PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

AN LTER PROGRAM FOR THE ALASKAN ARCTIC

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RESULTS FROM PRIOR NSF SUPPORT

Grant #DPP 8320544: "Response of Arctic Freshwater Ecosystems to Environmental Stress" $1,429,808 from May 1984-December 1987. In this project, ideas about the control of aquatic ecosystems were tested by changing the rate of nutrient input to enclosed parts of lake ecosystems, to half of a divided lake, and to an entire stream. Fish and zooplankton abundance was also manipulated. Aquatic systems are mostly nutrient limited and lakes and streams responded instantly to fertilization. Under natural conditions, the predators control the structure of lake zooplankton communities but stream grazers are controlled by food limitation. Zooplankton and stream grazers could not respond to enrichment for more than two years because of their multi-year life cycles. A list of over 50 peer-reviewed publications and 21 MS and PhD theses from the ten years of NSF funding is given in Appendix I.

Grant #BSR 8507493: "Nutrient Cycling in an Arctic Landscape: Interactions Between Ecosystems along a Riverside Toposequence" $810,000 from September 1985-September 1988. This project began only a year ago and builds on prior research funded by the NSF through the University of Alaska (F.S. Chapin and G.R. Shaver, grants #DEB 8205344 and #DEB 79-05842). Over the past seven years this series of projects has resulted in over 35 peer-reviewed publications; those directly related to Toolik Lake are listed in Appendix I. In the earlier work, we found that nutrient availability plays a key role in controlling the terrestrial community. The current project examines this in more detail by measuring nutrient movement between ecosystems dominated by different growth forms in the tundra landscape. After one full summer, this new work (Shaver, with A.E. Giblin and K.J. Nadelhoffer) has shown us that nutrient movement between ecosystems does differ in different tundra ecosystem types, and that the various ecosystem types differ greatly in their dependence in internal element recycling in comparison to external supply. Greater detail is provided in the text of this proposal.

ABSTRACT

Since 1975 terrestrial and aquatic ecologists have used the University of Alaska's Toolik Lake Camp, on the North Slope of Alaska, as a research base. Funding for this research has come from a variety of sources and the ecologists have come from many different home laboratories. A group of those ecologists with long experience at Toolik Lake now propose that it be added to the network of Long Term Ecological Research (LTER) sites.

The proposed LTER research has five separate but related sections: (1) baseline data collection, (2) experimental manipulations of whole ecosystems from the "bottom up" (i.e., nutrients, light, and temperature), (3) manipulations from the "top down" (grazers and predators), (4) linkages of land, water, and the atmosphere through exchanges of elements, and (5) regional extrapolations.

Research in all five sections will involve terrestrial ecosystems, lakes, and rivers. The major strengths of the research include our demonstrated ability to apply experimental techniques to whole ecosystems, both terrestrial and aquatic, and the application of new methods using stable isotopes. The relative simplicity of arctic ecosystems makes them particularly good models for whole ecosystem research, and their location in a region of climatic extremes makes them particularly important to include in the LTER network.

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I. INTRODUCTION

A. Overview. Since 1975, a series of aquatic and terrestrial ecological projects have worked near Toolik Lake, a foothill site in the Alaskan arctic. Eleven years later, the ecology of lakes, a river, and the tundra vegetation is well documented, detailed process studies have been made, there are a number of long-term data sets being collected, and several long-term experimental whole-ecosystem manipulations are underway. An excellent field station has been established by the University of Alaska where laboratories and logistics are available. Now, a group of 14 arctic investigators from seven institutions with a strong record of productive long-term ecological research on important questions, proposes that arctic research would be strengthened by the coordination and stability of an LTER program and that the arctic information, the investigators, and the expertise will help the nationwide LTER program.

Research tasks proposed are: baseline studies of climate and its relationship to plant growth, of atmospheric deposition, of soil chemistry, and of stream flow and chemistry; experimental studies of controls of ecosystem structure and function by resource limitations (nutrient, temperature) and by the higher trophic levels (predators, grazers); experimental and observational studies of land, air and water interactions (movement of N, P, C and trace gases), and the first steps to extrapolation of detailed process knowledge to gain understanding of the ecology of other regions of the North Slope.

Among the many ways to carry out ecosystem research, two will be emphasized in this LTER program. First, we have found that whole-ecosystem manipulations and perturbations work very well in the Arctic and have given valuable insights. On the tundra, the long-term plots investigating the interactions of added nutrients (N,P,K), of shading, and of increased temperature will be continued. We have successfully enclosed sections of lake ecosystems in small limnocorrals and divided lakes with polyethylene curtains to investigate effects of nutrient addition on herbivores (zooplankton, benthos) - we will continue the nutrient studies and begin manipulations (add, remove) of lake trout, the top predator. We will continue fertilization (continuous) of a section of the Kuparuk River and also darken sections and increase and reduce the number of fish (grayling) in other sections.

Second, we have recently found that the isotopes ^{13}C, ^{14}C, and ^{15}N work well in the Arctic to study nutrient transfers and food-chain links and that we have introduced stable isotope signals through fertilization. Old peat has different ^{14}C ages than stream algae (which do stream insects use?), stream-side willows have different δ^{15}N than vegetation higher on the slope (where does nitrification occur?), and lake trout feeding on snails will have different δ^{15}N than lake trout feeding on fish (what is the food of lake trout in a series of lakes over the North Slope? Will the protein in fish scales tell us?). We will use naturally occurring radioactive and stable isotopes both for process studies and for surveys. They become especially powerful when comparisons can be made of stable isotope distribution in control and experimental ecosystems.

B. Why an Arctic Alaska Long-Term Ecological Program? There are three reasons: First, basic science -- arctic tundra is a major biome and must be studied, some ecological questions are best studied in the Arctic, processes and their controls must be investigated at the ends of the climatic spectrum, some questions and experiments need 5-10 years. This is especially true where important components of the ecosystem have long life cycles such as 50 years for lake trout and 7 years for chironomids in tundra ponds. Second, applied science -- northern Alaska is developing rapidly and research can answer several applied questions, global warming may first manifest itself in the Arctic so a long-term data base must be collected. Third, efficiency and effectiveness -- ongoing projects provide a ten-year data base, experienced investigators, already operative sites, experiments, and a well set-up research station.

All of the basic ecosystem processes occur in the Arctic and fit together into functioning ecosystems -- yet these are relatively simple systems and the unraveling of the interactions of cycles and populations is often simplified. For example, in streams there is no litter input and most of the particulate carbon comes from eroding 1000-year-old tundra peat -- the ^{14}C isotope label will help determine the usefulness to the ecosystem of the old carbon vs. new carbon from algal photosynthesis. Here the ecosystem biota is microbes, four dominant species of insects and one species of fish. On land, light, temperature, and nutrient abundance and cycling control the growth form, productivity, and biomass of the vegetation. It is now known that near Toolik Lake the nutrient-rich sites are dominated by deciduous shrubs while nutrient-poor sites are dominated by evergreens and lichens. Light, temperature and nutrient cycle interactions can be sorted out over the next decade by experimental manipulations because of the low stature of the vegetation. A greenhouse or shade experiment needs only a 1 m high structure -- simple, cheap, and do-able.

Comparative studies of all LTER sites will also be enhanced by an arctic site. The data will fall at the extremes of any comparison of ecosystem properties (e.g., primary productivity of lakes, decomposition rates in soils).

Another basic research need arises from the global viewpoint of International Geosphere-Biosphere Program. IGBP requires information on input and cycling of elements in all types of ecosystems including the Arctic. It is also true that models predict that the greenhouse effects on temperature will be highest at high latitudes so long-term data sets are needed to test the prediction of ecosystem effects and the possible increased release of CO_2 and trace gases from the soils. Arctic ecosystems will be the first to experience large climatic changes and adequate baseline data are urgently needed.

There is an immediate need for applications of science in northern Alaska. As Larry Bliss recently stated, the Arctic is the only area virtually unmodified by man but the next 20 years will see more of man's impacts than the past thousand. The only road to northern Alaska will be opened to the public in 1987 and questions are being asked by the U.S. Bureau of Land Management and the North

Slope Borough about fertilization of streams to increase fish production, the effect of fishing pressure on as-yet undisturbed populations of lake trout, and the impact of wastes and road construction on tundra and streams. The North Slope Borough is asking about the possibility of success of introducing new species of fish to the North Slope of Alaska and about the impact of increased fishing by local populations. A number of studies have already been carried out at Toolik Lake aimed at finding the best strategies for revegetation of oil pipeline pads and former construction camps. The U.S. Fish and Wildlife Service has contracted for a synthesis of aquatic ecology on the North Slope in relation to the food webs supporting fish and waterfowl resources. The Department of Energy is sponsoring research to predict impacts of energy extraction on land ecosystems of the North Slope. Finally, there is a Congressional mandate that increased study of arctic ecosystems is in the national interest.

Finding answers to many of these basic and applied questions requires long-term measurements and large-scale experimental manipulations. An LTER program would provide a core of long-term planning, long-term environmental data, and funding to provide the continuity now lacking. LTER sites would be a magnet to attract other projects which would in turn add to the information and attractiveness. In addition, an LTER program would be effective to set up because a series of projects by a number of investigators over the past 12 years have provided a strong base of data and ecological understanding for the area around Toolik Lake and have allowed the University of Alaska (with state and federal help) to build an excellent field camp which allows state-of-the-art ecological measurements to be carried out. A number of long-term experiments are already set up and experienced investigators from a number of institutions are available. In fact, some are already working on various projects at the Toolik Lake site so maximum use will be made of affiliated projects.

C. Operating Procedures. We propose that an Arctic Alaska LTER Program be set up to focus research and investigators on several important questions, on several sites, and on long-term experimental manipulations. The goals of the program would be determined by 14 principal investigators drawn from seven institutions. The Program Director and five other P. I.'s would be housed at the Ecosystems Center of the Marine Biological Laboratory, the lead institution. Most of the field work will be carried out in June, July and August; some measurements will begin in May and extend into September.

Based upon the experience of 12 seasons of multi-investigator projects at the Toolik Lake site, project integration can be achieved by some practical rules: 1) select experienced scientists who take part in developing program goals; 2) insistence that principal investigators interact by spending six weeks each summer in the field; 3) ensure excitement by insisting that many of the samples (e.g., nutrients) be worked up in the field; 4) focus the work by insisting on a limited number of sites and a limited number of large-scale manipulations; and 5) make data available to all through annual reports and through a data base.

Under the ideal conditions of availability of research funds, LTER funds would be used to provide: 1) Field collection of baseline data on climate, stream flow, stream and lake chemistry, and phenology; 2) Setup and maintenance of manipulation experiments including stream and lake fertilization, changes in the top predators of lakes, and changes in the nutrients, light, and temperature of tundra plots; 3) Operation of a data base; 4) Management and logistics costs of field operations; and 5) If necessary, funding to P.I.'s for projects for continuity. If other research funds are not available, then the funding would shift towards #5.

The measurements would be carried out at the location best for that question. Most research would be near Toolik Lake. Additional research would be in the Colville River Delta because that is the best location for studies of top trophic levels such as migratory fish and waterfowl. Part of the research task presented in section III F is to begin to extrapolate the results from intensive measurements to other regions of the North Slope and this task also requires measurements and experiments away from Toolik Lake. Therefore, the LTER Program would be to some extent a regional one, encompassing the entire Alaskan tundra.

The program has an ambitious set of goals (see Section III). If the program is well planned and priorities clear, then the goals can be met with or without additional funding of projects in northern Alaska. Of course, outside funds (affiliated projects) will allow much more rapid progress and each investigator is expected to always seek outside funds. Thus, there are already two projects funded for one or two years more (DOE and NSF-Ecosystems to Shaver) that will add information to the LTER Program. Another large project (NSF-DPP) is being reviewed for renewal. If, as expected, the LTER sites become magnets for other research projects then new projects will be generated in addition to these listed here. The changing mix of funded projects argues for flexibility in the LTER Program, at least flexibility to fund necessary projects for two or three years at a time and then to bring in other projects.

II. SITE AND HISTORY OF RESEARCH

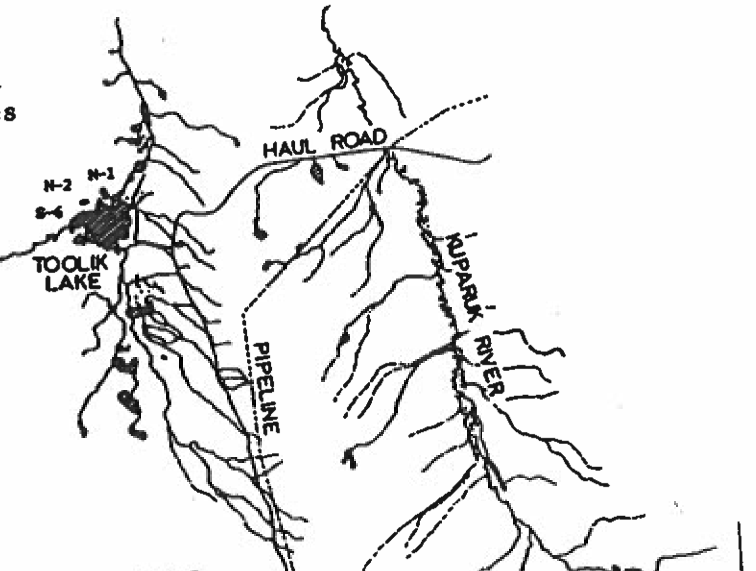
A. Site Location and Description. The North Slope is the 200,000 km^2 of northern Alaska which drains to the Arctic Ocean (Fig. 1). All of the North Slope has continuous permafrost, a general lack of trees, a complete snow cover for 7 to 9 months, winter ice cover on lakes, streams, and ocean, and cessation of river flow during the winter (Walker 1973). The North Slope is divided into the Coastal Plain (61,000 km^2), the Foothills (95,000 km^2), and the Mountains (40,000 km^2).

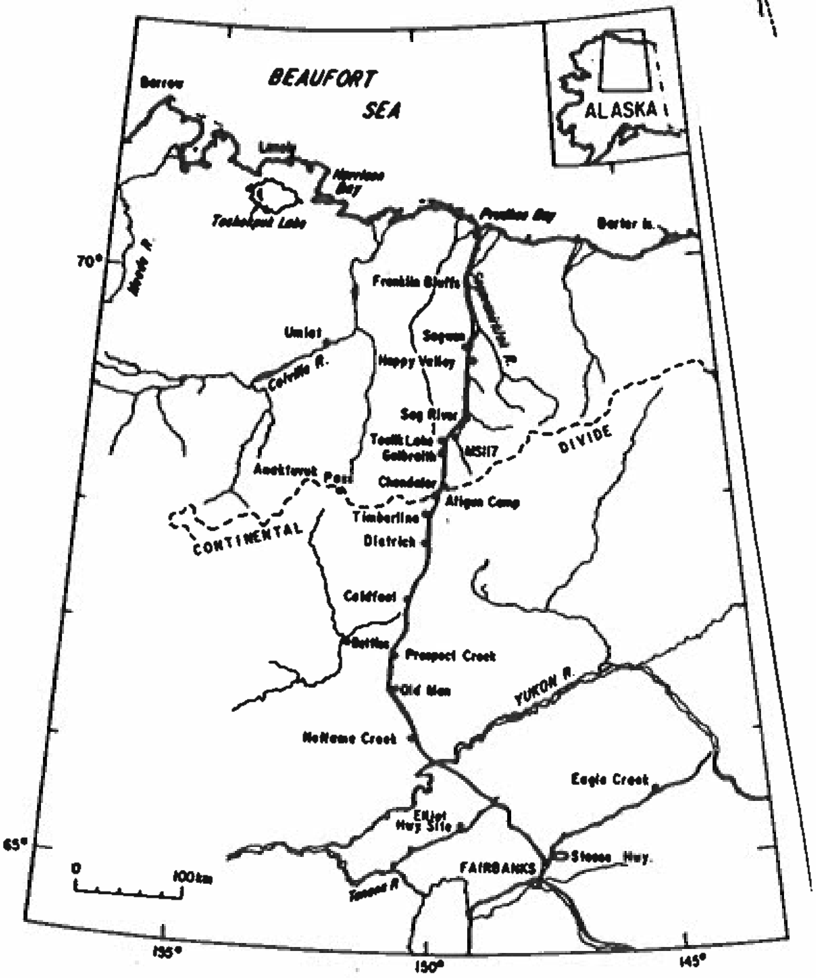
The population of the North Slope, less than 10,000, is located in villages along the coast and at the Prudhoe Bay oil field. The only road is the Dalton Highway constructed to build and service the oil pipeline. Between 1947 and 1977, most of the scientific research took place near Pt. Barrow, the location of the Naval Arctic Research Laboratory. After 1975 the Dalton Highway provided access to a 500 mile transect from Fairbanks north to the Arctic Ocean and scientific interest shifted to sites along the highway.

We propose field work for the Arctic Alaska LTER Program at a foothill site

Figure 1. Location maps of proposed LTER sites.

Top: Detail of Toolik Lake and Kuparuk River area, also showing the small lakes used for divided-lake experiments (N-1, N-2, S-6). The field camp is at the SE corner of Toolik Lake, near the inlet. MS117 is just off the map to the east (right) of the Kuparuk River. Sag River is 13 miles further north and east.





Bottom: The Dalton Highway and oil pipeline between Fairbanks and Prudhoe Bay, showing Toolik Lake, MS117, and Sag River in the northern foothills of the Brooks Range and the Colville River. The Kuparuk River is the unnamed river that flows into the Beaufort Sea between the Colville and Prudhoe Bay. A road now runs from Prudhoe to the mouth of the Colville.

near Toolik Lake, at the Colville Delta near the Arctic Ocean, and on transects of the foothills and coastal plain along the Dalton Highway (Fig. 1). Most work would be near the Toolik Lake Research Station (University of Alaska) at 68°38'N and 149°38'W. This site is located 10 miles north of the Brooks Range in rolling foothills. By road, the lake is 130 miles south of Prudhoe Bay (site of a regular airport) and 360 miles north of Fairbanks. Seven miles to the northeast of Toolik Lake, the Dalton Highway crosses the Kuparuk River (the stream site and MS 117 site) and 14 miles beyond that the highway meets the Sagavirnirktok River (Sag River), where another site is located on river bottom, river terraces, and upland. Extensions of the highway west along the coast allow access to the Colville Delta area, a site suitable for studies of waterfowl and fish.

During the summer in the foothills, the average monthly air temperature is 5-14°C and the rainfall is 30-40 mm. The annual temperature is -10°C and the total precipitation is 200-250 mm (Selkregg 1977). Despite the dry climate, the permafrost prevents downward drainage, cold temperatures lower the evapotranspiration, and the tundra is usually moist to soggy. As a result, there is a continuous vegetation cover and lots of mosquitoes. At the foothills research sites the vegetation is a mosaic of types from evergreen heaths on drier sites, to wet sedge tundra in flat lowlands, to riparian deciduous shrubs (Chapin and Shaver 1985a*). The most abundant vegetation type is cottongrass-tussock tundra. The composition on any site depends upon the time since glaciation, the soil type, exposure, drainage, and topography.

Toolik Lake (1.5 km^2) is a 25 m deep kettle lake in a terminal moraine (Miller et al. 1986). It is oligotrophic (annual production of 12 g C m^{-2}), stratifies with surface temperatures up to 15°C, and is ice-free from July through September. Lake trout and grayling dominate the fish, *Heterocope*, *Daphnia*, and *Bosmina* the zooplankton, and chironomids and snails the benthos (Hershey 1985b*). In the surrounding moraine lie a number of small lakes up to 10 m deep containing a variety of fish and zooplankton populations (O'Brien et al. 1979b*).

The Kuparuk River arises in the foothills of the Brooks Range and flows north draining a large area of the North Slope. Only the upper 25 km has been studied by our group. Some baseline data on the delta region is available from oil field development impact statement reports. It is a clear-water stream, frozen solid from late September until late May. Discharge at the Dalton Highway crossing ranges from 0.3 to 28 m^3 sec^{-1}. Nutrients, especially phosphorus, are low and dissolved organic carbon high (6 mg C $liter^{-1}$). Most of the carbon in the stream comes from eroding peat or dissolved organic carbon leaching from the tundra (Peterson et al. 1986*). The primary producers are mostly diatoms on rocks. Insects are dominated by black flies, a mayfly, chironomids, and a caddisfly. There is but one fish, the arctic grayling, and the entire population migrates to a lake in the headwaters each winter.

The coastal plain LTER site is the region comprising the Kuparuk Oilfield and the Colville River delta. Access is by all-weather road extension of the Prudhoe Bay system. Full logistic support is available at Kuparuk Center and limited accommodations and aircraft support are available at Colville Village and the native community of Nuiqsut in the Colville delta.

The Colville River drains over 60,000 km^2 or about one-third of the North Slope with an average annual flow of near 10^{10} m^3. A commercial fishery in the Alaskan Beaufort Sea exploits the abundant whitefish and cisco populations as they pass through the Colville delta and the marshy wetlands provide habitat for large populations of waterfowl and shorebirds during the summer months. The river flow ceases during the winter. Up to half of the annual flow may occur during the spring flood in June; freeze-up ends the flow in late October and November (Arnborg et al. 1966).

B. ECOLOGICAL STUDIES AND WHOLE-ECOSYSTEM EXPERIMENTS

1. Terrestrial Ecology

a. *Descriptive Ecology* Terrestrial research in the Toolik area began in 1976 with descriptive and baseline vegetation studies of many sites along the length of

SITE	TYPE OF RESEARCH	HOW FUNDED
TOOLIK LAKE	LAKE WHOLE-SYSTEM EXPERIMENTS, N,P, FISH	NSF-DPP
	TUNDRA WHOLE-SYSTEM EXPERIMENTS WITH NUTRIENTS, TEMPERATURE, LIGHT	LTER
	CO2-ADDITION GREENHOUSES	DOE
KUPARUK RIVER	STREAM WHOLE-SYSTEM EXPERIMENTS WITH NUTRIENTS, FISH PREDATION	NSF-DPP LTER
MS117	CLIMATE BENCHLINE	DOE
	TUNDRA PROCESSES, PHOTOSYNTHESIS, WATER	DOE
SAGAVIRNIRKTOK RIVER	LANDSCAPES, SOILS, N,P TRANSFER	NSF-BSR LTER
COLVILLE DELTA	TRANSFER OF CARBON TO FISH/WATERFOWL	LTER

the highway and at Toolik Lake (Brown and Berg 1980, Walker et al. 1982, Shaver and Chapin 1984*, Shaver et al. 1983*, Chapin and Shaver 1981*). The next phase, research on the response of plants to disturbances of pipeline and road construction (Johnson 1980, Chapin and Shaver 1981*, Shaver et al. 1983*), led to studies of plant demography and population dynamics (Gartner et al. 1986*, Fetcher and Shaver 1983*) and raised questions of long-term successional patterns and the regulation of plant growth form and composition of the vegetation (Shaver and Chapin 1984*, Chapin and Shaver 1985*).

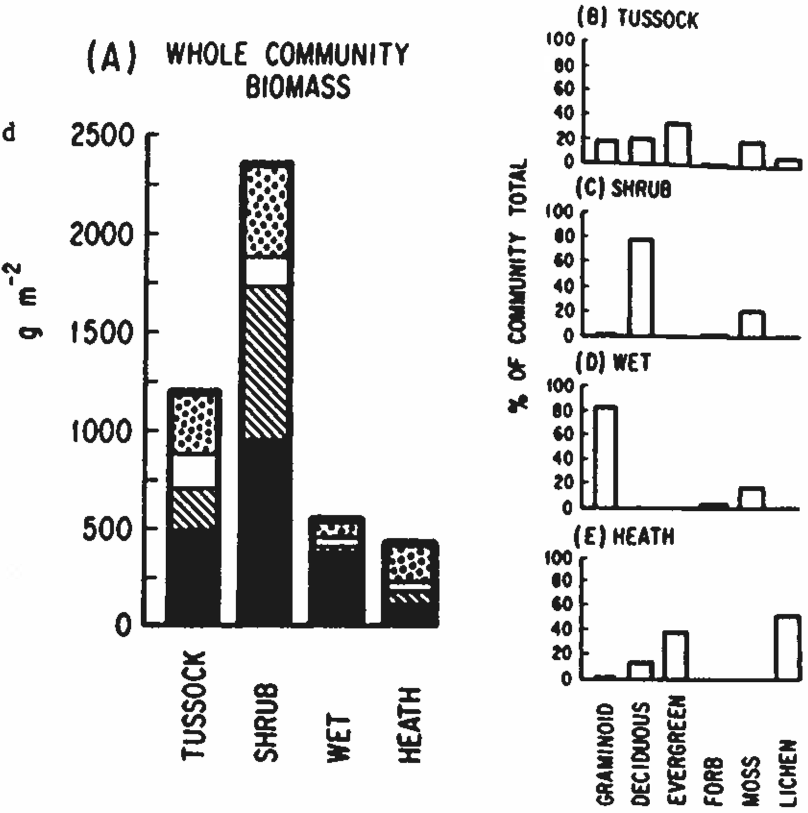
From 1979 to 1982, plant growth and its controls were analyzed and a number of long-term experiments (fertilization, light, temperature) were set up (Shaver et al. 1986*, Chapin et al. 1986*). Four replicate plots were used in each site; plots were 4-20 m^{-2}. Wooden greenhouse/shade structures were also constructed for some sites and emplaced only during the growing season. The principal conclusion, that soil processes and nutrient availability were more important than light and temperature in limiting annual productivity, led in 1984 to an NSF-Ecosystem project on element cycling in the tundra landscape (Shaver, Giblin, and Nadelhoffer are the LTER P.I.'s involved).

Since 1981, a DOE project (Oechel) has focused on response of plant processes (photosynthesis, respiration) to changes of atmospheric CO_2 and temperature. The low stature of the vegetation allowed multiple mini-greenhouses to be set up with controlled levels of CO_2. Another DOE project (Oechel) began in 1984 to work at Materials Site 117 (Fig. 1) on a detailed study of vegetation and water flow processes. The goal is to model terrestrial processes affected by energy-extraction related disturbance (Shaver, Linkens and Schell are on this project and are also LTER P.I.'s).

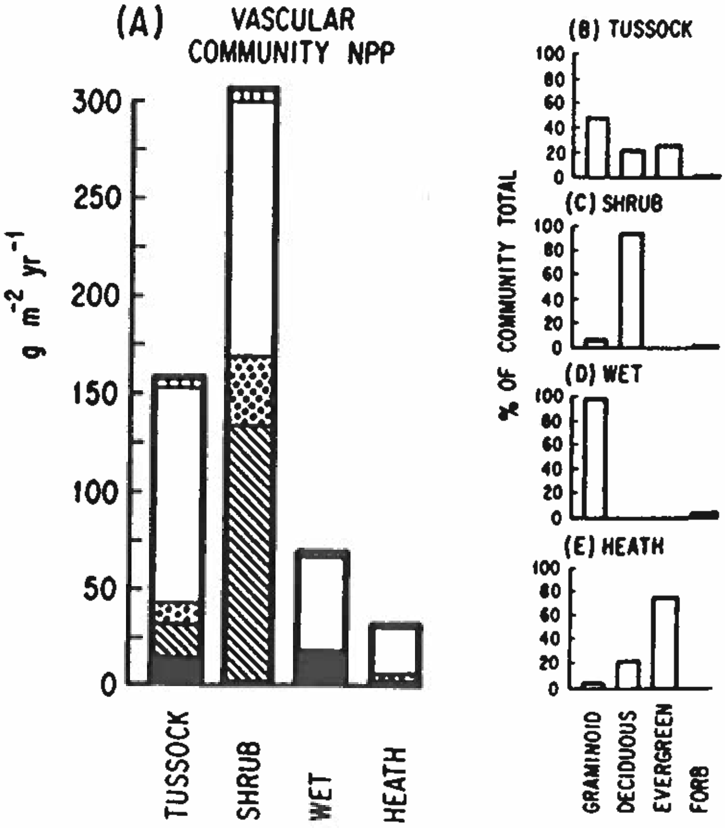
On the sites proposed for LTER research, we already know that the growth form composition, productivity, and biomass of the vegetation varies dramatically (Fig. 2). Although tussock tundra with its nearly equal mix of graminoids, deciduous shrubs, and evergreens is the most common vegetation type, we also have extensive

Figure 2. Primary production and plant biomass in four contrasting ecosystem types near Toolik Lake (Shaver and Chapin unpublished).

Top: (A) Whole community biomass including mosses and lichens (dotted bars), leaves (clear bars), aboveground stems (hatched bars), and belowground stems/rhizomes (filled bars). (B-E) For each ecosystem type in part A, biomass is broken down according to the proportion accounted for by each of six plant growth forms.



Bottom: (A) Total NPP by vascular plants including inflorescences (vertically hatched bars), leaves (clear), apical woody stem growth (dotted), secondary woody stem growth (diagonally hatched), and apical graminoid rhizome growth (filled). (B-E) For each ecosystem type in part A, NPP is broken down according to the proportion accounted for by each of four vascular plant growth forms.



areas dominated almost entirely by each of these growth forms individually. As one might expect, these ecosystems also differ strongly in element content and element cycling patterns (Shaver and Chapin unpublished). The most productive and nutrient-rich sites are dominated by deciduous shrubs, while the poorest sites are dominated by evergreens and lichens.

Vegetation biomass, primary productivity, and plant mineral nutrition have been described in detail for the Toolik Lake and MS117 research sites (Shaver and Chapin 1986* and unpublished). For several individual species (especially Eriophorum vaginatum), these data are available from 2-10 different years (Shaver et al. 1986* and unpublished), and for the tussock tundra sites we have at least two years of whole-community data (Shaver and Chapin 1986*). We thus have a good idea of how the vegetation of these sites compares with others around the North Slope (e.g., Wein and Bliss 1974, Walker et al. 1982, Brown and Berg 1980, Brown et al. 1980, Batzli 1980, Miller 1982), and how their productivity varies from year to year. Similar data are not yet available from the Sag River site (Fig. 1), but this is a major goal of our current research there and the data should be available by the end of 1988.

Descriptions of soils processes and their variation among our proposed LTER sites was a major focus of our work during the 1985 and 1986 field seasons. The data are still being worked up, but by the start of 1987 we should have a good description of soil solution element concentrations, exchangeable element concentrations, and N and P mineralization, and how they vary both among sites and within a year. The most detailed data will be from the Sag River sites, and from our long-term fertilization experiments at Toolik Lake. Also from the Toolik Lake area, a Ph.D. thesis on soils processes and soil/plant interactions is now in preparation (K. Kielland, University of Alaska). At MS117, Dr. Giles Marion is currently doing similar research with DOE sponsorship (Marion unpublished). Our major need for additional data on soils is for comparative information from a wider range of sites over the North Slope. Although basic soil descriptions are available from many areas (Everett in Brown and Berg 1980, Walker et al. 1980, 1982), comparable process studies are available only from a very few wet tundra and tussock tundra sites (Brown et al. 1980, Marion and Miller 1982).

Climatic data have not been collected as systematically as the vegetation and soils descriptions, either on our sites or elsewhere. Although Haugen (1982; Haugen and Brown 1982) has provided a useful long-term record of summer air temperature and precipitation in northern Alaska, his weather stations were mostly at different sites from where ecological research was done. Many of these weather stations have now been abandoned. There is no long-term climatic record for the Toolik Lake camp, although individual investigators have often collected data during the time they were at camp. The situation has improved recently, however. Since 1984 a climate and microlimate monitoring station has been maintained at the MS117 site by Dr. John Kelley of the University of Alaska, and in 1986 the Shaver project began collecting detailed data from two weather stations at the Sag River sites. Fortunately, the MS117 site was also one of Haugen's long-term sites. We still need consistently-maintained climate and microclimate data from Toolik Lake, and we need to set up long-term stations at several of our extensive sites along the Dalton Highway.

b. Landscape patterns and interactions We have been studying element cycling over the past two growing seasons in six ecosystem types along a mesotopographic gradient in the Sagavanirktok River watershed about 50 km north of Toolik Lake (NSF-BSR 85-07493). These ecosystems show obvious and striking differences in plant species and growth form composition, organic matter and nutrient stocks, soil structure and morphology, rate and maximum depth of thaw, microclimate, and hydrology. Boundaries between ecosystems are easily identified and ecosystem locations can be predicted using geomorphological data. We are measuring nutrient fluxes (primarily N and P) between soils and vegetation within ecosystems and fluxes across ecosystem boundaries.

Measurements made during the past two years strongly indicate that differences in nutrient cycling rates among ecosystem types are large and are responsible for differences in plant productivity and growth form among ecosystems in the watershed. For example, field measures of soil N mineralization are highest in two relatively productive ecosystems with deciduous shrubs as major growth forms -- Ridgetop Shrub-Heath and Riverside Shrub-Willow systems. While the former ecosystem exports nutrients to downslope terrestrial ecosystems where nutrients are sequestered in accumulating sedge-peat, the latter exchanges nutrients with the river. Some ecosystems with lower internal nutrient fluxes are also likely to exchange elements with the atmosphere and to control nutrient exports to downslope terrestrial and aquatic systems. For example, the broad expanse of upland tussock tundra at the top of the toposequence has intermediate N cycling rates, but our in situ measures suggest a large percentage of mineralized N is nitrified. Therefore, ground- and streamwater flow from tussock tundra is likely an important source of nitrate to terrestrial and aquatic ecosystems.

The most extensive comparisons yet available come from work based at Toolik Lake and along the Dalton Highway over the past 10 years (Chapin and Shaver 1981*, 1985*, Shaver and Chapin 1986*, Shaver et al. in press*). One of our most significant findings is that there is significant variation in the limiting nutrient for plant growth <u>within</u> as well as between ecosystem types. For example, wet or tussock tundras that are quite similar in terms of production, biomass, or species composition may be variously limited by N, P, or both elements. We also have shown that, although a "good" year for plant growth or flowering is apparently "good" throughout the North Slope, there is no clear relationship with annual temperature variation. Furthermore, the latitudinal correlation between average temperature and plant size is due more to ecotypic variation in plant size than to any direct climatic control. These results are important because they contrast sharply with predictions based on temperature and nutrient controls of single processes at single sites (Shaver et al. in press).

c. <u>Whole-Ecosystem Experiments</u> Our past research has shown that arctic vegetation is in general strongly nutrient-limited, with significant increases in production and biomass following fertilization (Shaver and Chapin 1980*, 1986*) or disturbances that increase nutrient availability (Chapin and Shaver 1981*). However, although this nutrient-limitation seems to be ubiquitous (we have performed the same experiment at 14 different sites throughout northern Alaska), the form of the vegetation response is quite variable. At some sites all species seem to be equally limited by the same nutrients (Shaver and Chapin 1980*), while at other sites there are dramatic changes in species and growth form composition (Shaver and Chapin 1986*). Moreover, even in sites that appear to have quite similar vegetation, the specific element that is most limiting (N, P, or K) is not predictable.

Much of the variability in response to our fertilization experiments seems to be due to interaction with light and temperature regimes. Apparently, each species responds individualistically to a given combination of light, temperature, and nutrient availability (Chapin and Shaver 1985*). For the one species that we have studied in most detail, Eriophorum vaginatum, it appears that nutrient availability (usually N) sets a limit on the total amount of productivity that is possible, with temperature and light determining the rate at which nutrient reserves are used up (Shaver et al 1986*, Chapin et al. 1986*). In the next step, we wish to expand to the level of the whole vegetation, testing the hypothesis that nutrient availability limits community productivity, with temperature and light determining the distribution of productivity among species and growth forms. We further suggest that the major direct effect of temperature at the ecosystem level is on soil mineralization processes that determine nutrient availability, not on photosynthesis.

There have been no experimental studies of the effects of grazers on terrestrial ecosystems at Toolik Lake, other than one clipping experiment on cottongrass tussocks (Shaver et al. 1986*). However, in 1985, Dr. George Batzli and students of his began working at Toolik on the relationships between small mammal abundance and vegetation composition. Batzli's study was a part of the DOE R4D project but unfortunately, it will be discontinued unless separate funding is obtained; Batzli currently has a proposal under consideration by NSF-OPP for this continuation. Assuming that this proposal is funded, our proposed experiments will complement his by examining long-term effects of removal of small mammals.

2. Aquatic Ecology - Lakes

a. Descriptive Ecology Aquatic research began in 1975 as a followup to the detailed IBP project on shallow tundra ponds at Barrow (summarized in Hobbie 1980). Little was known about deeper lakes in the Arctic and nothing about foothill lakes.

The first studies of Toolik Lake were descriptive. Organism and biomass studies include chemistry and budgets of N and P (Whalen and Cornwell 1985*), sediment age and accumulation rates (Cornwell 1985*), nitrification and denitrification (Klingensmith and Alexander 1983*), planktonic nitrogen cycling (Whalen and Alexander 1984*), bacteria (Hobbie et al. 1983*), planktonic algae (Miller et al. 1986*), primary productivity of plankton (Whalen and Alexander 1986*), epilithic algae (Cuker 1983a*), decomposition of particulate matter (Federle and Vestal 1980a*), benthic animals (Cuker and Mozley 1981*, Hershey 1985*), zooplankton (O'Brien et al. 1979b*, Luecke and O'Brien 1983*), zooplankton feeding (Peterson et al. 1978*), and feeding by fish (Schmidt and O'Brien 1982*, Kettle and O'Brien 1978*) (see Appendix I for complete list).

The low nutrient concentration in the inlet stream causes the primary production of the lake to be low; in fact, the annual production averaged 12 g C m^{-2} over 10 years (Miller et al. 1986*). Planktonic algae are dominated by nanoplanktonic chrysophytes and cryptophytes (Miller et al. 1986*). Despite the ultraoligotrophic conditions, bacterial numbers in the plankton are moderate (Hobbie et al. 1983*) because of the relatively high concentrations of dissolved organic carbon entering the lake (Whalen and Cornwell 1985*).

The planktonic algae and bacteria are fed upon by crustaceans (Peterson et al. 1978*) and microflagellates (Hobbie and Helfrich in press). The herbivorous zooplankton assemblages are fed upon by Heterocope and small fish (Fig. 3). These juvenile arctic grayling and small lake trout are the primary visual planktivores (O'Brien et al. 1979a*) and these are thought to be relatively rare in the open waters of the lake. The abundance or presence of these juvenile fish is probably controlled by adult lake trout. Presumably because of the rarity of these juvenile fish in open waters, the copepod Heterocope is also present in Toolik Lake in fair abundance; therefore the zooplankton in the lake face both large-size and small-size selective predation (O'Brien et al. 1979b*). The zooplankton in the lake do seem to be facing severe predation pressure because Bosmina longirostis and Daphnia longiremis populations decline in abundance throughout each summer. In other lakes in the area which lack Heterocope, populations of these two species increase throughout the summer.

Fishes also have a strong effect on the benthic community. In these lakes, there are no suitable fish species for food for large lake trout. Instead, they feed mainly on snails and appear to control the snail community through size-selective predation (Fig. 3) (Hershey submitted). Sculpin predation controls chironomid density in bare sediments (Hershey 1985a*) and when lake trout are abundant, sculpin density is low and chironomid density is relatively high.

We have an estimate of the pelagic fish species composition and their size distribution in experimental gillnets from 1977 (pre-exploitation) for Toolik Lake (O'Brien et al. 1979*). Since this time the lake has been subjected to moderate levels of fishing pressure. We have recently duplicated this survey (1986, McDonald and Hershey in prep) and found that the lake trout (char) population has shifted to a significantly smaller median size. Also, the round whitefish, which is rarely caught by hook and line, increased substantially in the proportion caught in the gillnets from 1977 to 1986. We have also identified some unexploited populations of lake trout and grayling within the proposed LTER area, and have begun to examine their population structure and life history parameters.

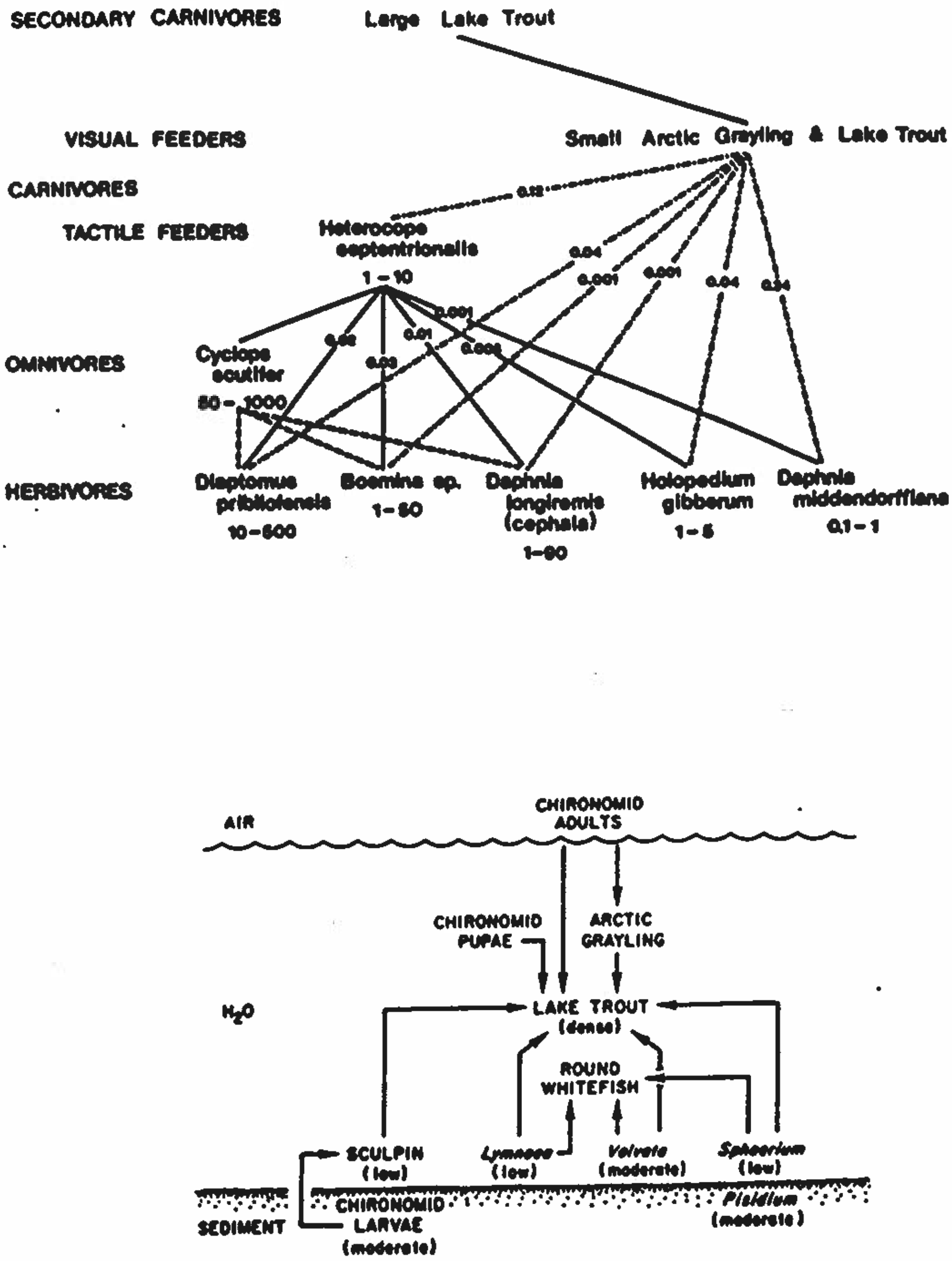


Figure 3. Food web dynamics of Toolik Lake Zooplankton Community and Planktivores. Lines leading upward indicate the direction of flow of energy to predators. The numbers below various species indicate a general range of abundance expressed as numbers of individuals per 100 liters. The numbers along the lines leading to Heterocope septentrionalis are typical feeding rate coefficients for that prey species being fed upon by the predators. The numbers along the lines leading to the fish planktivores indicate the probability of the fish locating that prey type within a 100 liter volume of lake water assuming the fish are searching a spherical volume with a radius equal to the average reactive distance for that prey species.

The slimy sculpin population in Toolik Lake was estimated and its life history characteristics examined in 1978 (McDonald et al. 1982*). Since that time, the slimy sculpin's interaction with its benthic food source has been examined (Cuker 1983*, Hershey 1985a*,b*, Hershey and McDonald 1985*). We have begun to examine the age and growth of slimy sculpin populations in area lakes which do not contain lake trout (Hershey et al. in prep.).

b. *Whole-Ecosystem Experiments* To test theories about factors controlling the aquatic food web, experimental manipulations were begun in 1983 (NSF-DPP). Six enclosures of polyethelene (each 60 m^3) were built to float in the lake. The effects of changes in nutrients (three levels of addition of N and P) and abundance of fish (small grayling) were examined throughout the ecosystem (O'Brien et al. in prep., Hobbie and Helfrich 1986). The objective of the nutrient additions was to stimulate phytoplankton growth and determine the extent to which this increased phytoplankton production was passed up through the planktonic and benthic food chains. The objective of the fish additions was to alter the density of *Heterocope*, a planktivorous copepod, thought to be a dominant zooplankton predator in Toolik Lake, and determine the extent to which release from this predator cascades down through the planktonic food chain. In 1983-85, the addition of N and P resulted in an immediate increase in phytoplankton production and biomass in proportion to the rate of addition (O'Brien et al. in press). At 10 x the natural rate, but not at 5 x, the algal species changed from flagellates to a small green alga. At high fertilization rates the bacteria responded to the algal increase by increasing their productivity and biomass. Microflagellates, their predator, followed suit and a classic oscillation of the two populations began (Hobbie and Helfrich in press*). This event allowed, for the first time, measurements of the clearance rate per cell of the flagellates and of the bacterial productivity per cell each day of the cycle. Another major finding, as yet unexplained, was the two-year lag before the zooplankton responded and *Daphnia* and *Bosmina* increased 10-fold.

Because limnocorrals are small relative to a lake, we next (1985-86) fertilized half a lake (cut off by a plastic curtain). All the responses, productivity, species, bacteria, lag of zooplankton, etc., occurred here as well. Data collected in 1986 will also show the response of benthic animals and algae to the fertilization.

Other aquatic studies included an EPA-sponsored investigation (1976) of effect of oil on a small lake (Miller et al. 1978, O'Brien 1978) and an EPA survey of the chemistry of small streams on the North Slope and of the effect of road dust on streams and sphagnum (Miller and Spatt 1981).

3. Aquatic Ecology - Streams

a. Descriptive Ecology The observations of production, N, P and C budgets, and nutrient limitations begun on the Kuparuk in 1978 were among the first of an arctic river (Peterson et al. 1983, 1986).

We have studied the Kuparuk River intensively since 1978. During 1978, 1979 and 1980, we took baseline data to describe the hydrology, sediment load, nutrient concentrations, productivity and carbon cycle of the river (Peterson et al. 1986*, Peterson et al. in revision). A series of bioassay studies of nutrient limitation in 1979 and 1980 demonstrated that phosphorus and nitrogen were the primary and secondary limiting nutrients for primary productivity (Peterson et al. 1983*).

b. Fluxes and budgets of carbon and nutrients Our research on the Kuparuk River has demonstrated experimentally that large changes in phosphorus and nitrogen inputs can control productivity at all trophic levels. We have several years of data on carbon, phosphorus and nitrogen concentrations in river water throughout the open water season and we know that there are important differences between years and during each year that correlate with discharge, weather and season (Peterson et al. 1983, 1986). Two important questions are (1) what controls the timing and amount of available phosphorus, nitrogen and carbon export from the tundra to rivers and lakes and (2) are these annual and seasonal differences in export of consequence to lake or river productivity. These difficult and subtle questions can best be addressed with long-term high quality data sets on nutrient concentration and productivity in a variety of aquatic sites in landscapes having different vegetation and soils.

c. Whole-Ecosystem Experiments - Kuparuk River To examine the response of the entire biota to fertilization, large-scale fertilization began in 1983 (NSF-DPP project). We fertilized the river by adding phosphorus continuously to give an average increase of 10µg P l^{-1} in the river. Enhanced algal growth could be measured for over ten kilometers (Peterson et al. 1985*) and fertilization changed the patterns of secondary production of insects (mayflies, caddisflies) and the sole fish (grayling).

We have tested the importance of nutrient limitation in regulating productivity and energy flow in the Kuparuk River by enriching the river with added phosphorus in 1983 through 1986 and with added nitrogen in 1986. During these four years, we have studied intensively nutrients, decomposition, heterotrophy, primary production, secondary production and fish production in the river. The responses to the added nutrient have been dramatic but the observed responses have changed from year to year reflecting a gradual long-term evolution in the structure of the stream community in response to chronic enrichment (Fig. 4). Algal productivity increased rapidly in response to phosphorus additions as predicted by our pilot bioassay experiments (Peterson et al. 1983*). In contrast, decomposition of allochthonous organic matter such as Carex detritus was not changed by nutrient addition. Bacterial numbers and activity were greatly stimulated not by nutrient directly but rather indirectly through substrate provided as a result of increased algal production. Most insect species grew faster in the fertilized reaches but over the course of four years, black fly and Orthocladius (a chironomid) populations declined while grazers such as mayflies and caddisflies increased. The increase in grazer abundance coincided with two years of low algal biomass in response to added nutrients. Possibly the epilithic algae are now controlled by grazers rather than by nutrient supply. Both larval

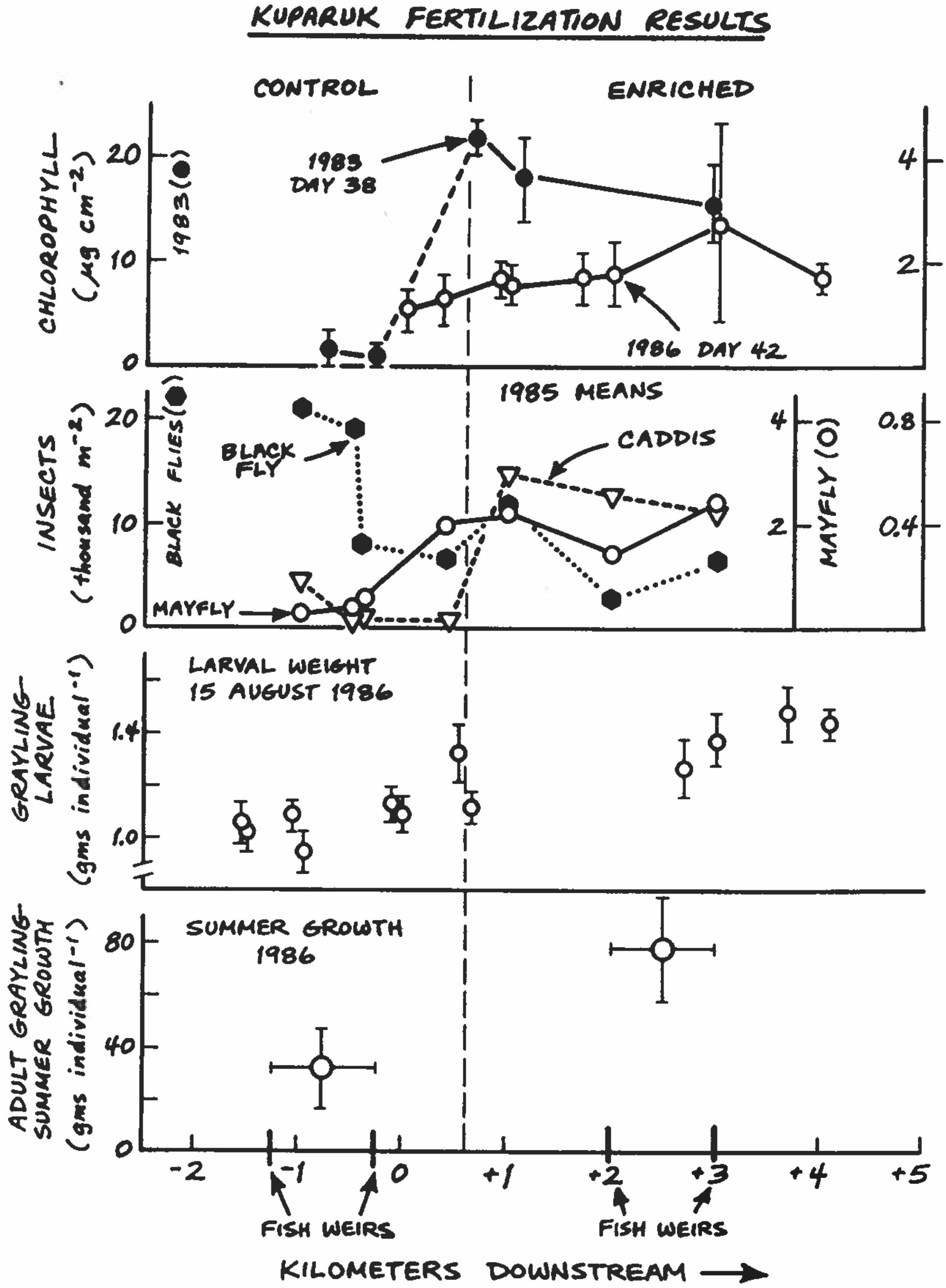


Figure 4. Transects for benthic chlorophyll, insects'abundance, larval grayling weight and adult grayling growth along the control and fertilized reaches of the Kuparuk River. Note the scale changes for chlorophyll between 1983 and 1986 and for different insect species.

and adult grayling have experienced sharply increased growth in the fertilized reach. In summary, we have found strong evidence for control of stream ecosystem function by nutrients (resources) but the magnitude and timing of the responses are strongly modified by interaction among the various trophic levels.

There may be important top-down controls operating in the river. It appears that after 3 to 4 years, the increased algal production which was stimulated by added phosphorus has resulted in large increases in grazers. The grazers appear to have eliminated any recurrence of the larger increases in algal biomass we observed in years 1 and 2. There may be similar feedback operating at the level of fish predation on insects but the response time for the grayling population is at least 7 to 10 years.

There appears to be a strong interaction between the omnivorous caddis (_Brachycentrus_) and other insects such as black flies and possibly _Orthocladius_. Black fly populations have declined as _Brachycentrus_ has increased in spite of the fact that individual black fly growth is stimulated by added nutrients. Cage experiments have shown that black flies numbers decline rapidly in cages with high caddis density (Hershey, unpublished).

These trophic interactions appear to strongly modify the long-term responses of the river ecosystem to fertilization and experiments to test our present tentative conclusions are needed. We could not have predicted the importance of the grazer-algal interaction or the caddis-black fly interaction in shaping the ecosystem responses on the basis of prior work. We feel strongly that these experiments must be continued and repeated to build understanding.

4. _Descriptive Ecology - Colville Delta_ The abundance of wildlife resources and the high potential of the Colville delta area for oil and gas development has resulted in a broad spectrum of scientific effort that continues today. Most of this effort has been applied directly to environmental impacts of the oil industry on fish, bird and mammal resources. Past basic research has addressed the physical processes governing the geomorphology, hydrology and chemistry of the

Colville delta and aspects of the microbiology and nutrient dynamics of sediments and water.

Work on nutrient dynamics in the Colville River began in the early 70's with support from NOAA-Sea Grant and the Environmental Protection Agency (Schell 1974, 1975). As the oil industry expanded westward from Prudhoe Bay, the Colville River, its delta, and nearshore lagoons became the focus for NOAA-OCSEAP sponsored interdisciplinary studies on the top trophic levels and the energy flow supporting them. These studies used the combination of stable carbon isotope ratios and radiocarbon abundances to describe the importance of peat in the aquatic foodwebs (Schell 1983) and further work quantified the inputs of peat to the system (Schell and Ziemann 1983). By the end of the winter season, grayling in the Colville River contain over 50 percent peat carbon in their make-up indicating that the processes converting peat to biomass at lower trophic levels may be essential for overwinter survival of top predators. We have recently been trying to determine the importance of peat versus "new" autochthonous carbon to individual species of arctic fishes and this work would continue under the LTER.

III. SCIENTIFIC TASKS

A. OVERVIEW

In the following sections (IIIB - IIIF), we describe five research tasks and the particular questions we will attempt to address. Because of the number of major research projects at the general site over the past decade, parts of some of the goals have been met (e.g., nutrient and carbon budgets for the stream) and some are partially met (see Section II above for description of past research).

The *first* task is to carry out baseline studies of climate and of effects of climate changes on plant growth, of the spatial distribution of nutrients in soil solution, of the changes in flow and chemistry of the Kuparuk River with climate, and of amounts and type of atmospheric deposition. The goal is to relate changes in climate, atmospheric deposition, and soil nutrients to spatial and annual changes in ecosystem properties. Although not a part of this present proposal, this LTER site would be an appropriate place for a direct tie-in to networks for IGBP measurements of land-atmospheric transfers of elements and trace gases.

A second and third task take up a central question of ecosystem science -- how is ecosystem structure and function controlled? There are two schools of thought, control is through resource limitation such as nutrients or food versus control is through the higher trophic levels such as grazing of zooplankton on algae or the grazing of ungulates on grass. Although we separate discussion of experiments to test resource control from those to test predator/grazer control, the same experiments are often used for both questions and, in fact, both types of controls are present in any ecosystem.

A fourth task deals with chemical and nutrient linkages within and between terrestrial and aquatic systems. This is actually a subset of the resource control question for we already know that nutrients are extremely important in structuring arctic ecosystems, both on the tundra and in lakes and streams. We will address questions such as how do annual variations in N fixation inputs affect soil processes and subsequent N transfer into streams?

A fifth task takes up the question of what is the distribution and variability of various ecosystem types and of various ecosystem processes (e.g., primary production) in northern Alaska and of how to extrapolate the insights and understanding of the controls of processes at Toolik Lake to other ecosystems throughout northern Alaska. This extrapolation is important because of the many types of habitats in northern Alaska and because of questions about how to manage arctic ecosystems under man's impacts or about the amount of trace gas released (e.g., methane, oxides of nitrogen) throughout the entire region.

B. ECOLOGICAL BASELINES FOR RESEARCH SITES

1. Introduction. The methodological themes of this LTER project are

experimental whole ecosystem manipulations and stable isotopes as techniques to gain new insights into ecosystem questions. Yet, descriptive ecology can not be left out for a description of the ecology is a necessary first step before experiments can be designed and is vital to the interpretation of any isotope measurement. The chief biotic actors and their abundance, productivity, cycles of nutrients, and different types of variability (spatial, seasonal, annual) must be identified in any ecosystem under study.

It is also true that descriptive ecology produces many insights about how ecosystems operate. Comparisons between sites and the natural experiments of different climate from micro-site to micro-site or of year-to-year differences in stream hydrology have been very useful in the development of our science. For example, O'Brien et al. (1979b*) sampled the plankton of the many small lakes in the moraine around Toolik Lake and used the variation in distribution of fish and plankton from lake to lake to demonstrate the control of zooplankton community structure by an invertebrate predator.

In northern Alaska, there have been intensive descriptive and process studies at Barrow (ONR and IBP projects), descriptive studies at Atkasuk, a foothills site near Barrow, descriptive studies at Prudhoe Bay, and descriptive and process studies at Toolik Lake. The only aquatic studies have been descriptive and process studies of shallow ponds at Barrow and of the lakes and streams at Toolik.

How far along are descriptive studies at Toolik? The lake and stream systems are well described and a long-term data base exists for lake and stream physics and lake productivity. The climate record exists for various intervals but has only been regularly collected during the past three years. Detailed descriptions of terrestrial productivity, soils, and annual variations have been published for tussock tundra, the most common vegetation type in the Toolik area. Descriptions of other ecosystem types are now in progress and will be completed in two years.

2. Baseline research tasks

a. Continue to describe the comparative climate and microclimate of contrasting ecosystems. We need to establish long-term weather stations at all of our major sites and to maintain them consistently. This is already being done at the MS117 terrestrial site with DOE funding, but we will not be able to keep up our observations at Toolik Lake, Sag River, or the Kuparuk River unless a stable funding source is obtained. The work involves comparison of microclimates among contrasting ecosystem types at Toolik Lake and Sag River, as well as comparison of macroclimatic differences between these sites which are separated by over 500 m elevation.

b. Establish the relationships between annual climatic variation and plant growth and flowering. There is a long-term (6-10 yr) record of plant growth and flowering at 34 sites between Fairbanks and Prudhoe Bay. We know from this record (Shaver et al. in press*) that growth and flowering vary uniformly from year to year over large regions of Alaska. Yet, this annual variation is apparently uncorrelated with any of the regional climate data available to us. In part, this lack of correlation may be due to the paucity of climate information in general, and to the fact that the sites and timing of climatic observations are often not coincident with the plant data collections. A second explanation may be that annual climatic variation is "buffered" in its effects on plants, either through biochemical storage of growth metabolites, or through climatic effects on soil nutrient availability. We favor the latter hypothesis based on our previous work (Shaver et al. 1986*), but in order to test alternatives we need to continue our annual observations and combine them with much better and more consistent climatic data. This research will involve annual phenological observations (to establish the length of the growing season and its variation) at our primary sites, in addition to continuing growth and flowering observations for Eriophorum vaginatum.

c. Establish the relationships between composition of the vegetation and the soil chemistry and soil nutrient cycles. We already know that the major species and plant growth forms of the Arctic each have characteristic patterns of element uptake and accumulation (Shaver and Chapin 1980*, Shaver and Lechowicz 1985*). However, we have not yet been able to document a relationship between the multivariate patterns of plant element use and multivariate patterns of element availability in the soil. This is a particularly important relationship to establish, given our broad interests in how terrestrial biogeochemistry controls the chemistry of element inputs to rivers and lakes. This objective will be met by sampling and multivariate analysis of the available element content of soils on sites where we have already determined the element content of the vegetation (Toolik, MS117, and Sag River), and looking for correlations. We will also use the vegetation classification scheme of Walker et al. (1982) to collect soil solution samples from several replicate stands of each of his vegetation types, to see if we can use vegetation type as a predictor of soil solution chemistry and, perhaps, stream chemistry.

d. Characterize the discharge and chemistry of the Kuparuk River. One baseline task will be to continue to characterize the discharge characteristics and nutrient chemistry of the Kuparuk River. The flow and chemistry are highly variable and depend both on the weather and the state of the tundra. Data on discharge and nutrient chemistry are needed for both studies of the tundra landscape and of river metabolism. We will record river stage continuously with a Stevens gauge from ice out to freeze up in the fall. Weekly samples of river water will be analyzed for pH, alkalinity, dissolved reactive phosphorus, total phosphorus, ammonium, nitrate and total nitrogen.

e. Characterize the amount and chemical species of atmospheric deposition. We will collect wet and dry precipitation at Toolik and the Sag River using Aerochem Metrics 210 wet/dry collectors. One is presently in operation at the MS117 site and these are the collectors presently being used nationwide by the National Acid Deposition Program (NADP). (The nearest NADP site is south of

Fairbanks in Denali National Park.) Wet deposition will be collected weekly and dry deposition will be collected bi-monthly through the spring, summer and fall. As at the NADP site, samples will be analyzed for pH, conductivity, alkalinity, SO_4, NO3, NH_4, Cl, PO_4, Na, Ca, K, and Mg. In addition, pooled samples will be analyzed for total N, P, and organic carbon. These measurements will be supplemented by data from samples from bulk collectors at several sites along the haul road transect. These precipitation stations will not regularly be maintained through the winter. Instead, snow will be sampled at the beginning of the spring using standard snow survey procedures.

C. CONTROLS OF ECOSYSTEM STRUCTURE AND FUNCTION: NUTRIENT, LIGHT, AND CLIMATE DRIVEN

1. Introduction. Ecologists have long been interested in the mechanisms regulating community structure and population densities (Hairston et al. 1960, Brooks and Dodson 1965, Paine 1966) as well as those regulating such ecosystem properties as energy flow. One way to look at the whole question of control is to ask the question, is the control exerted through resource limitation (nutrients, water, light, temperature) or is it through predation or grazing? This can be restated as bottom-up versus top-down control. In many food webs or ecosystems, both mechanisms of control are operating and different parts of the same system may well be controlled by different mechanisms.

The idea that aquatic ecosystems are regulated by nutrient supply began with Thienemann (1928) who coined the word eutrophic for lakes well fed with nutrients and rich in algae. Eutrophication is well studied but little is known about how much of the increased productivity is passed up the food chain. Experimental fertilization always increases primary production but in some cases zooplankton production increased (Le Brasseur and Kennedy (1972) in British Columbia) and in some cases zooplankton did not increase (ELA Lake 227, Malley et al. 1980). In a lake in northern Sweden, added phosphorus (but not added nitrogen) stimulated algal biomass and productivity but the effect on the zooplankton lagged by two years (Persson et al. 1977, Holmgren 1984, Jansson 1978). The conclusion from the literature is that there is no doubt that phosphorus (and sometimes nitrogen) stimulates plant production in lakes, but this is not always followed by increases in the herbivores. Understanding the linkage between primary productivity and secondary production in lakes is essential to predicting the effects of nutrient additions and in understanding how ecosystems operate.

Changes in primary production and plant community structure along gradients of resource availability on land have been documented in a number of studies (e.g., Whittaker 1956, 1967, Waring and Major 1964, Whittaker and Niering 1965, Beals 1969). These and other early attempts at gradient analysis typically stressed changes in temperature, moisture availability, and elevation. More recent studies of nutrient cycling in terrestrial ecosystems have shown that the availability of growth limiting nutrients (primarily N and P) in soil accounts for a large amount of the variation in productivity and structure of terrestrial ecosystems (Lea et al. 1979, Gosz 1981, Melillo 1981, Nadelhoffer et al. 1983, 1985, Pastor et al. 1984). It is likely that variables like temperature and moisture influence production and structure of terrestrial systems primarily by controlling decomposition and nutrient mineralization rates (Chapin and Shaver 1985*, Shaver et al. 1986*). Fertilization studies strongly suggest that nutrient availability is the primary controlling variable of production in tundra vegetation (Shaver and Chapin 1986*).

2. Research Questions

a. <u>Which nutrients (N, P, or K) are most limiting to terrestrial productivity in the various vegetation types of the site?</u> Most of our past factorial NPK fertilization experiments (described in section II B) were done in tussock tundra or wet tundra. We need to add factorial experiments in other vegetation types in order to determine the variation in limiting elements within each type, and to extend our comparisons among arctic ecosystems from descriptive to experimental. Some of this work has been started already in six contrasting ecosystems at our Sag River site. The major need is to reestablish experiments in the major ecosystems near Toolik, so we can compare responses between sites within a given ecosystem type as well as among ecosystems.

We also would like to perform the same fertilization experiment at the same site several years in a row, in order to examine the interaction between annual climatic variation and fertilization. We know from our previous work that this interaction is important for flowering, but we have not examined growth responses in this way.

b. How do light, temperature, and nutrient availability interact to control growth form and productivity of the vegetation? In this component of our research, we need to maintain the experiments in tussock tundra that are already established, and to expand the design to include a deciduous shrub site, an evergreen heath, and a wet sedge site, also at Toolik Lake. The experimental design includes a control area, an NPK-fertilized plot, and the building of small greenhouses or shade frames (Shaver et al. 1986*) both with and without fertilizer. The plot size is 10-15 meters squared, large enough to include a fairly complete sample of the community but small enough that the entire greenhouse/shade frame can be lifted off for sampling. Fertilizer-alone plots are much larger, to allow for more frequent sampling.

These will be long-term experiments, and only need to be sampled in detail every 3-4 yr. The detailed sampling will thus require a major effort in only one of the first 5 yr of this LTER, following set-up in yr 1. The sampling will include detailed biomass and productivity measurements by harvest methods, and detailed characterization of soil nutrient availability. In the intermediate years, the only effort required will be some minor growth measurements, soil solution sampling, and annual fertilizer application. The greenhouses and shade frames will be removed every fall and replaced in the spring.

c. How do changes in nutrients and light affect the relative importance of autochthonous and allochthonous organic matter in the stream? A dominant theme in river research has been the question about the relative utilization of allochthonous (terrestrial) versus autochthonous (algal) organic matter. Most of the organic matter in the Kuparuk River water and on the river bottom is derived from the tundra vegetation and soils by leaching as DOC or via erosion as POC (Peterson et al. 1986*). However, the utilization of this material is evidently very limited in spite of the large quantity present (Peterson et al. 1985*). One approach is analytical. We will characterize different classes of DOC in water entering the river and at different downstream locations.

These approaches to the question include (1) continuous flow bioassays which test the use of allochthonous DOC, (2) bioassays to test black fly growth using eroded peat particles, (3) whole river nutrient enrichments which greatly increase algal production, (4) river segment darkness experiments which eliminate photosynthetic carbon inputs to the epilithon and (5) stable and radioisotope tracer experiments to quantify the use of peat-derived versus algal carbon by consumers. These approaches combined with more traditional stomach content analyses and feeding studies will establish the relative importance of these two primary organic matter resources.

Experiment I. DOC. Soil solution water containing high concentrations of DOC leached from the tundra will be used to augment the DOC supply to epilithon developing in light and dark continuous flow bioassay tubes. Microbial biomass and activity on the substrates exposed to the elevated DOC should increase relative to controls if DOC is utilized.

Experiment II. POC. Peat eroding from the stream banks provides a continuous source of fine organic-rich particulates which are filtered by black flies. To test whether or not black flies utilize this organic matter for growth we will take advantage of the availability of old peat which is greatly depleted in ^{14}C. By adding this peat continuously to a small stream and monitoring the "^{14}C-age" of the black flies downstream, we will estimate the contribution of the allochthonous organic matter to black fly growth.

Experiment III. Whole River Enrichment. Fertilization with phosphorus and nitrogen stimulates algal growth but does not increase the decomposition of allochthonous organic matter (Peterson et al. 1985*). Thus, one approach we will utilize to judge the relative importance of these two organic matter resources will be whole-river enrichments. Phosphorus will be added continuously to give 10 $\mu g\ Pl^{-1}$ and nitrogen to give 100 $\mu g\ Nl^{-1}$ in the river. Already we know that increasing algal production produced dramatic changes in the food web. We do not know if the changes will continue or not.

Experiment IV. Darkness. We can experimentally eliminate both algal biomass and algal production from the epilithon by removing light (Peterson et al. 1985*,Vestal unpublished electron micrographs). We propose to cover stream segments with reinforced black plastic to apply this technique at the ecosystem level. This will allow us to follow the evolution of the epilithic community which develops in darkness and is thus primarily dependent on allochthonous DOC and POC. We will carefully monitor the growth of insects in this reach as well.

Experiment V. Our nutrient enrichment experiments have introduced stable isotopic tracers into the river food web that we can use to differentiate between algal and allochthonous organic matter sources. Fertilizing the river with nitrogen and phosphorus has resulted in large changes in $\delta^{15}N$ and $\delta^{13}C$ values in algae, insects and the grayling at the top of the food web. Through comparisons of the isotopic distributions at all trophic levels in control and fertilized reaches, we can calculate the relative contribution of autochthonous and allochthonous organic matter to riverine consumers under both natural and enriched conditions. The advantage of the whole-river enrichment is that we can experimentally introduce stable isotope tracers which help determine carbon and nitrogen flows.

d. How does the structure and function of the food web change during long-term, chronic fertilization of a lake trout lake? We know from our past experience with the limnocorrals that additions of inorganic nitrogen and phosphorus will produce a nearly proportional response of phytoplankton primary productivity and biomass (section II B). Microbial metabolism and population growth rates will also be stimulated as well as the rate of nutrient regeneration from the sediments. However, the response of the higher trophic levels was not clear -- we believe this is in part due to the limitations of the limnocorral approach with higher organisms.

We propose to use sectors of lakes to both validate our findings from the limnocorrals and extend the experiments to zooplankton, benthic invertebrates, and fish. These will be cut off by plastic curtains. In experiments, we will add a total of 0.5 g PO_4 m^{-2} and 7 g NH_4 m^{-2} over 40 days to two of the four sectors of lake N-2 and both sectors of lake N-1 (small lakes within 1 km of Toolik Lake). The nutrient solution will be pumped into each sector by solar-powered peristaltic pumps. Natural wind mixing will distribute the nutrients throughout the sector.

Certain processes that are controlled by predation when nutrients and rates of reaction are slow may not be affected under more eutrophic conditions. For example, a prey population may grow slowly under the natural arctic conditions and will be controlled by predation. However, when the prey population is growing much faster because of better nutrients or food, then the impact of predation might be much diminished. This will be particularly true when the predator is a slow-growing, long-lived species with a slow reproductive rate such as lake trout.

In the research we will measure planktonic primary production, benthic primary production, the extent of winter anoxia, rates of remineralization of nutrients, biomass of mosses and rooted plants found down to 2 m depth, and species and abundance of zooplankton. In the benthos, the snail growth and reproduction will be tested for food limitation and chironomid growth will be measured (although they should not be affected). The population of the slimy sculpin, the prey of the lake trout, will also be followed. Small grayling growth, expected to improve because of increased zooplankton, will be measured as will lake trout growth.

D. CONTROLS OF ECOSYSTEM STRUCTURE: PREDATOR AND GRAZER DRIVEN

1. Introduction Terrestrial and aquatic ecosystems are frequently strongly affected by the activities of grazers and predators and this is commonly termed "top down" control. In arctic Alaska there have been numerous studies of the effects of grazing on plant processes, and of the effects of various food sources on herbivore nutrition (e.g., Batzli 1980). However, except in wet coastal tundra there is little information on the long-term effects of herbivory on plant community composition or overall productivity. In the wet tundra at Barrow a detailed hypothesis was developed that linked the 3-4 year lemming population cycle with both predator abundance and changes in productivity and element storage in plants (Schultz 1964, 1969). This "nutrient-recovery" hypothesis (in which lemming grazing was proposed as a key to releasing nutrients tied up in plant biomass) was tested during the IBP study in the early 1970's; the results were equivocal but intriguing (Batzli et al. 1980). Batzli (1975) also showed in long-term exclosure experiments that prevention of lemming grazing sometimes had significant effects on plant biomass. Yet, relatively little work has been done on these ecosystem-level questions since the 1970's.

The idea that lake ecosystems are also regulated through top down control is a concept first put forth for plankton systems by Hrbacek (1962) and Brooks and Dodson (1965). In these papers, they noted that when planktivorous fish were introduced into lakes, the size and species composition of the zooplankton changed dramatically. Several studies in which high densities of planktivorous fish have been added to ponds or enclosures in ponds have found zooplankton to be severely reduced and phytoplankton generally stimulated (Hrbacek 1962, Hurlbert et al. 1972, and Losos and Hetesa 1973). In a study by Lynch and Shapiro (1981), fish addition led to an order of magnitude increase in phytoplankton abundance but the addition of nitrogen or phosphorus had no effect. Stenson et al. (1978) removed fish from a small Swedish lake and found that large zooplankton soon dominated the zooplankton community. Subsequently, primary productivity declined by 90% and large phytoplankton increased in importance. There is evidence that arctic plankton communities are also structured by predation. Nilsson and Pejler (1973) stocked various combinations of fish species in Swedish lakes and noted that when obligate planktivorous forms were stocked, small-sized zooplankton communities developed.

Experimental work on lake benthic communities has clearly implicated predation as an important control mechanism (Ball and Hayne 1952, Hayne and Ball 1956, Hall et al. 1970, Crowder and Cooper 1982). The effect of fish predation is generally greatest on large invertebrates for most benthic communities (Hall et al. 1970, Crowder and Cooper 1982). However, susceptibility to fish predation may be determined by habitat structure on lake bottoms (Crowder and Cooper 1982, Gilinsky 1984, Hershey 1985a*), and fish predation on chironomids does not appear to be size-selective on large larvae (Werner et al. 1983, Hershey 1985a*).

The evidence for top-down control in rivers suggests that fish exert control over benthic insects in some systems but not in others. Although trout (Allan 1982; Newman and Waters 1984) and sculpin (Newman and Waters 1984) are size-selective on stream invertebrates, experimental removal of trout resulted in little change in densities of benthic or drifting invertebrates (Allan 1982). In contrast to Allan's finding Bowlby and Roff (in press) found strong evidence for top-down control of benthic invertebrates in an Ontario trout stream. When piscivorous brown trout were present, the biomass of non-piscivorous (invertebrate feeding) fish was significantly lower and the abundance of benthic invertebrates was higher than when trout were absent. Also, in contrast to Allan, Flecker (1984) found fewer midges after sculpin were added while midges increased in exclusion cages. Another type of regulation is on the distribution of the prey. Trout affected the distribution but not the density of gerrids in stream pools (Cooper 1984). Invertebrate predators also affect prey distributions, but probably not prey densities, through complex behavioral interactions (Peckarsky and Dodson 1980; Peckarsky 1980).

Both invertebrate and vertebrate grazers can control stream epilithic community structure and biomass. Experimental manipulations of stream caddisflies have shown that these dominant grazers control not only microspatial distribution patterns (Hart 1985) but also abundance of other grazers through competition for space (Lamberti and Resh 1983; McAuliffe 1984). Where grazing fish occur, they also can control epilithic standing stock (Power and Matthews 1983), although distribution of grazing fish may be controlled by predators (Power 1984). Algal biomass can also be reduced by snails as has been shown for laboratory streams (Earnest 1967, McIntire 1973).

2. Research Questions

a. Is the long-term grazing or browsing by large and small mammals an important control of growth form composition or productivity of terrestrial vegetation? We need to know more about how herbivores influence the structure and productivity of arctic vegetation. We propose to do this by building a series of exclosures of two kinds: one to eliminate large herbivores, and another to eliminate small herbivores. These will be long-term experiments that will not need to be sampled more than once every few years (probably at the same time as the greenhouse/shade/fertilizer experiments). Except for these occasional harvests, the only costs involved will be the costs of construction and fence maintenance. The aim of the harvests will be to determine how the vegetation within the enclosures changes in terms of species composition, biomass, and NPP.

We have already done the initial descriptive work in our comparison of species/growth form composition, biomass, NPP, and element cycling among four vegetation types near Toolik (Shaver and Chapin unpublished). The four vegetation types include a tussock tundra, a wet sedge tundra, an evergreen heath, and a deciduous shrub area (Fig. 2). Thus one part of this research will be a comparison of the long-term effects of herbivory in contrasting ecosystems, with the expectation that herbivory will be more important in some systems than in others.

b. Does either grazing by invertebrates or algae or predation of fish on invertebrates control energy flow in a stream ecosystem? These questions can be addressed as part of our long-term river fertilization experiment. The grazing question will be addressed in two ways. The first approach is to exclude grazing insects from both artificial substrates and from patches of river bottom rocks in both control and fertilized segments of the rivers. By monitoring algal biomass inside and outside of the exclusion cages, we can determine if grazers are cropping the algae. The second approach exploits the fact that there is a year or more lag in the response of the grazer population to increases in algal production. We can test whether grazers can control algal biomass by moving the phosphorus fertilizer input site upstream to repeat the year 1 fertilization experiment. This would create three zones - a control reach, a 1st year fertilization reach and a 5th year fertilization reach. In the control reach we predict low algal biomass, low grazer biomass and low fish production, in the 1st year fertilization reach we predict high algal biomass, low grazer biomass and low fish production, and in the 5th year fertilization reach we predict low algal biomass, high grazer biomass and high fish production.

We calculate that grayling are abundant enough to consume a large fraction of the production of invertebrates such as mayflies and caddisflies in the Kuparuk River. A calculation of the number of opportunities for grayling to feed on drifting insects also suggests they could have a significant impact (O'Brien unpublished). This is a common observation in stream salmonid studies but experiments designed to demonstrate such impacts by fish removal have failed to show any change in the benthic or drift insect community (Allan 1983).

We propose to repeat these fish density manipulation experiments on this arctic river where 24 hour daylight eliminates the ability of insects to avoid predation by drifting and foraging at night. We will establish river reaches isolated by weirs where fish are decreased or eliminated and where fish densities are increased by a factor of 5. Benthic and drift insect collections will be made throughout the season in both riffles and pools. The weirs will be held in place until the fish migrate in August and will be reestablished with the same treatments at the same locations the following year.

This fish density manipulation will be maintained in both the control and fertilized river reaches. Individual fish growth and total fish production will be measured for each reach by mark-recapture. Recapture is facilitated by the fact that the entire population migrates upstream at the end of the summer during August.

c. How are lake ecosystems changed when lake trout are exploited by fishing or when lake trout are introduced into lakes with no lake trout? How do the effects of adding nutrients or forage fish to lakes and manipulating lake trout populations interact? Initially, we propose to examine growth rates, age, and size structure and make estimates of population size of the dominant species within several lakes near Toolik. Some research has been done on unexploited salmonid populations in the Canadian arctic, but the fish populations of these Canadian lakes contain many interacting species and the top predators are primarily piscivorous (Johnson 1972, 1976). The fish community in the proposed LTER area is less complex and has a simpler food web so that we can attain a better understanding of the trophic interactions. Also, in these arctic systems the top predator control point may be on the benthic community, rather than on a pelagic forage fish as in Canadian arctic and temperate systems.

Expanding on our work on the Toolik Lake fish population, we will experimentally reduce the top predators (lake trout) in previously unexploited lakes and follow the subsequent shifts in the structure of the other populations to determine if and when a new equilibrium community is reached. We will also continue to study the exploited fish population of Toolik Lake. We predict that remaining lake trout in newly exploited lakes will grow faster, but will be of smaller size than the pre-exploitation populations. We also hypothesize that the grayling populations in these lakes will decline and sculpin and round whitefish will increase. Examination of the food habits of these fishes before and after exploitation will provide insight into resource partitioning changes and the effects of top down control.

In other lakes which have no lake trout, we will add lake trout at a normal density. By adding a top predator to the system we can examine the restructuring of the community by predation from the top down. We predict that: the lake trout will show an initial increase in growth due to high resource availability, the sculpin population will decrease, the snail population will decline, and the chironomid population will increase. The relationship between the lake trout and the benthic community may be the key to the regulation of arctic lake ecosystems.

In other experiments we will enhance several systems containing lake trout by fertilization or by the addition of a forage fish. Since both these disturbances may occur either intentionally or unintentionally as this area becomes more accessible to the public, we hope to assess their impacts on the ecosystem. If fertilization increases benthic production, we would expect to see some growth response by the lake trout. However, by inserting a larger, higher energy forage for the lake trout into the trophic structure, we would expect to see more rapid and substantial growth gains by the predators.

E. LAND/AIR/WATER INTERACTIONS

1. <u>Introduction</u> There is ample evidence from temperate zone studies that terrestrial ecosystems can regulate outputs of growth limiting elements to aquatic ecosystems (Likens et al. 1977, Schlosser and Karr 1981, Lowrance et al.

1981). For example, Dillon and Kirchner (1975) showed that P inputs to 34 Ontario lakes were influenced by watershed land use patterns and geology. Carbon inputs to lower order Boreal Forest streams are primarily from terrestrial ecosystems (Naiman 1983). Peterjohn and Correll (1984) showed that riparian forests in temperate agricultural watersheds filter large amounts of C, N, and P from surface and subsurface water flowing into rivers.

Element exchanges between the atmosphere and ecosystems can be relatively large for some elements in a watershed or region. Precipitation inputs of nitrogen supply most of the N that eventually accumulates in many terrestrial ecosystems (Likens et al. 1977, Kelly and Levin 1986). Nitrogen fixation is not as well quantified but may be equal to or more important than precipitation in some systems (see studies quoted in Kelly and Levin 1986). Denitrification losses vary widely and depend largely upon temperature, pH, dissolved organic matter, and aeration.

The Alaskan North Slope consists of readily identifiable ecosystems arranged in predictable patterns along topographic gradients within watersheds (Nadelhoffer et al 1986*). These ecosystems display characteristic patterns of community structure, primary production, and organic matter distribution (Chapin and Shaver 1985*). Rates of nutrient cycling are probably critical in controlling ecosystem locations in arctic regions (Miller 1982). Furthermore, soil water movement and drainage and concomitant effects on soil temperature and aeration control many aspects of nutrient cycling (Tilton 1978, Gosselink and Turner 1978, Mendelssohn & Seneca 1980). Therefore, current studies of terrestrial ecosystems at the Sag River and R4D sites are now focusing heavily on hydrology and nutrient cycling. This work should lead to a fundamental understanding of controls on element exchanges between adjacent terrestrial ecosystems. As a result, we will gain an ability to predict how arrangements of ecosystems within watersheds affect element exchanges with the atmosphere and element exports to aquatic systems.

2. Research Questions

a. What is the source of nitrogen in the mosaic of ecosystem types in arctic watersheds and how is nitrogen modified as it moves across the landscape and into streams? The typically low levels of atmospheric N deposition in the Arctic (Barsdate and Alexander 1975) together with the presence of potential N fixers in most ecosystem types we have studied suggest that dinitrogen fixation is likely to be the ultimate source of most organic N in arctic watersheds. Along the Sag River toposequence, blue-green algae (free living and lichen associated) are present in Tussock Tundra, Ridgetop Heath, Hillslope, Footslope, Sedge Bog, and Riverside Shrub ecosystems. In addition, symbiotic N fixing vascular plants (e.g., Lupinus arcticus, Alnus crispa) are common in Hillslope and Footslope ecosystems. Nitrogen fixed and cycled within one ecosystem has several potential fates. It can be: 1) accumulated in buried and frozen soils; 2) exported downslope as litter and in dissolved organic and mineral forms; or 3) exported to the atmosphere as N_2 or N_2O. We have measured nitrification and detected nitrate, the most mobile dissolved N species, in soils of most of the Sag River sites. Of the six Sagavanirktok River sites, nitrification rates are relatively high in our upland Tussock Tundra, Riverside Shrub and Wet Sedge sites. Therefore, these ecosystem types may be important donors of nitrate-N to downslope and downstream terrestrial and aquatic systems. However, conditions are also favorable for denitrification losses, particularly in the Wet Sedge Tundra. Cold, saturated soils with high organic carbon contents could result in gaseous N losses approaching or exceeding N fixation rates.

Another aspect to nitrogen transfer is the N in dissolved organic matter. This is formed by decomposition of organic matter which appears to have seasonal peaks in tussock tundra soils (Linkins et al. 1984). Fall, during early freeze up, seems to be a time of maximum activity (Linkins, in press). At that time, vascular plants are senescent and soil microbial activity is minimal if soil pH is negative. However, plant roots still have nutrient uptake potential from both organic and inorganic sources, but there may still be nutrient accumulation in the soil solution or loss to the aquatic ecosystem (Kroehler et al. in press). These circumstances during the fall peak in decomposition may be responsible for the spring peak in nutrient transfer from the soil to the aquatic ecosystem. The seasonal timing and nature of decomposition and its interaction with plant and microbial immobilization are the key elements determining the type and amount of nutrient and energy transfer from the soil to aquatic ecosystem. Seasonal decomposition and immobilization patterns in different soils must be established so that the long term allochthonous input into and support of the aquatic continuum can be understood.

A complete characterization of N movement across terrestrial ecosystem boundaries, exchanges with the atmosphere, and exports to aquatic ecosystems requires the use of hydrological models. We are collecting data on surface water, soil water, and first-order stream flow at the Sag River site. In addition, we hope to collaborate on hydrologic modelling with DOE funded researchers working on a sloping tussock tundra (the R4D Project at MS 117).

Nitrogen stable isotopes will be used extensively in these studies of nitrogen cycling because the importance of processes such as nitrogen fixation and nitrification in soils can be assessed very efficiently using isotopes. For example, we know from our work to date that the stable isotope ratios in streamside dwarf willows reflect the nitrification process in well-drained riverbank soils. In this zone, ammonium is transformed to nitrate as water draining the hillslopes seeps into the river. We also know from our previous work that we can trace nitrogen flow in the river with stable isotope ratios.

b. What are the sources and sinks of phosphorus in the arctic landscape? New phosphorus inputs due to weathering and precipitation are very low in wet and mesic tundra sites. Decomposition of organic matter supplies most of the P taken up by the vegetation (Chapin, Barsdate & Barel 1978). Much less is known about mid-slope ecosystems, such as the deciduous lupine zone and the grass/sedge/Equisetum zone at the Sag river, or drier ecosystems such as ridge top heath and alluvial willow sites. Warmer temperatures and good aeration are likely to increase both organic matter decomposition and mineral weathering rates in these ecosystems. However, soils and organic matter may serve as sinks as well as sources of phosphorus. Phosphorus may be fixed in soils by adsorption or precipitation, taken up by bacteria or trapped by burial in permafrost. The balance between these processes determines not only the productivity, distribution, and species composition of an individual ecosystem but its ability to exchange nutrients with adjacent ecosystems as well. Therefore, we need to know how differences in temperature, hydrology, and geology affect the relative importance of soil and plant processes releasing and immobilizing phosphorus. One approach to help make field measures more generalizable to other sites are laboratory experiments such as our experiment on the effect of temperature on rates of P release. The next step is to make some of our measures of P cycling to areas where similar ecosystem types are found on different geology, in different climatic regimes, or exhibit different patterns of nutrient limitation and primary production. For example, we are especially interested in comparing the results of our study on phosphorus cycling in the P limited wet sedge site at the Sag river to nitrogen limited wet sites at Atigun gorge.

Our long term LTER goal, which links these projects with the aquatic research, is to determine how nutrient cycling patterns in the terrestrial ecosystems affect the timing and the amount of phosphorus entering arctic streams and rivers. Fully answering this question will require workable hydrologic models, and a knowledge of how P cycling changes with climate and geology. Hydrologic measurements are currently being made at both the MS117 and Sag river sites and as part of our LTER studies basic hydrological measurements will be undertaken at the Kuparuk. The soil solution chemistry of terrestrial ecosystems along the Kuparuk will be compared to sites of similar vegetation on the Sag and MS117 sites. We will also examine the chemistry of small streams which drain watersheds of distinct geology and vegetation.

These studies of the controls and variability of nutrient export from land will be accompanied by studies of primary and secondary productivity in the receiving rivers and lakes. We know that there are large differences in temperature and precipitation patterns from year to year that have important impacts on nutrient export. We think that these differences probably contribute to important variation in primary productivity in lakes and rivers. To address this point we will measure standing stocks of algae, primary production and secondary production in the Kuparuk River and in Toolik Lake and correlate the seasonal patterns and annual totals with nutrient loading for both N and P.

c. <u>Does peat-derived organic carbon in streams ultimately fuel the top trophic levels (fish, birds)?</u> Stable isotope techniques allow the discrimination between marine and terrestrial derived carbon in the anadromous fishes migrating in and out of the Colville River and the waterfowl and shorebird populations feeding in tundra ponds and lakes (Schell 1983). By comparing the radiocarbon content of top consumers and the carbon sources available through prey organisms, it is possible to allocate the peat, freshwater algal, and marine algal carbon contributions to the energy budgets. This study would compare the isotope abundances in different species of anadromous and obligate freshwater fishes and determine the critical energy sources to the organisms over the annual cycle. By comparing both nitrogen and carbon isotopes, it should be possible to allocate habitat dependencies for both nutrients and energy supply. Migratory waterfowl and shorebirds should also be amenable to determination of the respective roles of the separate carbon sources deriving from overwintering habitats and their prey from the tundra environments.

Once specific energy sources have been determined, emphasis will be shifted to determining the mechanisms by which the carbon is converted to biomass and transferred through the food web. Several species of aquatic invertebrates have been found to have lowered concentrations of radiocarbon as a result of consuming peat (Schell and Ziemann, in press) and the mechanisms by which this is accomplished is poorly known. Through the use of radiolabeled substrates, it may be possible to gain further insight into the mechanisms of consumption and assimilation of peat.

F. REGIONAL ECOLOGY: EXTRAPOLATION TO OTHER REGIONS OF THE NORTH SLOPE AND THE ARCTIC

1. Introduction Most people think of the Arctic as uniformly cold and barren, with spectacular scenery but not much biotic diversity. In fact the Arctic includes an unusually wide range of climatic regimes, geologic conditions, and topography. This wide range of habitat conditions is reflected in a wide range of ecosystem characteristics. For example, the dominant plant in a "typical" North Slope Alaskan ecosystem may be a moss, a lichen, a graminoid, or a deciduous or evergreen shrub (Chapin and Shaver 1985*). In contrast, most other biomes are characterized by the single plant growth form that dominates them, e.g., "deciduous forest", "tallgrass prairie", or "mediterranean shrub". In the Arctic the relative simplicity within ecosystems is confounded by variation between ecosystems.

The ecosystem-level variability in the Arctic represents both a challenge and an opportunity. On one hand it means that we must be very careful in extrapolating our knowledge from one site to another, and there is a particular need for comparative studies among sites. On the other hand the relatively small total number of species at any one site, and the fact that many species and genera are held in common between quite different ecosystems, means that comparative studies among sites are often easier to interpret than in other biomes.

On the North Slope of Alaska there is a particular need for us to be able to extrapolate our results from site to site. The exploration and development of economic resources is proceeding rapidly throughout the Arctic, over the entire range of natural ecological variation. Yet, almost all of our information comes from only a few, mostly similar sites. The Toolik Lake area, and the transect across Alaska opened up by the Dalton Highway, represent an ideal opportunity to test our ability to extrapolate from site to site because for the first time virtually the whole range of variation in arctic ecosystems is available to us by road and within reasonably close proximity.

2. Past Research

a. Terrestrial There have been intensive studies of Alaskan arctic ecosystems at Barrow (Brown et al. 1980), Meade River (Batzli 1980), Prudhoe Bay (Brown 1975, Walker et al. 1982), and Eagle Creek (Miller 1982). Other intensive arctic ecosystem studies include the Canadian high arctic research at Devon Island (Bliss 1977) and the Scandinavian IBP projects (Weilgolaski 1975). Most of this work, particularly in North America, has focused on either wet sedge tundra or tussock tundra, the two most common ecosystem types on the North Slope. As a result we now know a great deal about these two ecosystem types, and especially much about individual processes such as photosynthesis or nutrient uptake. The current DOE R4D project is continuing this tradition, with a number of excellent, detailed process studies in tussock tundra. However, in the past and at present there have been few if any direct comparisons among the Alaskan sites (e.g., Wein and Bliss 1974), and little work outside of wet or tussock tundra (Chapin and Shaver 1985*). Within Alaska the major means of extrapolation has been useful but essentially unvalidated simulation modeling (e.g., Miller et al. 1984*). An international synthesis was pulled together from the IBP studies of the early 1970's (Bliss et al. 1981), but since then there has been little additional comparative work.

The most extensive comparisons yet available come from work based at Toolik Lake and along the Dalton Highway over the past 10 years (Chapin and Shaver 1981*, 1985*, Shaver and Chapin 1986*, Shaver et al. in press*). One of our most significant findings is that there is significant variation in the limiting nutrient for plant growth within as well as between ecosystem types. For example, wet or tussock tundras that are quite similar in terms of production, biomass, or species composition may be variously limited by N, P, or both elements. We also have shown that, although a "good" year for plant growth or flowering is apparently "good" throughout the North Slope, there is no clear relationship with annual temperature variation. Furthermore, the latitudinal correlation between average temperature and plant size is due more to ecotypic variation in plant size than to any direct climatic control. These results are important because they contrast sharply with predictions based on temperature and nutrient controls of single processes at single sites (Shaver et al. in press*).

b. Aquatic Large thaw lakes and shallow ponds may cover 50% of the area in some regions of the Coastal Plain. Large lakes are much rarer in the foothills and mountains and are restricted to glacial end-moraines. Lakes and wetlands are such a dominant part of the landscape that they have attracted much scientific attention; various features (biota, physics, chemistry) of the lakes and ponds of northern Alaska have been described since the early 1950's (see reviews by Livingstone 1963, Kalff 1970, and Hobbie 1973).

Intensive research on rates and processes in lakes and ponds as ecosystems has been carried out only at two sites, shallow ponds at Barrow (summarized in US/IBP Synthesis Series vol. 13, Hobbie (ed.) 1980 and in Hobbie 1984) and at Toolik Lake (summarized in this proposal and in papers referenced in Appendix I).

There are only a handful of studies on streams in the Arctic anywhere; in Alaska Craig and McCart (1975) classified streams, Schell (1974, 1975) and Arnborg et al. (1966) have reported on the Colville River. Peterson and associated scientists have carried out the only intensive study of any arctic stream (see Section II and Appendix I for references). At the R4D site (MS 117), Mark Oswood is investigating stream insects and carbon cycling and the entire DOE project has monitoring and modeling of micro-watersheds as one of its goals.

3. Research Questions

<u>What is the distribution and range of variability in the chemistry, patterns of primary production, limiting factors and trophic structure of North Slope Ecosystems? How do the intensively studied sites fit within the range ? How can we use the intensively studied sites to understand the ecology of all parts of the North Slope?</u>

a. <u>Terrestrial</u> We have been intensively studying several sites around Toolik for more than ten years. From these intensive studies we are finding some simple measures that are good predictors of ecosystem characteristics such as limiting factors or number of trophic levels. We will survey a variety of ecosystems on the North slope and measure what we believe are key variables which will indicate how similar these sites are to our intensively studied sites. Then to test the robustness of our predictions, we will make intensive measures in a few sites which appear to be very similar or very different.

Element ratios in soils and tissues have been shown to be good predictors of plant nutrient status (Shaver and Melillo 1984). From our factorial fertilization studies we have found that similar ecosystems are not always limited by the same nutrient. We will return to these sites and examine C/N, C/P and N/P ratios in soils, soil solutions, and plant tissues to determine if these predict the response we observed in our fertilization treatments. The next step is to survey areas using these simple measures and see how general the patterns we find are for the rest of the North Slope. We than can go to a few sites and repeat some of our experiments and intensive measurements.

b. <u>Aquatic</u> Our river studies have focused primarily on the 4th order reach of a tundra river. In order to establish the basis for generalizing our findings, we must carry out a survey of other types and sizes of rivers. One survey which we will do is to compare rivers of different order within a watershed. We have access to first through fifth order reaches of the Kuparuk near Toolik and can sample the mouth of the river where the Kuparak becomes a 7th or 8th order river. A second aspect of the survey will be to investigate the characteristics of different rivers of similar sizes. Craig and McCart (1975) have classified North Slope rivers into three broad categories; tundra rivers, mountain glacier-fed rivers, and spring-fed rivers. Our objective is to obtain enough information for a detailed comparison of other stream orders and other river types to the Kuparuk and other well studied rivers. We plan to sample nutrients, suspended particulate matter, benthic algae, insect drift, and fish. Some samples will be taken for stable isotopes (see below).

Stream water chemistry will not only give us information on processes occurring in aquatic ecosystems but will also reveal variability in the pattern of nutrient export from the terrestrial ecosystem. We will sample water chemistry and soil solution chemistry in a number of first through third order watersheds dominated by different terrestrial plant communities and by different types of bedrock.

From our work at Toolik and Barrow we already have a sense of how lake processes vary with lake size and latitude. This needs to be quantified. We will examine the dissolved nutrients and primary production in a number of lakes between Toolik and Barrow in conjunction with our stream survey. Although a great deal is known about nutrient cycling less is known about trophic structure. Fish removal and introduction experiments are planned in the Toolik area to examine these questions. We believe that stable isotopes can revel much about trophic structure (see below). Therefore we will sample fish and invertebrates in lakes and measure their stable C,N and S isotope content.

The stable isotopes of carbon, nitrogen and sulfur provide naturally occurring tracers of biogeochemical processes in all ecosystems and their distribution in the components of each ecosystem is determined by the same principles. Since the isotopes integrate the effects of processes occurring over various time intervals, a survey of isotopes in components of ecosystems at one point in time can tell a lot about the history of ecosystem function. One of the most effective and efficient ways to establish differences in function between ecosystems with similar structure is to compare stable isotope values for similar components. If the relative stable isotope distributions are different, then one must assume that the biogeochemical pathways in the two systems are also different.

For example, if the organic nitrogen in the soil organic matter has a $\delta^{15}N$ value of +5.0 ‰, one would expect a plant growing at this site and using remineralized ammonium to have a $\delta^{15}N$ value of +5.0 ‰. Any plant with a $\delta^{15}N$ value of +1 ‰ would be suspected of using recently fixed atmospheric nitrogen or having a symbiotic nitrogen fixer. Thus, in many systems, a survey using $\delta^{15}N$ can indicate times or places where nitrogen fixation is important.

For lakes, one would like to know, for example, if lake trout in all lakes fed at the same trophic level. In this instance carbon and nitrogen isotopes may provide a very efficient way to compare trophic structure. For each trophic transfer ^{13}C and ^{15}N are enriched by about 1 ‰ and 3 ‰ respectively. Thus the difference between the primary producers in a lake and the lake trout would be 3 ‰ in $\delta^{13}C$ and 9 ‰ in $\delta^{15}N$ if the lake trout were feeding on average at trophic level three. It seems likely that as both the population density and the individual size of lake trout change their position in the overall trophic structure will shift. These shifts, if they involve changes in either the ultimate source of the organic matter or in the number of links in the food chain, will be reflected in the stable isotope values of lake trout relative to other components in the ecosystem. The rapidity of the shifts can be assessed by examining trout tissues with different turnover times.

While these examples are overly simplistic, we want to make the point that comparison of ecosystems using stable isotopes is one very efficient approach to testing our ideas about the similarities between ecosystems or the generality of ecosystem function. We propose that this would be an ideal approach to integration of the research at a wide variety of LTER sites.

Ecologists have begun to use remote sensing to look at broad scale vegetation patterns across a landscape (Walker et al. 1982). This tool works well in the arctic where vegetation is of low stature and understory communities are absent. In addition, information on biomass, phenology, chlorophyll a, woody biomass, elevation, and perhaps nitrogen/lignin may all be sensed remotely. Our sites and those studied by others provide convenient locations where this tool can be calibrated. This will provides another way in which to examine the distribution and range of variability within the range of North Slope Ecosystems.

IV. RESEARCH SCHEDULE AND WORKPLAN

The LTER Program is a blend of ongoing affiliated (DOE and NSF-BSR), proposed (NSF-DPP), and LTER projects. A research schedule of the order in which projects are to be carried out will allow LTER funding to be allocated year-by-year as the mix of funding of affiliated projects changes. The ideal mix with all pending projects funded is:

Task	Question	Funding
<u>Baseline studies</u>		
IIIB	Vegetation related to soil chemistry and nutrients	NSF-BSR
IIIB	Climate variation related to plant growth and flowering	LTER
IIIB	Climate and microclimate of contrasting ecosystems	NSF-BSR
IIIB	Flow and water chemistry of Kuparuk River	NSF-DPP
IIIB	Composition and quantity of atmospheric deposition	LTER
<u>Ecosystem structure: Predator/grazer control</u>		
IIID	Experimental changes in lake trout populations and their prey	NSF-DPP
IIID	Grazer or predator control of energy flow in stream	NSF-DPP
IIID	Effect of mammal grazing on vegetation, long term	LTER
<u>Ecosystem structure: Resource control</u>		
IIIC	Structure of lake food web after fertilization	NSF-DPP
IIIC	Controls of growth form and productivity in vegetation	LTER
IIIC	Use of autochthonous vs. allochthonous carbon in stream	NSF-DPP
IIIC	Tests of limitations of vegetation elsewhere on North Slope	LTER
<u>Atmosphere/land/water interactions</u>		
IIIE	Transfer of organic carbon from peat to fish and waterfowl	LTER
IIIE	Sources and sinks of N and P as they move across the landscape	NSF-BSR
<u>Extrapolation to other North Slope ecosystems</u>		
IIIF	Regional patterns of limitation, how to extrapolate?	LTER

WORKPLAN	88	89	90	91	92	93	94	95	96	97
Vegetation related to soil chemistry and nutrients	X	X	X	X	X	X	X	X	X	X
Climate variation: plant growth and flowering	X	X	X	X	X	X	X	X	X	X
Climate and microclimate of contrasting ecosystems	X	X	X	X	X	X	X	X	X	X
Flow and water chemistry of Kuparuk River	X	X	X	X	X	X	X	X	X	X
Composition and quantity of atmospheric deposition	X	X	X	X	X	X	X	X	X	X
Experimental changes: lake trout and prey	X			X			X			X
Grazer/predator control of energy flow in streams	X	X	X	X						
Effect of mammal grazing on vegetation, long term	X				X				X	
Structure of lake food web after fertilization	X			X			X			X
Controls of vegetation: growth form/productivity	X	X			X			X		X
Autochthonous vs. allochthonous carbon in streams	X	X	X	X	X					
Tests of limitations of vegetation, North Slope				X			X			X
Transfer of organic carbon, peat to fish/waterfowl	X	X	X							
Sources and sinks of N and P in landscape	X	X	X	X	X					
Regional patterns of limitation, how to extrapolate				X		X	X	X		

V. MANAGEMENT AND ORGANIZATION

A. Arctic Alaska LTER Program. The program management will consist of a Program Director (John E. Hobbie) and an Executive Committee (Hobbie, Bruce J. Peterson, Gus Shaver, W. John O'Brien, Don Schell) who will make most of the day-to-day decisions. Members will communicate by Telemail (already in place for all except for O'Brien). A Research and Policy Committee consisting of all of the current principal investigators will meet once a year to decide upon scientific goals and policy (this group met in the summer of 1986 to decide upon the goals outlined in this proposal). This annual meeting is an important part of the program and will consist of three days of scientific presentations and discussions of goals and policy.

The responsibility for setting up and maintaining the field experiments, logistics, and data collection will be given to a Field and Program Coordinator, to be hired at the R. A. III level. This person, who will report to the Director, will be experienced in finances, logistics, and the management of field research. His task is made easier by the presence of a logistics coordinator at the University of Alaska whose office will arrange for transportation and shipping, buying of equipment and supplies in Fairbanks, lodging at the University, and communications in the field. Some of these services are included in the per diem charge for staying at the field camp; other services are billed.

Two senior staff members, J. Helfrich and J. Laundre, will bear joint responsibility for Data Management. For this part of their duties they will report to Peterson (aquatics) and Shaver (terrestrial).

Three non-arctic scientists from outside the project will visit the field site each year and attend the coordinating meeting. They will constitute an Advisory Committee whose task is to bring an outside viewpoint and contribute to the cooperation with other projects.

B. Data Management. The series of multi-investigator projects in arctic Alaska since 1970 have operated with the following rules for data management: 1) all data are available to all investigators, 2) investigators must publish their results in reviewed journals, 3) the collection and maintenance of routine data (e.g., streamflow, water temperature, climate, etc.) is assigned among the various subprojects, 4) an annual data report is required from each subproject and is distributed to all investigators. These rules have worked as evidenced by the many multi-authored papers (Appendix I) and the published synthesis volume from the IBP (1980. Limnology of Tundra Ponds, Hobbie ed.). Yet, the LTER project is for a longer term and also has the goal of intersite comparisons. A greater emphasis on data management is needed; until we have the opportunity to find out what is happening among LTER projects, we propose the following.

We will modify the above rules by assigning to two staff members the responsibility for the assembling and reporting of data, responsibility for archiving of data, and responsibility for interacting with other LTER projects to achieve comparability of units and ways of reporting data collected on the project. Investigator responsibility would be Peterson (aquatic) and Shaver (terrestrial). Each staff person (Laundre and Helfrich) would work half-time on this. Each is very experienced with a variety of ecological research, with statistics, and with computers. Both are already working at the site and doing extensive data management.

James Laundre has an M.S. in Botany with 27 other course credits in Electrical Engineering and Computer Science. He is experienced in chemical analyses, ecological surveys, limnology, bogs, etc., and has worked on the IBM 3081, PDP 11/60 and PDP 11/35 computers in PL/I, Fortran, Pascal, and Assembler languages. He has used various statistical packages such as SAS, BMD, and SPSS. He is currently employed at the Marine Biological Laboratory on the landscapes project.

John Helfrich has undergraduate degrees in mathematics and biology. He is experienced in microscopy (epifluorescence, autoradiography of microbes), radioisotopes, computers (PDP 11/35, IBM micros, spreadsheets, graphics), water quality analysis, and electronics. He is co-author on three papers and is currently employed on the arctic lakes and streams project.

C. Principal Investigators. The principal investigators of the Arctic Alaska LTER include scientists currently working at the site on three separate projects. All of these projects contribute, to a significant degree, to the goals of this LTER program. One project (NSF Landscapes with Shaver, Giblin, Nadelhoffer) continues for two more field seasons. One project (DOE R4D with many scientists including Shaver, Linkins, Schell) continues for one more field season at least. One project (NSF Lakes and Streams with Hobbie, Deegan, Hershey, Kipphut, McDonald, Miller, O'Brien, and Peterson) is being reviewed for renewal for the 1987-1989 field seasons. The scientists in the following table have C.V.'s in this proposal and all are likely to contribute data to the program and possibly receive support from LTER funds over the next five years; but not all of them will take an active role in the LTER program in any given year. Some scientists are necessary for setting up long-term experiments (e.g., McDonald, Schell) so will receive funds at the start of the program. Some (Hobbie, Peterson, O'Brien, Shaver) have important management roles.

Linda Deegan	Univ. Mass.	Fish ecology, aging, growth
Brian Fry	MBL	Stable isotopes in plants and animals esp. S, N
Anne Giblin	MBL	Chemical ecology of wetlands, P, Fe
Anne Hershey	Univ. Minn.	Insect ecology, competition
John Hobbie	MBL	Arctic limnology, planktonic microbes
George Kipphut	U. Alaska	Geochemistry, sediments, carbon dioxide
A. Linkins	Clarkson Tech	Soil and stream organic matter, enzymes
Mike McDonald	U. Minn.	Fish ecology
Michael Miller	U. Cincinn.	Phytoplankton, production, chemistry
Knute Nadelhoffer	MBL	Plant/soil interactions
John O'Brien	U. Kansas	Zooplankton, fish
Bruce Peterson	MBL	Stream ecology, isotopes
Don Schell	U. Alaska	Feeding of birds, fish, stable isotopes
Gus Shaver	MBL	Physiology of arctic plants, nutrients

D. Control of Site. The North Slope of Alaska is entirely public lands under the control of the North Slope Borough, the Bureau of Land Management (BLM) and the State of Alaska. The field station at Toolik Lake and the foothills research sites are technically in the pipeline corridor and controlled by BLM. However, all agree that both BLM and BSB use permits should be obtained for the research station and for research sites. There have been no problems obtaining these use permits over the past decade and no problems are foreseen for the future. Hobbie has contacted both BLM in Fairbanks and the Planning Office of the North Slope Borough in Barrow about use permits for research, as suggested by Frank Williamson (Appendix II). Neither office foresaw any problems for future permits but could not make definite permit promises at this time. Letters have been promised by these two offices and will be sent to NSF when received. The Director of the Institute of Arctic Biology, Dr. Frank Williamson, states (letter in Appendix II) that the research station will be available to an LTER project.

What does this mean for a long-term project? First, all research sites in northern Alaska fall under these rules and researchers have obtained permits for 15 years or more (see Appendix II for list of current permits). Second, the ownership and control of the sites will not change in the foreseeable future. Third, the BLM and NSB are in favor of continued research in the Arctic and NSF now has a Congressional mandate to foster and coordinate arctic research. Fourth, it is true that the opening of the road to the public removes some protection from the sites but this will never be a heavily used region because it is so remote. The projects are designed so that the control areas are miles away from the nearest roads and will not be harmed by occasional hunters or fishermen. There will be scientists at the sites during the summer when recreational use would be highest. Finally, the use permits are under the control of BLM which recognizes the value of research and the need for undisturbed control sites.

E. Facilities. At Toolik Lake the University of Alaska Field Station rents laboratory and living space to projects from any institution. Currently, the camp supports 40 scientists. There are five heated laboratory trailers (2500 sq ft), kitchen and dining room, five sleeping trailers, workshop and storage buildings and tents. Electricity is provided by 30 kw generators and communication by single side-band and meteor-burst radios. There are five small boats and motors. Staff consists of a camp manager, his assistant, a cook, and assistant cook. The camp is open from approximately 1 May until 15 September but may be used for short periods in the winter as well. The camp is operated by the Institute of Arctic Biology, U of A, and the costs to investigators, $90/day in 1986, are based upon operational costs.

The camp was begun in 1975 by the NSF aquatic project (DPP, Project Rate) with Hobbie as P.I. This aquatic project has continued under various names and in the last five years there have been a number of terrestrial projects at the camp as well (DOE and NSF funding). Until 1982, the funds for construction came from appropriations from the State of Alaska, from indirect cost recoveries, and revenue from operation. In 1978 and 1979, two trucks were bought as a part of the logistics proposal on the NSF project. In 1982-83, DOE contributed $40,000 for operation. An additional $37,000 from DOE and overhead recovery allowed purchase of 13 trailers from the pipeline service company. In 1984, the State of Alaska (Legislature plus U of Alaska) appropriated $45,000 for upgrading the wastewater collection system and the kitchen. All human and kitchen wastes are trucked to Prudhoe Bay for disposal.

In 1986 NSF (Biological Research Resources Program, BSR) approved an equipment and facilities award of $60,000 to the University of Alaska for the Toolik Lake camp. The funds were for generators, dining hall, communications, and scientific equipment.

The scientific equipment is mostly furnished by projects although the camp owns freezers, balances, drying ovens, a dissecting microscope, and a PC. During summer 1986 additional instruments in camp included four PC's, two spectrophotometers, a gas chromatograph, a liquid scintillation counter, a large incubator, a flow-through microcalorimeter, a T.V. recording system for fish behavior studies, an inverted microscope, and an epi-illuminated fluorescence microscope. Field instrumentation included water samplers, light meters, pH meters, temperature-conductivity meter, and diving equipment.

At the University of Alaska the special equipment available is the mass spectrometer (VG Isogas) in the laboratory of D. Schell. At the Marine Biological Laboratory the special equipment is a Finnigan 251 Mass Spectrometer (paid for by NSF-BSR and the A. W. Mellon Foundation).

The laboratories of the principal investigators at the Universty of Kansas, University of Cincinnati, Clarkson University, University of Minnesota, University of Alaska, University of Massachusetts and MBL also contain standard laboratory instrumentation and facilities suitable for counting bacteria, counting benthic animals, making organic matter determinations, etc.

F. Institutional Cost Sharing. A strength of past projects in the Arctic has been the bringing together of scientists from many institutions. This proposal also involves seven institutions. This unusual arrangement for an LTER raises the problem of which institution should cost share? As noted above, the site cannot be owned and the field station is complete; in fact, the State and the University of Alaska has already contributed more than $50,000 to the construction and upgrading of the Toolik Lake field station. The other major institution is the Marine Biological Laboratory, a non-profit organization obtaining its operating funds from overhead and space rental. The Ecosystems Center of the MBL has used funds from private foundations and from its Reserve Fund to support the salaries of principal investigators to ensure project completion -- and has done this for the arctic projects described here.

VI. INTERACTION WITH OTHER LTER SITES

A. Interaction with the Northern Lakes LTER Site. J. Magnuson, T. Frost and T. Kratz are interested in working closely with us to compare the fish communities of their LTER site with those of arctic lakes. One interesting question to be addressed is the stability of large aquatic ecosystems. If stability is the maintenance of the basic community structure, then unexploited arctic fish communities are extremely stable. However, when disturbed, the fish communities of an exploited arctic lake may be far less stable than the more complex fish communities of the exploited Northern LTER lakes. There, the study of the responses of lake ecosystems to disturbance and stress has focused on turnover events, species invasions, and acid deposition. Our work will complement this by extending the database to include ecosystem responses to fertilization and overfishing.

Our data on unexploited fish populations will likely provide the Northern Lakes LTER researchers with ideas about the community structure of their lakes before disturbance; this is a benchmark to which they have previously had no access. Also, as we gradually increase the fishing pressure on a previously unexploited lake, we may be able to provide insights into the development of the present species composition of certain Northern LTER lakes containing the same species and/or functionally analogous species. By adding top predators to a lake ecosystem, which previously had few or none, and by introducing a new forage species to a lake containing top predators, we can not only gain insight into the effects of these potential anthropogenic stresses in arctic lakes, but also compare our results with data from the Northern Lakes LTER, where these types of stresses have been occurring for some time. These experiments could help us understand some of the observed variability in fish communities resulting from changes in the top trophic level and also allow intersite tests of ecological theory.

B. Niwot Ridge

The Niwot Ridge LTER site, in the Rocky Mountain alpine zone, makes a natural pairing with our arctic site. The flora and fauna are quite similar, with many of the dominant species or genera held in common between the two sites. Both sites are cold, with a short growing season. Species diversity is low in both sites, and the low vegetation stature and fine-grained scale of heterogeneity offer similar opportunities for whole-system experiments. On the other hand the two sites differ in daylength, light intensity, precipitation, potential and actual evapotranspiration, and the presence of permafrost.

The similarities and differences between arctic and alpine ecosystems are almost a classic subject for research in ecology (e.g., Billings 1973), yet most research has been at the process level rather than the whole-system level. A fine opportunity exists to build on this research heritage by doing comparative, ecosystem-level measurements and experiments at Toolik and Niwot. The opportunity is strengthened by virtue of the fact that the Niwot Ridge site, like our Toolik Lake site, includes both a variety of terrestrial ecosystems dominated by different plant growth forms and a chain of lakes within the same watershed.

We already have good working relationships with scientists involved in the Niwot Ridge LTER, extending back to the IBP program based at Barrow and Niwot. Two of the Niwot P.I.'s, Drs. Pat Webber and Skip Walker, have very extensive experience on the North Slope of Alaska and for the past three summers have participated in the DOE R4D research program based at Toolik Lake (Shaver, Linkins, and Schell are also involved). Several of the P.I.'s in our group have visited Niwot Ridge in the past, so we are familiar with the facilities and potential collaborations. Pat Webber, the director of the Niwot LTER, has been quite encouraging about future collaboration and has sent us copies of their proposals, data reports, and planning documents.

To start, we would like to make some of the same observations, experiments, and isotopic tracer studies at Niwot Ridge as described under the "Regional Ecology" section above. We would also invite Niwot ecologists to make comparative measurements on our sites and experimental plots. An initial goal might be simply to determine, "What are the limits of extrapolation of our knowledge between arctic and alpine ecosystems?"

C. Stable isotopes as a comparative tool. A new stable isotope laboratory capable of measuring C,N,S isotopic variations is now operative at the Ecosystems Center under the direction of Brian Fry. Its goal is collaborative ecological research and enhancing the use of stable isotopes as an ecological tool.

Stable isotope measures are an important part of this proposal but we believe that they can also be very useful for cross-site comparisons with other LTER programs. To this end, LTER funds were used to bring Brian Fry to Wisconsin in the spring of 1986 for seminars and consulting. As a result of that trip, plans are being developed with Tom Frost (Northern Lakes LTER), James Hodgson (St. Norbert College, WI), and Steve Carpenter (Notre Dame, IN) for stable isotope investigations of food webs in freshwater habitats.

We would like to collaborate with other LTER groups, both terrestrial and aquatic, for cross-site comparisons of stable isotopes to answer questions about nutrient cycling and C,N,S element flows between different landscape units and about food webs. It would be appropriate to begin with a workshop of interested LTER scientists.

D. Affiliated Projects. The proposed LTER Program will interact with affiliated projects in northern Alaska in a number of ways. Some projects (e.g., the NSF-BSR project on landscapes) will be closely integrated (personnel, goals) into the LTER so that some extra data and data management will be provided by the LTER personnel and some of the LTER questions will be answered by the NSF-BSR research. If the NSF-DPP project is funded, then the situation will be similar but if it is not funded then some of the parts of that project will be paid for by LTER funds. Other projects, such as the DOE-R4D project, will share data, insights, and models with the LTER project through informal arrangements fostered by investigators sharing the same field station and by some overlap of investigators. Oechel's DOE-R4D project has included three of the LTER P.I.'s on that project and has included Hobbie and MIller as a part of their review panels. Still other projects will want to make measurements of all types at the experimental sites and build on the data sets.

Some of the measurements, such as the climate measures at MS117, may have to be funded by the LTER program if DOE funding ends. If this occurs, then we would call on J. Kelley, of the University of Alaska, for advice and possibly for a proposal to continue his climate station.

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APPENDIX II

UNIVERSITY OF ALASKA-FAIRBANKS
Institute of Arctic Biology
Fairbanks, Alaska 99775-0180

Office of Director
(907) 474-7648

14 October 1986

Dr. John Hobbie
Marine Biological Laboratory
Woods Hole, MA 02453

Dear John:

This letter is in response to your request for comments from the Institute of Arctic Biology on the long-term planning aspects of three areas of your Long-Term Ecological Research (LTER) proposal to the National Science Foundation. The areas of concern as listed in the LTER announcement are (1) site integrity and security, (2) resolution of conflicts in use of the site, and (3) long term agreements with site owners.

Site Integrity and Security

The Institute's Toolik Field Station, and associated 20 acre site, are subject to permit renewals from the Bureau of Land management (BLM), the North Slope Borough (NSB) and the Department of Environmental Conservation (DEC). We are confident that these permits will be in effect as long as there is research being done in the area of Toolik Field Station which utilizes our logistic support. We feel comfortable in giving you our assurance that the integrity of the field station is sound and see no reason to believe that permit renewals will be denied.

Site security is relatively good due in part to the Dalton Highway being a restricted access road. In the winter we have some vandalism from hunters and snowmachine operators. We expect to reduce or eliminate such winter violations by having regular inspection trips to the station. The State Troopers are expected to keep a lookout for unauthorized activity when they pass the camp on regular road trips.

Resolution of conflicts in use of the site

Since the field station and associated site are operated under permits, the chance of there being any conflicting use of the site is perceived as being slight. As long as we continue to operate within the terms of our agreements we should maintain a good relationship with the permitting agencies. If our use of the site were challenged by another potential permittee, the conflict would be resolved through adjudication by either the NSB or the BLM, or both. Our position in such an instance would be strengthened by the acceptability of the research being done, and we would look to users of the field station to support our case.

Long term agreements with site owners

We operate the field station subject to the terms and conditions of the following permits:

A. Bureau of Land Management
  1. f-81426
     Site use - 20 acres

This permit is being renewed annually until the utility corridor land use review is completed. After 1988 the permit period will be for a longer period, perhaps three to five years.

  2. ff-85215
     Wastewater disposal - 1 acre
     Renewal 31 January 1989

B. State of Alaska - Department of Environemtnal Conservation
  1. 350146
     Public water supply

  2. 853H4025
     Food service permit

Both permits are indefinite.

C. North Slope Borough
  1. 83-1
     Site permit
     Renewal 31 January 1990

In your telephonce call of 6 October you identified the areas which you are proposing as LTER research sites. For the record, our understanding of the areas proposed for your LTER activity are:

1. Toolik Lake Watershed
2. Itigaknit Lake Watershed
3. Kuparuk River Warershed downstream to the confluence with the Toolik/Itigaknit drainage stream
4. The R-4-D site
   T-9-S, R-12-E Sec. 33, 34
   T-10-2, R-12-E Sec. 3, 4
5. Dr. Shavers study area
   Sagavanirktok River
   East of the Slope Mountain camp of the Dept. of Transportation, on the left bank of the river. T-8-S, R-14-E, Sec. 8, 16-17.

All of the above areas are in the Umiat Meridian.

We feel that is is inappropriate for us to comment on the long term use of these proposed study areas since our logistics support is confined to activities on the 20 acrea site authorized for use by the NSB and the BLM.

I believe that is important now for you to discuss your proposal with the BLM and the NSB.

With best regards, I am,

Sincerely,

Frank

Francis S.L. Williamson
Director
INSTITUTE OF ARCTIC BIOLOGY

FSLW/na