux and photosynthetic rates. However, at ambient temperatures and nutrient availabilities, homeostatic adjustments result in net ecosystem flux rates dropping to those found at contemporary CO_2 levels within three years. Evidence for ecosystem-level acclimation in the first season of elevated CO_2 exposure was found in 1987. Photosynthetic rates of *Eriophorum vaginatum*, the dominant species, adjusts to elevated CO_2 within three weeks.

Past research also indicates other changes potentially important to ecosystem structure and function. Elevated CO_2 treatment apparently delays senescence and increases the period of positive photosynthetic activity. Recent results from the 1987 field season verify the results obtained in the 1983-1986 field seasons: elevated CO_2 resulted in increased ecosystem-level flux rates. Regressions fitted to the seasonal flux rates indicate an apparent 10 d extension of positive CO_2 uptake reflecting a delay of the onset of plant dormancy. This delay in senescence could increase the frost sensitivity of the system.

Changes in tillering rate, bud size, and proportion of sexual:vegetative buds, leaf survival rate, number of growing points produced per growing point, and number of flowers reaching fruition were detected in response to CO_2. By changing leaf area, canopy structure, and composition, these effects could influence ecosystem function despite there being homeostatic adjustment in photosynthesis to elevated CO_2. The interaction of elevated temperature and increased nutrient availability with elevated CO_2 on ecosystem structure and function deserves further study.

In the arctic, an 11°C mean annual temperature rise and a 3-4° summer air temperature rise have been predicted for a doubling of atmospheric CO_2. The resulting translation to soil heating may be a critical factor in the synergy of the effects of global warming and elevated atmospheric CO_2 on the functioning of tundra ecosystems. Our previous work indicates prolonged enhancement of net ecosystem CO_2 uptake with elevated air temperature and elevated CO_2. This aspect of the study was preliminary, and it is not possible to separate the effects of warming alone from the combined effects of warming and elevated CO_2. The past experiments were not designed to determine to what extent the observed effect was due to increased nutrient availability following soil warming.

A test of the "greenhouse effect" using the interactive effects of carbon dioxide enrichment and increased soil temperature and, later, nutrient addition, is proposed. The whole ecosystem, closed-chamber design used previously is ideal to determine a change in ecosystem carbon balance due to soil heating. In ambient carbon dioxide chambers, we have found a net seasonal loss of carbon (ecosystem respiration > photosynthesis). With a doubling of chamber atmospheric CO_2, we have shown a significantly greater ecosystem flux rate relative to controls resulting in a net ecosystem sequestering of carbon. From three years of CO_2 enrichment, we have found that the initial increase in ecosystem flux is lost through time. The research proposed here will address the effects of increases in soil temperature, elevated CO_2, their interaction, and apparent ecosystem-level homeostatic adjustment. If ecosystem-level adjustment does occur during the first two years of treatment, we will further attempt to stimulate increased ecosystem flux 1) in the elevated CO_2 treatment with nutrients; 2) in the increased soil-temperature treatment with elevated CO_2; and 3) in the

elevated CO_2 and soil-temperature treatment with nutrients. These experiments will be among the first CO_2 experiments to test the response of ecosystem-level flux to both single and multiple physical factors in the field. A two-way factorial experiment will be used to test the interactions between elevated carbon dioxide and soil temperature.

By heating soil directly, we can speed up the translation of elevated air temperature to elevated soil temperature, and thereby mimic a major aspect of the "greenhouse effect." Increased soil temperatures and altered nutrient availabilities are expected to follow a CO_2 rise. Nutrient limitation is thought to be a major factor explaining the lack of long-term response of tussock tundra to elevated CO_2. Research proposed will explore whether soil heating or nutrient addition increases the response of tussock tundra to elevated CO_2. If soil heating does result in an interactive effect with CO_2, the contribution to this effect of increased nutrient availability will be evaluated.

Simultaneous experiments of elevated soil temperature in the boreal forest near Fairbanks as part of the Taiga Long-Term Ecological Research (LTER) program of NSF will allow direct comparison of the response of two biomes to elevated soil temperature throughout the duration of the proposed study.

The initial phases of this research indicated gross differences in ecosystem flux with carbon dioxide enrichment and with the resolution available, showed step-function responses. We have a quality, null-balance photosynthetic system for ecosystem-level studies. In addition to the experiments outlined above, we can test general ecosystem theory with ecosystem-level experiments, and obtain ecosystem-level response curves to carbon dioxide, temperature, and light. The time-response resolution is much better than that initially available.

Major end points proposed for this research include the effects of elevated CO_2 and the interaction of elevated atmospheric CO_2 with elevated soil temperature and increased nutrient availability on:

1) Net ecosystem CO_2 flux;
2) Net photosynthetic rates;
3) Patterns and resource controls on homeostatic adjustment in the above processes to elevated CO_2;
4) Plant-nutrient status, litter quality, and forage quality;
5) Soil-nutrient status;
6) Plant-growth pattern and shoot demography.

This research is designed to complete a Phase I contribution to the University Consortium on Carbon Dioxide Research (present member institutions are San Diego State, Harvard, and Duke Universities). The object is to contribute to a diverse data base which will help structure the processes and patterns included in mechanistic and phenomenological models developed by Reynolds *et al.* and to identify areas requiring additional research. The information obtained and not used in model development will provide initial validation of model performance.

This information will also be incorporated in and used to advance existing models of the response of arctic ecosystems (ARTUS-CO_2) and plant growth to elevated atmospheric CO_2. Existing plant population models will be used predict new steady state assemblages from observed changes in shoot demography.

1. INTRODUCTION

1.1 BACKGROUND

Far northern ecosystems are an important component of the global carbon budget. In these ecosystems, a vast quantity of organic carbon is stored as peat. Conclusions of a workshop held in San Diego in 1980 were that tundra and taiga contain over 200 billion metric tons of organic carbon in live biomass and peat, representing 10-27% of the total terrestrial carbon in the biosphere (Miller, 1981). Despite low rates of production, tundra alone has accumulated 59 BMT of carbon, equal to nearly 12% of that in the global atmosphere. Furthermore, the workshop concluded that tundra was a sink for carbon dioxide and had the capacity to increase sequestering of carbon under appropriate conditions. Based on historical data, general theory, and ecosystem models, tundra ecosystems are expected to increase the rate of accumulation of carbon under elevated atmospheric CO_2 and air temperature, but rates and amounts are unknown in the absence of relevant data. A primary effect in the arctic tundra of global warming certainly will be soil warming and its effects on decomposition rates, nutrient availability, and the carbon pool stored in the peat.

In addition to their importance in the long-term carbon balance, northern ecosystems are of interest because they occur in the zones of the greatest seasonal amplitude in CO_2 flux (Harris and Bodhaine, 1983). Northern ecosystems are also important because they are major sources of methane to the atmosphere (Sebacher, *et al.*, 1986). Changes in soil temperature, water table, and soil organic matter content associated with global changes in atmospheric CO_2 can affect the atmospheric injection of this important greenhouse gas. It is particularly relevant that global circulation models predict that CO_2-induced warming will be three to four times greater in polar regions than the global average (Seidel and Keyes, 1983; Manabe and Wetherald, 1980). This raises the possibility of a number of direct and indirect temperature effects on ecosystem response. The direct effects of elevated air and soil temperature include more rapid metabolic rates and a possible CO_2 and temperature interaction which yields a greater relative response to elevated CO_2 at higher temperatures (Kimball, *et al.*, 1986). The indirect effects of soil heating include increased depth to the permafrost, decreased water logging, and increased nutrient supply through increased mineralization. These direct and indirect temperature effects may be more important to future ecosystem carbon balance than are the direct CO_2 effects (Billings, *et al.*, 1982, 1983, 1984).

The potential for simultaneous increases in CO_2 and temperature, and the potential for complex system interactions to occur in nature, make it virtually impossible to accurately predict *a priori*, all important ecosystem responses including production rates, carbon sequestering and litter, and forage quality (Oechel and Strain, 1985). In the arctic and elsewhere, the ability of native plants to respond to elevated CO_2 varies by species (Oberbauer, *et al.*, 1986a; Oechel and Strain, 1985; Bazzaz, *et al.*, 1985). The innate capacity to respond can be reduced further by complex interactions among other limitations to growth such as nutrient and water supplies, and by the way in which these supplies are sequestered by neighboring plants. As ecosystem interactions can limit the extrapolation of single species phytotron studies to the field, homeostatic adjustments occurring in plant and ecosystem processes can limit the relevance of short-term experiments in predicting longer-term effects.

Our initial research was designed to determine the effects of elevated CO_2, and to a very limited extent, elevated temperature on key ecosystem parameters. Special emphasis was placed on net changes in ecosystem carbon flux, changes in growth and photosynthesis of individual species to incorporate this information in extant models, especially ARTUS CO_2 and NECS, and to share the resultant understanding with other researchers and modelers. Below we summarize the progress made to date towards these objectives. This summary is brief as the work has been published or summarized elsewhere (see e.g., Oechel, *et al.*, 1984, 1987, subm., Appendix B; Oechel and Strain, 1985). Recent progress for the 1987 field season has not yet been published and is detailed in Appendix B.

In 1983 we initiated field studies to determine key responses of tussock tundra to elevated CO_2 and temperature. The work was primarily conducted in the field to determine responses under realistic system interactions and resource limitations. The research site at Toolik Lake, Alaska was chosen in part because of the presence of representative tussock tundra, an important vegetation type and abundant store of carbon, the existence of a remote field camp operated by the University of Alaska, road access from Fairbanks and Prudhoe Bay, and extensive baseline information on the ecosystem (e.g. Miller, *et al.*, 1984; Shaver, *et al.*, 1986; Chapin and Shaver, 1985). The site has become more desirable with funding of related studies including an arctic LTER study (NSF), several other NSF ecosystems projects including a landscape project, and the DOE R4D project.

Despite resource limitations, the tussock tundra initially responds to elevated CO_2 with a marked increase in net ecosystem carbon flux (Figure 1) at both 510 (2.5 g m^{-2} d^{-1}) and 680 (6.5 g m^{-2} d^{-1}) µl/l CO_2. This marked increase in carbon storage primarily due to increased photosynthesis belies Kimball, *et al.*'s (1986) assertion that plants growing in cold climates will not respond to elevated CO_2. This marked increase in carbon accumulation means that if it persisted, there could be major new storage of carbon at elevated CO_2 and an important negative feedback on global atmospheric increases.

It was recognized that stimulation in net ecosystem sequestering while initially potentially quite large, should dissipate as ecosystem-level adjustments occur in the rates of photosynthesis and ecosystem respiration. Ecosystem respiration was predicted to increase as biomass accumulated in response to the greater rates of photosynthesis. Photosynthesis was predicted to peak, and then partially decrease as resources became more limiting, *e.g.* as nutrients were sequestered in accumulating biomass and soil organic matter. This process was expected to take a number of centuries (Oechel and Strain, 1985).

While the predicted pattern explained above occurred, it developed more rapidly than anticipated. During the second season of treatment, the mean net daily CO_2 flux was still greater in the 510 and 680 µl/l chambers, but the increase over the ambient CO_2 chambers was not as great as the first year of treatment. By the third season, daily fluxes at 340 and 680 µl/l were nearly identical; nearly complete homeostasis had occurred at elevated CO_2. At this time, the 510 µl/l treatment still showed a greater net daily CO_2 flux than the ambient chamber suggesting that, due to lesser response in production at 510 compared to 680 µl/l CO_2 acclimation did not occur as rapidly, presumably limitation by resources other than CO_2 concentration were not reached as quickly in a lower CO_2 treatment.

The 1987 data indicate a much faster ecosystem adjustment to elevated CO_2 than previously thought possible. The initial increase in production during the first year of treatment was confirmed by short-term experiments performed from mid-July through August 1985 and in 1987 (Figure 2). In 1987, CO_2 treatments were reversed on

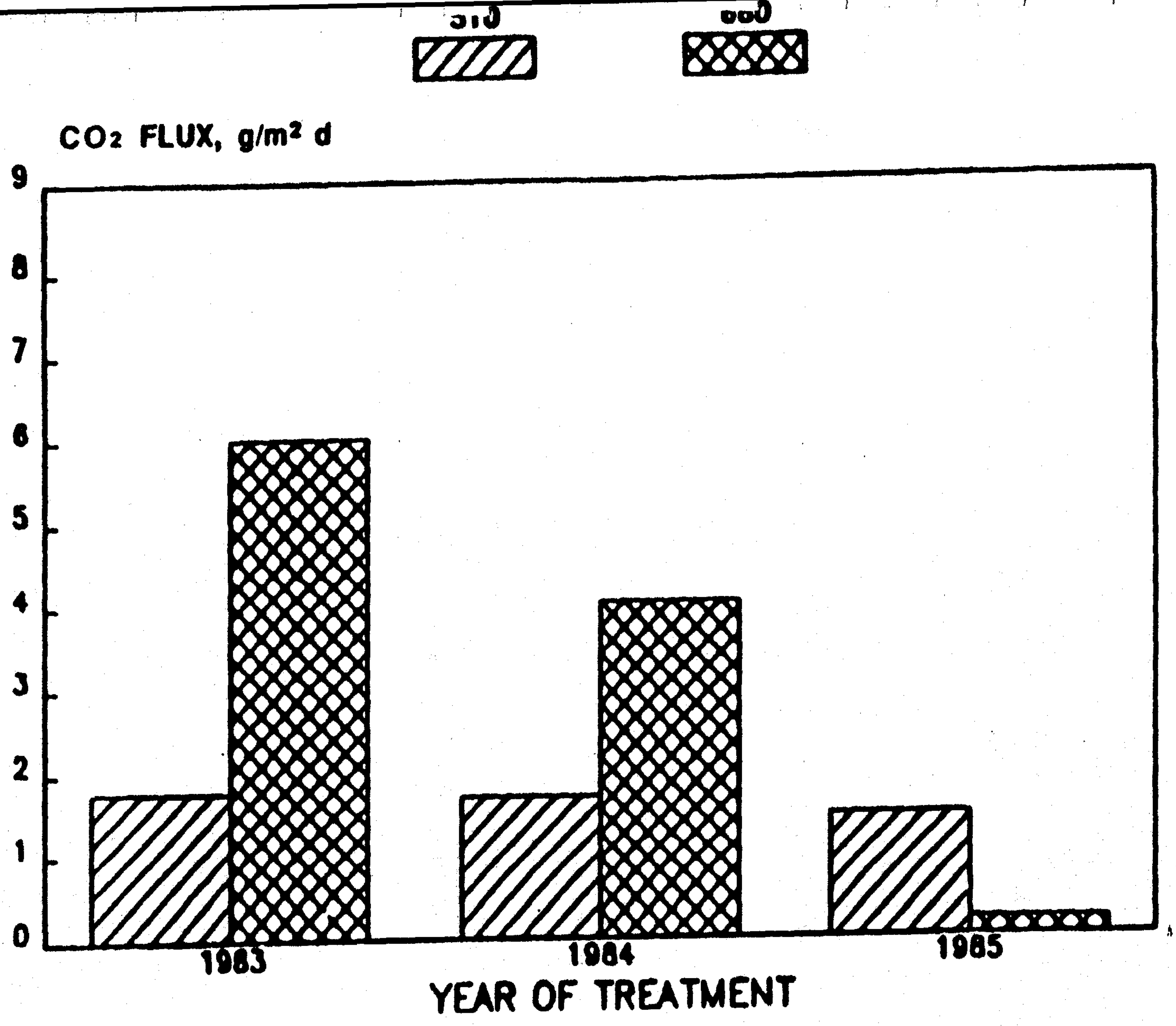


Figure 1 Mean net daily carbon fluxes (g $m^{-2} d^{-1}$) for the three years of study. Bars represent the differences in the mean flux rates between 510 and 340 µl/l CO_2 treatments.

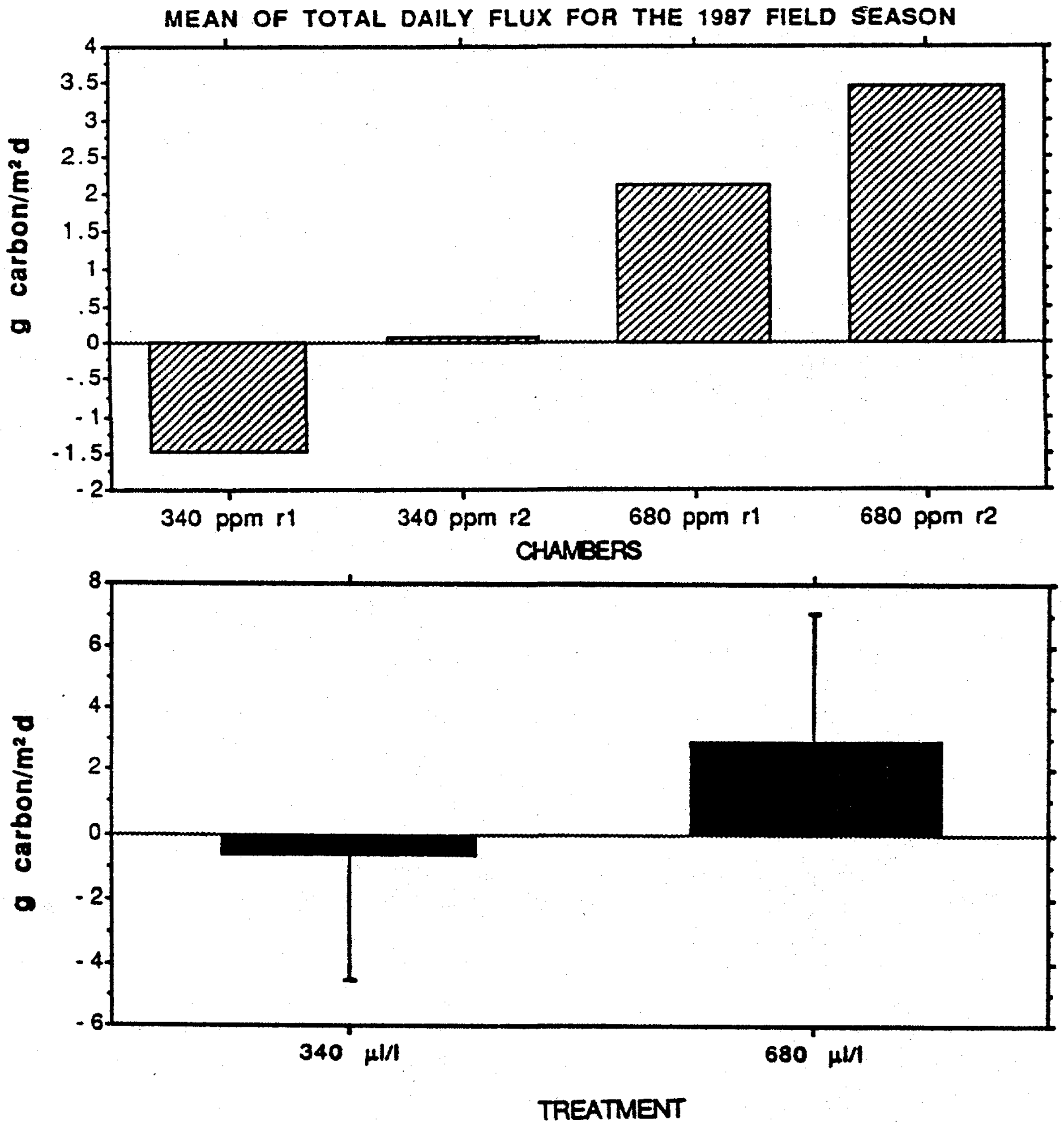


Figure 2 The mean of total daily flux rates for the 1987 field season is presented for each chamber (replicate) with ambient CO_2 (340-1,340-2) and elevated CO_2 (680-1,680-2) treatments in the top graph. In the bottom graph, the mean and standard deviation of each treatment is indicated. The mean total daily flux for the elevated CO_2 treatment [680 µl/l] was significantly greater (Fs = 44.05.05; $p <$ .01) than the ambient chamber [340 µl/l].

Julian days 197-200 (Figure 3). The results show a depression in the photosynthetic rates of the 680 µl/l treatment at 340 µl/l and enhancement of the 340 µl/l treatment at 680 relative to both treatments during the reciprocal exchange (Figure 3, Appendix B). These data show rapid adjustments in the photosynthetic capacity to CO_2 availability occurring over a matter of days.

Our studies indicate a stronger short-term response to elevated CO_2 than that predicted by Billings, *et al.* (1982, 1983, 1984) and others, some of whom anticipated that resource limitation would prevent a CO_2 response. However, over the course of three years, resource limitation appears to have restricted the response and at this level their predictions appear correct. We feel that it is likely that this lack of longer-term response to elevated CO_2 reflects severe nutrient limitation in the tussock tundra. We feel that greater nutrient availability would result in prolonged response in net ecosystem response to elevated CO_2. This increased nutrient supply could occur if warmer soil temperatures, a lower water table, or an increased soil active layer result in greater rates of mineralization.

Seasonal CO_2 fluxes indicate a lengthened period of photosynthetic activity at elevated CO_2. The photosynthetic period in 1987 was extended by about ten days at elevated CO_2 (Figure 4, Appendix B). This may have been due to a delay in senescence similar to that found with fertilization and reported for other CO_2 experiments (Oechel and Strain, 1985). Similar results were found in 1983 when ecosystem carbon flux and plant photosynthetic rates were maintained at higher values for longer at elevated CO_2 (Tissue and Oechel, 1987). There is an indication that early season photosynthetic rates are noticeably higher at elevated CO_2, possibly reflecting high rates of photosynthesis before homeostatic adjustment occurs.

Short-term CO_2 treatment has a pronounced effect on the light response of tussock tundra ecosystems. At ambient light, net diurnal CO_2 uptake is greater at 680 µl/l CO_2. The light compensation point for the ecosystem is substantially lower at higher CO_2 (Figure 5). At 340 µl/l, the light compensation point occurs at about 3/5% of ambient light, whereas at 680 µl/l, it drops 2/5% or less. Daily carbon uptake is higher over a greater light range at 680 µl/l compared to 340 µl/l. Gas exchange at very low light was more similar than at high light, and at 20% of full ambient sunlight levels, the rates were the same.

In the first year of treatment in 1987, after some homeostatic adjustment has occurred, the enhancement of photosynthesis at elevated CO_2 is greater on clear days than cloudy (Figure 6, Appendix B). This may reflect initial homeostatic adjustment of photosynthetic capacity at elevated CO_2. When light is limiting, the decreased photosynthetic potential of plants grown at 680 µl/l results in lower photosynthetic rates. However, in the first year, homeostatic adjustment is not yet complete, and photosynthetic rates are still enhanced at elevated CO_2 and saturating light (see e.g. daily flux on 6/27, Appendix C). More work is necessary to confirm this explanation of the differential response to elevated CO_2 under varying light conditions.

Increased temperature, anticipated with increasing atmospheric CO_2, may result in greater response to elevated CO_2. Kimball, *et al.*, (1986) report a positive interaction between temperature and CO_2 on growth in agricultural plants. Unfortunately, their data is based on the effects of changes of within-season temperature variation on growth rates. Such data may not be transferable to situations of climate change or to differing bioclimates. Climatic differences or climate change may result in differing patterns of response and variation compared to short-term, daily, or seasonal variation. The effects of short-term, within-season variation of temperature are likely

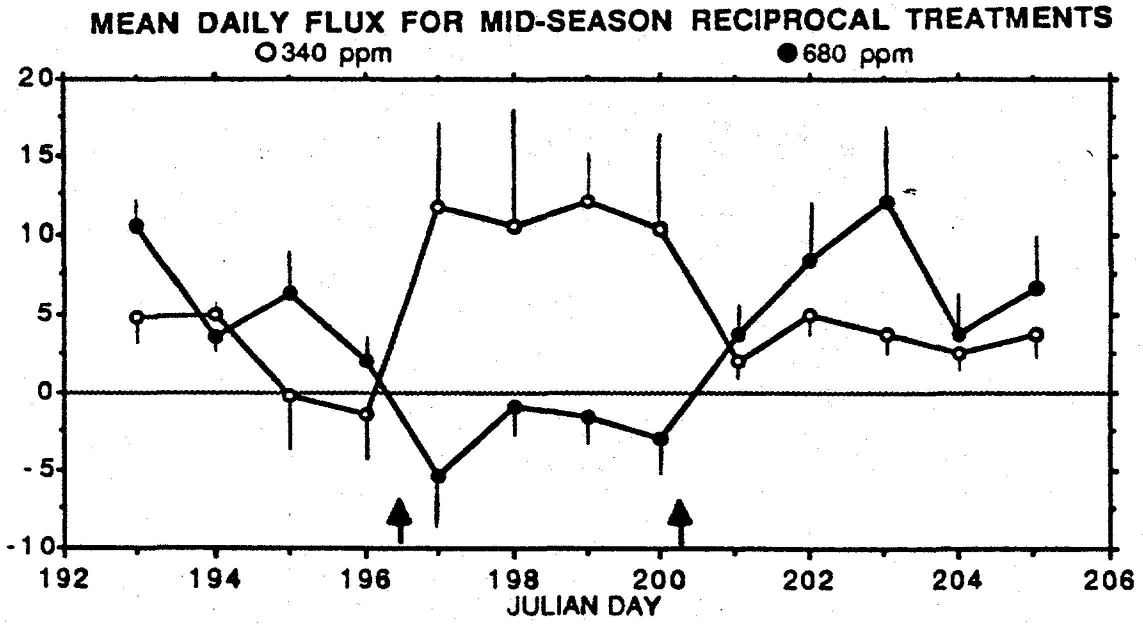


Figure 3 Mean total daily flux for the long-term 340 µl/l (open circles) and 680 µl/l (closed circles) treatments during mid-season. For Julian day 197 through 200 (July 17-20), the continuous 340 µl/l treatment was set at 680 µl/l, and vice versa to test for homeostatic adjustment. Bars are standard error.

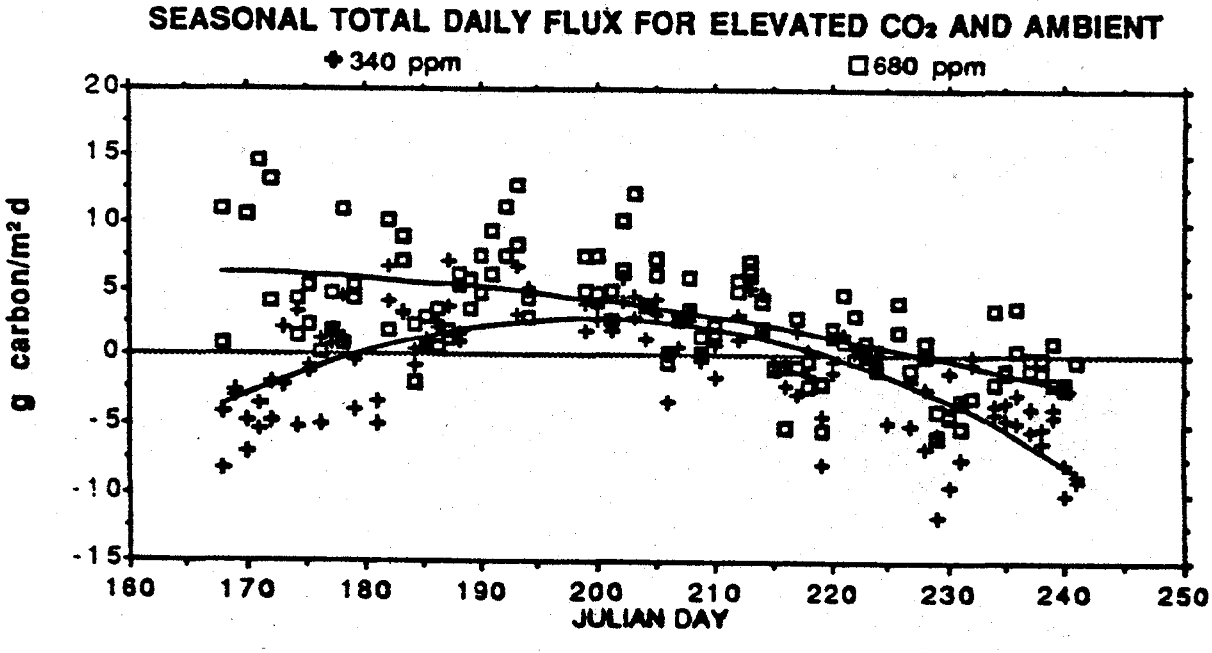


Figure 4 Regressions to seasonal daily CO_2 flux for 1987 for the 340 µl/l and 680 µl/l over the growing season.

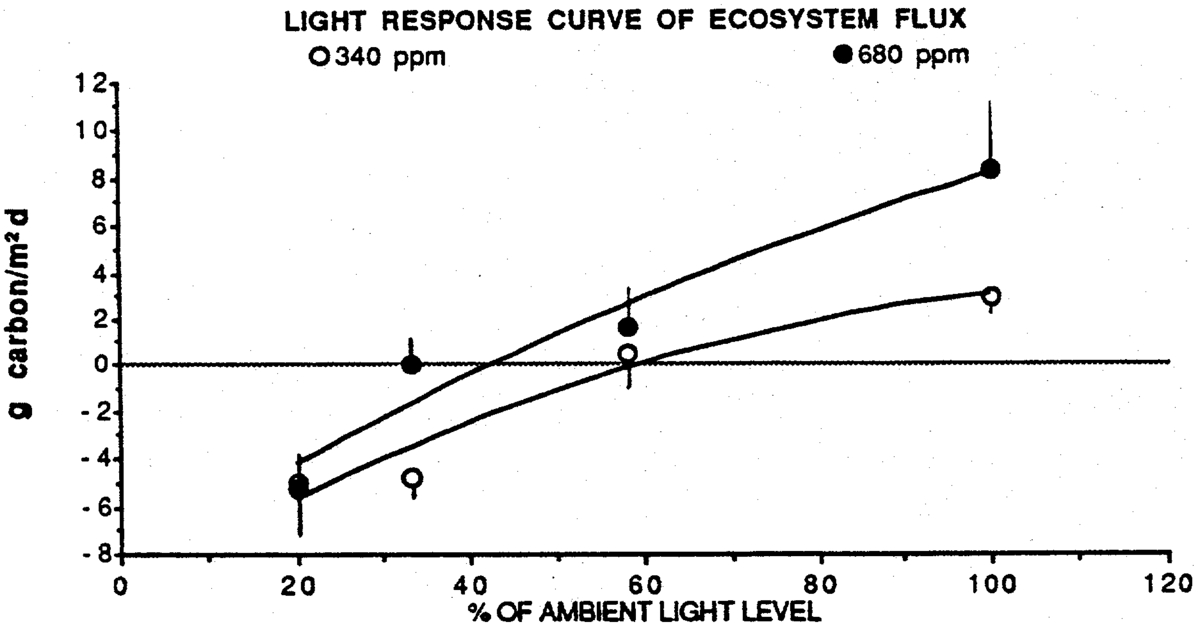


Figure 5 Light response of net ecosystem CO_2 flux at 340 and 680 µl/l CO_2. For 340 $y = 5.97 \ln(x) - 24.63$, $r^2 = 0.52$, $n = 54$. For 680 CO_2 $y = 7.53 \ln(x) - 27.06$ $r^2 = 0.27$, $n = 44$.

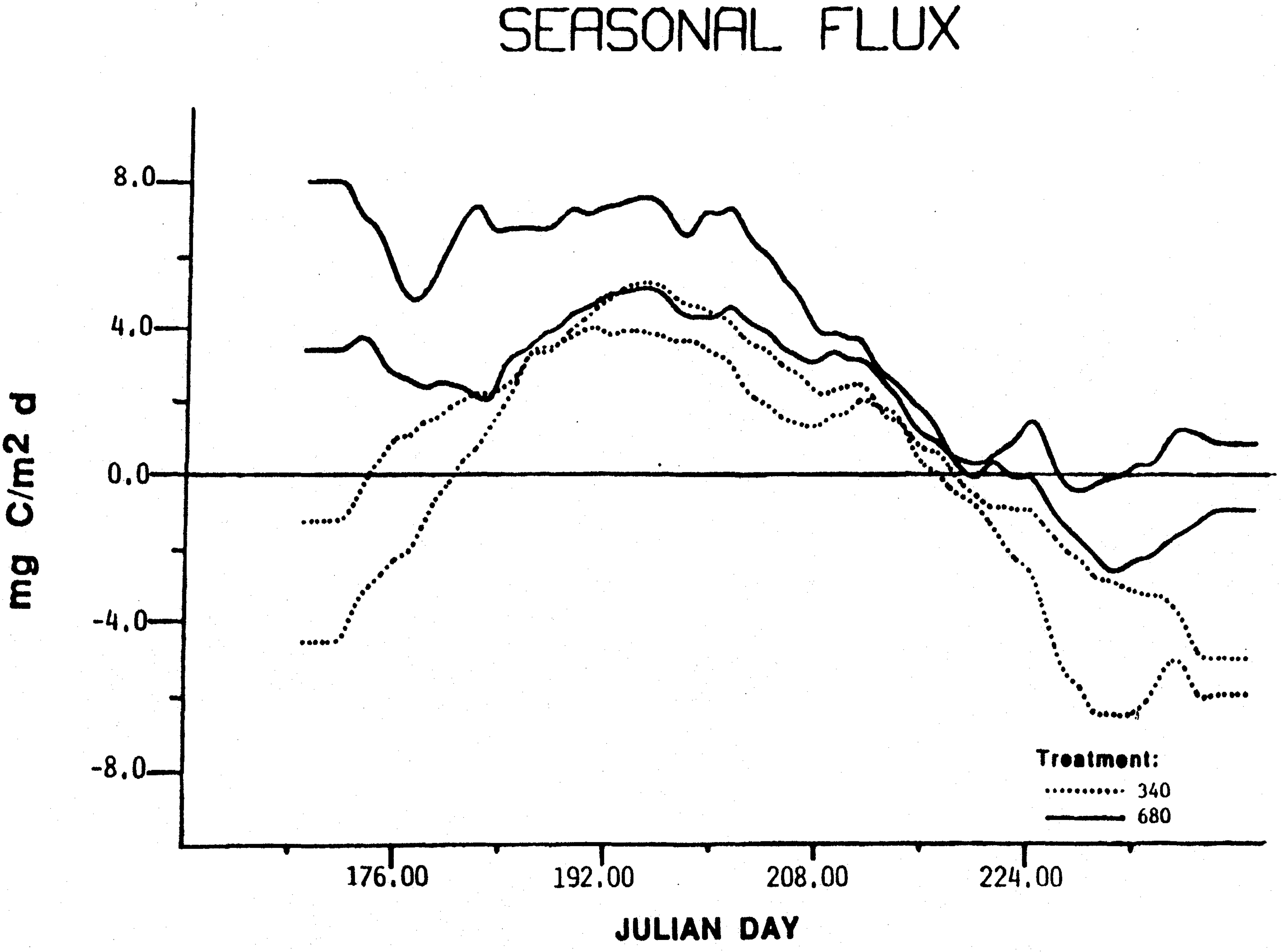


Figure 6 The 1987 seasonal flux rates for the two 680 μl/l chambers (solid lines) and the two 340 μl/l chambers (dotted lines). The response curve was developed from a spline function over a local nine-point average of the total daily flux for each chamber.

to be different from shifts in mean temperature of the growing season where acclimation is more likely to be an important factor.

We found that the pattern of response of net ecosystem carbon accumulation to elevated CO_2 was quite different at ambient and elevated temperatures (Table 1, 1983-1985). In the first year of treatment, elevated temperature and CO_2 resulted in an increase in carbon uptake compared to the ambient treatment. This initial stimulation at elevated temperature and CO_2 was less than that with elevated CO_2 only, presumably due to temperature effects on respiration. Interestingly, increased carbon uptake with elevated CO_2 was maintained in the temperature treatment over the three seasons of the experiment. This may reflect the temperature enhancement of the CO_2 effect reported by Kimball, *et al.*, (1986) or the effect of greater nutrient availability following increased mineralization. It was not possible to undertake a full temperature experiment, and to observe the effects of temperature at all CO_2 levels. It is therefore not possible to calculate the CO_2 and temperature interaction. These experiments indicate that we can expect increased carbon sequestering under future proposed arctic conditions at elevated temperature and CO_2.

It is important to know to what extent the stimulation of CO_2 uptake at elevated CO_2 and temperature is directly due to elevated temperature, and to what extent it is due to increased nutrient status following increased mineralization and uptake. It is also important to know whether there is an interactive effect between soil temperature or nutrient supply and ambient CO_2 concentration on net ecosystem CO_2 flux. Perhaps homeostatic adjustment to elevated CO_2 only occurs when there is inadequate resource availability or when carbon sinks are otherwise restricted.

In contrast to carbon balances developed for wet coastal tundra (Miller, 1981; Billings, *et al.*, 1982; Schell, pers. comm.), our research does not indicate carbon accumulation in the tussock tundra at Toolik Lake under current environmental conditions (Oechel, *et al.*, subm., Appendix A). This is in agreement with results of Schell (pers. comm.) who, using carbon-14 dating found no evidence of peat accumulation in this area in the last 2000 y. These recent data differ from earlier estimates which indicated a current accumulation of 90 g C $m^{-2} y^{-1}$ (Miller, 1981). Additional studies are needed to test the generality of our results and to insure that this result is not the result of minor local heating due to heat conduction through the chamber bases.

Whole ecosystem dark respiration rates are higher at warmer temperatures as expected. At any temperature, respiration rates are lower at elevated CO_2 (Figure 7, Appendix B). This pattern has been observed previously (Oechel *et al.*, subm.) and does not seem to be due to altered rates of soil respiration (Oberbauer *et al.*, 1986b). Experimentation with more replication and additional experiments will be necessary to determine if respiration rates are truly lower at elevated CO_2, and if this pattern is due to lower leaf respiration, reflecting lower photosynthetic capacity, RUBISCO concentration, and lower protein turnover.

In some species there was a homeostatic adjustment of photosynthesis to elevated CO_2 which was similar, but more rapid than that found in the whole ecosystem. In the first year of CO_2 enrichment (1983), a very rapid adjustment to elevated CO_2 was found in *Eriophorum vaginatum* (Tissue and Oechel, 1987). These data show that CO_2 enrichment reduced the photosynthetic capacity of *E. vaginatum* within a growing season so that rates of photosynthesis in plants growing at 680 µl/l were similar to those growing at 340 µl/l. This rapid photosynthetic adjustment suggests elevated atmospheric CO_2 may have relatively little effect on this and possibly other tundra

Table 1 Effects of CO_2 treatment and duration of treatment on net daily CO_2 fluxes. Replicate chambers nested under CO_2 treatment. Level for rejection of the null hypothesis of 0.05.

	Treatment:			
Year:	340 µl/l	510µl/l	680µl/l	680µl/l+4°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 CO2	37.805	<0.001	2/380
Effects of temperature	2.471	=0.112	1/236

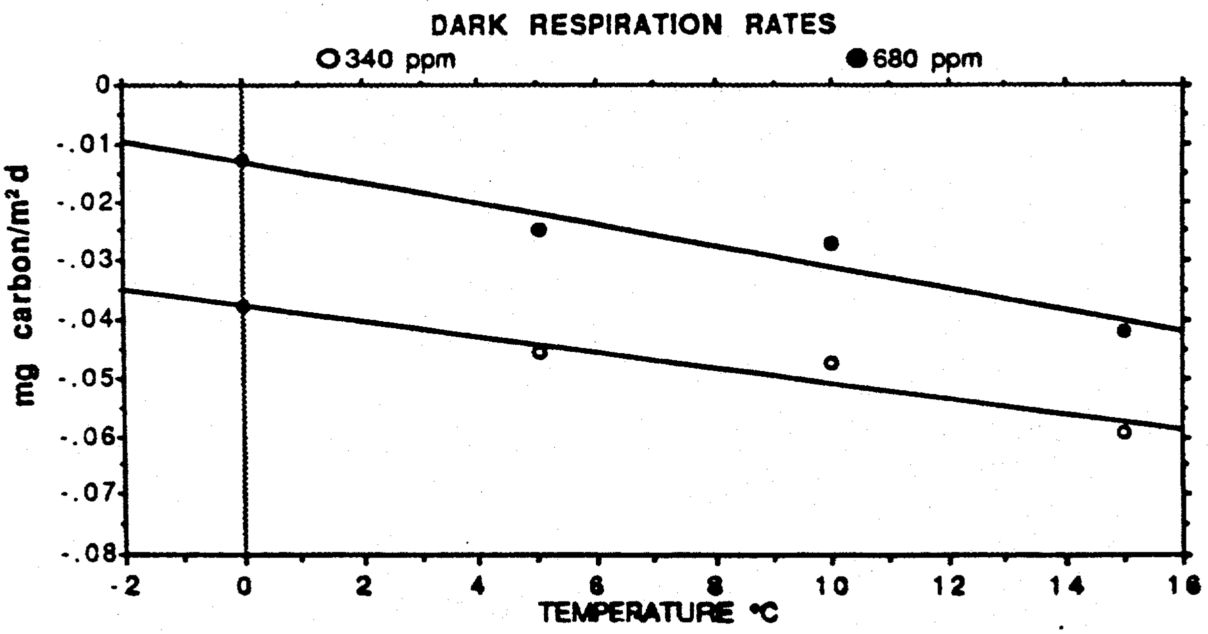


Figure 7 Dark respiration rates on August 24, 1987 for the ambient (340 µl/l, open circles) and the elevated CO_2 (680 µl/l, closed circles) treatments at various controlled temperatures. The treatments are significantly different.

species. It is further suggested that growth in *Eriophorum vaginatum* is less limited by carbohydrate supply than by other resources. These data suggest that predicted photosynthetic response to elevated CO_2 may have been commonly overestimated for environments where plants are limited by resources other than CO_2 (see e.g. Lemon, 1983). Increasing nutrient supply, for example accompanying elevated soil temperatures, might result in enhanced photosynthetic response to elevated CO_2.

This homeostatic adjustment in photosynthesis rate to elevated CO_2 persists several years, if not indefinitely. In the third year of treatment at 680 μl/l CO_2, *Eriophorum vaginatum* had the same photosynthetic rate as those grown at 340 μl/l. However, this response is not universal among arctic plants. *Ledum palustre* maintained enhanced photosynthetic rates when grown for three seasons at elevated CO_2. Perhaps this evergreen species has a better developed mechanism for storage of excess carbohydrate or is less resource limited than is *Eriophorum vaginatum*. Field experiments to determine the interaction of soil temperature and nutrient availability with elevated CO_2 would help identify the reasons for the pronounced homeostasis found in this species.

Photosynthetic measurements made in the third year of treatment in some cases contradict results obtained in laboratory studies (Oberbauer, *et al.*, 1986a), emphasizing the caution which must be taken in extrapolating laboratory studies to the field or even a manipulated field situation. Laboratory experiments performed on *Carex bigelowii, Betula nana*, and *Ledum palustre* ssp. *decumbens* were performed to determine the interaction between CO_2 enrichment and nutrient availability. Contrary to previous controlled-environment studies on crop species (Sionit, *et al.*, 1981; Sionit, 1983), this study did not discover CO_2 enrichment or CO_2-nutrient interaction effects resulting in a stimulation of photosynthesis at elevated CO_2. However, in the field, *Ledum palustre*, and possibly the other two species showed enhanced photosynthetic rates at elevated CO_2.

There is insufficient information to predict from growth form or other characteristics those species which will respond positively to elevated CO_2. From other studies, it appears that those species with well-developed storage organs or other strong sinks or with only modest resource limitation will be most likely to respond to elevated CO_2 (Sasek, *et al.*, 1985). The mechanism for homeostatic adjustment to elevated CO_2 likewise has not been fully elucidated. Possible mechanisms include starch accumulation, especially in the chloroplasts (DeLucia, *et al.*, 1985), decreasing RUBISCO content or activity, and triose phosphate limitation (Oechel and Strain, 1985; Sharkey and Badger, 1984).

Long-term exposure to elevated atmospheric CO_2 concentration did not significantly affect soil CO_2 efflux on a surface area basis. There was an apparent, non-significant trend for soil respiration to be higher, under similar test conditions, after treatment at 4°C above ambient temperature compared to the ambient temperature treatment (both at 680 μl/l CO_2) (Oberbauer, *et al.*, 1986b). Respiration would, of course, be higher at the higher temperature. The results from this study indicated that the effects of CO_2 enrichment on litter quality and decomposition rates, if existent, were small in the third season of treatment.

Impacts of CO_2 treatment on soil solution chemistry and plant-nutrient status were modest. The pH tended to be lower at elevated CO_2 (Appendix B). Greater dissolved CO_2 or more abundant organic acids could cause this effect. There was no statistical difference in soil solution ammonium, nitrate levels, or phosphate levels with CO_2 treatment in the first year of treatment (1987, Appendix B). Sampling restrictions within the chambers prevented determination of total available nitrogen or phosphorus.

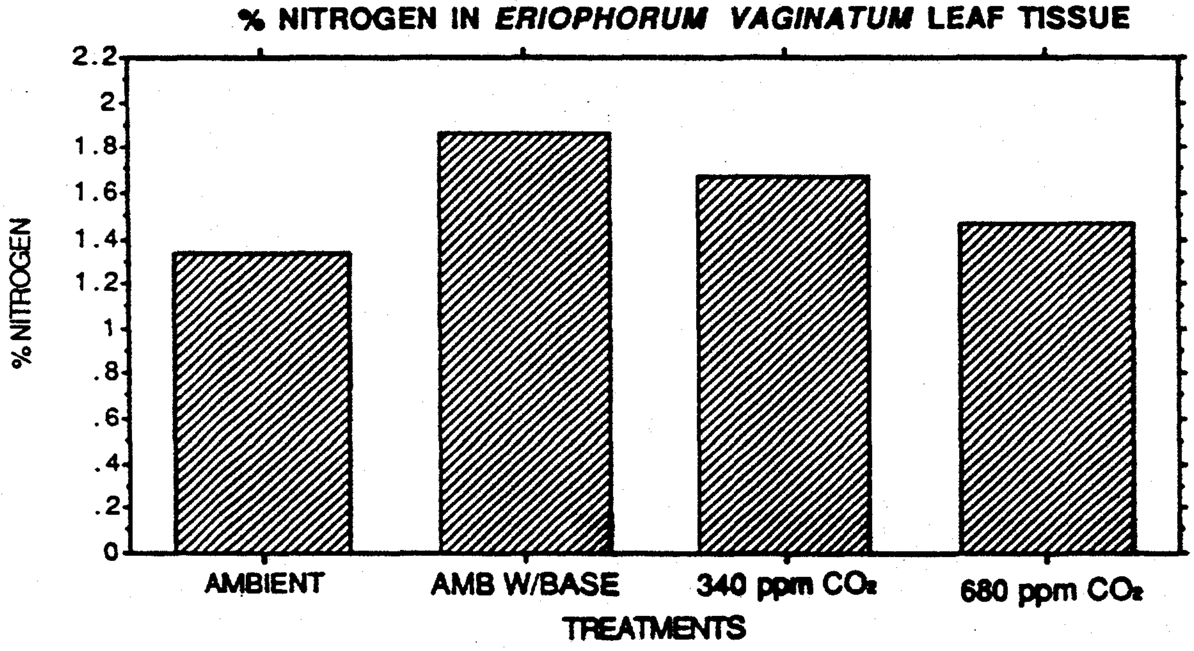
Plant-tissue nutrient content was more sensitive to CO_2 treatment. As expected, and except in the case of *Betula nana*, nitrogen content of the 680 µl/l treated vascular plants tended to be lower than the 340 µl/l grown plants. However, treatment effects were only significant in the case of *Carex* (Figures 8-10). These data imply increased nutrient limitation, decreased litter quality, and decreased forage quality at elevated CO_2. Additional observations will be necessary to document changes in C/N, lignin/N, C/P, and lignin/P following prolonged exposure to elevated CO_2. These variables can be helpful in predicting decomposition rates and forage quality (Norby, *et al.*, 1986a; Melillo, 1983).

Recent information indicates changes in soil enzyme activity at elevated CO_2 (Linkins and Oechel, unpubl. data). Cellulase activity decreases with CO_2 treatment, possibly indicating greater availability of labile carbohydrates to the microflora obviating the need for cellulose as a carbon source. This labile carbon may be from root exudation or from increasing carbohydrate content of litter. Phosphatase activity at elevated CO_2 increases, suggesting greater phosphate limitation under conditions of improved carbon supply. Alternate oxidase activity also increases, possibly indicating greater carbohydrate supply to the roots at elevated CO_2. These are intriguing observations and may represent early change in the belowground system following exposure to elevated CO_2.

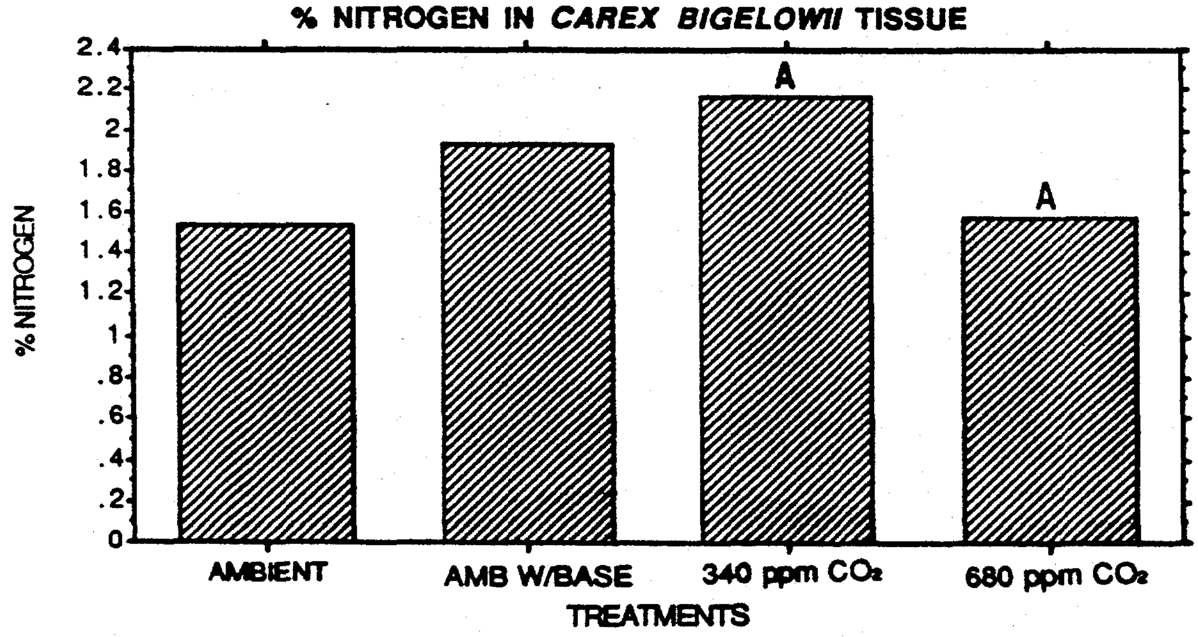
Sensitive parameters to elevated CO_2 seem to be plant growth and shoot demography. Changes in growth and shoot demography are important since they are early indicators of change in vegetation composition and structure, and because they can presage a change in ecosystem function. This change in function can occur even if the physiology and metabolism of the individual elements is fairly conservative with respect to CO_2. CO_2-induced changes in the production and development of vegetative and sexual buds can be used to model and project species response to elevated CO_2 (*e.g.* McGraw and Antonovics, 1983 and others).

In the first year of treatment, 1987, there was no significant effect of CO_2 on leaf number or leaf length for *Vaccinium vitis-idaea*. Leaf number is fixed prior to bud break, and possible CO_2-enrichment effects could only be expected next spring. The bud mortality was similar in the two CO_2 treatments. Slightly fewer buds remained dormant at 680 than at 340 µl/l CO_2, and the proportion that are vegetative are much higher at 680 µl/l CO_2 (Figure 11). Statistical tests have not yet been completed, but these data indicate a likely direction of change in the vegetation. Other factors being equal, *Vaccinium vitis-idaea* should become more important in the vegetation at elevated CO_2, but slightly fewer sexual buds may be available to produce seed for re-establishment in disturbed areas. No studies have yet been carried out on seed size, seed set, or viability in *Vaccinium vitis-idaea* at elevated CO_2, but there was a decrease in the proportion of flowers setting fruit between the 340 and 680 µl/l treatments.

In *Vaccinium vitis-idaea,* leaf number was decreased more at 680 µl/l than at 340 µl/l. This has implications for canopy leaf area and photosynthesis and for nutrient cycling. The 680 µl/l treatment had a slightly greater number of new growing points (Figure 12) than did the control CO_2 treatment. Double buds and lateral buds were more common. As found for white oak (Norby, *et al.*, 1986a), bud weight was greater at elevated CO_2 suggesting larger shoots in the following year. It appears that elevated CO_2 may have important effects on vegetative growth. These effects, in turn, would be expected to have major impacts on ecosystem structure and functioning including vegetative structure, productivity, palatability, and net carbon flux. Longer-term experiments will be required to verify these trends and to obtain a similarly



% NITROGEN IN *ERIOPHORUM VAGINATUM* LEAF TISSUE



% NITROGEN IN *CAREX BIGELOWII* TISSUE

Figure 8 Leaf total Kjeldahl nitrogen in a tussock-forming sedge, *Eriophorum vaginatum* (upper graph) and a caespitose sedge, *Carex bigelowii* (lower graph) collected August 1-4, 1987. Similar letters denote statistically significant differences at the $p < .01$ level.

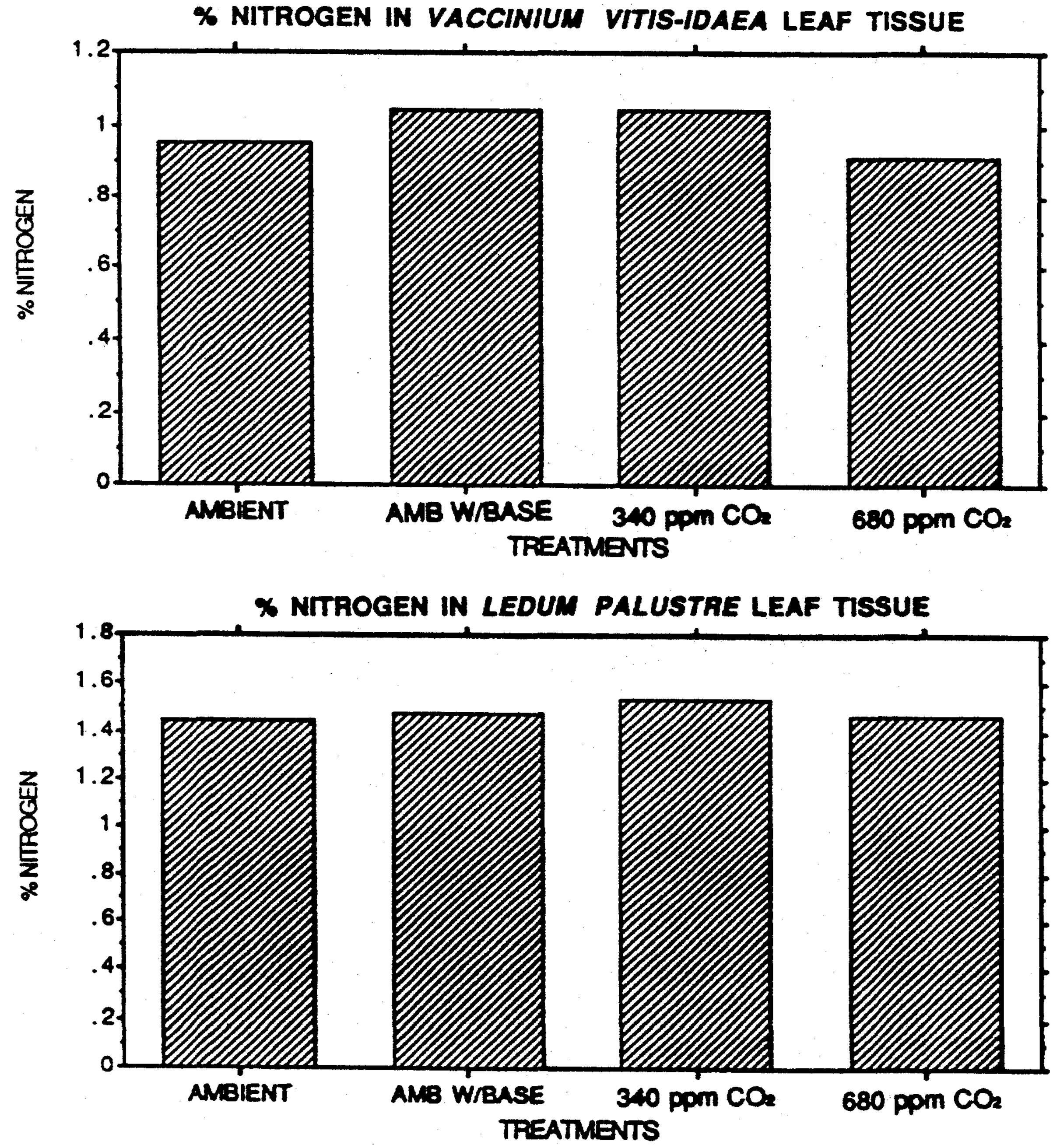


Figure 9 Leaf total Kjeldahl nitrogen in two dwarf heaths, *Vaccinium vitis-idaea* (upper graph) and *Ledum palustre* ssp. *decumbens* (lower graph) collected August 1-4, 1987. There were no significant differences between treatments.

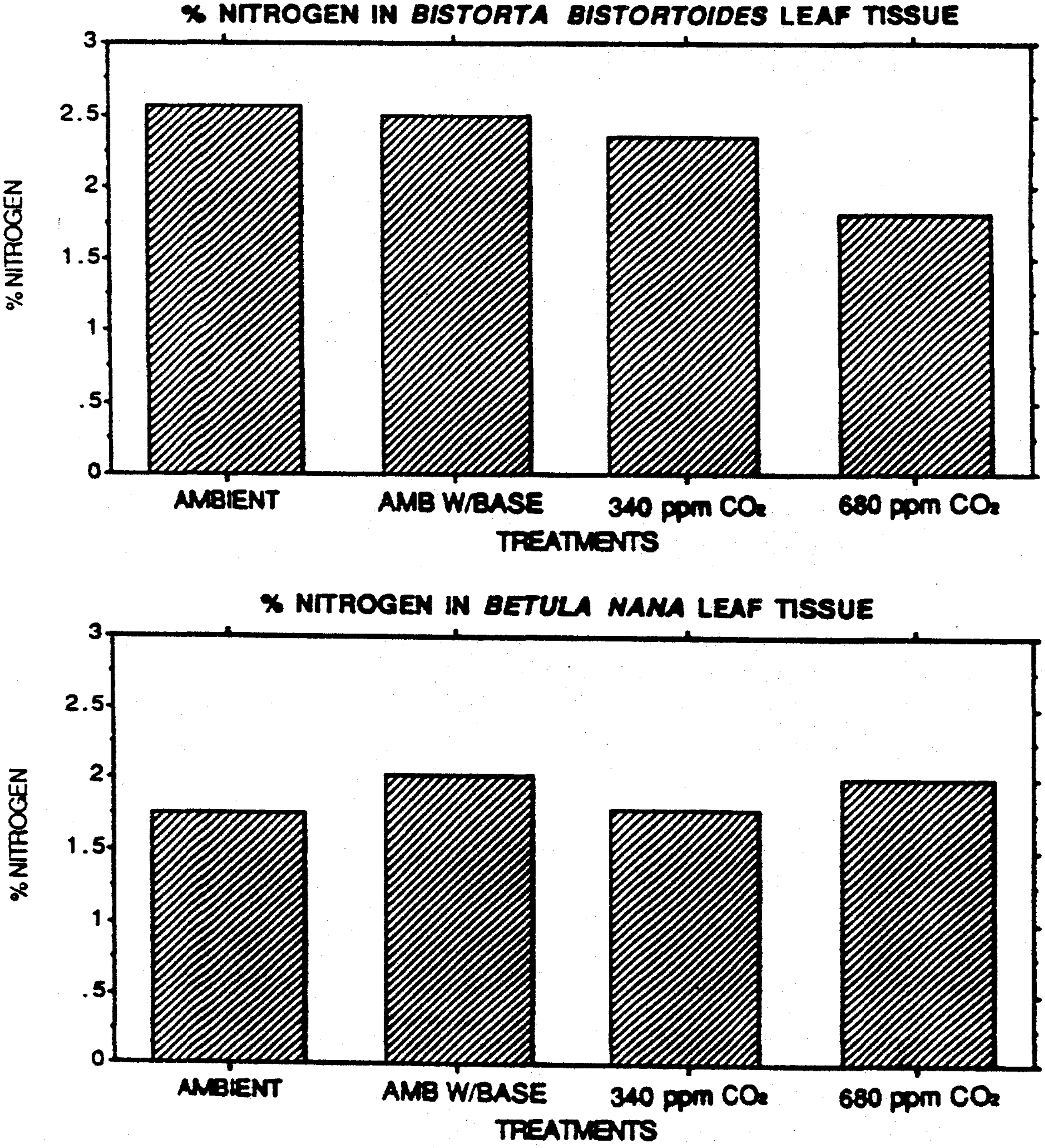


Figure 10 Leaf total Kjeldahl nitrogen in a forb, *Bistorta bistortoides* (upper graph), and a dwarf deciduous shrub, *Betula nana* (lower graph) collected August 1-4, 1987. There were no significant differences between treatments.

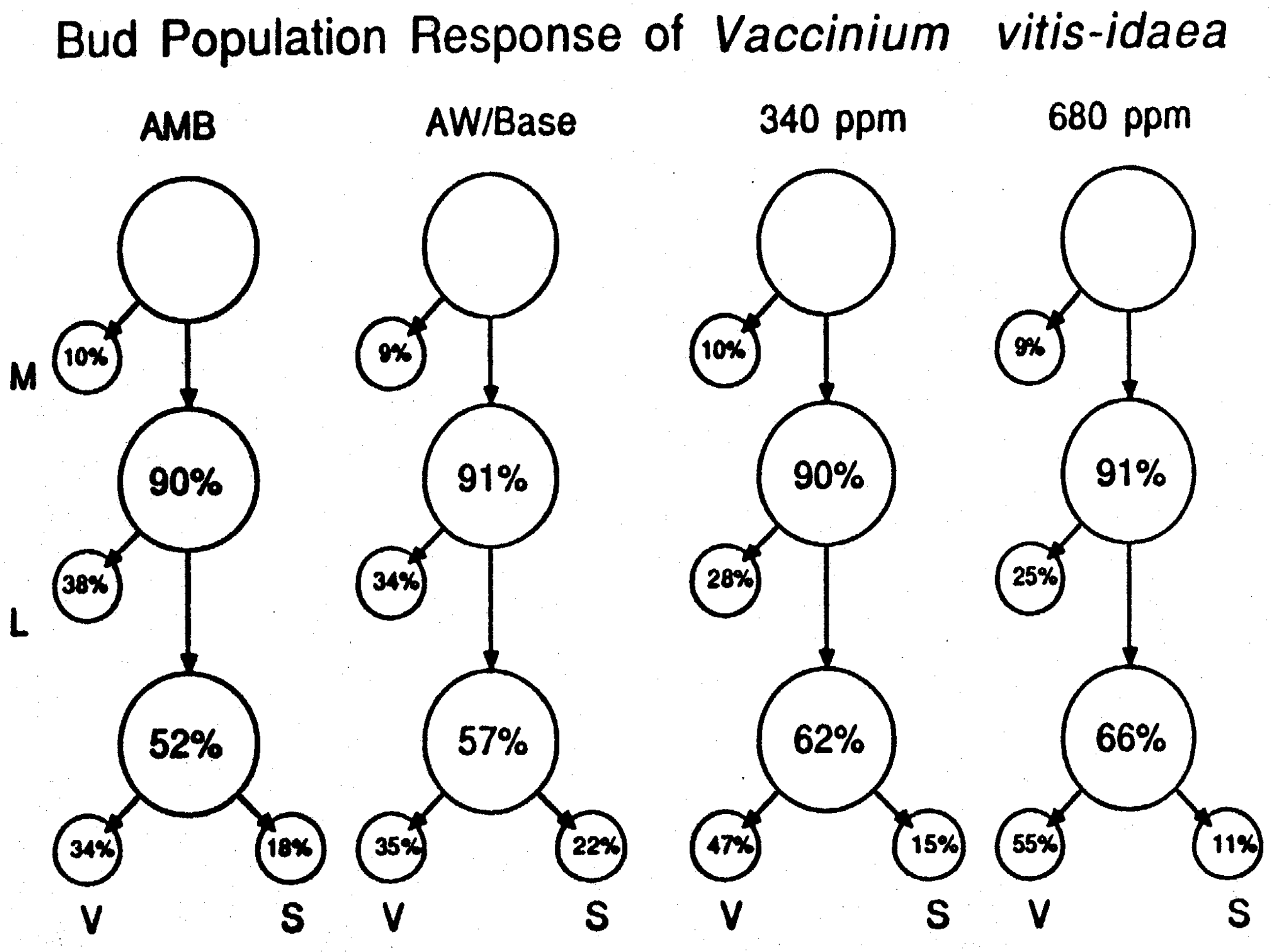


Figure 11 Fate of growing points in *Vaccinium vitis-idaea*. Mortality (M), latency (L), vegetative bud production (V), or sexual bud production (S), as affected by CO_2 and experimental manipulation.

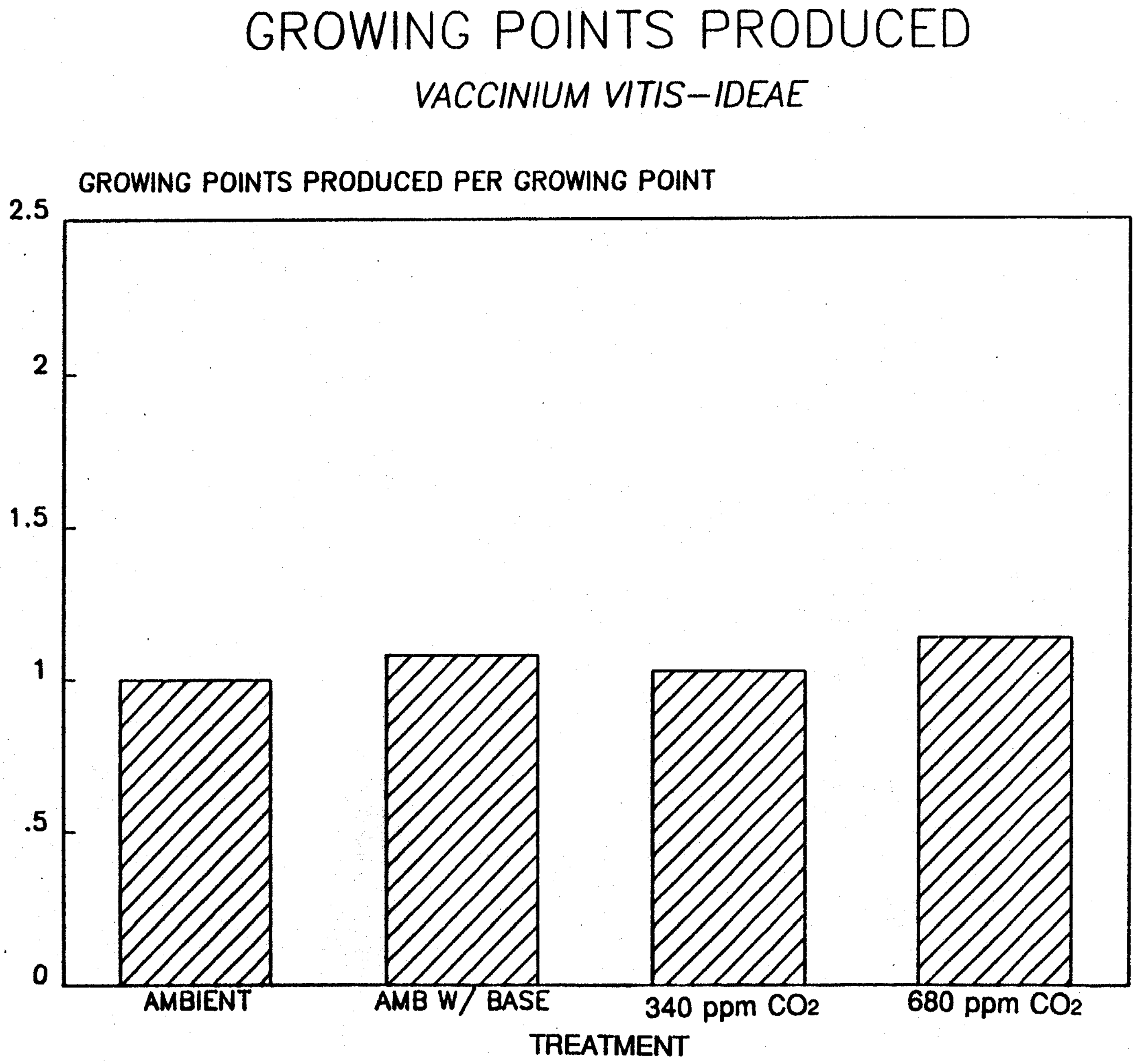


Figure 12 Effects of CO_2 treatment and chambers on population dynamics of growing points: number of growing points produced per growing point for *Vaccinium vitis-idaea*. No statisitcal analyses available yet.

comprehensive set of observations for other vascular and nonvascular species. Some preliminary observations exist, however.

Elevated CO_2 had a consistently positive effect on leaf area in *Betula nana*. Mean leaf length, number of leaves per growing point, and mean number of leaves per current year's growing point were all greater at elevated CO_2 (Table 2).

There were few observed effects of elevated CO_2 on branch demography of *Ledum palustre*. Leaf length was slightly shorter at elevated CO_2, possibly reflecting the depletion of nutrient reserves within the plant or the effect of higher photosynthetic capacity at elevated CO_2.

For *Eriophorum vaginatum*, current year's leaf area, total leaf area, and the final mean number of leaves per tiller was significantly lower at 680 µl/l CO_2 (Table 3). However, if tillering rate continues higher at elevated CO_2 as initially indicated (Tissue and Oechel, 1987, Appendix B), leaf area of *Eriophorum vaginatum* could increase at elevated CO_2, despite the depressing effects of CO_2 on the leaf area of an individual tiller. As a result of higher leaf area, total canopy photosynthesis could increase despite homeostasis in the photosynthetic rate.

No statistical difference was found after one year at elevated CO_2 in the rates of mortality and recruitment in the four mosses *Aulacomnium turginatum*, *Hylacomnium splendens*, *Sphagnum angustifolium*, or *Sphagnum girgensonii* (Appendix B). Longer-term exposure may be necessary to uncover any differences that may exist.

It seems quite apparent that short-term CO_2 enrichment has differential effects on vegetative growth, leaf size and number, and shoot demography among species. Detailed, longer-term studies will be necessary to obtain the information essential to predict new steady-state populations.

1.2 COMPARISON WITH WET COASTAL TUNDRA

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 present carbon dynamics may be somewhat different. Each system appears to respond similarly to elevated CO_2, temperature, nutrients, and other environmental factors.

Wet coastal tundra is accumulating carbon under current climatic and atmospheric conditions (Miller, 1981; Billings, *et al.*, 1982; Schell, pers. comm.). The rate of carbon accumulation may be about 40-120 g C m^{-2} y^{-1} resulting in a current store of about 20 kg C m^{-2} in peat in the upper 20 cm (Billings, *et al.*, 1984). Phytotron experiments using microcosms of natural ecosystems indicate carbon accumulation of 78-340 g CO_2 m^{-2} per season depending on site, temperature, and water level. Increasing CO_2 may have a positive effect on net ecosystem carbon sequestering in the first year of treatment. In one experiment, a doubling of CO_2 from 400-800 µl/l increased seasonal CO_2 uptake by 174 g CO_2 m^{-2} per season (Billings, *et al.*, 1984).

However, phytotron-determined carbon balance from tundra microcosms does not necessarily predict net carbon gain for a future warmer and drier climate. Phytotron measurements of microcosms under current ambient temperature and CO_2 conditions, but with a water table of -5 cm, resulted in a measured seasonal loss of

Table 2 Summary of *Betula nana* population dynamics. In all statistical tests below, the biologically important tests are between the ambient (1) versus the base (2) to test for possible chamber effects, the ambient (1) versus the 340 (3) to test for possible chamber effects, and between the 340 (3) and 680 µl/l (4) treatments to test for CO_2-enrichment-effects.

TISSUE TYPE:	SIGNIFICANCE[a] (2-WAY ANOVA)	(1-WAY ANOVA)[b]			
mean leaf area (mm^2)	(1-way only)	1	2	3	4
	n = 1600	1	*	*	*
	680 > 340	2		NS	*
		3			*
mean # leaves per growing point	* * *	1	2	3	4
	n = 1170	1	*	NS	*
	680 > 340	2		*	*
		3			*
mean # leaves per current yr's growing point	(1-way only)	1	2	3	4
	n - 152	1	NS	NS	NS
	680 > 340	2		NS	*
		3			*

[a] treatment (ambient, ambient with base, 340 ppm CO_2, 680 ppm CO_2) by chamber (replicate); *** = ($p < .001$); ** = ($p < .01$); * = ($p < .05$)

[b] between treatments only; significance at 95% level

Table 3 Summary of *Eriophorum vaginatum* population dynamics. In all statistical tests below, the biologically important test is between the ambient (1) versus the base (2) to test for possible chamber base effects, the ambient (1) versus the 340 treatment (3) to test for possible chamber effects, and between the 340 (3) and 680 µl/l (4) treatments to test for CO_2-enrichment effects.

SUMMARY OF *Eriophorum vaginatum*

TISSUE TYPE:	SIGNIFICANCE[a] (2-WAY ANOVA)	(1-WAY ANOVA)[b]			
current yr's leaf area (mm^2)	* *	1	2	3	4
	n = 439	1	NS	*	NS
	340 > 680	2		*	NS
		3			*
current yr's and overwintering leaf area (mm^2)	* * *	1	2	3	4
	n = 739	1	*	*	*
	340 > 680	2		NS	NS
		3			*
mean # leaves per tiller	NS	1	2	3	4
	n = 633	1	*	NS	NS
	initial: 680 > 340	2		NS	*
	final: 340> 680	3			*

NO STATISTICS HAVE BEEN CALCULATED FOR THE FOLLOWING:

Seasonal change in total leaf # (in 100 cm^2 per treatment)
AMB > 340 > 680 > AMB W/BASE

Seasonal change in total # of tillers
AMB > 340 = 680 > AMB W/BASE

Seasonal change in mean leaf # per tiller
AMB W/BASE > 340 > 680 > AMB

---

[a] treatment (ambient, ambient with base, 340 ppm CO_2, 680 ppm CO_2) by chamber (replicate); *** = ($p < .001$); ** = ($p < .01$); * = ($p < .05$)

[b] between treatments only; significance at 95% level

49 g C m^{-2} y^{-1} (Billings, *et al.*, 1982). Doubled CO_2 concentration to 800 µl/l caused an increase in net CO_2 uptake of 48% with the water table at the surface, versus only 35% with the water table at -10 cm. This increase was not sufficient to 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). Despite this effect, the authors conclude that the wet coastal tundra is not presently limited by CO_2.

Exposure to elevated CO_2 could affect soil decomposition and respiration through effects on litter quality, soil nutrient status, and root exudation. In general, higher C/N ratios and the presence of toxic or recalcitrant compounds should slow rates of decomposition. Availability of labile carbon sources such as sugars and starches in the soil and litter should speed rates of decomposition as they act as an energy source for soil microbes. One would expect no direct effects of elevated atmospheric CO_2 on soil microbial activity. The metabolic activity of soil microbes *in vitro* has been shown to be depressed at high CO_2 concentrations (50,000-900,000 µl/l; Strotsky and Goos, 1964). However, the CO_2 application in the chamber was low relative to CO_2 concentration in the soil atmosphere and should have little effect on the soil atmosphere CO_2 gradient and, therefore, on the soil CO_2 concentration.

A predicted net effect of a global rise in CO_2 on wet coastal tundra 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. It also appears that other factors possibly associated with a CO_2 rise have more of an effect than the direct effects of CO_2. Changes in available temperature, nutrient supply, and water table in particular can have large effects on net CO_2 flux. Therefore, the final effect of a long-term global change in CO_2 concentration and climate in either mesic or wet coastal tundra ecosystems is difficult to accurately predict.

No experiments of longer than one growing season nor 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, an even sign of carbon flux indicates that medium-term field experiments of several years should be conducted. These 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.

As stated earlier, tussock tundra in the region of Toolik Lake, Alaska may not be currently accumulating carbon. Our work indicates a net loss of carbon under ambient CO_2 and temperature conditions. This result 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 could be interpreted that the peat is in equilibrium near the surface, or that it is in recession. Carbon-14 dating from material within the active zone may be unreliable because of the yearly incorporation of new carbon from dying roots and mixing due to cryoturbation.

Although data on upland tussock tundra come 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 processes influence much of the energy and carbon budget across the North Slope so it should be possible to generalize our results to other similar permafrost-dominated regions. It is essential to understand the change in carbon stores and fluxes under anticipated changes in CO_2 and climate to predict the future global carbon balance. Additional studies are needed to document historic and current rates of carbon accumulation in wet and mesic tundra areas throughout the circumpolar arctic.

1.3 LITERATURE REVIEW: IMPACTS OF SELECTED ENVIRONMENTAL FACTORS ON TUNDRA AND RELATED ECOSYSTEMS

1.31 EFFECTS OF ELEVATED SOIL TEMPERATURE ON CARBON BALANCE

Elevated soil temperature can affect the carbon balance of the ecosystem. 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. They also emphasized the importance of water table on net CO_2 flux. 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. They found the depth of the water table to have a major impact on the respiration rate of the system and, therefore, on the net CO_2 balance. Differences due to temperature and water table were more pronounced than those due to site. A water table lowered from the surface to -10 cm during the course of the season resulted in a conversion from CO_2 uptake to CO_2 loss.

In wet tundra ecosystems, root and rhizome respiration accounted for 50-90% of total soil respiration (Billings, *et al.*, 1977) and factors which affect live tissue respiration rate can potentially mask the net gain or loss of soil carbon due to temperature-increased decomposition rate. Following treatment by elevated air temperature (+4°C) and CO_2 enrichment, soil respiration under similar temperature conditions was slightly, but not significantly elevated compared to other treatments in the tussock tundra (Oberbauer, *et al.*, 1986b). However, the C/N ratio, which can affect decomposition rate, was not measured in the study. Tundra ecosystem dark respiration rates are decreased with lower air temperature over a 24 hr period (Appendix B, see Figure 7) presumably due to decreasing aboveground tissue respiration rates.

Climatic changes associated with rising global 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. While increased decomposition would increase nutrient availability and system productivity, any decrease in thermal insulation could cause melting of the ice wedges and ice lenses resulting in thermokarst erosion of tundra soils (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.

In the boreal forest, elevation of soil temperature by 8-10°C and the heat sum from 563 to 943 degree days has been shown to increase nutrient status and productivity of black spruce in central Alaska (Van Cleve and Oechel, in prep). In three years of temperature treatment, there was a $\approx$20% or 1878 $g \cdot m^{-2}$ loss in soil organic matter from the forest floor. This increased decomposition resulted in an increase in soil solution concentration of organic N, available P, exchangeable NH_4^+, and tissue N, P, and K concentrations. Photosynthetic rates improved by 20%.

Mosses generally showed little effect from soil heating, possibly because of their usually shallow stems and rhizoids and limited conductive tissue. Even *Polytrichum* which grows to the mineral layer did not benefit from the increased nutrient availability. The interaction of soil heating and CO_2 availability was not explored in this experiment.

The direct effects of increased soil and air temperatures at the species level involve physiological processes, individual plant responses, and ecosystem level processes. The major responses are:

Physiological processes:

1) root resistance to water uptake;
2) nutrient uptake rates;
3) root respiration;
4) CO_2 diffusion into the leaf (as affected by the effect of root resistance on stomatal conductance);
5) photosynthetic rate (as affected by leaf nutrient (nitrogen) content); and
6) carbon fixation (as limited by temperature effects on enzyme activity).

Individual plant responses include:

1) shifts in resource (carbon and nutrients) storage versus utilization for growth;
2) shifts in types of compounds (secondary plant compounds);
3) root:shoot resource allocation; and
4) shifts in resource allocation to vegetative versus sexual reproduction.

The direct effects of increased soil and air temperatures at the ecosystem level primarily affect:

1) soil decomposition, with effects on
2) mineralization and nutrient availability and nutrient turnover rates, with an indirect feedback on
3) soil temperature via changes in the amount of litter or
4) a direct effect on the total volume of soil via increased depth of thaw.

These effects may interact with elevated CO_2 to produce a larger effect than otherwise anticipated.

1.32 EFFECTS OF ELEVATED SOIL TEMPERATURE ON NUTRIENT AVAILABILITY

Species response to temperature-mediated nutrient increases may be analogous to and interpreted from low-level and/or long-term fertilizer treatments. With fertilization, a number of plant characteristics are affected, including nutrient uptake rates, tissue-nutrient content and allocation, photosynthetic rates, biomass allocation, allocation to specific plant compounds (protein, carbohydrates), and growth rates (leaf size, leaf number, and/or changes in numbers of growing points such as tillering). With long-term response to nutrient addition, plant tissue has greater nutrient content

(Ulrich and Gersper, 1978; Shaver, *et al.*, 1986; Chapin, *et al.*, 1986; Chapin and Shaver, 1985; Shaver and Chapin, 1980; plus many others).

Unlike many temperate plants, there is some evidence that arctic plants do not shift biomass allocation (root:shoot ratios) with long-term fertilization (Dennis, *et al.*, 1978; McCown, 1978), although certain components of biomass (such as protein) may be reallocated or synthesized with fertilization (Chapin, *et al.*, 1986; Chapin, 1978).

In this study, CO_2 enrichment decreased survivorship of older leaves and increased the number of new buds produced for next year in *Vaccinium vitis-idaea*. With CO_2 enrichment, there was a decrease in leaf mortality in *Betula nana*. An increase in tillering rate was apparent in *Eriophorum vaginatum* with elevated CO_2 and with elevated CO_2 and soil temperature (Tissue and Oechel, 1987). Whether this is due solely to short-term stimulation of existing bud primordia or whether there is allocation of resources to new production of bud primordia is not known. If only the former were true, we could expect to find a short-term increase in tillering followed by a depression of tillering rate. If the latter were true, we would expect to find a new, higher tillering rate, and an expansion of the species would result. In this study, the number of leaves per tiller was greater with CO_2 enrichment.

Nutrient availability as a function of soil temperature has been analyzed in detail for a black spruce stand which occupies the lowest soil temperature and wettest microenvironments (often underlain by permafrost) in the boreal forest (Van Cleve, *et al.*, 1983; Van Cleve and Oechel, in prep.). Low soil temperature was correlated to the lowest biomass, lowest production, lowest tissue-nutrient content, and lowest nutrient turnover rates of any of the different forest types described. The poorest litter quality (lower nutrients, higher lignin) is associated with the cooler black spruce stands. These characteristics further decrease microbial decomposition rates and nutrient cycling. With increased soil heating within a black spruce stand, there was increased forest floor nutrient cycling, increased nutrient availability [available NH_4^+, P], increased tissue-nutrient content [N,P,K], and increased plant biomass (Van Cleve and Oechel, in prep.; Hom, 1986). These data on heating effects are the most complete for any permafrost-dominated stand to date and provide a valuable indicator of what we can expect to find in the response of soil processes to heating of the tundra ecosystem.

Heating wet tundra soil results in higher microbial respiration rates and three times greater ammonium concentration in soil solution (Barel and Barsdate, 1978). Heating soil can also increase phosphate absorption twofold (Chapin, 1978). The long-term result of stimulation of decomposition rates is not known.

1.33 DIRECT EFFECTS OF ELEVATED CO_2 ON PLANTS AND ECOSYSTEMS AND INTERACTIONS WITH OTHER FACTORS

The direct and indirect effects of elevated CO_2 on native plants and unmanaged ecosystems have been thoroughly summarized in several recent reviews and position papers (see e.g., Lemon, 1983; Strain, 1985; Strain and Cure, 1985). Known and possible effects of elevated CO_2 on plants and ecosystems are myriad and will not be exhaustively reviewed here. Rather, we briefly review information particularly relevant to understanding and predicting the response of arctic systems to elevated CO_2.

In the very short term, CO_2 availability limits photosynthesis in most species. This observation led some to the conclusion that elevated global atmospheric CO_2 will almost universally increase photosynthetic rates, and that we currently know enough about the physiology of photosynthesis to predict these effects (Lemon, 1983). Evidence indicates that predicting the response of species to elevated CO_2 is more complicated. Genetic constraints, metabolic pathway, growth form, resource availability, and temperature can all affect the species response to elevated CO_2 (Oechel and Strain, 1985; Bazzaz *et al.*, 1985). In the absence of an experimental data base, the number of variables involved makes accurate predictions difficult. Some generalizations are possible, however.

1.331 Single Factor Effects of Elevated CO2

This section is fairly brief because single factor interaction rarely applies. In nature, there is competition for limiting resources with other individuals and species in the community. In the laboratory, resources are set at some level, and therefore interact with the CO_2 availability. Even when these other factors are not treated as a variable, they are influencing the plant response to elevated CO_2. In very few experiments are all non-CO_2 variables continuously held at optimal levels. Whether explicitly recognized or not, these other factors influence the response to elevated CO_2. For a comprehensive list of known and suspected effects of elevated CO_2 on plant physiology, growth, and development, see Strain, 1985.

Photosynthesis

C-3 species are inherently more responsive to elevated CO_2 than are C-4 species. Plants with strong sinks for carbohydrate, such as those with active storage organs or those with indeterminate growth patterns, are more likely to exhibit prolonged enhancement of photosynthetic rates with elevated CO_2.

Water-Use Efficiency

Water-use efficiency is often increased by elevated CO_2. C-3 species are likely to show a larger improvement than are C-4 species. Improvements in water-use efficiency are greater in xeric than in mesic situations (Oechel and Strain, 1985). Water is not limiting in much of wet tundra and tussock tundra, and CO_2 effects on water-use efficiency have not been shown to be important. Where CO_2 effects on water-use efficiency were investigated, no effect was found (Strain, unpubl. data, Appendix B). Perhaps in dry microsites or in periods of drought, this could be a significant factor.

Branching, Tillering, Population Biology, Growth Rates, and Growth Patterns

Tillering rates have been shown to increase at elevated CO_2. This is true for the sedge, *Eriophorum vaginatum* in the arctic (Tissue and Oechel, 1987), and for agricultural grasses in the phytotron (Sionit, *et al.*, 1980). Leaf production, leaf mortality, the percentage of bud primordia which become sexual, and bud size are all affected by CO_2 treatment (Appendix B, Oechel, *et al.*, subm.). Allocation to roots and shoots are also affected by CO_2 treatment.

Litter Quality, Forage Quality

There is an indication that in the arctic, nutrient content of the tissue can decrease with elevated CO_2 (below, Oechel, *et al.*, subm.). We anticipate that with other factors constant, elevated CO_2 should result in higher C/N and lignin/N ratios in litter and higher carbohydrate contents in living tissue and litter. To date, these effects have been modest in the arctic (Tissue and Oechel, 1987; Oechel, *et al.*, subm.). Lincoln, *et al.*, (1984) found that decreasing litter quality occurred in plant material grown at elevated CO_2 in the phytotron, and that this resulted in increased consumption by insect herbivores. Such a pattern, if it occurs in the arctic, could affect ecosystem structure and function.

1.332 INTERACTION OF CO_2 AVAILABILITY WITH OTHER FACTORS

The direct effects of CO_2 on vegetation is constrained by resource availability and climate. Resource availability and climate can be affected fairly directly by changes in global atmospheric CO_2 (e.g. changes in temperature, growing season, precipitation, and humidity), or indirectly through ecosystem interactions (e.g. nutrient availability). We know relatively little about the interaction of CO_2 with key climate and resource variables. We suspect that nutrient limitation and suboptimal climatic conditions can restrict the magnitude and duration of a response to elevated CO_2. Listed below are some of the major known or suspected interactions.

Temperature

Temperature is one of the factors thought to have the potential for a strong interaction with CO_2. Kimball, *et al.*, (1986) present information showing a positive interaction between CO_2 and temperature on the growth of a number of agricultural plant species. Such an interaction means that the response of plants to elevated CO_2 and temperature is greater than would be expected from knowledge of the responses to each of the factors separately. Such an effect, if it occurs, could have great relevance to the arctic where marked increases in growing season temperature are anticipated. Kimball, *et al.*, (1986) report inhibitory effects of low temperature on response to CO_2. However, their information is primarily based on within-season temperature variability; sensitivity to short-term changes in temperature may not translate to response to longer-term differences in temperature which occur in different vegetation zones or which may exist in response to CO_2-induced climate change. Also, conclusions of Kimball *et al.* are based on experiments with agricultural plants selected for growth under temperate conditions. Native species adapted to low temperatures may show a very different response in terms of the actual temperatures which cause inhibition or promotion of a CO_2 response if not the actual pattern of response to temperature.

We found a marked increase in net ecosystem carbon flux after three seasons of treatment with a CO_2 and 4°C temperature increase. Initially, net ecosystem carbon flux was reduced at elevated CO_2 and temperature compared to the CO_2 treatment only. Presumably, this reflects higher respiration rates at elevated temperature. However, the homeostatic adjustment which occurred at ambient temperature and elevated CO_2 was not seen at elevated CO_2 during the three years of treatment. The reason for this lack of homeostatic adjustment is not clear, but may reflect a direct temperature affect, possibly by increasing sink activity, or an indirect affect through increased mineralization and nutrient availability.

Unfortunately, resources did not permit a full factorial experiment, so a temperature-CO_2 interaction cannot be evaluated. With the data in hand, we cannot separate the direct effect of heating on ecosystem response from indirect affects due to increased mineralization and nutrient availability following soil heating. Proposed experiments will separate soil heating and nutrient effects and their interaction with elevated CO_2.

Any factors which increase the growth potential or sink strength should increase the ability of the plant to respond to elevated CO_2. Since temperature is frequently suboptimal, one would expect many situations where increased temperature will stimulate the response to CO_2. However, growth at elevated temperature did not seem to circumvent homeostatic adjustment of photosynthesis in *Eriophorum vaginatum* to elevated CO_2.

The full extent of interaction between CO_2 and temperature is yet to be learned.

Nutrients

Plants in many natural ecosystems are nutrient limited. This is certainly true for the tussock tundra. Severe nutrient limitation could restrict the response of plants and the ecosystem to elevated CO_2. To date, no field test of nutrient-CO_2 interaction has been performed. However, results of the temperature treatment discussed above indicates that increased nutrient availability with increased temperature could explain the increased CO_2 uptake at elevated temperature. The resolution to this question must await future experiments.

Billings, *et al.*, (1984) report trends for laboratory experiments utilizing field collected cores which indicate the highest CO_2 flux at elevated CO_2 and nutrients. However, two-way ANOVA indicates that the effect of CO_2 and the nutrient CO_2 interaction are significant for only one sampling period each of nine. The answer to whether there is a temperature-nutrient interaction which was obscured by variability also awaits further experimentation.

Phytotron studies with arctic species indicated relatively little effect of CO_2 or interaction of CO_2 and nutrients on growth parameters in three arctic species. Photosynthesis rates, on the other hand, were most often affected both by the growth CO_2 concentration, and by nutrient status, but not by nutrient-CO_2 interaction (Oberbauer, *et al.*, 1986a).

Experiments with *Quercus alba* seedlings growing in nutrient-poor native soil showed that in the first season of growth, an enhancement in growth was possible at elevated CO_2 (Norby, *et al.*, 1986b). A decrease in tissue-nitrogen content was found at elevated CO_2. This increase in nutrient-use efficiency under elevated CO_2 indicates that plants grown at ambient conditions were not under severe nutrient deficiency, since plants growing under the most severe nutrient limitations have already reduced tissue concentrations to a minimal level below which little additional decrease in concentration is possible (Chapin, 1980). It is unclear whether the growth response in *Quercus alba* can be carried into subsequent years since, as the authors point out, no increase in nutrient uptake at elevated CO_2 was found. There is a reduction in nutrient content in litter fall which may decrease the nutrients available through mineralization in subsequent years, and there was a reduction in nitrogen available for internal remobilization to support new growth.

In any case, the pattern found by Norby *et al.* was different from that which occurs in the arctic. The difference may be due to relatively greater nutrient limitation in the arctic or the relative responsiveness of the respective species to resource availability. Arctic species can be quite conservative in nutrient-use efficiency, often holding tissue content constant over a wide range of availability.

Research proposed here is intended as a conclusion to this arctic research program. The focus is on better understanding the limitations on response of arctic ecosystems to elevated CO_2. To accomplish this, three initial treatments are planned:

1) CO_2 enrichment; 2) increased soil temperature; and 3) a "greenhouse effect," the interactive effects of CO_2 and soil temperature. In conducting this research, emphasis will be placed on understanding the effect of the above factors on the shape of the response in ecosystem flux and on determining whether homeostatic adjustment has occurred. If net ecosystem flux adjusts in response to the above treatments, we will attempt to stimulate a response with nutrient addition or soil heat. This will indicate the factors limiting the response to elevated CO_2 and will provide important information when predicting the response of other ecosystems to elevated CO_2.

2. EXPERIMENTAL APPROACH

2.1 OVERVIEW

The arctic was chosen for the first field experiment on the response of native vegetation to elevated CO_2 because of the importance of tundra to the global carbon balance and because it was viewed as a tractable system for the closed, null balance greenhouse-cuvette system proposed. The short growing season and short stature of the vegetation were advantages in the development and implementation of this novel system.

The structure of the tundra ecosystem makes it particularly amenable to investigation of long-term effects of carbon dioxide enrichment. The low stature of tussock tundra and the small scale of the spacing between its basic physiognomic units (tussocks and intertussock) allow a representative subsample of the ecosystem to be enclosed within a controlled-environment chamber of reasonable size. Chambers were 1.22 m square and less than 0.5 m tall, and each was able to enclose three to five tussocks and associated intertussock vegetation (Oechel, *et al.*, subm., Appendix A; Prudhomme, *et al.*, 1984; Riechers, *et al.*, in prep.).

The net effect of a long-term increase in atmospheric CO_2 concentration in the world's biosphere is difficult to predict accurately from single-species responses. CO_2 enrichment of single species performed in growth chambers have clearly demonstrated that the magnitude to which plants are able to respond varies widely among species and that the capacity to respond is further reduced by complex interactions among other limitations to growth such as nutrient and water supplies. Increases in net productivity predicted from short-term experiments may be offset over the longer term by photosynthetic acclimation to elevated CO_2 or by end-product inhibition. Nutrient limitation may restrict potential increases in primary production resulting from elevated levels of CO_2, decreasing litter quality, slowing decomposition, and decreasing nutrient availability. Increasing litter fall may result in an increased litter layer which may cause a decrease in soil temperature, perhaps affecting the depth of the active layer and resulting in massive carbon storage in the soil.

The most direct means of determining ecosystem response to CO_2 enrichment is to experiment at that level for a long enough period to allow interactions among its various components. In natural ecosystems, limitations imposed by water, nutrients, and irradiance may moderate the impact of CO_2 enrichment, but the degree of this moderation is generally unknown (Oechel and Strain, 1985). CO_2 enrichment initially enhances the growth of some tundra species, but the effect is expected to decrease with time because nutrient limitations reduce the demand for the additional carbohydrate. Enhanced photosynthesis from CO_2 enrichment should increase the carbohydrate content of litter and increase soil C/N ratios. These two factors can cause competing effects. Increases in carbohydrate can stimulate decomposition while increasing C/N ratios, especially when accompanied by an increase in lignin or other recalcitrant material, may result in a decrease in decomposition rates. Because tundra soils are already nitrogen limited (Ulrich and Gersper, 1978), the net result of atmospheric CO_2 enrichment is likely to decrease soil respiration.

During the initial phase of this research, we were able to show marked differences in ecosystem acquisition of carbon with carbon dioxide enrichment and with elevated CO_2 and elevated air temperatures. We have a quality, null-balance photosynthetic system for ecosystem-level studies. With much of the development behind us, we are now poised to address both quantitative (how much) and qualitative (nature of response curve) questions. We can test general ecosystem theory with ecosystem-level experiments where CO_2 is one of the major system stressors, and obtain ecosystem-level response curves to carbon dioxide, temperature, and light.

A test of the "greenhouse effect," including carbon dioxide enrichment and increased soil temperature of 3-4°C, is proposed. The whole ecosystem, closed-chamber design is ideal to test loss of respired carbon through soil heating. In ambient carbon dioxide chambers, we have found a net seasonal loss of carbon (ecosystem respiration > photosynthesis). With a doubling of chamber atmospheric CO_2, we have shown a significantly greater initial ecosystem flux rate relative to controls resulting in a net ecosystem sequestering of carbon. From three years of CO_2 enrichment, we have found that the initial increase in ecosystem flux is lost through time. The research proposed here will address the effects of increases in soil temperature, elevated CO_2, their interaction, and ecosystem-level homeostatic adjustment. If ecosystem-level adjustment does occur during the first two years of treatment, we will use nutrients to attempt to re-stimulate increased ecosystem flux in 1) the elevated CO_2 treatment; 2) the increased soil-temperature treatment and; 3) the elevated CO_2 and soil-temperature treatment. The nutrient addition is to be a complete nutrient addition (plus sucrose to maintain microbial decomposition). The results presented above, and these experiments will be the first field test of ecosystem-level flux to elevated CO_2 with both single and multiple physical factors. The proposed experiments will indicate the whole ecosystem response to elevated CO_2 and soil temperature, interactions between the two factors, and the factors limiting a long-term response to elevated CO_2 and temperature.

This research is designed to test the interaction of CO_2, soil temperature, and nutrient availability on specific parameters important to ecosystem functioning.

Major end points proposed for this research include the effects of elevated CO_2 and the interaction of elevated atmospheric CO_2 with elevated soil temperature and increased nutrient availability on:

1) Net ecosystem CO_2 flux;
2) Net photosynthetic rates;
3) Patterns and resource controls on homeostatic adjustment in the above processes to elevated CO_2;
4) Plant-nutrient status, litter quality, and forage quality;
5) Soil-nutrient status;
6) Plant-growth pattern and shoot demography.

This information will be incorporated in and used to advance existing models of the response of arctic ecosystems (ARTUS-CO_2) and plant growth to elevated atmospheric CO_2. Existing plant population models will be used to predict new steady state assemblages from observed changes in shoot demography.

This research focuses on what we believe to be the key limitation to utilization of elevated CO_2, nutrients, and the key environmental response to elevated CO_2 (soil temperature). The proposed research will investigate the most important primary biological responses to elevated CO_2 (CO_2 flux, nutrient status, growth, and demography). The manipulations will be carried out in the field where the normal limitations on response and system level interactions will occur.

We feel that it is particularly important to conduct these final proposed experiments. Past research in the arctic has raised important and currently unanswered questions. It seems worthwhile to answer these questions before moving to a new biome. The likelihood of returning to the arctic, and regaining lost momentum, is small once the arctic site is left and a new site established.

2.2 EXPERIMENTAL DESIGN

The established research site is within the tussock tundra at Toolik Lake, Alaska, in the northern foothills of the Central Brooks Range (68°38'N, 149°34'W). For the closed-chamber experiment, there are an existing 14 chamber bases installed in mid-July 1985 (Figure 2a). Two of these chambers are not suitable for future experimentation because they have had the seasonal elevated CO_2 treatment in 1987. Seven were used for the light, air temperature, carbon dioxide, and dark respiration experiments in 1987 (see Results, Appendix B). In addition, two chamber bases were a type of control ambient with base. Chamber flux was tested periodically at 340 µl/l (ambient) throughout the season on the experimental chambers. After examining the flux rates and comparing them to the seasonal 340 µl/l treatments, we do not believe that the experimentation has had a lasting effect on whole ecosystem flux. These chamber bases, in addition to a new one with a cuvette will be used in the following two-way factorial design with three chambers per treatment. In addition to those bases to which cuvettes are attached, an additional six bases will be installed, three for control and three to which a full fertilizer (nutrients and sucrose to maintain microbial populations and activity) will be added twice during the summer in 1988 (not shown in Figure 2a).

The 1987 chamber base assignment is shown in Figure 13, with a three-year projection of treatments for the 1) 340 µl/l; 2) 340 plus elevated soil temperature; 3) 680 µl/l; 4) 680 µl/l plus elevated soil temperature; 5) chamber bases alone with no cuvettes attached; 6) true ambients (no cuvette or base; not shown in Figure 2a); 7) full-fertilizer treatments (treated twice a growing season) as a future control and used for comparing individual species response. The first two years will have the same treatment with three chambers per treatment. Between 1989 and 1990, we will examine the data and test for acclimation in flux in each of the treatments. If we find an initial increase in treatment flux rate (for 2, 3, or 4 above), we will test for a subsequent decline in 1989. If homeostatic adjustment in ecosystem flux can be determined, then additional manipulations will be conducted to ascertain underlying controls on this adjustment.

To attempt to restimulate ecosystem flux, we propose to add three chambers at 340 µl/l CO_2 as a control while enriching nutrient availability with a complete nutrient solution in all others. We propose to also monitor field photosynthetic response of individual species to the above treatments (*Eriophorum vaginatum* (tussock sedge, a competitive species, *sensu* Grime, 1979), *Ledum palustre* ssp. *decumbens* (dwarf heath, a conservative species), *Vaccinium vitis-idaea* (dwarf heath, a relatively

Closed Chamber Experiment

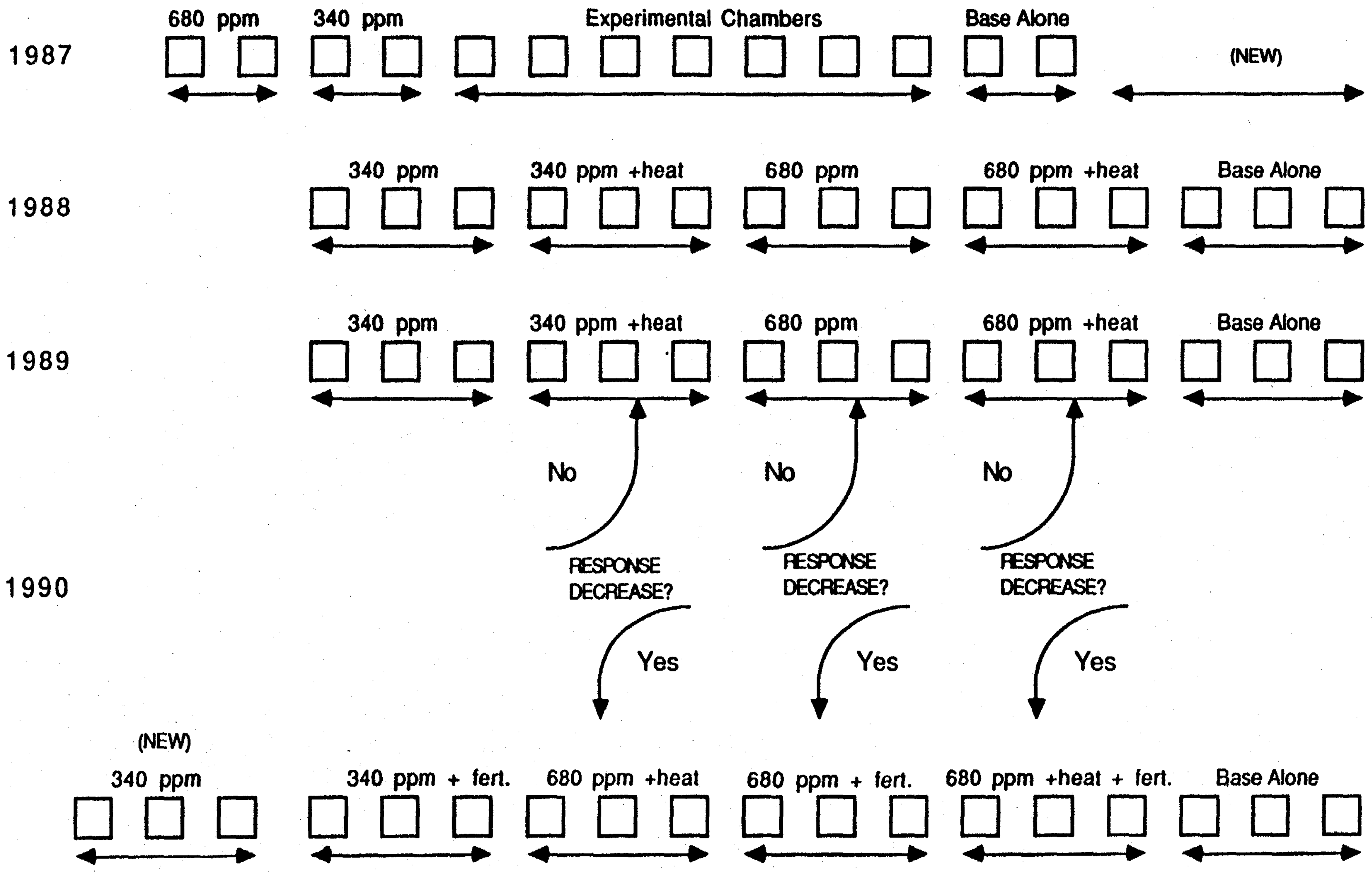


Figure 13 Experimental layout for the 1988 through 1990 closed-chamber treatments, including reassignment of 1987 chamber bases. New chamber bases will be installed to complete the 2-way factorial design. 'Heat' denotes soil heating of 3-4°C, and 'fert' denotes a complete fertilizer treatment including sucrose. If homeostatic adjustment of ecosystem flux occurs by the beginning of the 1990 field season 'Response decrease?,' then the 1988 and 1989 treatments will be further modified to the 1990 reassignment. Otherwise, the treatment will remain the same for the three years.

conservative species), and *Betula nana* (deciduous dwarf shrub, a relatively competitive species), which are the dominant vascular plant species locally and regionally in the tussock tundra. We support a supplemental proposal from Dr. Bart Sveinbjornsson (University of Alaska, Anchorage) to test for responses in the two dominant cryptogams (mosses): *Aulacomnium turginatum* and *Sphagnum angustifolium.* If this proposal is not funded, we will attempt to monitor moss photosynthetic response using a cuvette similar to that designed for very small high arctic grasses with similar low photosynthetic rate (Grulke, unpubl. data).

2.3 QUESTIONS AND HYPOTHESES

The effects of manipulations will be analyzed at three levels: the ecosystem flux rate (priority) and whole ecosystem "integrators" (lignin/N, C/N, lignin/P, and C/P ratios), population response (leaf, bud, shoot, and tiller population dynamics), and individual species' response (nutrient uptake, photosynthetic response). The experimental design outlined above will allow us to address the following questions and hypotheses, concerning ecosystem flux:

1) Maintenance of long-term 340 µl/l chamber: How variable is the yearly net ecosystem flux? Is carbon acquisition or loss the *status quo* for upland tundra ecosystems?

Net ecosystem carbon gain has been documented for the coastal wet tundra at Barrow, Alaska. The Toolik Lake site is a drier, warmer example of tussock tundra and representative of much of the moist upland tundra in the arctic. This is an ideal ecosystem in which to test whether there is net carbon gain or loss and the associated variability. We hypothesize that the upland tussock tundra will continue to show a net negative CO_2 flux (respiratory loss).

2) 340 µl/l plus soil heating of 3-4°C: Is soil heating or elevated carbon dioxide more limiting to ecosystem flux (in conjunction with 3 below)? Is the response to soil heating a medium- or long-term response relative to CO_2 enrichment?

A 4°C rise in global air temperature is predicted, but the resulting translation to soil heating may be the critical factor in the synergy of global warming on tundra ecosystems. We hypothesize that the net result of soil heating will be nutrient enrichment, similar to appropriate level fertilization treatments. We expect plant response (photosynthetic gains) under ambient CO_2 levels and soil heating of +3-4°C to be similar to a low or moderate nutrient enrichment. We expect an increase in plant photosynthesis (both single species and ecosystem-level flux) resulting from a general increase in tissue-nutrient content (and specifically nitrogen; Oberbauer, *et al.*, in prep.) with an accompanying increase in litter quality (decreased lignin/N, C/N). The increase in plant photosynthetic gain should be then translated to a net increase in ecosystem flux and a seasonal carbon sequestering. We expect an initial increase in soil respiratory losses (Oberbauer, *et al.*, 1986b; Oechel, *et al.*, subm.) and net carbon loss with an increase in soil temperature.

3) 680 µl/l: With CO_2 enrichment, how much is ecosystem-level flux rate increased? How long does it last? How early in the growing season can competing species (*Eriophorum vaginatum, Betula nana, Salix pulchra*) respond to the elevated CO_2? Does this period of early response represent a significant portion of the seasonal carbon budget? Once the ecosystem acclimation to CO_2

enrichment has occurred, can we re-stimulate enhanced flux with increased soil-nutrient availability? How will elevated atmospheric carbon affect leaf-nutrient content, litter quality, and types and quantities of secondary plant compounds?

We know from the 1983-1985 as well as 1987 seasonal data that with CO_2 enrichment, we will initially see a significant net carbon gain in an upland tundra ecosystem. The ecosystem flux shows signs of acclimation to elevated CO_2 even within the growing season. However, we further hypothesize that the 340 µl/l CO_2 treatment plus soil heating of 3-4°C will eventually (2-3 years) result in a greater ecosystem carbon gain than will the elevated CO_2 treatment. In other words, we believe that ecosystem carbon gain is more limited over the medium term by temperature and nutrient availability than by carbon availability. Again, this closed-chamber design offers a unique opportunity to test short- and medium-term ecosystem response and acclimation.

We expect that lignin/N, lignin/P, C/N, and C/P ratios (as whole ecosystem integrators) will increase in both leaf tissue and leaf litter as a result of elevated CO_2 availability (with no soil heating or fertilization). We hypothesize that in a nutrient rather than a carbon-limited ecosystem, there will be an increase in secondary plant compounds including tannins and phenols with CO_2 treatment. In addition to the expected decrease in food quality with long-term CO_2 enrichment, the exacerbation of poor palatability could have serious implications on levels of herbivory and herbivores (Lincoln, *et al.*, 1984).

4) 680 µl/l plus soil heating of 3-4°C: Will the effects of elevated CO_2 and soil temperature be additive or synergistic? Is the acclimated ecosystem flux rate more similar to the elevated CO_2, or the elevated soil temperature effect? Is the response to the "greenhouse effect" medium term (2-3 y) or long term (> 3 y) (distinguished by time it takes to become acclimated)?

We propose to manipulate only soil (not air) temperature, and to ignore an associated longer snow-free period which could result from increased air and soil temperature. We hypothesize that enriching both carbon and nutrients (via soil heating) will have synergistic effects on net ecosystem flux and that the combined effects will be greater than the additive effects that could be predicted from carbon enrichment or nutrient enrichment alone. We expect that it will take longer for homeostatic adjustment of the ecosystem to occur under both carbon and nutrient enrichment.

The summary of predicted relative net ecosystem flux response to treatment ("heat" below refers to elevated soil temperature of 3-4°C):

1988 late mid-season ecosystem flux rate:

[680 µl/l] > [680 µl/l + heat] > [340 µl/l] > [340 µl/l + heat]

1989 late mid-season ecosystem flux rate:

[680 µl/l + heat] ≈ [340 µl/l + heat] > [680 µl/l] ≈ [340 µl/l]

1990 late mid-season ecosystem flux rate (see Figure 2a for acclimation experiments):

1990 [680 µl/l + heat + fert*] > 1988 [680 µl/l + heat]

1990 [680 µl/l + fert*] > 1988 [680 µl/l + heat]

1990 [340 µl/l + heat + fert] > 1988 [340 µl/l + heat]

* = appropriate (low to moderate) fertilization plus sucrose (see below)

2.4 METHODS

Considerable effort has been devoted to developing a quality, null-balance photosynthetic system. Flux rates will be measured in the closed chambers as has been described in previous reports and publications (Oechel, *et al.*, subm., Appendix A; Riechers, *et al.*, in prep.). Supporting data for the flux measurements include photosynthetically active radiation, air, leaf and soil temperature, and air humidity (vapor pressure deficits). These data will be used to determine light and temperature response curves for ecosystem flux at 340 µl/l, 680 µl/l, 340 µl/l + heat, and 680 µl/l + heat treatments. This is currently being carried out with the 1987 seasonal fluxes and will provide the next step of refining models of ecosystem CO_2 flux with respect to these factors (see Results 3.411 in Appendix B for description of data reduction) except as noted, methods will follow those used previously (Oechel, *et al.*, subm.; Tissue and Oechel, 1987; Oberbauer, *et al.*, 1986a,b, Appendix A below). Chamber modification, repair, and expansion by two greenhouses is proposed.

2.41 CHAMBER MODIFICATION AND MAINTENANCE

One new chamber is requested for a balanced two-factor analysis of the interaction between CO_2 enrichment and soil heating. Complete parts for an additional chamber are requested for back-up, and an additional six bases will be needed to round out the experimental design.

The chambers have now had four field seasons of use and a number of components need to be repaired or replaced. For 12 chambers, the following mortality of components has been noted in the 1987 field season: solenoids (3); solid-state relays (3); air pumps (6); mass flow valves (4); chamber tops and sides (2); fans (3); mylar tops (1); refrigerator compressor, repair (1); and overhaul of the rest of the compressors.

In order to reduce possible chamber contamination with soda lime dust, high quality air filters will be installed prior to the return of sample air to the chamber. The mass flow controllers are a vast improvement over rotameters. However, we need a means for manually checking flow on occasions when due to weather conditions the mass flow controllers may be undependable. To eliminate possible soil heating effects, the steel chamber bases will be replaced with linear polyethylene bases (chemically inert with a low thermal conductivity).

2.42 SYSTEM MODIFICATION AND MAINTENANCE

We feel that we have an excellent system for controlling CO_2 concentration and related environmental factors of interest. The accuracy of environmental control and reliability of the greenhouse system are outstanding. The ability to accurately and continuously measure whole ecosystem CO_2 flux while modifying the CO_2 and climatic environment is unique (Oechel, *et al.*, subm., Appendix A). However, there are still a few, relatively minor modifications proposed to further improve system performance.

One weak component in the system are the air pumps which draw air from the chambers, pump it through the scrub tubes, and return it to the chambers. To circumvent this problem, we are requesting a dependable industrial air pump that can handle the air volume of all the chambers. A high quality pump prior to IRGAs is also necessary to maintain steady air flow. Large variations in air flow to the IRGA can cause erratic readings. To obtain a more accurate estimation of leak rates, the Liston-Edwards nitrous oxide IRGA needs to be replaced. The Liston-Edwards has proved unstable and has a high noise-to-signal ratio (highly sensitive to temperature fluctuations and vibrations). High quality alternatives at modest price are now available.

The rainfall simulator will be modified with better quality, clog resistant, mister heads, swage-lock fittings throughout the system that can withstand the water pressure applied, and valves in line just prior to each mister head to more precisely control water flow to each chamber.

Manual override for temperature control on all chambers is proposed to prevent freezing of the chambers in the event of control program failure since the compressors must be plugged in at all times to provide a constant load on the generator.

Early in the season, during program failures, and during necessary system shutdown for repair, we lack complete microenvironmental data which could be useful in simulating and estimating total season CO_2 flux. A Campbell data logger will be installed to obtain these data.

The research shack will be increased in size so that mass flow controllers and integrators can be brought inside to maintain constant temperature environment and to provide a temperature-controlled field calibration and trouble-shooting facility. Moving the flow valves into the shack will require some minimal re-plumbing of the gas lines.

The homemade integrating circuits used in 1987 had erratic noise, and high noise-to-signal ratio. We are proposing to place a relatively inexpensive analog to digital converter in line after the mass flow controllers to reduce noise sent to the data acquisition system. A professional systems engineer is budgeted to evaluate and trouble-shoot the entire electronics and electrical system, and to oversee smooth operation in the field.

At least five people have contributed to the control program. A professional modification and clean-up of control program is in order at this point and is proposed.

2.43 SOIL HEATING

The technique of applying long-term soil heating to northern ecosystems has been well established (Van Cleve and Oechel, in prep.). Hom (1986) has described a simple mechanical approach to soil heating via capillary-type thermostats which activated relays for the heat cables ("heat tape") spaced at 20 cm intervals in the soil. This system was able to maintain temperatures at 8-10°C above ambient soil conditions over three field seasons (Hom, 1986; Hom, *et al.*, in prep.; Van Cleve and Oechel, in prep.). The heat tape will be threaded through the organic soil, approximately 20 cm below the average tussock surface. Comparison between ambient and heated soil temperature will be carefully monitored; this is already a component of the control program. Care will be taken to insulate all chambers and heating apparatus from the surrounding intact tundra.

2.44 FERTILIZATION

Fertilizer will be applied within chamber bases (not shown in Figure 12) at low levels twice a growing season within (early June and early July). "Low levels" are considered to be equivalent to twofold the amount found in ecosystem annual growth, and can be estimated from nutrient analyses (macro- and micronutrients available, Grulke, unpubl. data) of the dominant vascular species in the chambers: *Bistorta bistortoides, Betula nana, Carex bigelowii, Eriophorum vaginatum, Ledum palustre* ssp. *decumbens,* and *Vaccinium vitis-idaea.* Other vascular species which occur in the chambers, but not dominantly or consistently include: *Empetrum nigrum* ssp. *hermaphroditum, Kalmia polifolia, Pedicularis verticillata, Pedicularis capitata,* and *Salix pulchra.* Estimates of nutrient content of these species will be obtained from the literature (e.g. Wein and Bliss, 1974).

2.45 MONITORING AND EXPERIMENTAL METHODS

Ecosystem CO_2 Flux

Diurnal and seasonal CO_2 flux will be continuously measured during the growing season using the null balance greenhouse system described here. Data recording and data analysis will follow the most recent protocol developed (Oechel *et al.*, subm., Appendix A, B).

Photosynthetic response to CO_2

Photosynthetic response characteristics will be determined for representative species in each of the treatments at peak season as previously reported (Tissue and Oechel, 1987). In addition, curves of assimilation versus internal leaf CO_2 concentration will be established and stomatal conductance and water-use efficiency measured for the dominant, representative species. Species to be measured include: *Eriophorum vaginatum, Carex bigelowii, Salix pulchra, Betula nana, Ledum palustre, vaccinium vitis-idaea, Aulacomnium turginatum,* and *Sphagnum angustifolium.*

Microenvironmental Monitoring

Although the system already monitors photosynthetically-active radiation, air, leaf, soil temperature, and air humidity (Riechers, *et al.*, in prep.; Oechel, *et al.*, subm.), we lose this valuable data when the system is down (as for example during weekly generator maintenance or with system maintenance). We are currently developing ecosystem-level response curves to light, air, and soil temperature. A Campbell data logger will be added to provide continuous environmental monitoring that is independent of the system. In this way we will be able to simulate ecosystem flux response to known environmental factors during periods for which there are no data. This will greatly improve our ability to estimate net seasonal ecosystem flux in each treatment.

Decomposition

The direct effect of soil heating will be on the temperature-controlled rates of decomposition. The easiest and most inexpensive way to determine decomposition rates is with "litter bags." Eight vascular plant species and two mosses were found to be ubiquitous in all 12 chambers and two chamber bases (see Appendix B, 2.423). They include: *Eriophorum vaginatum, Carex bigelowii, Salix pulchra, Betula nana, Ledum palustre* ssp. *decumbens, Vaccinium vitis-idaea, Aulacomnium turginatum,* and

Sphagnum angustifolium. Equal amounts of similar tissue will be combined (both sedges, both deciduous shrubs, both dwarf heaths, and both mosses) for determining decomposition rates. Approximately 0.5 g of air-dried, mixed material will be used for each litter bag, approximately three bags per growth form, per chamber (total of 12 bags per chamber) will be used. Loss of dry weight and nutrient content of the samples will be tested after two growing seasons at the end of 1989.

In addition to litter bags, a relatively new technique for determining decomposition has been developed involving various types of compounds (simple and complex organics) impregnated in a porous, polymer plate. The decomposition rate of the compound or group of compounds can then be calculated from weight loss of the plate. Although relatively expensive, this is a specific, sensitive technique. Due to their cost and to minimize impact within the chambers, these plates are proposed for the 1989 treatments to test the difference between heat, fertilization, and heat and fertilization in combination with the 680 µl/l atmosphere (Figure 2a).

Nutrient Content and Secondary Plant Compound Analysis

The treatment effects on the nutrient content of soil solution will be closely monitored using the miniature lysimeters developed and tested during the 1987 field season (see Results, Appendix B). Three replicates for each chamber will be pooled (three replicates of solutions per treatment), and the solutions will be handled in the same manner as in 1987 (see Results, Appendix B). Leaf tissue at the end of mid-season, and senescent tissue collected at the end of August will be collected from the dominant species (listed in *Decomposition* above plus *Bistorta bistortoides*). The collection of 0.3 g of tissue of each species per each of three replicates will allow sufficient material for analysis of nutrient content (specifically N and P). The replicates of leaf material from each species will be combined for each chamber. This combined sample will be analyzed for total carbon (loss on ignition, equipment available to N. Grulke at the University of Washington), total hydrolyzable tannins, and lignin content. Statistical analyses will test for differences between the lignin/N, lignin P, C/N, C/P ratios, and quantities of tannins and lignins between the treatments. Alkaloids were not present in any appreciable quantities in three deciduous and a dwarf evergreen heath species at any time during the growing season at another North Slope Brooks Range site (Grulke and Rhoades, in prep.). The total plant material that will be extracted yearly is slightly greater than 1% of the total live standing biomass, and is not expected to significantly affect the overall flux rate or nutrition of the chambers.

Population Dynamics

The growing-point analysis (location and fate probabilities) used in the 1987 field season was an effective means of detecting first-year responses to elevated CO_2 (see Results, Appendix B, 3.431), and the same approach and sample sizes will be taken with the same vascular plant species as outlined. For the mosses, the population dynamics of *Aulacomnium turginatum* and *Sphagnum angustifolium* only is proposed for population dynamics studies (see Results, Appendix B, 3.431). Other vegetative characteristics such as leaf length and number will not be used because these characters respond at a timescale greater than one year, and are time-consuming (see Results, Appendix B, 3.432). The growing-point analysis can be performed without opening the chambers through the summer except for mapping bud location and type on each ramet (see Appendix B, 3.431) early and late in the season. This method also has the advantage of providing the basis for population dynamics models, and projecting probable population sizes of growing points (and therefore biomass estimates) forward in time.

2.5 PERSONNEL AND STRUCTURING OF FIELD TIME

In the past, the project has been staffed with four to five people. Loss of temperature control during program or system kill necessitated 24 hr attendance. We propose to set up and take down the system with four people, but run the system with three to four people. We will install mechanical overrides (thermostat control) on temperature control which will prevent freezing or overheating of the system. Although these mechanical shut-offs will not control the CO_2 levels in the chambers, temporary variation in CO_2 levels will not seriously harm the plants for a possible 7 hr excursion (00:00 to 07:00) if the program or system kill were to occur at midnight. The mechanical override will free up time for the additional physiological measurements and population characterization as proposed.

Personnel will largely continue as in 1987 with several changes. George Riechers will not continue with the project. Nancy Grulke will assume responsibilities for on-site field supervision. Riechers' technical contributions will be assumed by on-site technicians and consulting engineers. One field assistant is to be an upper level or graduate student engineer from the Engineering School at SDSU backed up by a faculty engineer. Dr. Riechers' scientific contribution will be covered by the other senior personnel on the project.

W. C. Oechel is primarily responsible for the project. He will oversee general program development, progress, budgeting, and reporting. Nancy Grulke, a research associate and co-principal investigator is the continuous on-site supervisor for the field aspect of the program. She will oversee successful chamber operation and the field sampling schedule. Dr. Grulke will work on the project 75% time in the first year and full time thereafter. She has one-year's experience with the CO_2 program at Toolik Lake and many years' experience conducting research in remote arctic locations.

Steve Hastings is the chief technician for the project. He is budgeted 75% time in the first year and 100% thereafter. Mr. Hastings has responsibility for the smooth running of the chamber system, chamber maintenance and implementation of new upgrades, and for the field sampling. Mr. Hastings has four seasons' experience in the arctic at Toolik lake and has been with the group since 1980.

A systems engineer, John Celto, will be contracted to consult on current system design and planned modifications and to troubleshoot in the event a problem arises which is not easily resolved by the field crew. Flight connections are such that the engineer can be in the field within one or two days of a problem being identified. The systems engineer will be consulted on the implementation of system overrides, audio and visual alarm systems, other additions to the system including integrators and analog to digital converters. Additional help is anticipated from the Engineering School as part of their system of senior honors theses in mechanical and electrical engineering.

Dr. Steve Roberts, President of Data Design Group, is familiar with the operation and design of the system. He has agreed to evaluate the current design, initiate needed changes, oversee their construction and implementation, and consult in the event of a system failure. Walt Merek, the refrigeration technician for the Biology Department, will be available should any refrigeration problems develop in the field. He will be also responsible for bringing current refrigeration units to specifications this spring.

We will contract with a systems analyst for profession evaluation and modification of the control program. The control program has benefited from the programming input of more than five individuals, and would now benefit from streamlining and consolidation of the 30+ pages of code and notation.

Marty Blake-Jacobson, or another familiar with the ARTUS-CO_2 model, will be contracted to program revisions in the model to incorporate recent information on the response of arctic ecosystems to elevated CO_2 and to exercise the model for comparison to experimental data and for scenario development.

Two field assistants will be employed to assist in system maintenance and sampling. It is our intention that one or both of these individuals be returning veterans to the arctic CO_2 project.

Ulf Hjelm will continue as the computer technician responsible for data reduction, analysis, and presentation. Next-day analysis and graphing of the data will occur in the field to give a general overview of system performance and ecosystem response. Due to time constraints and limited computer capacity in the field, final analysis must be carried out at the University.

Sufficient hardware will be placed in the field to allow next-day synoptic data analysis and graphing. Next-day analysis was routine earlier in the program, but this activity was suspended due to constraints on storage space and field time. It will be resumed in 1988. The same assignment of field time is outlined in Figure 14 for 1988, 1989, and 1990. In 1991, we propose a reduced field crew of three (WCO, NG plus FA) to spend three weeks in June to sample the fate of the growing points for population modeling (assignment not listed in figure).

3. SIGNIFICANCE OF PROPOSED RESEARCH

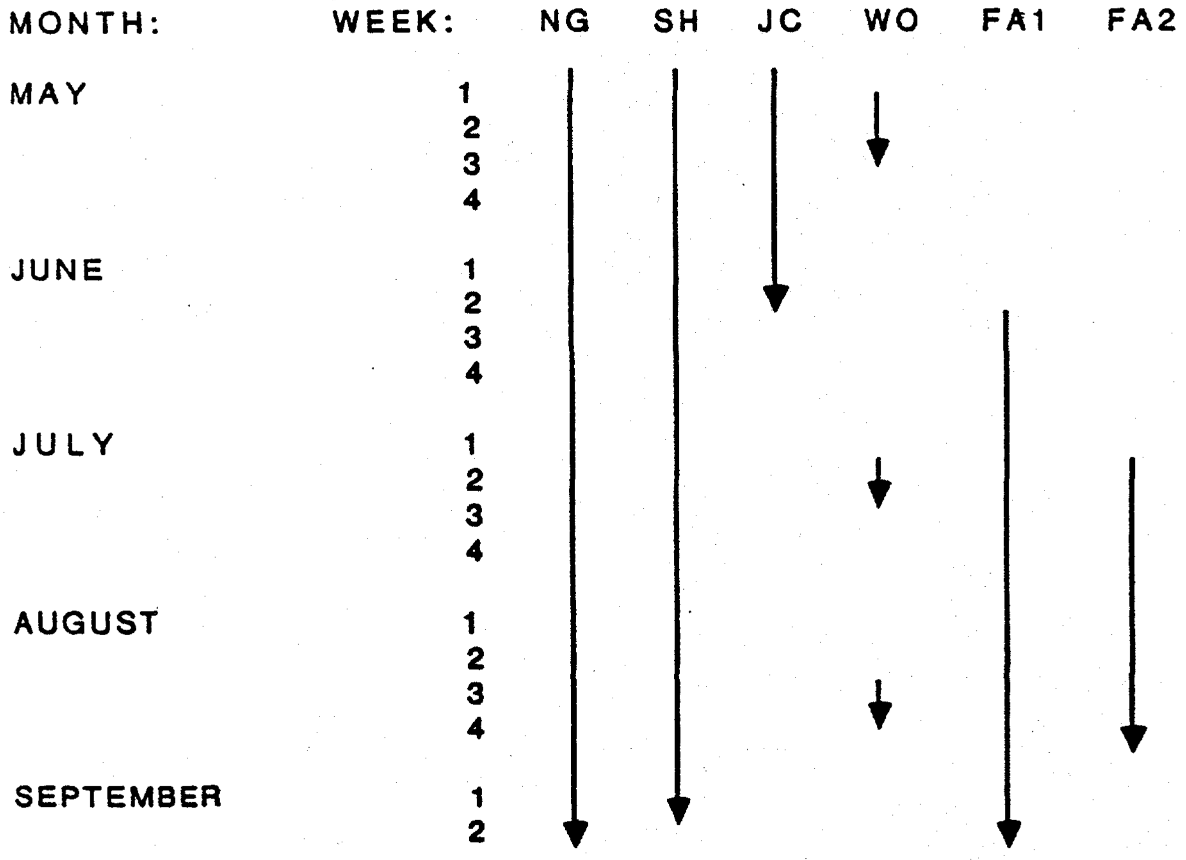
Given the importance of the arctic to the world's carbon budget and seasonal pattern of variation in atmospheric CO_2 and trace gas emissions, it is important to gain a thorough knowledge of the response of the arctic to elevated CO_2 and temperature. Furthermore, we are at a point of equipment development, familiarity with the system, and familiarity with initial responses to enhanced CO_2 where rapid progress towards new understanding of response to elevated CO_2 and interactions of CO_2 with other factors can be expected. Such information gained for the arctic will have relevance to understanding and predicting the response of other unmanaged ecosystems to elevated CO_2 and climate change.

Eventually a number of unmanaged ecosystems need to be studied and their response to elevated atmospheric CO_2 in interaction with other limiting factors determined (Oechel and Strain, 1985). Nevertheless, it seems important to capitalize on our high level of understanding and technical competence in the arctic to answer questions concerning ecosystem response to elevated CO_2. We will not be in a position to answer similar questions in other systems for a number of years.

This four-year study is proposed as a conclusion to our arctic CO_2 program and is anticipated to provide the following information and to contribute to the following areas.

1. We are confident that the upland tundra is not accumulating carbon at the rates previously assumed (Miller, 1981). In the research proposed it will be possible to refine the seasonal and annual ecosystem CO_2 fluxes. These values have relevance to understanding the world's carbon balance, and the relevance of CO_2-induced changes.

SCHEDULING OF FIELD TIME:



NG = NANCY GRULKE
SH = STEVE HASTINGS
JC = JOHN CELTO, SYSTEMS ENGINEER
WO = WALT OECHEL
FA1 = FIELD ASSISTANT #1
FA2 = FIELD ASSISTANT #2

Figure 14 Assignment of personnel and field commitments for the 1988, 1989, and 1990 field seasons. The 1991 field season will consist of two people to sample population dynamics parameters in June 1991.

2. The arctic ecosystem and component plant species adjust to elevated CO_2 more fully and quickly than previously realized. Our past research has shown and confirmed that ecosystem flux adjusts within three years to elevated CO_2, and that some adjustment appears to occur within several days. Similarly, photosynthesis of the dominant plant (*Eriophorum vaginatum*) adjusts completely within several weeks to elevated CO_2. However, the controls on these patterns are less well understood. Modification of soil temperature and available nutrient supply will indicate whether this response is entirely due to nutrient limitation, or if genetic constraints in the individuals present or limitation by other resources is restricting the response to elevated CO_2. This information obviously has relevance to other ecosystems where genetic or resource limitation to response to elevated CO_2 may exist.

3. A major impact of elevated CO_2 may be changes in branching patterns, growth patterns, and sexual and asexual reproduction. Even if there is little long-term effect of elevated CO_2 on the metabolic rates of the species present, changes in community composition and structure could have a major impact on ecosystem functioning. Replacement of a less productive species by more productive species could have a significant impact on ecosystem performance. Observed changes in the tillering rate of *Eriophorum vaginatum*, the bud size of *Ledum palustre*, or the relative production of vegetative versus sexual shoots in *Vaccinium vitis-idaea* if they persist, could cause major and significant changes in the vegetation.

4. Billings, *et al.*, (1982, 1983, 1984) have speculated that indirect effects of elevated CO_2 on the water table, depth to permafrost, and soil temperature will have more important effects on net carbon flux in the wet tundra than the direct effect of increased CO_2 supply. We have shown that the initial effect of elevated CO_2 on ecosystem CO_2 flux is large, but that in the absence of a change in other factors such as nutrient availability or temperature, this effect is transitory. Contrary to predictions by Billings, but consistent with the predictions of the SDSU Workshop (Miller, 1981) and the NECS model (Miller, *et al.*, 1983), elevated CO_2 and temperature caused a continued increase in carbon uptake compared to contemporary ambient conditions. The soil heating experiment proposed will separate the effects of increases in air and soil temperature, tested previously, from the effects of elevated soil temperature only. Measurements of soil solution and tissue-nutrient levels during heating, and subsequent fertilization of the heated and unheated treatment plots, will indicate the extent to which enhancements due to elevated soil temperature may have resulted from increased nutrient availability.

   This information will greatly improve our ability to define and model the response of the tussock tundra to elevated CO_2 and temperature. Furthermore, it will give us information about interacting factors in a way that will improve our ability to predict responses to other combinations of factors and to other ecosystems.

5. The tussock tundra consists of a number of different growth forms including mosses, sedges, forbs, deciduous shrubs, and evergreen shrubs. These growth forms represent a diversity of patterns with respect to aspects thought to be important in response to elevated CO_2 including life history, resource status, and resource allocation (storage versus utilization). Patterns of response identified in the arctic will form a good starting point for hypotheses and predictions for the response of individuals in other ecosystems.

6. This information will be used to help set the bounds on and the structure of generic, modular plant growth and ecosystem models of Reynolds (Reynolds, 1987a,b). Independent data sets will also be used as initial verification of these models.

7. This information will allow further development of arctic ecosystem models. ARTUS-CO_2 was developed to the point it reflected current knowledge and understanding. Recent results and information from the experiments proposed here will allow a major advancement in arctic ecosystems and growth modeling of the effects of elevated CO_2 and interacting factors. This will not only aid scenario forecasting of the effects of elevated CO_2 in the arctic, it should also provide approaches relevant to modeling of other ecosystems.

8. The arctic tundra is a major store of carbon. Much of this is present as soil organic material. Unlike the wet tundra, upland tussock tundra may have minimal levels of accumulation under current conditions. The fate of the stored carbon under future conditions is of relevance to the global carbon balance. Changes in local carbon balance will affect production and nutrient status of the system. The work proposed should give good estimates of current carbon balance, the effect of increases in atmospheric CO_2 on carbon balance, and interactions with soil temperature and nutrient availability. It may continue for some time to be impossible to wholly predict the state of carbon balance in the tussock tundra for the middle of the next century. However, with the information available from past research and that proposed here, we should be able to predict the effects of an increase in CO_2 and certain aspects of climate change on selected processes of interest.

4. RELATION TO OTHER STUDIES

This research represents a contribution to the DOE Carbon Dioxide Research objective of predicting changes in carbon balance, growth, productivity and function of plants, communities, and ecosystems resulting from rising atmospheric CO_2 and associated climate change (Dahlman, 1984; Dahlman *et al.*, 1985) (Figure 15). This research is part of a Phase I effort intended to build a diverse data base. This data base will be used to identify the needed structure of plant growth and ecosystem models. Independent Phase I data will be used to verify these models.

Phase II research is designed to investigate the patterns of plant and ecosystem responses in order to set some of the likely bounds of response to be encompassed by native plants and unmanaged ecosystems. Initially a number of plant and ecosystem processes were selected to represent a range of response types where important CO_2-induced changes could be expected. Material from a range of ecosystems has been studied which are diverse with respect to water, temperature, and nutrient availability. Response of plants and ecosystems in plant physiology, growth, population dynamics, and field ecosystem carbon flux, productivity, and species composition are being studied.

The ecosystems and processes investigated are not comprehensive, but rather selected to represent a range of potentially important response patterns from a range of habitats (Strain and Bazzaz, 1983; Oechel and Strain, 1985). This information is intended to set some general bounds on the responses anticipated. In Phase I, work in these diverse systems and environments will be completed. Resultant information will be used to structure the plant growth and ecosystem models.

This work will continue to be coordinated with members of the University Consortium on Carbon Dioxide Research (currently San Diego State, Harvard, and Duke Universities) and the generic, modular modeling program of Jim Reynolds. This proposed research represents the conclusion of our involvement in Phase I of the Consortium research. At the end of this research, we will be prepared for concentration

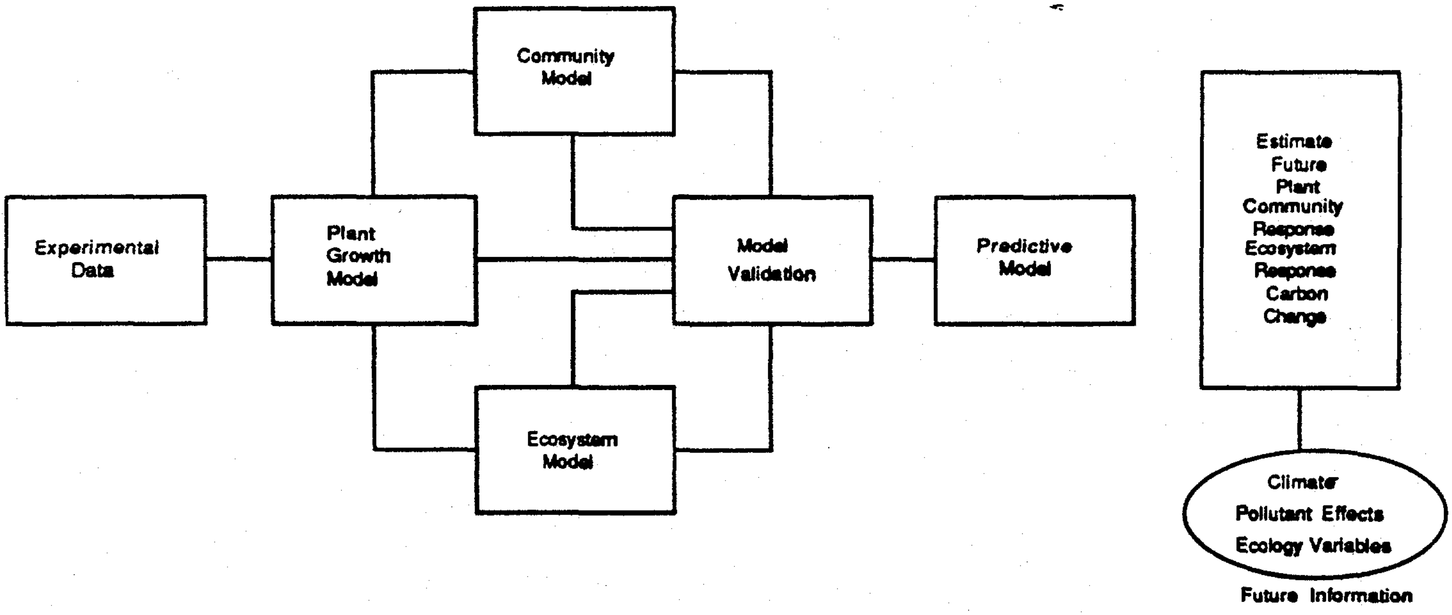


Figure 15 A graphical model of CO_2 research goals of the Office of Carbon Dioxide Research, Department of Energy (from Dahlman, 1985).

on Phase II research on a single coordinated, integrated research site or system to be used by members of the Consortium. Here integrated research can lead to a complete data base developed with good interchange among modeling and experimental programs.

In addition to our continued involvement in the University Consortium on Carbon Dioxide Research, we will continue to actively communicate with other members of the CO_2 research community concerned with CO_2 effects on vegetation.

5. RECENT PUBLICATIONS, ABSTRACTS, AND MANUSCRIPTS

PUBLICATIONS

Reports:

Oechel, W.C., S.J. Hastings, D. Hilbert, W. Lawrence, T. Prudhomme, G. Riechers, and D. Tissue. 1984. The response of arctic ecosystems to elevated CO_2 regimes. (DOE DE-AC03-82ER60079) U.S. Department of Energy, Washington, D.C., Progress Report on Research, No. 019, 99 pp.

Oechel, W.C. and G.H. Riechers. 1987. Response of a tundra ecosystem to elevated atmospheric carbon dioxide. (DOE DE-AC03-82ER60079) U.S. Department of Energy, Washington, D.C., Progress Report on Research, No. 037, 87 pp.

Oechel, W C., G.H. Riechers and N. Grulke. 1987. The effect of elevated atmospheric CO_2 and temperature on an arctic ecosystem. (DOE DE-AC03-82ER60079) U.S. Department of Energy, Washington, D.C., 72 pp.

Oechel, W.C. 1987. Response of tundra ecosystems to elevated atmospheric carbon dioxide. U.S. Department of Energy Final Report, 74 pp.

SELECTED LITERATURE PUBLICATIONS

Oechel, W.C. and B.R. Strain. 1985. Native species responses to increased carbon dioxide concentration. In: B.R. Strain and J.D. Cure (eds.), Direct Effects of Carbon Dioxide on Vegetation. U.S. Department of Energy, Carbon Dioxide Research, State of the Art Report, pp. 117-154.

Oberbauer, S.O., N. Sionit, S.J. Hastings, and W.C. Oechel. 1986. Effects of carbon dioxide enrichment on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. Can. J. Bot. 64:2993-2998.

Oberbauer, S.O., W.C. Oechel, and G.H. Riechers. 1986. Soil respiration of Alaskan tussock tundra at elevated atmospheric carbon dioxide concentration. Plant and Soil 96: 145-148.

Blake-Jacobson, M.E. and W.C. Oechel. 1986. ARTUS-CO_2: Arctic tundra simulator with CO_2 effects. U.S. Department of Energy CDIC Code Package Carbon Dioxide Information Center, ORNL, Oak Ridge, TN, 328 pp.

Tissue, T.D. and W.C. Oechel. 1987. Physiological and growth response of *Eriophorum vaginatum* to field elevated carbon dioxide and temperature in the Alaskan tussock tundra. Ecology. 68:401-411.

Hilbert, D.W., T.I. Prudhomme, and W.C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: Analysis of ecosystem flux through nonlinear modeling. Oecologia 75:466-472.

Oechel, W.C. and M. Blake-Jacobson. Modeling possible responses of arctic tundra to elevated atmospheric CO_2. (in prep.).

Larigauderie, A., D.W. Hilbert, and W.C. Oechel. Interaction between high CO_2 concentrations and multiple environmental stresses in *Bromus mollis*. (in prep.).

Riechers, G.H., T.I. Prudhomme, and W.C. Oechel. A System for *In Situ* temperature and carbon dioxide control at the ecosystem level: System description and evaluation of performance. (in prep.).

PUBLISHED ABSTRACTS OF PRESENTED PAPERS

1984

Hastings, S.J. and W.C. Oechel. 1984. Carbon balance of six arctic plant species grown under ambient and elevated carbon dioxide with high and low nutrient regimes. Bull. Ecol. Soc. Amer. 65(2):85.

Hilbert, D.W., W.C. Oechel, T.I. Prudhomme, and W.T. Lawrence. 1984. The effects of increasing atmospheric carbon dioxide concentration on ecosystem carbon flux in Alaskan tussock tundra. Bull. Ecol. Soc. Amer. 65(2):59.

Oechel, W.C. and M. Blake-Jacobson. 1984. Modeling the responses of arctic tundra to elevated atmospheric carbon dioxide. Bull. Ecol. Soc. Amer. 65(2):59.

Prudhomme, T.I., W.T. Lawrence, and W.C. Oechel. 1984. A field based system for studying community level responses to elevated atmospheric carbon dioxide. Bull. Ecol. Soc. Amer. 65(2):84.

Tissue, D.T. and W.C. Oechel. 1984. Physiological and growth responses of *Eriophorum vaginatum* to elevated carbon dioxide and temperature. Bull. Ecol. Soc. Amer. 65(2):85.

1985

Riechers, G.H., W.C. Oechel, and S. J. Hastings. 1985. Effects of elevated atmospheric carbon dioxide concentrations on tussock tundra at Toolik Lake, Alaska. Bull. Ecol. Soc. Amer. 66(2):256.

Tissue, D.T. and W.C. Oechel. 1985. Growth response of *Eriophorum vaginatum* to elevated carbon dioxide and temperature in the Alaskan tundra. Bull. Ecol. Soc. Amer. 66(2):283.

1986

Oechel, W.C. and G. Riechers. 1986. Impacts of increasing CO_2 on natural vegetation, particularly the tundra. Proceedings of Workshop on Climate-Vegetation Interactions, Goddard Space Flight Center, New York, New York.

Beyers, J.L. and W.C. Oechel. 1986. Comparison of photosynthetic response to long-term growth under atmospheric CO_2 enrichment by *Eriophorum vaginatum* and *Ledum* *palustre* in Alaskan tussock tundra. Proceedings IV. International Congress of Ecology, Syracuse, New York, p. 91.

Larigauderie, A. and W.C. Oechel. 1986. The response of growth, allocation patterns and gas exchange parameters to CO_2 enrichment in two California grassland species as influenced by limited nitrogen and water availability. Proceedings IV. International Congress of Ecology, Syracuse, New York, p. 211.

Oberbauer, S.F., W.C. Oechel, and G.H. Riechers. 1986. Soil respiration of Alaskan tundra at elevated atmospheric carbon dioxide concentrations. Proceedings IV. International Congress of Ecology, Syracuse, New York, p. 258.

Riechers, G.H., W.C. Oechel, and T.I. Prudhomme. 1986. Comparison of short- and long-term effects of elevated atmospheric carbon dioxide concentrations on tussock tundra. Proceedings IV. International Congress of Ecology, Syracuse, New York, p. 286.

1987

Riechers, G.H., S. Cowles, W.C. Oechel and T.I. Prudhomme. Long-term effects of elevated atmospheric carbon dioxide on Alaskan tussock tundra. Bull. Ecol. Soc. Amer. 68(3) 398.

6. LITERATURE CITED

Barel, D., and R.J. Barsdate. 1978. Phosphorus dynamics of wet coastal tundra soils near Barrow, Alaska. In: D.C. Adriano and I.L. Brisbin, (eds.) *Environmental Chemistry and Cycling Processes.* U.S. Department of Energy Symposium Series.

Bazzaz, F.A., and J.L. Harper. 1977. Demographic analysis and growth of *Linum usitatissimum.* New Phytologist 78:192-203.

Bazzaz, F.A., K. Garbutt, and W.E. Williams. 1985. *The Effects of Elevated Atmospheric CO_2 on Plant Communities* (DOE/EV/04329-5). U.S. Department of Energy, Washington, D.C. Available from NTIS, Springfield, Virginia.

Beyers, J., G.H. Riechers, and W.C. Oechel. (in prep.). Photosynthetic response to elevated CO_2 in arctic species after three years of treatment.

Black, C.A. 1965. Methods of soil analysis. Part 2. Chemical and microbiological properties. Society of Agronomy, Madison, Wisconsin.

Billings, W.D., K.M. Peterson, G.R. Shaver, and A.W. Trent. 1977. Effect of temperature on root growth and respiration in a tundra ecosystem, Barrow, Alaska. In: J.K. Marshall (ed.). *The Belowground Ecosystem: A Synthesis of Plant-Associated Processes.* Range Science Department, Science Series No. 26, Colorado State University, Fort Collins, Colorado, 351 pp.

Billings, W.D., K.M. Peterson, and G.R. Shaver. 1978. Growth, turnover, and respiration rates of roots and tillers in tundra graminoids. In: L.L Tieszen (ed.). *Vegetation and Production Ecology of an Alaskan Arctic Tundra.* Springer-Verlag, New York, pp. 415-434.

Billings, W.D., J.O. Luken, D.A. Mortensen, and K.M. Peterson. 1982. Arctic tundra: A source or sink for atmospheric carbon dioxide in a changing environment? Oecologia 53:7-11.

Billings, W.D., J.O. Luken, D.A. Mortensen, and K.M. Peterson. 1983. Increasing atmospheric carbon dioxide: possible effects on arctic tundra. Oecologia (Berl.) 58:286-289.

Billings, W.D., K.M. Peterson, J.D. Luken, and D.A. Mortensen. 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. Oecologia 65:26-29.

Callaghan, T.V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment. Strategies of growth and population dynamics of tundra plants. 3. Oikos 27:402-413.

Callaghan, T.V., N.J. Collins, and C.H. Callaghan. 1978. Photosynthesis, growth, and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. Strategies of growth and population dynamics of tundra plants. 4. Oikos 31:73-88.

Chapin, F.S. III. 1978. Phosphate uptake and nutrient utilization. In: L.L. Tieszen (ed.). *Vegetation and Production Ecology of an Alaskan Arctic Tundra.* Ecological Studies. 29. Springer-Verlag, New York, pp. 484-507.

Chapin, F.S. III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11:233-60.

Chapin, F.S. III and G.R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66:564-576.

Chapin, F.S. III, G.R. Shaver, and R.A. Kedrowski. 1986. Environmental controls over carbon, nitrogen, and phosphorus fractions in *Eriophorum vaginatum* in Alaskan tussock tundra. Journal of Ecology 74:167-195.

Chester, A.L. and J.B. McGraw. 1983. Effects of nitrogen addition on the growth of *Vaccinium uliginosum* and *Vaccinium vitis-idaea.* Canadian Journal of Botany 61:2311-2322.

Clymo, R.S. 1970. The growth of *Sphagnum:* methods of measurement. Journal of Ecology 58:13-49.

Collins, N.J. 1976. Growth and population dynamics of the moss *Polytrichum alpestre* in the maritime Antarctic. Strategies of growth and population dynamics of tundra plants. 2. Oikos 27:389-401.

Dahlman, R.C. 1984. *Vegetation Response to Carbon Dioxide Research Plan.* DOE/ER0187. U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C., 32 pp.

Dahlman, R.C., B.R. Strain, and H.H. Rogers. 1985. Research on the response of vegetation to elevated atmospheric carbon dioxide. Journal of Environmental Quality 14:1-8.

DeLucia, E.H., T. W. Sasek, and B.R. Strain. 1985. Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. Photosynthesis Research 7:175-184.

Dennis, J.G., L.L. Tieszen, and M.A. Vetter. 1978. Seasonal dynamics of above- and belowground production of vascular plants at Barrow, Alaska. In: L.L Tieszen (ed.) *Vegetation and Production Ecology of an Alaskan Arctic Tundra.* Springer-Verlag, New York, pp. 113-140.

Grime, J.P. 1979. *Plant Strategies and Vegetation Processes.* Wiley, New York, 222 pp.

Grulke, N.E. and L.C. Bliss. 1988. Comparative life history characteristics of two high arctic grasses, Northwest Territories. Ecology 69(2): (in press).

Grulke, N.E. and D. Rhoades. (in prep.). Phenology of leaf area, leaf nutrients, and secondary plant compounds in low arctic dwarf shrubs.

Harper, J.L. and J. White. 1974. The demography of plants. Annual Review of Ecology and Systematics 5:419-463.

Harris, J.M. and B.A. Bodhaine (eds.). 1983. *Geophysical Monitoring for Climate Change,* No. 11: Summary Report, 1982. Environmental Research Laboratories/NOAA, U.S. Dept. of Commerce, Washington, D.C.

Hom, J. 1986. Investigations into some of the major controls on the productivity of a Black Spruce (*Picea mariana* [Mill.] B.S.P.) forest ecosystem in the Interior of Alaska. Ph.D. Dissertation. University of Alaska, Fairbanks.

Hom, J., W.C. Oechel, and K. Van Cleve. (in prep.). Studies on elevated root temperature and nutrient enhancement on the photosynthesis of black spruce.

Kimball, B.A., J.R. Mauney, J.W. Radin, F.S. Nakayama, S.B. Idso, D.L. Hendrix, D.H. Akey, S.G. Allen, M.G. Anderson, and W. Hartung. 1986. *Response of Vegetation to Carbon Dioxide, 039: Effects of Increasing Atmospheric* CO_2 *on the Growth, Water Relations, and Physiology of Plants Grown Under Optimal and Limiting Levels of Water and Nitrogen.* U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C., 125 pp.

Lemon, E.R. (ed.). 1983. CO_2 and plants: The response of plants to rising levels of atmospheric carbon dioxide. Westview Press, Boulder, Colorado.

Lincoln, D.E., N. Sionit, and B.R. Strain. 1984. Growth and feeding responses of *Pseudoplusia includens* (Lepidoptera: Noctuidae) to most plants grown in controlled carbon dioxide atmospheres. Environmental Entomology 13:1527-1530.

Longton, R.E. 1979. Studies on growth, reproduction, and population ecology in relation to microclimate in the bipolar moss *Polytrichum alpestre.* The Bryologist 82(3):325-367.

Manabe, S. and R. Wetherald. 1980. On the distribution of climate change resulting from an increase in the CO_2 content of the atmosphere. Journal of Atmospheric Science 37:99-118.

McCown, B.H. 1978. The interactions of organic nutrients, soil nitrogen, and soil temperature and plant growth and survival in the arctic environment. In: L.L. Tieszen (ed.). *Vegetation and Production Ecology of an Alaskan Arctic Tundra.* Springer-Verlag, New York, pp. 435-56.

McGraw, J.B. and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes. II. A demographic model of growth, branching, and fecundity. Journal of Ecology 71:899-912.

Melillo, J.M. 1983. Will increases in atmospheric CO_2 concentrations affect decay processes? In: The Ecosystems Center. 1983 Annual Report. Marine Biology Laboratory, Woods Hole, Massachusetts, pp. 10-11.

Miller, P.C. (ed.). 1981. *Carbon Balance in Northern Ecosystems and the Potential Effect of Carbon Dioxide Induced Climate Change.* U.S. Department of Energy, Carbon Dioxide effects. Research and Assessment Program. Report No. 015. NTIS, Springfield, Virginia, 109 pp.

Miller, P.C., P.M. Miller, M. Blake-Jacobson, F.S. Chapin, III, K.R. Everett, D.H. Hilbert, J. Kummerow, A.E. Linkins, G.M. Marion, W.C. Oechel, S.W. Roberts, and L. Stuart. 1984. Plant-soil processes in *Eriophorum vaginatum* tussock tundra in Alaska: A systems modeling approach. Ecological Monographs 54:361-405.

Norby, R.J., J. Pastor, and J.M. Melillo. 1986a. Carbon-nitrogen interactions in CO_2-enriched white oak: physiological and long-term perspectives. Tree Physiology 2:233-241.

Norby, R.J., E.G. O'Neil, and R.J. Luxmoore. 1986b. Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. Plant Physiol. 82:83-89.

Oberbauer, S.F., N. Sionit, S.J. Hastings, and W.C. Oechel. 1986a. Effects of CO_2 enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan Tundra Plant Species. Canadian Journal of Botany 64:2993-2998.

Oberbauer, S.F, W.C. Oechel, and G.H. Riechers. 1986b. Soil respiration of Alaskan tundra at elevated atmospheric CO_2 concentrations. Plant and Soil 46:145-148.

Oberbauer, S.F., J.L. Beyers, S.J. Hastings, and W.C. Oechel. (in prep.). Micronutrient influences on Alaskan tundra photosynthesis and productivity.

Oechel, W.C. and M. Blake-Jacobson. (in prep.). Modeling possible responses of arctic tundra to elevated atmospheric carbon dioxide.

Oechel, W.C., S. Hastings, D. Hilbert, W. Lawrence, T. Prudhomme, G. Riechers, and D. Tissue. 1984. *Response of Vegetation to Carbon Dioxide, 019: The Response of Arctic Ecosystems to Elevated Carbon Dioxide Regimes*, U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C., 99 pp.

Oechel, W.C., G.H. Riechers, J. Beyers, S. Cowles, N.E. Grulke, S. Hastings, S. Oberbauer, T. Prudhomme, and N. Sionit. 1987. *Response of Vegetation to Carbon Dioxide, 037: The Response of Arctic Ecosystems to Elevated Carbon Dioxide Regimes.* U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C., 87 pp.

Oechel, W.C., G.H. Riechers, and N.E. Grulke. (subm.). *Response of Vegetation to Carbon Dioxide: The Response of Arctic Ecosystems to Elevated Carbon Dioxide Regimes* (DOE/EV/DE-FG03-86ER60479) U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C. NTIS, Springfield, Virginia, 72 pp.

Oechel, W.C., and B.R. Strain. 1985. Native species responses. Ch. 5. In: B.R. Strain and J.D. Cure (eds.). *Direct Effects of Carbon Dioxide on Vegetation, State of the Art Report.* U.S. Department of Energy, Office of Basic Energy Sciences, Carbon Dioxide Research Division, Washington, D.C., pp. 118-154.

Prudhomme, T.I., W.C. Oechel, S.J. Hastings, and W.T. Lawrence. 1984. Net ecosystem gas exchange at ambient and elevated carbon dioxide concentrations in tussock tundra at Toolik Lake, Alaska: An evaluation of methods and initial results. In: J. McBeath (ed.). School of Agriculture and Land Resources Management, University of Alaska, Fairbanks, pp. 155-161.

Reynolds, J.F. 1987a. *Response of Vegetation to Carbon Dioxide, 041: SERECO: A model for the simulation of ecosystem response to elevated* CO_2. Parts I-III, U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C., 127 pp.

Reynolds, J.F., R. L. Dougherty, and J. Tenhunen. 1987b. *Response of Vegetation to Carbon Dioxide, 042, PRECO: Plant response to elevated* CO_2 *simulation model.* Parts I-III, U.S. Department of Energy, Carbon Dioxide Research Division, Washington, D.C.

Riechers, G.H., T.I. Prudhomme, and W.C. Oechel. (in prep.). A system for *in situ* temperature and carbon dioxide control at the ecosystem level: System description and evaluation of performance.

Sasek, T.W., E.H. DeLucia, and B.R. Strain. 1985. Reversibility of photosynthetic inhibition in cotton after long-term exposure to elevated CO_2 concentrations. Plant Physiology 78:619-622.

Sebacher, D.J., R.C. Harris, K.B. Bartlett, S.M. Sebacher, and S.S. Grice. 1986. Atmospheric methane sources: Alaskan tundra bogs, and alpine fen, and a subarctic boreal marsh. Tellus 38B:1-10.

Seidel, S. and D. Keyes. 1983. Can we delay a greenhouse warming? Office of Policy and Resources Management, Washington, D. C. 20460.

Sharkey, T.D. and M.R. Badger. 1984. Factors limiting photosynthesis as determined from gas exchange characteristics and metabolite pool sizes. In: C. Sybesma (ed.), advances in photosynthesis research. Vol. IV, Dr. W. Junk Publ., The Hague, The Netherlands, pp. 325-328.

Shaver, G.R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub. *Ledum palustre* ssp. *decumbens*. Oecologia (Berlin) 49:362-365.

Shaver, G.R., and F.S. Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. Ecology 61:662-675.

Shaver, G.R., F.S. Chapin III, and B.L. Gartner. 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. Journal of Ecology 74:257-278.

Sionit, N. 1983. Response of soybean to two levels of mineral nutrition in CO_2 enriched atmosphere. Crop Science 23:329-333.

Sionit, N.H. Hellmers, and B.R. Strain, 1980. Growth and yield of wheat under CO_2 enrichment and water stress. Crop Science 20:687-690.

Sionit, N., D.A. Mortensen, B.R. Strain, and H. Hellmers. 1981. Growth response of wheat to CO_2 enrichment and different levels of mineral nutrition. Agronomy Journal 73:1023-1026.

Sokal, R.R. and F.J. Rohlf. 1969. Biometry: the principles and practice of statistics in biological research. W.H. Freeman and Co., San Francisco, California, 776 pp.

Strain, B.R. 1985. Physiological and ecological controls on carbon sequestering in ecosystems. Biogeochemistry. 1:219-232.

Strain, B.R. and J. D. Cure. *Direct Effects of Carbon Dioxide on Vegetation* (DOE/ER-0238), State of the Art Report, U.S. Department of Energy, Office of Basic Energy Sciences, Carbon Dioxide Resesarch Division, Washington, D.C., 286 pp.

Strotsky, G., and R.D. Goos. 1964. Effect of high CO_2 and low O_2 tensions on the soil microbiota. Canadian Journal of Microbiology 11:853-868.

Tissue, D.T., W.C. Oechel. 1987. Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan arctic tundra. Ecology 68(2):401-411.

Torstensson, P. and A. Telenius. 1986. Plastic morphological response to density in *Spergularia mariana* (L.) Griseb.: Leaf demography and meristem activity. Holarctic Ecology 9:13-19.

Ulrich, A., and P.L. Gersper. 1978. Plant-nutrient limitations of tundra plant growth. In: L. Tieszen (ed.). *Vegetation and Production Ecology of an Alaskan Arctic Tundra*. Springer-Verlag, New York, pp. 457-481.

Van Cleve, K. and W.C. Oechel. In prep. Response of black spruce (*Picea mariana* [Mill] B.S.P.) to soil temperature modification in interior Alaska.

Van Cleve, K., L. Oliver, R. Schlentner, L.A. Viereck, and C.T. Dyrness. 1983. Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Resources 13:747-766.

Wein, R.W. and L.C. Bliss. 1974. Primary production in arctic cottongrass tussock tundra communities. Arctic and Alpine Research 6:261-274.

7. CURRICULA VITAE

A. Walter C. Oechel

B. Nancy E. Grulke

C. Steven J. Hastings

D. Ulf Hjelm

CURRICULUM VITAE

NAME: Oechel, Walter C.

BIRTHDATE: [redacted]

BIRTHPLACE: [redacted]

EDUCATION: A.B., San Diego State University, San Diego California 1966

Organization for Tropical Studies, Tropical Ecology Course, Costa Rica, Summer 1967

Duke University, 1969-1970

Ph.D., University of California, Riverside, California, 1970

EXPERIENCE:

1983-date	Professor, Biology Department, San Diego State University
1982-6/30/87	Director, Systems Ecology Research Group, San Diego State University
1982-1986	Member, Watershed Research Advisory Committee, California Department of Forestry, University of California
1982-1986	Member, Watershed Management Task Force, County of San Diego, Department of Agriculture
1982-1985	Consultant on "Plant materials release model," USDA, Southern Plains Research Station, Woodward, Oklahoma. P.L. Simms, Research Leader
1982-1983	Chairman, Physiological Ecology Section, Ecological Society of America
1978-1982	Research Professor, Systems Ecology Research Group, San Diego State University
1976-1978	Visiting Research Professor, Systems Ecology Research Group, San Diego State University
1975-1978	Associate Professor, Biology Department, McGill University
1970-1975	Assistant Professor, Biology Department, McGill University

1967-1970	NDEA Title IV Fellow, Department of Life Sciences, University of California, Riverside
1967-1968	Research Assistant, Department of Life Sciences, University of California, Riverside
1967	National Science Foundation Fellowship to attend Organization for Tropical Studies Summer Tropical Ecology Course, Costa Rica
1966-1967	Graduate Teaching Assistant, Department of Life Sciences, University of California, Riverside

RESEARCH EXPERIENCE:

1987-1988	Principal Investigator, U.S. Department of Energy, R^4D Program "Interactive effects of carbohydrate and nutrient availability on vascular plant allocation and productivity" $75,000/yr
1984-1988	Principal Investigator, National Science Foundation "Mechanisms controlling resource use, community organization, and succession in fire-dominated chaparral ecosystems" $900,000/yr
1984-1987	Principal Investigator, Scientific Coordinator, U.S. Department of Energy, R^4D Program "Effect of perturbation of tundra drainage systems on ecosystem dynamics of tundra and riparian vegetation" $850,000/yr
1984-1987	Principal Investigator, U.S. Department of Energy, CO_2 Project, "The response of arctic ecosystems to elevated carbon dioxide regimes" $470,000/18 mo
1983-1984	Principal Investigator, U.S. Forest Service, "The effect of stand age on allelopathy in chaparral soils"
1983-1984	Principal Investigator, University of California, Davis, "A data synthesis on chaparral management and the effects of prescribed burning on vegetation"
1982-1984	Principal Investigator, U.S. Department of Energy, "Potential responses of tundra ecosystems to perturbations from energy development"
1982-1984	Principal Investigator, U.S. Department of Energy, "Response of arctic ecosystems to elevated CO_2 regimes"
1982-1984	Principal Investigator, National Science Foundation, "Mechanisms controlling resource use, community organization, and succession in fire dominated chaparral ecosystems"
1982-1983	Principal Investigator, USDA Forest Service, "Controls on growth and carbon balance of resprouts and seedlings following fire and harvesting for biomass"

1982-1983	Principal Investigator, MAB-UNESCO, "A proposal for cooperative research in Mediterranean-type ecosystems"
1981-1982	Principal Investigator, USDA Forest Service, "Primary production and stand development in chaparral communities at the San Dimas Biosphere Reserve"
1981-1982	Principal Investigator, USDA Forest Service, "Development of a guide to the vegetation communities along a transect from the Pacific Coast to the Anza Borrego Desert State Park"
1981-1982	Principal Investigator, USDA Forest Service, "Patterns and control of carbon assimilation in chaparral and associated ecosystems"
1981-1982	Co-Principal Investigator, National Science Foundation, "International symposium on dynamics and management of Mediterranean-type ecosystems," P. Zedler, Principal Investigator
1981-1982	Co-Principal Investigator, UNESCO-MAB, "International symposium on dynamics and management of Mediterranean-type ecosystems," Paul Zedler, Principal Investigator
1979-1980	Principal Investigator, USDA Forest Service, "Controls on growth and photosynthesis in chaparral regrowth following fire"
1978-1980	Co-Principal Investigator, National Science Foundation, "The structure and function of a black spruce (*Picea mariana* [Mill] B.S.P.) forest in relation to other fire affected taiga ecosystems," K. Van Cleve, Principal Investigator
1977-1981	Co-Principal Investigator, National Science Foundation, "Community organization and resource utilization by vegetation in convergent ecosystems," P.C. Miller, Principal Investigator
1977-1982	Co-Principal Investigator, U.S. Department of Energy, "Research on dynamics of tundra ecosystems and their potential response to energy resource development," P.C. Miller, Principal Investigator
1977-1978	Principal Investigator, National Research Council, Canada, Travel Grant
1977-1978	Principal Investigator, National Research Council, Canada, Capital Equipment Grant for Growth Chambers
1974-1978	Principal Investigator, National Research Council, Canada, "Factors controlling the evolution and selection of the photosynthetic response patterns in boreal plants"

1974-1978	Co-Principal Investigator, FCAC, Quebec Ministry of Education, "Systems analysis of production and nutrient cycling in a subarctic open lichen woodland," four annual grants
1974-1975	Principal Investigator, National Research Council, Canada, Capital Equipment Grant for a Data Acquisition System
1973-1974	Principal Investigator, National Research Council, Canada, "Factors controlling photosynthesis in arctic and subarctic bryophytes"
1972-1973	Principal Investigator, National Research Council, Canada, "The ecology and productivity of subarctic plants"
1971-1978	Principal Investigator, Department of Indian Affairs and Northern development, "Northern biology project," seven annual grants
1971-1977	Co-Principal Investigator, FCAC, Quebec Ministry of Education, "The ecology and productivity of subarctic mosses and lichens," six annual grants
1971-1973	Principal Investigator, National Research Council, Canada, "The ecology and productivity of subarctic plants"

OTHER:

1987-	Editorial Review Board Member, Tree Physiology

PUBLICATIONS: (SINCE 1982 40 TOTAL)

Moreno, Jose and Walter C. Oechel. A simple method for estimating fire intensity after a burn in California chaparral. Oecologia Planatarum (submitted).

Moreno, Jose and Walter C. Oechel. Nutrients and water addition effects on the post-fire establishment of *A. fasciculatum* and *C. greggii* in a southern California chaparral. Ecology. (submitted).

Matthes-Sears, U., W. C. Matthes-Sears, S. J. Hastings and W. C. Oechel. Variation in nutrient status, biomass, vegetative characteristics, and gas exchange of two deciduous shrubs on an arctic tundra slope. Arctic and Alpine Res. (submitted).

Hastings, S. J., Luchessa, S. A., Oechel, W. C., and Tenhunen, J. D. Biomass attributes of two plant communities within a small watershed in the Brooks Range Foothills, Alaska. Holarctic Ecology. (submitted).

Marion, G. M., S. J. Hastings, S. F. Oberbauer, and W. C. Oechel. Soil-plant nutrient relationships in a tundra ecosystem. Holarctic Ecology. (submitted).

Oberbauer, S. F., S. J. Hastings, J. L. Beyers, and W. C. Oechel. Impacts of downslope water and nutrient movement on plant nutrition, photosynthesis, and growth in Alaskan tundra. Holarctic Ecology. (submitted).

Oberbauer, S. F., S. J. Hastings, J. L. Beyers, and W. C. Oechel. Variation in nutrient status, biomass, vegetative characteristics, and gas exchange of two deciduous shrubs on an arctic tundra slope. Arctic and Alpine Research. (submitted).

Reid, C. D. and Walter C. Oechel. Physiological ecology of two chaparral shrubs along a fire-induced chronosequence in California. Ecology. (submitted).

Skre, O., W. C. Oechel and P. M. Miller. Standing biomass and production of four moss species in stands with evergreen conifer or deciduous tree overstories. Holarctic Ecology. (submitted).

Hastings, Steven J., Walter C. Oechel and Nasser Sionit. Water relations and photosynthesis of chaparral resprouts and seedlings following fire and hand clearing. In: S. Keeley (ed.) Proc. of the Symp., The California chaparral Paradigms reexamine (7-8 Nov. 1986, Los Angeles Natural History Museum). (submitted).

J. D. Tenhunen, F. M. Catarino, O. L. Lange and W. C. Oechel. Plant Response to Stress. Functional analysis in Mediterranean ecosystems series G: Ecological Sciences, Vol. 15, Springer-Verlag, Heidelberg, West Germany, 1987, 668 pp.

Y. Mauffette and W. C. Oechel. Seasonal photosynthate allocation of the Californian coast live oak Quercus agrifolia. In Plant response to stress. Functional analysis in Mediterranean ecosystems. Series G. Ecological Sciences, Vol. 15, Springer-Verlag, Heidelberg, West Germany, 1987, 437-444.

Tissue, D.L. and W.C. Oechel. 1987. Physiological response of *Eriophorum vaginatum* to field elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology. 68: 401-410.

Hilbert, D.W., T.I. Prudhomme, and W.C. Oechel. 1987. Response of tussock tundra to elevated carbon dioxide regimes: analysis of ecosystem CO_2 flux through nonlinear modeling. Oecologia. 75: 466-472.

Alpert, Peter and Walter C. Oechel. 1987. Comparative patterns of net photosynthesis in an assemblage of mosses with contrasting microdistributions. Amer. J. Bot., 74: 1787-1796.

Oberbauer, S., W.C. Oechel, and G.H. Riechers. 1986. Soil respiration of Alaskan tundra at elevated atmospheric CO_2 concentration. Plant and Soil 46: 145-148.

Oechel, W.C. and B. Strain. 1986. Response of native species and ecosystems. *In:* Direct Effects of Increasing Carbon Dioxide on Vegetation. Department of Energy DOE/ER-0238.

Oechel, W.C. and K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the taiga, pp 121-137. *In:* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness (eds.), Forest Ecosystems in the Alaskan Taiga: A Synthesis of Structure and Function, Springer-Verlag, New York.

Oberbauer, S.F., N. Sionit, S.J. Hastings, and W.C. Oechel. 1986. Effects of CO_2 enrichment and nutrition on growth, photosynthesis and nutrient concentration of Alaskan tundra species. (Can. J. Bot. 64: 2993-2998).

Oechel, W.C. and W.T. Lawrence. 1985. Taiga. *In:* H. Mooney and B. Chabot (eds.), The Physiological Ecology of North American Vegetation. Chapman and Hall Publishers.

Kruger, F.J., P.M. Miller, J. Miller, and W.C. Oechel (eds). 1985. Simulation modelling of fynbos ecosystems: Systems analysis and conceptual models. South African Scientific Programmes Report No. 105, March.

Miller, P.C., P.M. Miller, M. Blake-Jacobson, F.S. Chapin III, K.R. Everett, D.W. Hilbert, J. Kummerow, A.E. Linkins, G. M. Marion, W.C. Oechel, S.W. Roberts, and L. Stuart. 1984. Plant-soil processes in *Eriophorum vaginatum* tussock tundra in Alaska: A systems approach. Ecol. Monogr. 54: 361-405.

Sparks, S. and W.C. Oechel. General Shrubland Management Procedures. *In*: J.J. DeVries (ed.), Shrublands in California: Literature Review and Research Need for Management, Water Resources Center, University of California, Davis. Report No. 191, November 1984.

Reid, C. and W.C. Oechel. Effects of Shrubland Management on Vegetation. *In:* J.J. DeVries (ed.), Shrublands in California: Literature Review and Research Needed for Management, Water Resources Center, University of California, Davis. Report No. 191, November 1984.

Curry, R. and W.C. Oechel. Shrubland ecosystem dynamics. 1984. *In*: J.J. DeVries (ed.), Shrublands in California: Literature Review and Research Needed for Management. Water Resources Center, University of California at Davis, Report No. 191, November 1984.

Alpert, P. and W.C. Oechel. 1984. Microdistribution and water loss resistances of selected bryophytes in an Alaskan *Eriophorum* tussock tundra. Holarctic Ecology 7: 111-118.

Margaris, N.S., W.C. Oechel, and M. Arianoutsou-Faraggitaki (eds). 1984. Proceedings of the symposium on adaptations of plants to their environ-ment. Tasks for Vegetation Science, Dr. W. Junk Pubs., The Hague.

Reid, C.D. and W.C. Oechel. 1984. Water relations of two chaparral shrubs along a fire-induced age gradient in southern California. *In:* Proceedings of the Mediterranean Bioclimatology Symposium, 18-20 May 1983. Montpellier, France. Bull. Soc. Bot. Fr., 131. Actual Bot. 1984 (2/3/4), 601-602.

Oechel, W.C. and C.D. Reid. 1984. Photosynthesis and biomass of chaparral shrubs along a fire-induced age gradient in southern California. *In:* Proceedings of the Mediterranean Bioclimatology Symposium, 18-20 May 1983. Montpellier, France. Bull. Soc. Bot. Fr., 131 Actual. Bot., 1984 (2/3/4) 399-409.

Hom, J.L. and W.C. Oechel. 1983. The photosynthetic capacity, nutrient content and nutrient use efficiency of different needle age classes of black spruce (*Picea mariana*) found in interior Alaska. Can. J. For. Res. 13: 834-839.

Lawrence, W.T. and W.C. Oechel. 1983. Effects of soil temperature of carbon exchange of taiga seedlings. I. Root respiration. Can. J. For. Res. 13: 840-849.

Lawrence, W.T. and W.C. Oechel. 1983. Effects of soil temperature on carbon exchange of taiga seedlings. II. Photosynthesis. Can. J. For. Res. 13: 850-859.

Read, D. J. (convener), C.B. Field, S. Gulmon, S.M. Jongens-Roberts, O.A.M. Lewis, D.T. Mitchel, and W. Oechel. 1983. Plant Nutrition and Assimilation. *In:* J.A. Day (ed.), Mineral Nutrients in Mediterranean Ecosystems. South African National Scientific Report No. 71.

Chapin, F.S. III and W.C. Oechel. 1983. Photosynthesis, respiration and phosphate absorption by *Carex aquatilis* ecotypes along latitudinal and local environmental gradients. Ecology 64: 743-751.

Miller, P.C., R. Kendall, and W.C. Oechel. 1983. Simulating carbon accumulation in northern ecosystems. Simulation 40: 119-131.

Oechel, W.C., and S. J. Hastings. 1983. The effects of periodic fire on photosynthesis in chaparral resprouts, pp. 274-285. *In:* F.J. Kruger, D.T. Mitchell, and J.U.M. Jarvis (eds.), Nutrients as determinants of the structure and functioning of Mediterranean type ecysystems. Springer-Verlag, New York-Heidelberg-Berlin.

Skre, O., W.C. Oechel, and P.M. Miller. 1983. Patterns of translocation of carbon in four common moss species in a black spruce (*Picea mariana*) dominated forest in interior Alaska. Can. J. For. Res. 13: 869-878.

Skre, O., W.C. Oechel, and P.M. Miller. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. Can. J. For. Res. 13: 860-868.

Strain, B.R. and J. Bazzaz with W.D. Billings, J. Detling, J.P. Grime, P. Grubb, O.T. Loucks, J. Melillo, J.A. Mooney, W.C. Oechel, D. Overdiech, D. Patterson, W. Reiners, H. Rogers, M. Rutter, P. Vitouset, and D. West. 1983. Terrestrial plant communities, pp. 177-222. *In*: E.R. Lemon (ed.), CO_2 and Plants: The response of plants to rising levels of atmospheric carbon dioxide. AAAS Selected Symposium 84. Westview Press, Inc., Boulder, Colorado.

Sveinbjornsson, B. and W.C. Oechel. 1983. The effect of temperature preconditioning on the temperature sensitivity of net CO_2 flux in geographically diverse population of the moss, *Polytrichum commune* Hedw. Ecology 64: 1100-1108.

Van Cleve, J., C.T. Dyrness, L.A. Viereck, J. Fox. J.S. Chapin III, and W.C. Oechel. 1983. Taiga ecosystems in interior Alaska. Bioscience 33: 39-44.

Alpert, P. and W.C. Oechel. 1982. Bryophyte vegetation and ecology along a topographic gradient in montane tundra in Alaska. Hol. Ecol. 5(2): 99-108.

Bigger, C.M. and W.C. Oechel. 1982. Nutrient effect on maximum photosynthesis in arctic plants. Hol. Ecol. 5(2): 158-163.

Conrad, C.E. and W.C. Oechel, (eds.). 1982. Proceedings of the Symposium of the Dynamics and Management of Mediterranean-Type Ecosystems, June 22-26, 1981, San Diego, California. Pacific Southwest Forest and Range Experiment Station, Berkeley, California, 637 pp.

Limbach, W.E., W.C. Oechel, and W. Lowell. 1982. Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. Hol. Ecol. 5(2): 150-157.

Marion, G.M., P.C. Miller, J. Kummerow, and W.C. Oechel. 1982. Competition for nitrogen in a tussock tundra ecosystem. Plant and Soil 66: 317-327.

Oechel, W.C. 1982. Carbon balance studies in chaparral shrubs: Implications for biomass production, pp. 158-165. *In:* C.E. Conrad and W.C. Oechel (eds.), Proceedings of the International Symposium on the Dynamics and Management of Mediterranean-Type Ecosystems, June 22-26, 1981, San Diego, California. Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Oechel, W.C. and J. Mustafa. 1982. Photosynthetic variability along an elevational gradient in the chaparral, pp. 417-433. *In:* P. Quezel (ed.), Definition and localization of terrestrial and marine Mediterranean biota. Plenum Press, New York.

Oechel, W.C., W. Lowell, and W. Jarrell. 1982. Environmental controls on carbon flux in Mediterranean shrubs from California and Chile. *In:* N.S. Margaris and H.A. Mooney (eds.), Components of productivity of Mediterranean-climate regions, basic and applied aspects. Dr. W. Junk Publishers, The Hague. 279 pp.

Prudhomme, T.I., W.C. Oechel, S.J. Hastings, and W.T. Lawrence. 1982. Net ecosystem gas exchange at ambient and elevated carbon dioxide concentrations in Tussock Tundra at Toolik Lake, Alaska: An evaluation of methods and initial results. *In:* Jenifer H. McBeath (ed.), The potential effects of carbon dioxide-induced climatic changes in Alaska. Proceedings of a Conference. April 7-8, 1982. School of Agriculture and Land Management, University of Alaska. Misc. Publication 83-1, pp. 155-16.

SELECTED TECHNICAL REPORTS: (SINCE 1982)

Oechel, Walter C. and George H. Riechers. 1987. Response of a tundra ecosystem to elevated atmospheric carbon dioxide. U.S. Department of Energy Greenbook Report 037.

Oechel, W. C. and B. R. Strain. 1986. Native species responses to increased carbon dioxide concentration. In: B. R. Strain and J. D. Cure (eds.), Direct Effects of Carbon Dioxide on Vegetation, Carbon Dioxide Research, State of the Art Report.

Blake-Jacobson, M. E. and W. C. Oechel. 1986. ARTUS-CO_2: Arctic tundra Simulator with CO_2 effects. U.S. Department of Energy CDIC Code Package Carbon Dioxide Information Center, ORNL, Oak Ridge, TN.

Oechel,W. C. 1985. United States Forest Service. Controls on carbon balance of resprouts.

Oechel, W. C. 1985. Planning Document for Proposed Research. Department of Energy R^4D. Model development to describe the response to disturbance in an Alaskan arctic tundra watershed.

Oechel, W. C., S. Hastings, D. Hilbert, W. Lawrence, T. Prudhomme, G. Riechers, D. Tissue. 1984. Department of Energy CO_2 Report #019, The response of arctic ecosystems to elevated CO_2 regimes. Progress Report.

Hastings, S. J. and W. C. Oechel. 1984. Primary Report of Research. Primary production and stand development in chaparral communities at the San Dimas Biosphere Reserve. U. S. Forest Service, 31 December 1982-30 April 1983, Agreement No. 59-PSW-81-002G.

Oechel, W. C. 1984. Annual Report, Sky Oaks Biological Field Station, 1983-1984.

Oechel, W. C. 1983. Annual Report, Sky Oaks Biological Field Station, 1982-1983.

MANUSCRIPTS IN PREPARATION:

Van Cleve, K. and W. C. Oechel. Response of black spruce (Pilcea mariana [Mill] B.S.P.) to soil temperature modification in interior Alaska.

Swank, Sarah E. and Walter C. Oechel. Effects of predation, competition and resource limitation on chaparral herbs.

Oechel, W. C. and F. Kruger. Drought tolerance in different species of chaparral and trees of Southern California and fynbos of South Africa.

Mauffette, Y. and Walter C. Oechel. Seasonal variation in leaf chemistry of the coast live oak *Quercus agrifolia* and implications to the California oak moth *Phryganidia californica.*

Mauffette, Y., Walter C. Oechel and Steve Sparks. Seasonal photosynthate allocation in relation to growth and herbivory for an evergreen tree species. The coast live oak, *Quercus agrifolia* Nee.

Sparks, Steven R. and Walter C. Oechel. Controls of postfire sprouting vigor in *Adenostoma fasciculatum,* a California chaparral shrub.

Sparks, Steven R., Walter C. Oechel and Yves Mauffette. ^{14}C-Labeled photosynthate allocation in chaparral shrubs along a fire-induced age sequence.

Oechel, Walter C. Seedling establishment and water relations after fire in a Mediterranean ecosystem.

Oechel, Walter, C. and Nasser Sionit. Lethal water potentials for chaparral seedlings.

Hastings, S. J., W. C. Oechel and Nasser Sionit. Controls on growth and carbon balance of chaparral resprouts and seedlings following fire and above-ground clipping.

Oberbauer, S. F. J. L. Beyers, S. J. Hastings and W. C. Oechel. Micronutrient influences on Alaskan tundra photosynthesis and productivity.

Oberbauer, S. F. and W. C. Oechel. Seasonality of photosynthesis in Alaskan arctic tundra species.

Oberbauer, S. F. and W. C. Oechel. Light and temperature responses of photosynthesis of Alaskan arctic tundra species.

Oberbauer, S. F. and W. C. Oechel. CO_2 exchange along an arctic tundra toposequence.

Oechel, W.C. and M. Blake-Jacobson. Modeling the responses of arctic tundra ecosystems to elevated atmospheric CO_2.

Grulke, N. E. and W. C. Oechel. Effects of elevated CO_2 on population dynamics of vascular plants and moss in tussock tundra.

Grulke, N. E. and W. C. Oechel. Effects of elevated carbon dioxide on available soil nutrients and nutrient content of plant tissue.

Larigauderie, A., D. W. Hilbert, and W. C. Oechel. Interaction between high CO_2 concentrations and multiple environmental stresses in *Bromus mollis.*

Riechers, G. I., T. I. Prudhomme, and W. C. Oechel. A System for *In situ* temperature and carbon dioxide control at the ecosystem level: System description and evaluation of performance.

Sionit, N., Oechel, W.C., Kruger, F.J., Hastings, S.J. and Smith, F.R. Photosynthesis and Growth of Seedlings of Evergreen Sclerophylis under Varying Rates of Nitrogen Supply.

Hastings, S.J., Oechel, W.C. and Prudhomme, T.I. Primary production and stand development in chaparral communities at the San Dimas Biosphere Reserve.

Moreno, J.M., Hastings, S.M. and W.C. Oechel. Controls on growth of resprouts following fire in southern California chaparral.

ABSTRACTS AND SEMINARS:

G. H. Riechers, S. Cowles, W., C. Oechel and T. I. Prudhomme. Long term effects of elevated atmospheric carbon dioxide on Alaskan tussock tundra: Carbon dioxide flux rates and biomass production. 72nd Annual Meeting of the Ecological Society of America, Columbus, Ohio, 9-14 August, 1987.

W. C. Oechel and J. D. Tenhunen. Integrated ecosystem research on a small arctic watershed: Controls on nutrient, movement and uptake, an overview. 72nd Annual Meeting of the Ecological Society of America, Columbus, Ohio, 9-14 August, 1987.

Moreno, Jose and Walter C. Oechel. Controlling factors of the post-fire shrub establishment in a *Ceanothus greggii-Adenostoma fasciculatum* chaparral of southern California. 72nd Annual Meeting of the Ecological Society of America, Columbus, Ohio, 9-14 August, 1987.

Oechel, W. Invited participant. Impacts of Changes in Climate and Atmospheric Chemistry on Northern Ecosystems and their Boundaries. International Institute for Applied Systems Analysis, Laxenburg, Austria, 3-7 August, 1987.

Oechel, W. Tundra responses. Invited participant, round-table presentation on the effects of global increases in atmospheric CO_2. International Botanical Congress, Berlin, West Germany, 30 July, 1987.

Oechel, W. Water limitation to seedling establishment and survival in Mediterranean climates. Invited symposium presentation. Vth International Conference on Mediterranean-Climate Ecosystems, Montpellier, France, 15-21 July, 1987.

Moreno, J. and W. Oechel. Post fire establishment of *Adenostama fasciculatum* and *Ceratonus greggii* in a Southern Californian chaparral: influence of herbs and increased soil nutrients and water. Invited symposium presentation. Vth International Conference on Mediterranean-Climate Ecosystems. Montpellier, France, 15-21 July, 1987.

Oechel, W. C. Status of the CO_2 greenhouse problem in global climate change. Invited speaker. University of Alaska, Fairbanks, Alaska,1 July, 1987.

Beyers, J.L. and W.C. Oechel. Comparison of photosynthetic response to long-term growth under atmospheric CO_2 enrichment by *Eriophorum vaginatum* and *Ledum palustre* in Alaskan tussock tundra. IV International Congress of Ecology 1986, State University of New York, College of Environmental Science and Forestry, and Syracuse University, Syracuse, New York, 10-16 August, 1986.

Larigauderie, A. and W.C. Oechel. The response of growth, allocation patterns and gas exchange parameters to CO_2 enrichment in two California grassland species as influenced by limited nitrogen and water availability. IV International Congress of Ecology 1986, State University of New York, College of Environmental Science and Forestry, and Syracuse University, Syracuse, New York, 10-16 August, 1986.

Oberbauer S.F., W.C. Oechel, and G.H. Riechers. Soil respiration of Alaskan tundra at elevated atmospheric carbon dioxide concentrations. IV International Congress of Ecology 1986, State University of New York, College of Environmental Science and Forestry, and Syracuse University, Syracuse, New York, 10-16 August, 1986.

Riechers, G.H., W.C. Oechel, and T.I. Prudhomme. Comparison of short- and long-term effects of elevated atmospheric carbon dioxide concentrations on tussock tundra. IV International Congress of Ecology 1986, State University of New York, College of Environmental Science and Forestry, and Syracuse University, Syracuse, New York, 10-16 August, 1986.

Sparks, S.R. and W.C. Oechel. Relative importance of current photosynthesis and energy reserves in determining postfire resprouting vigor in the California chaparral shrub, *Adenostoma fasciculatum*. IV International Congress of Ecology 1986, State University of New York, College of Environmental Science and Forestry, and Syracuse University, Syracuse, New York, 10-16 August, 1986.

Oechel, W.C. The Reconstruction of Disturbed Arid Ecosystems. AAAS Symposium, Philadelphia, 25-30 May, 1986.

Oechel, W.C. Impacts of increasing CO_2 on natural vegetation, particularly the tundra. Workshop on Climate-Vegetation Interactions, Goddard Space Flight Center, New York, New York, 27-29 January, 1986. NASA, Goddard Institute for Space Studies, New York, New York.

Oechel, W.C. Ecophysiological Field Research. NATO Advanced Research Workshop. Plant Response to Stress - Functional Analysis in Mediterranean Ecosystems, Sesimbra, Portugal, 13-19 October 1985.

Oechel, W.C., F. Sproul, and S. Roberts. Non-lethal water potentials in chaparral shrub seedlings. ESA Annual Meeting in Minneapolis, Minnesota, 7-21 June 1985.

Reid, C.D., M.A. Rehse, and W. C. Oechel. Patterns of respiration and net photosynthesis in two dominant southern California chaparral shrubs over a long fire cycle. ESA Annual Meeting in Minneapolis, Minnesota, 7-21 June 1985.

Riechers, G.H., W.C. Oechel, and S.J. Hastings. Effects of elevated CO_2 concentrations on tussock tundra at Toolik Lake, Alaska. ESA Annual Meeting in Minneapolis, Minnesota, 7-21 June 1985.

Tissue, David T. and W.C. Oechel. Growth response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tundra. ESA Annual Meeting in Minneapolis, Minnesota, 7-21 June 1985.

Oechel, W.C. and C.D. Reid. The physiological response of chaparral to aging. Chaparral Ecosystem Research, 16-17 May 1985. University of California, Santa Barbara.

Oechel, W.C. Carbon dioxide stimulation in unmanaged ecosystems. Electric Power Research Institution, sponsor, Carbon dioxide transfer in the atmosphere-ocean-terrestrial system Conference, UCSD, Scripps Institution of Oceanography, 5-10 May 1985, Lake Arrowhead.

Oechel, W.C. Photosynthesis, growth, carbon, and nutrient allocation. The Arctic Program and HERAC Meeting, Washington, D.C., 25 September 1985. Department of Energy Ecology Program Review.

Oechel, W.C. Participant in SIGMA XI Teleconference on The Effects of Increases in Atmospheric Carbon Dioxide, 19 September 1985. Co-Sponsored by U.S. Department of Energy.

Oechel, W.C. Carbon balance of chaparral shrubs over a disturbance cycle of 85 years. Fourth International Conference on Mediterranean Ecosystems, MEDECOS IV, Perth, Western Australia, 13-17 August 1984.

Oechel, W.C., and Martha Blake-Jacobson. Modeling the responses of arctic tundra ecosystem to elevated atmospheric CO_2. ESA/ISEM symposium, AIBS Annual Meeting, Ft. Collins, Colorado, 5-9 August 1984. Symposium title: Modeling approaches to predicting responses of plants and ecosystems to global carbon dioxide enrichment.

Oechel, W.C., and S. Cowles. Growth equations from shrub dynamics models. ESA/ISEM symposium, AIBS Annual Meeting, Ft. Collins, Colorado, 5-9 August 1984. Symposium title: Mathematics of plant growth form modeling.

Oechel, W.C. Invited Participant, Symposium on the Biogeography of Mesoamerica. Tulane University, 26-30 October 1984.

Oechel, W.C. Research on Plant Physiological Ecology. Invited workshop. Stanford University, 21-24 October 1984.

Oechel, W.C. Invited Speaker. Environmental Controls of oak woodland and grassland communities in southern California. Sky Oaks Conference. San Diego State University, 8 September 1984.

Oechel, W.C. Changes in the storage of carbon in terrestrial systems for reasons other than changes in land use. Topic Chairman. Carbon Cycle Numeric Data Workshop at the 6th Life Science Symposium. Knoxville, Tennessee, 30 October-2 November 1983.

Oechel, W.C. Research on the effects of elevated CO_2 on arctic ecosystems. Invited workshop. Univ. of Illinois, 20-21 October 1983.

Oechel, W.C. The DOE/R^4D Program, Arctic Terrestrial Environmental Research Liaison Conference, Prudhoe Bay, Alaska, 28-29 August 1984. University of Alaska, Fairbanks, Alaska, Institute of Marine Sciences.

Oechel, W.C. Costs of poikilohydry in mosses, Invited symposium presentation. Evolutionary constraints on primary productivity: Adaptive strategies of energy capture in plants. Chabot Symposium. Harvard Forest, Petersham, Massachusetts, 21-25 August 1983.

Chester, A.L. and W.C. Oechel. The effect of nitrogen availability and leaf position of patterns of nitrogen distribution from leaves of an evergreen and a deciduous shrub. Invited symposium presentation. 1983 ESA Annual Meeting with AIBS. University of North Dakota, Grand Forks, North Dakota, 7-11 August 1983.

Mauffette, Y. and W.C. Oechel. Herbivory on *Quercus agrifolia* in relation to carbon allocation. Invited poster session. 1983 ESA Annual Meeting with AIBS. University of North Dakota, Grand Forks, North Dakota, 7-11 August 1983.

Oechel, W.C. Infrared gas analyzer systems: Open systems. Invited symposium presentation. 1983 ESA Annual Meeting with AIBS. University of North Dakota, Grand Forks, North Dakota, 7-11 August 1983.

Oechel, W.C., C.M. Bigger, and J. Miller. Micronutrient limitation of photosynthesis in tussock tundra plants in the Alaskan arctic. Invited symposium presentation. 1983 ESA Annual Meeting with AIBS. University of North Dakota, Grand Forks, North Dakota, 7-11 August 1983.

Reid, C.D. and W.C. Oechel. Physiological changes of two chaparral shrub species within the fire cycle. Invited poster session. 1983 ESA Annual Meeting with AIBS. University of North Dakota, Grand Forks, North Dakota, 7-11 August 1983.

Oechel, W.C. Production and nutrient dynamics of selected taiga mosses and their effect upon ecosystem development. Invited talk. Taiga Synthesis Meeting. University of Alaska, Fairbanks, Alaska, 6-10 June 1983.

Oechel, W.C. and C.D. Reid. Photosynthesis and biomass of chaparral shrubs along a fire-induced age gradient in southern California. Invited symposium presentation. Mediterranean Bioclimatology Symposium. Montpellier, France, 18-20 May 1983.

Reid, C.D. and W.C. Oechel. Water relations of two chaparral shrubs along a fire-induced age gradient in southern California. Invited poster session. Mediterranean Bioclimatology Symposium. Montpellier, France, 18-20 May 1983.

Hilbert, D.W. and W.C. Oechel. Simulation of plant and soil processes in Alaskan tussock tundra. Invited talk. DOE Plant Uptake and Soil-Plant Processes meeting. Gaithersburg, Maryland, 9-10 May 1983.

Oechel, W.C. Ecology of chaparral. Invited talk. Brush Management Workshop, USDA, Soil Conservation Service, San Diego, California, 21 April 1983.

Oechel, W.C. Effects of elevated CO_2 on tussock tundra: experimental methods and preliminary results. Invited seminar presentation. Response of vegetation to CO_2. U.S. Department of Energy, Germantown, Maryland, 2 March 1983.

Oechel, W. C. Effects of elevated global atmospheric CO_2 on plants and terrestrial ecosystems. Invited talk. Sierra Club, San Diego, California, 14 October 1982.

Lawrence, W. T. and W. C. Oechel. Soil temperature effects of carbon balance, water relations, and succession of taiga tree species. Invited symposium presentation. International symposium of Plant, Animal and Microbial Adaptations to Terrestrial Environment. Sponsored by UNESCO-MAB. Kriopigi-Kassandra-Halkidiki, Greece, 26 September-2 October 1982.

Oechel, W. C. and W. T. Lawrence. Role of mosses on functioning of taiga ecosystems. Invited symposium presentation. International symposium of Plant, Animal and Microbial Adaptations to Terrestrial Environment. Sponsored by UNESCO-MAB. Kriopigi-Kassandra-Halkidiki, Greece, 26 September-2 October 1982.

Oechel, W.C. Invited participant. International Seminar on Forest Management and Biomass Utilization in Mediterranean-type Climates: An Interdisciplinary Approach. Kassandra-Halkidiki, Greece, 3-10 October 1982.

Oechel, W.C. Invited participant. Research Conference on "Carbon Dioxide, Science, and Consensus." Carbon Dioxide Research Division, Office of Energy Research, U.S. Department of Energy. Coolfont Conference Center, Berkeley Springs, WV, 19-23 September 1982.

Hom, J. and W.C. Oechel. Photosynthetic rates and nutrient levels found in needle age classes of black spruce (*Picea mariana*) growing in permafrost dominated areas in the taiga of central Alaska. 63rd Annual Meeting, AAAS Pacific Division. University of California, Santa Barbara, 20-25 June 1982.

Prudhomme, T.I. and W.C. Oechel. Seasonal priorities for the use of current photosynthate in the leaves of an evergreen and a deciduous subarctic shrub species. 63rd Annual Meeting, AAAS Pacific Division. University of California, Santa Barbara, 20-25 June 1982.

Oechel, W.C. The measurement of the impact of rising global CO_2 on arctic plant communities. Invited symposium presentation. International Conference on Rising Atmospheric Carbon Dioxide and Plant Productivity. Sponsored by AAAS. Athens, Georgia, 24-28 May 1982.

Oechel, W.C. Control by forest floor mosses of ecosystem functions in the taiga of central Alaska. Invited seminar at California State University, Fullerton, 18 May 1982.

THESES AND DISSERTATIONS SUPERVISED:

CURRENT GRADUATE STUDENTS

Knoll, D. Controls on nutrient uptake in water hyacinth. M.Sc. Thesis, San Diego State University (in progress).

Langsford, Derek. Controls on seedling establishment after fire. Ph.D. Dissertation, San Diego State University (in progress).

Sparks, S. Competitive interactions among seedlings of obligate seeder and resprouter species of chaparral shrubs. Ph.D. Dissertation, San Diego State University (in progress).

PAST GRADUATE STUDENTS

Perry, S. 1987. Photosynthesis and Carbon Allocation in the Macrophytes *Hydrilla verticillata* and *Potamogetton pectinatus,* M.Sc. Thesis, San Diego State University.

Mauffette, Y. 1987. Controls of herbivory on *Quercus agrifolia.* Ph.D. Dissertation, San Diego State University.

Prudhomme, T. 1984. A comparison of seasonal allocation priorities for carbon and nutrients in an evergreen and a deciduous subarctic shrub species. Ph.D. Dissertation, McGill University, Montreal, P.Q., Canada.

Reid, C. 1984. Controls on senescence in chaparral. M.Sc. Thesis, San Diego State University. 159 pp.

Tissue, D. 1984. The effect of increased carbon dioxide concentration of photosynthesis, carbohydrate allocation, and litter decomposibility in five arctic tundra plant types. M.Sc. Thesis, San Diego State University. 104 pp.

Chester, A. 1984. Controls on nitrogen allocation in two *Vaccinium* species in the arctic at Eagle Creek, Alaska. Ph.D. Dissertation, Duke University. Co-Supervisor - Boyd Strain, Supervisor.

Houpis, J. 1983. Photosynthesis, water relations and plant distribution: A physiological-ecological study. M.Sc. Thesis, San Diego State University.

Lawrence, W. 1983. Soil temperature effects on carbon exchange in taiga species of interior Alaska. Ph.D. Dissertation, San Diego State University. 131 pp.

Bigger, M. 1981. Effect of nutrient enhancement on photosynthesis in native vascular and nonvascular plants growing in the Alaskan tundra at Eagle Creek., M.Sc. Thesis, San Diego State University. 103 pp.

Sveinbjornsson, B. 1979. Controls on the CO_2 exchange in arctic *Polytrichum* mosses. Ph.D. Dissertation, McGill University. 190 pp.

Mustafa, J. 1978. The effect of growth and species specific variability on photosynthesis along an elevational gradient in the chaparral. M.Sc. Thesis, McGill University. 74 pp.

Carstairs, A. 1976. The physiological ecology of *Cladonia alpestris* in the subarctic at Schefferville, Quebec. M.Sc. Thesis, McGill University. 88 pp.

Hicklenton, P. 1975. The physiological ecology of *Dicranum fuscencens* Turn. in the subarctic. M.Sc. Thesis, McGill University. 146 pp.

Auger, S. 1974. Growth and photosynthesis of *Larix laricina* (Du Roi) K. Koch in the subarctic at Schefferville, Quebec. M.Sc. Thesis, McGill University. 114 pp.

Vowinckel, T. 1974. The effect of climate on the photosynthesis of *Picea mariana* at the subarctic tree line. Ph.D. Dissertation, McGill University (with W. Boll). 147 pp.

Professional Memberships:

American Association for the Advancement of Science (AAAS)
California Native Plant Society
Ecological Society of America
International Association of Bryologists
International Association of Ecology (INTECOL)
New York Academy of Sciences
Sigma Xi
Western Society of Naturalists

CURRICULUM VITAE

NAME: Grulke, Nancy Elizabeth

BIRTHDATE: [redacted]

BIRTHPLACE: [redacted]

EDUCATION:

Ph.D., Botany, University of Washington, 1983

Dissertation Title: Comparative Morphology, Ecophysiology and Life History Characteristics of Two High Arctic Grasses, N.W.T. Advisor: Lawrence C. Bliss

B.Sc., Honors in Botany, Duke University, 1978

H.S. Diploma, Valedictorian, Berea High School, Berea, OH, 1974

RESEARCH INTERESTS: Ecophysiological and life historical characteristics of plant species; Cold and drought stress physiology; Relationship of plant nutrients and phenological stage; Revegetation of high arctic, low arctic, alpine, and subalpine sites.

EXPERIENCE:

1987-date	Post-doctoral Research Associate, Biology Department San Diego State University
3/1984-date	Research Associate, Institute of Arctic and Alpine Research, University of Colorado, Boulder, CO
9/86-12/86	Plant Ecologist, Seattle City Light, Seattle, WA
10/85-3/86	Plant Ecologist, Montana Natural Heritage Program, Helena, MT
5/84-9/84 5/85-9/85	Ecological Consultant, College of Forest Resources, University of Washington, Seattle, WA
Winter Quarters 1984, 1985	Adjunct Assistant Professor of Biology, Montana State University, Bozeman, MT; Plant Physiology
9/83-12/83	Post-doctoral Research Associate, University of Washington
1/79-8/83	Research and Teaching Assistant, University of Washington

9/80-9/81	Conservation Representative for the Washington Native Seattle, WA
9/79-9/80	President, Botany Graduate Student Organization, University of Washington
Summers 1973-1977	Field and Laboratory Assistant including two seasons in the Central Rocky Mountain alpine, two seasons on the North Slope, Alaska

RESEARCH EXPERIENCE:

1987	Post-doctoral Research Associate; field experiments testing tussock tundra ecosystem response to elevated carbon dioxide; responsible for response of plant phenology, population biology, and nutrient dynamics (North Slope, central Brooks Range, Alaska); PI: W.C. Oechel, G.H. Riechers, Biology Department, San Diego State University, San Diego, CA. Funded by Department of Energy, CO_2 Program.
1984-1985	Ecological consultant; two field seasons; floristics, community analysis of upland tundra, food chemistry of low shrubs, Okpilak Valley, NE Alaska; PI: F.C. Ugolini, D.J. Marrett, College of Forest Resources, University of Washington, Seattle, WA. NSF DPP-8409614.
1983	Post-doctoral Research Associate; photosynthetic capacity of two high arctic grasses; PI: L.C. Bliss, Botany Department, University of Washington. NSF 81-07520.
1979-1983	Research Assistant; three field seasons in the high arctic and growth chamber experiments to characterize adaptations of two grasses; ecophysiology and population dynamics; designed and constructed ecophysiological equipment; PI: L.C. Bliss, Botany Department, University of Washington. NSF 78-23260, 81-07520.
1977, 1983	Senior honors thesis research, "Regeneration of vegetation 50 yrs after fire at treeline, Niwot Ridge, Colorado;" Supervisor: W.D. Billings, Botany Department, Duke University, Durham, NC. Funded by Duke University Grant for Undergraduate Research. Follow-up research was conducted in 1983 funded by a Sigma Xi Grant-in-Aid of Research, Botany Department, University of Washington, Seattle, WA.
1976	Field Assistant; soil-landform mapping and nutrient cycling at Meade River (coastal plain), Alaska. PI: K.R. Everett, Institute of Polar Studies, Ohio State University, Columbus, OH. NSF OPP 75-12950-A01.

1975	Field Assistant; chemical and morphological changes in soil after oil spills, Barrow, Alaska; PI: K.R. Everett, Institute of Polar Studies, Ohio State University. NSF OPP 75-12950-A01.

PUBLICATIONS:

Grulke, N.E. and L.C. Bliss. 1988. Comparative life history characteristics of two high arctic grasses, N.W.T. Ecology 69(2), in press.

Bliss, L.C. and N.E. Grulke. 1988. Revegetation in the high arctic: its role in reclamation of surface disturbance. In: Kershaw, P. (ed.) Knowing the north: integrating tradition, technology, and science. Proceedings of a symposium held in Edmonton, Alberta.

Grulke, N.E. and L.C. Bliss. 1985a. Environmental control of the prostrate growth form in two high arctic grasses. Holarctic Ecology 8: 204-210.

Grulke, N.E. and L.C. Bliss. 1985b. Growth forms, carbon allocation, and reproductive strategies of high arctic saxifrages. Arctic and Alpine Research 17(3): 241-250.

Grulke, N.E. and L.C. Bliss. 1983. A note on winter seed rain in the High Arctic. Arctic and Alpine Research 15(2): 261-265.

MANUSCRIPTS IN PREPARATION:

Grulke, N.E. Micro-distribution of a high arctic grass, *Phippsia algida*.

Grulke, N.E. Regeneration at treeline in the front range after fire.

Grulke, N.E. and Bliss, L.C. Experimental field manipulations of two high arctic grasses.

Grulke, N.E., Hahn S., Marrett, D.J., and Tenhunen, J. Community analysis and above-ground biomass of two upland tundra plant communities at two sites on the North Slope, Alaska.

Grulke, N.E. and Marrett, D.J. Primary plant succession and soil development on an upland tundra surface, NE Alaska.

Grulke, N.E., Oechel W.C. Effects of elevated CO_2 on population dynamics of vascular plants and moss in tussock tundra.

Grulke, N.E. and Oechel, W.C. Effects of elevated carbon dioxide on available soil nutrients and nutrient content of plant tissue.

Grulke, N.E. and Rhoades, D. Phenology of nutrients and secondary compounds of low arctic shrubs.

PRESENTATIONS AT PROFESSIONAL MEETINGS:

Grulke, N.E. and Marrett, D.J. Primary plant succession and soil development on an upland tundra surface, NE Alaska. Poster session, INTECOL, ESA meetings, Syracuse, NY, 1986.

Grulke, N.E. and Bliss, L.C. Comparative life history strategies of two high arctic grasses. AIBS meeting, Fort Collins, CO, 1984.

Grulke, N.E. Drought Tolerance of two high arctic grass species. AAAS, Arctic Division, Fairbanks, AK, 1982.

Grulke, N.E. and Bliss, L.C. Demography of *Phippsia algida* in a heterogeneous environment. AIBS meeting, State College, PA, 1982.

Grulke, N.E. Ecology of Alaska. Invitational public lecture. Smithsonian Institute, Washington, DC, 1982.

Grulke, N.E. Population dynamics of saxifrages in the High Arctic. 11th Annual Arctic Workshop, INSTAAR, University of Colorado, Boulder, CO, 1982.

Grulke, N.E. Ecology of two high arctic grass species. 10th Annual Arctic Workshop, INSTAAR, University of Colorado, Boulder, CO, 1981.

Grulke, N.E. Vegetational regeneration 50 yrs after fire at treeline in the Front Range, CO. 52nd Annual Meeting, Northwest Science Association, Bellingham, WA.

CURRICULUM VITAE

NAME: Steven J. Hastings

BIRTHDATE: [redacted]

BIRTHPLACE: [redacted]

EDUCATION: B.A., Zoology, University of Nebraska, Lincoln, Nebraska, 1974

M.A., College of William and Mary, Williamsburg, Virginia, 1980.

EXPERIENCE:

1985-Present	Adjunct Faculty, San Diego State University, College of Sciences, San Diego, California.
1985-present	Logistics Coordinator, Systems Ecology Research Group. Facilitate multi-institutional research activities at arctic field stations. Responsibilities includes personnel, laboratory and data management, experimental design, mapping, site protection, logistics and technical services.
1984-1985	Manager, Systems Ecology Research Group. Coordinate and monitor research facilities and equipment amongst principal investigators and technicians, forecast and monitor research budgets and equipment inventories, prepare annual technical reports.
1980-1983	Research technician, in physiological plant ecology in California Chaparral, Systems Ecology Research Group, San Diego State University. Duties include field determination of plant water relations, water potentials, leaf conductances, photosynthetic rates, root biomass, laboratory determination of RUBP carboxylase/oxygenase activity and leaf carbohydrate levels in resprouts following fire.
Fall 1979	Biological Aid (Fisheries), Northeast Fisheries Center, National Marine Fisheries Service, Sandy Hook Laboratory. Duties included determination of seabed oxygen consumption using a Pamatmat multiple corer, and maintenance and calibration of equipment.
1976-1979	Graduate Research Assistant, Ecology Pollution, V.I.M.S., Gloucester Point, Virginia. Duties included cruise preparation, lab maintenance, determination of primary productivity, heterotrophy, concentration of nutrients and chlorophyll a and oxygen, and physical measurements of water columns within the Chesapeake Bay, marshes and seagrass beds.

Summer 1975	Laboratory Technician, University of Nebraska Soil Testing Laboratory, Lincoln, Nebraska. Duties included extraction and measurement of metals in soil and water samples using an atomic absorption spectrophotometer.
Spring 1975	Laboratory Instructor, General Physiology, University of Nebraska, Lincoln, Nebraska.
1974-1975	Student Research Assistant, University of Nebraska, Lincoln, Nebraska. Temperature acclimation in trout. Duties included the extraction and purification of fatty acid synthetase from chicken livers and livers from cold and warm acclimated trout utilizing column chromatography. Enzyme assays included determination of pH optima, Ea, and kinetic constants.
Summer 1974	Team member on Student Originated Studies Program (National Science Foundation): A Limnology Study of Perry Reservoir With Emphasis on Primary Productivity. Benedictine College, Atchison, Kansas. Duties included biweekly field sampling, followed by the identification and enumeration of phytoplankton samples and physical measurements of the water column.

PUBLICATIONS:

Kummerow, J., J.N. Mills, B.A. Ellis, S.J. Hastings, and A. Kummerow. 1987. Downslope Fertilizer Movement In Arctic Tussock Tundra. Accepted, Holarctic Ecology.

Oberbauer, S.F., N. Sionit, S.J. Hastings, and W.C. Oechel. 1986. Effects of CO_2 enrichment and nutrition on growth, photosynthesis and nutrient concentration of Alaskan tundra species. Can. J. Bot. 64:2993-2998.

Prudhomme, T.I., W.C. Oechel, S.J. Hastings, and W.T. Lawrence. 1984. Net ecosystem gas exchange at ambient and elevated carbon dioxide concentrations in tussock tundra at Toolik Lake, Alaska: An evaluation of methods and initial results, pp. 155-161. In: J.H. McBeath (ed.), The potential effects of carbon dioxide-induced climactic changes in Alaska: Proceedings of a conference. School of Agriculture and Land Resources Management, University of Alaska, Fairbanks. 208 pp.

Oechel, W.C., and S.J. Hastings. 1983. The effects of fire on photosynthesis in chaparral resprouts. In: F.J. Kruger and W.R. Siegfried (eds.). Nutrients as determinants of the structure and functioning of Mediterranean-type ecosystems. Springer-Verlag, New York-Heidelberg-Berlin.

Hastings, S.J., and W.C. Oechel. 1981. Photosynthesis and Water Relations of Mature and Resprout Chaparral Vegetation. In: Eugence, C.C. and W.C. Oechel (eds.), Proceedings of the symposium on dynamics and management of Mediterranean-type ecosystems, June 22-26, San Diego, California. Gen. Tech. Rep. PSW-58. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 1982, p. 602.

Haas, L.W., S.J. Hastings, and K.L. Webb. 1981. Phytoplankton responses to the stratification-mixing cycle in the York River estuary during late summer. In: B.J. Neilson and L.E. Cronin (eds.), Estuaries and nutrients. Humana Press, Inc., Clifton, New Jersey, pp. 619-636.

Hastings, S.J. 1980. Aspects of diel variation of 14 CO_2 uptake in cyclostat grown Chlorella sp. population exposed to varying lengths of photoperiods. Master thesis, College of William and Mary, Williamsburg, Va.

PAPERS SUBMITTED:

Hastings, S.J., Luchessa, S.A., Oechel, W.C., and Tenhunen, J.D. Biomass attributes of two plant communities within a small watershed in the Brooks Range Foothills, Alaska. Submitted to Holarctic Ecology.

Marion, G.M., S.J. Hastings, S.F. Oberbauer, and W.C. Oechel. 1987. Soil-plant nutrient relationships in a tundra ecosystem. Submitted to Holarctic Ecology.

Matthes-Sears, U., W.C. Matthes-Sears, S.J. Hastings, and W.C. Oechel. Variation in nutrient status, biomass, vegetative characteristics, and gas exchange of two deciduous shrubs on an arctic tundra slope. Submitted to Arctic and Alpine Research.

Oberbauer, S.F., S.J. Hastings, J.L. Beyers, and W.C. Oechel. Impacts of variation in water and nutrient supply on nutrition, photosynthesis, and growth in Alaskan tundra. Submitted to Holarctic Ecology.

Hastings, S.J., W.C. Oechel, and N. Sionit. 1987. Water Relations and Photosynthesis of Chaparral Resprouts and Seedlings Following Fire and Hand Clearing. In: S. Keeley (ed.) Proc. of the Symp., The California chaparral Paradigms reexamined (7-8 Nov. 1986, Los Angeles Natural History Museum, L.A.) (submitted).

PAPERS IN PREPARATION:

Sionit, N., Oechel, W.C., Kruger, F.J., Hastings, S.J., and Smith, F.R. 1987. Photosynthesis and growth of seedlings of evergreen *Sclerophylis* under varying rates of nitrogen supply.

Hastings, S.J., and K.L. Webb. 1987. Diel changes in photosynthetic parameters of a nitrate limited cylostat population of a marine *Chlorella sp.* subjected to varying photoperiods.

Hastings, S.J., Oechel, W.C., and Prudhomme, T.I. 1987. Primary production and stand development in chaparral communities at the San Dimas Biosphere Reserve.

Hastings, S.J., Luchessa, S A., Oechel, W.C., and Tenhunen, J.D. 1987. Aboveground biomass, nutrients and annual production in natural and disturbed arctic plant communities.

Oberbauer, S.F., J.L. Beyers, S.J. Hastings, and W.C. Oechel. Micronutrient influences on Alaskan tundra photosynthesis and productivity. To be submitted to Ecology.

CURRICULUM VITAE

NAME:	Hjelm, Ulf
EDUCATION:	M.Sc., Mathematics, San Diego State University. Full-time graduate studies in computer science: anticipated completion of degree, Spring 1988 B.A., Mathematics, University of California, San Diego
HONORS:	Member, Upsilon Pi Epsilon Honor Society Provost's Honor List
SPECIAL PROJECTS:	Programming and data reduction of CO_2 flux rates, mathematical analysis, compiler construction, alpha-beta search for game trees, load average servers, Xinu operating system, and replicated file servers
EXPERIENCE:	
1986-date	Research assistant, Systems Ecology Research Group, San Diego State University, San Diego, CA Fully responsible for data transfer, cleanup, manipulation and graphing of CO_2 flux rates. Administration and maintenance of Hewlett Packard microcomputer, graphics programming
1979-date	Freelance graphic artist, San Diego, CA Three-dimensional design of soft-sculptured toys, graphics for advertising and promotions
1981-1982	Planning Department, Stockholm Subway, Stockholm, Sweden
1979-1981	Undergraduate teaching assistant in mathematics, University of California, San Diego
COMPUTER LANGUAGES AND SYSTEMS:	C, Pascal, Assembly for PEP-11 and Motorola 68000, Simscript, Fortran,UNIX, VMS, NOS

Walter C. Oechel

A. Current Support

1. National Science Foundation

   "Mechanisms Controlling Resource Use, Community Organization and Succession in Fire-dominant Ecosystems"
   $900,000 for three years
   Award ends 3/31/89 25% effort

2. National Science Foundation

   "The Influence of Fire and Disturbance on Research Use in the Chaparral of Southern California and Oak Woodlands of Southern France"
   $20,000 for two years
   Award ends 3/31/88 5% effort

3. U.S. Department of Energy

   "Response of Tundra Ecosystems to Elevated Atmospheric CO_2"
   $470,000 for twenty-one months
   Award ends 3/31/88 25% effort

4. U.S. Department of Energy

   "Effect of Perturbation of Tundra Drainage Systems on Ecosystem Dynamics and Tundra and Riparian Vegetation"
   $850,000 for one year (this is the total grant amount for eight investigators)
   Award ends 12/31/87 50% effort

5. NATO
   "Mineral nutrition and irrigation effects on production in *Eucalyptus* plantations"
   $5,000 for one year
   Award ends 2/15/88 5% effort

B. Pending Support

1. U.S. Department of Energy

   "Effect of perturbation of tundra drainage systems on ecosystem dynamics and tundra and riparian vegetation"
   $54,860 for one year
   Award ends 12/31/88 25% effort

2. This proposal 50% effort

Nancy E. Grulke

A. Current Support

U.S. Department of Energy

"Response of Tundra Ecosystems to Elevated Atmospheric CO_2"
$37,372 for three months
Award ends 3/31/88 100% effort

B. Pending Support

National Science Foundation

"Reproduction Biology of White Spruce"
$252,000 for three years
Award ends December 31, 1991 25% effort

Nancy E. Grulke

A. Current Support

U.S. Department of Energy

"Response of Tundra Ecosystems to Elevated Atmospheric CO_2"
$37,372 for three months
Award ends 3/31/88 100% effort

B. Pending Support

National Science Foundation

"Reproduction Biology of White Spruce"
$252,000 for three years
Award ends December 31, 1991 25% effort

Steven J. Hastings

A. <u>Current Support</u>

None

B. <u>Pending Support</u>

None

Ulf Hjelm

A. <u>Current Support</u>

None

B. <u>Pending Support</u>

None

9. BUDGET AND BUDGET JUSTIFICATION removed at

BUDGET JUSTIFICATION

W. C. Oechel is primarily responsible for the project. He will oversee general program development, progress budgeting, and reporting. He is budgeted 25% time in the first year and 33% thereafter. However, Dr. Oechel will devote approximately 50% time to this project.

Nancy Grulke, a research associate and co-principal investigator, is the continuous on-site supervisor for the field aspect of the program. She will oversee successful chamber operation and the field sampling schedule. Dr. Grulke will work on the project 75% time in the first year and full time thereafter. She has one year experience with the CO_2 program at Toolik Lake and many years' experience conducting research in remote arctic locations. Steve Hastings is the chief technician for the project. He is budgeted 75% time in the first year and 100% thereafter.

A systems engineer will be contracted to consult on current system design and planned modifications, and to troubleshoot in the event a problem arises which is not easily resolved by the field crew. Several possibilities for engineering and technical design assistance exist. Dr. Steven Roberts, President of Data Design Group is familar with the CO_2 system, having worked with hardware and software aspects in 1983. He has agreed to evaluate the system design, to design and oversee system modifications in the spring of 1988, and to be on call to assist with system troubleshooting during the summer of 1988. Dr. Celto, an electronics engineer, familar with aspects of the greenhouse system, has also agreed to assist in system evaluation and design modifications. He would also be available to assist with troubleshooting during the field season should the need arise. In addition, the Engineering School at SDSU has agreed to provide whatever other engineering, technical, or systems services required. Walt Merek, the refrigeration technician for the Biology Department, will be available to the project to assist with refrigeration design and repair.

We will contract with a systems analyst for profession evaluation and modification of the control program.

Two field assistants will be employed to assist in system maintenance and sampling. It is our intention that one or both of these individuals be returning veterans to the arctic CO_2 project.

Ulf Hjelm will continue as the computer technician responsible for data reduction, analysis, and presentation.

Kathleen Turner is budgeted 75% time as administrative assistant and secretary but will be available to the project full time.

Five trips per year to the field site, two program meeting trips, and two national meeting trips are budgeted. Trips to the field are budgeted at the APEX fare where trip durations are sufficiently short (less than 60 days). Additional trips will be funded from other sources.

Supplies for system maintenance and modification are indicated in the budget particulars. Vehicle rental is based on rental from the University of Alaska at $1/mi. Nutrient analyses are based on rates for use of equipment and supplies at F.C. Ugolini's laboratory at the University of Washington. Camp fees are budgeted at the University of Alaska rate of $90/d for 505 days in the first three years and 90 days in the third year. Generator fuel is budgeted at 6,000 gallons at $1.10/gal.

Most equipment and facilities necessary for this project are already available to it. Therefore, equipment purchases proposed are minimal. Equipment requested in the first year includes refrigeration compressors and mass flow controllers for the two additional chambers to be constructed, mass flow valves for system repair, an enlarged research hut to allow space for all temperature sensitive equipment, air pump and compressor to replace worn and inadequate units, and a DAS board to allow expansion for addition to the two new chambers.

In the second year, a more stable N_2O IRGA is budgeted to improve the precision and reduce the time required for adequate leak determination. A LiCor 6200 photosynthesis system is budgeted for determination of photosynthetic response to elevated CO_2. LiCor photosynthesis systems have been borrowed from other projects in the past, but to assure availability to this project, the purchase of a dedicated unit is requested. No equipment is budgeted in the third or fourth years.

Indirect costs are based on the new off campus rate of 41% of the modified total direct costs (which exclude camp fees and equipment).