The Arctic LTER Project:

Terrestrial and Freshwater Research on Ecological Controls

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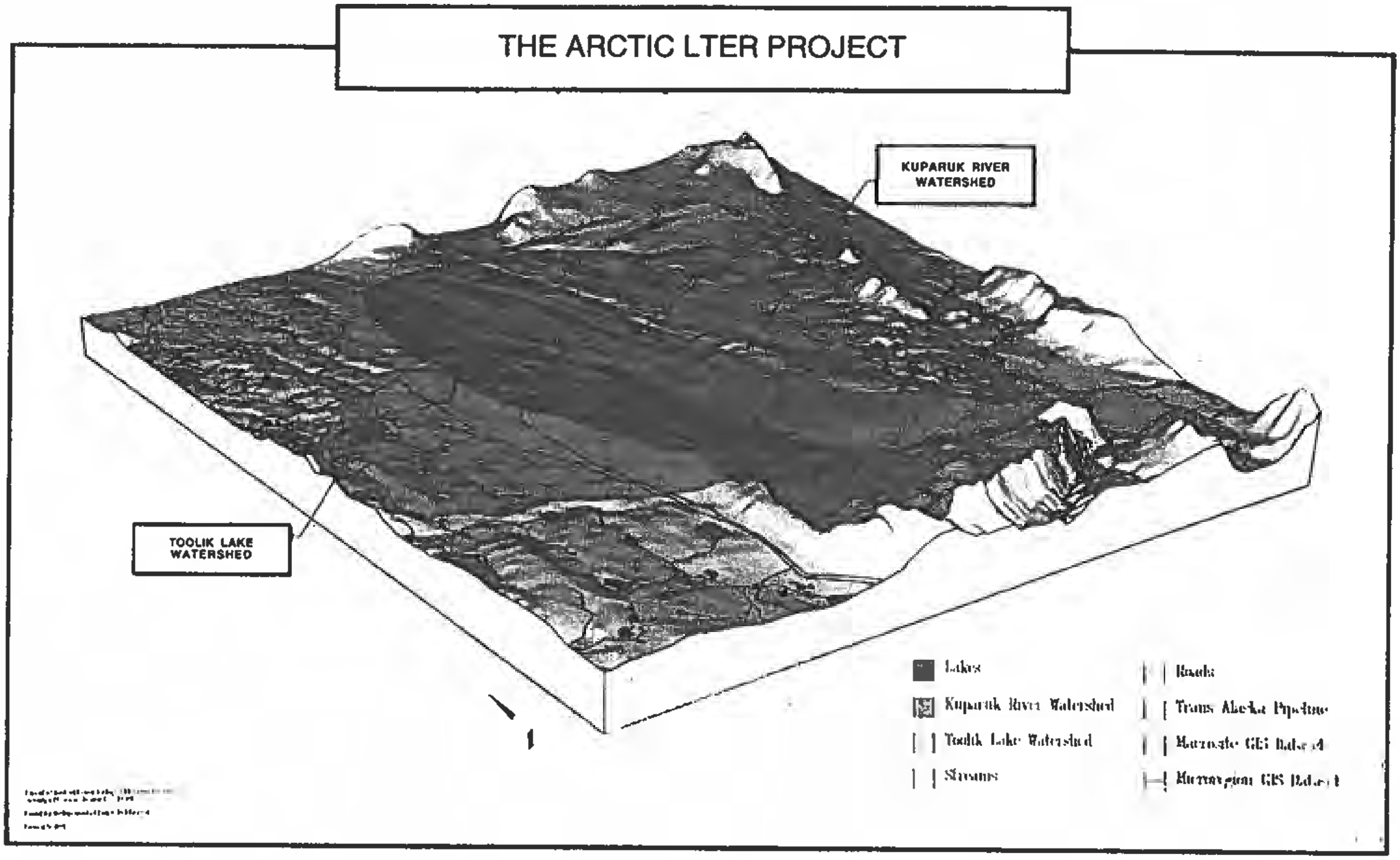

Frontispiece: Perspective view of the Arctic LTER research site from the southwest, showing the Toolik Lake (blue) and upper Kuparuk River (green) watersheds in topographic relief. The small and large rectangles within each watershed indicate intensively studied sites, mapped at several scales by D. Walker of the University of Colorado as part of the DOE-R4D and Arctic LTER research programs.

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PROPOSED RESEARCH

TWELVE TOPIC DESCRIPTION (required sections)

SUPPORTING MATERIALS

PROJECT SUMMARY

During the first five years of the Arctic LTER at Toolik Lake, Alaska, we began systematic measurements of climate, of tundra plant distribution and productivity, and of lake and stream physics, chemistry, and biology. Whole system experiments were set up on the tundra, in streams, and in lakes to examine the ecological effects of changes in environmental and biological factors such as air temperature, added nutrients, and changes in the density of the top predators and grazers. These measurements and long-term experiments are designed to help us reach the overall goal: To understand how tundra, streams and lakes function in the Arctic and to predict how they respond to human-induced changes including climate change. Under this broad goal we have three specific goals:

(1) Determine year-to-year ecological variability in these systems and measure long-term changes.
(2) Understand the extent of control by resources (bottom-up control) or by grazing and predation (top-down control).
(3) Measure rates and understand the controls of the exchange of nutrients and organic matter between land and water.

Long-term experiments are the heart of the Arctic LTER program. We have found that arctic systems often do not respond for many years, and that long-term responses are often not predictable from short-term responses. We still are finding changes in the responses of both streams and terrestrial vegetation to nutrients after 9 years. Lake trout manipulations take many years to show effects as these long-lived fish may change their diet from invertebrates to fish when they reach a certain size. As a result, we will continue most of our long-term experiments, and continue the measurements for determining ecological variability. Other long-term experimental manipulations will be discontinued in order to observe long-term recovery patterns.

We propose to continue pursuing these same goals of the Arctic LTER project for the next six years. The results of the long-term experiments will continue to be measured as we find out more about the long-term ecosystem controls by resources and predation. We also will begin new research on the controls of the exchange of nutrients between land and water. A major watershed experiment will be carried out to measure the movements of water and dissolved gases through the groundwater and into the streams. We will cooperate closely with new projects studying the hydrology in order to construct a model of the movement of water and nutrients through small watersheds and through a large watershed such as the upper Kuparuk River.

RESULTS FROM PRIOR NSF SUPPORT

The current LTER grant is titled: AN LTER PROGRAM FOR THE ALASKAN ARCTIC
NSF GRANT #BSR-8702338, Sept. 1987 to Sept. 1992, $2,250,000

History.

Ecological research in northern Alaska has been carried out since 1947 in the Coastal Plain Province of the North Slope. The terrestrial and freshwater research culminated in the Tundra Biome IBP at Pt. Barrow (1971- 74). Little was known about the Foothills Province at that time but the opening of the pipeline haul road allowed scientists access; research began at Toolik Lake in 1975 and has continued with a series of NSF, EPA, and DOE grants. The Arctic LTER, funded in 1987, was designed to build on the ecological information developed at Toolik Lake on the tussock tundra, streams, and lakes of this foothills region. In 1991-92 there are two cooperative NSF projects working at Toolik Lake that share many of the personnel and goals of the LTER project. Accordingly, the LTER serves as the framework and long-term component of the total research; the results are those of the combined projects. Since 1987, some 95 papers, one book, and one special journal issue have been published by the LTER scientists about the Toolik Lake research (see following list). These same scientists published some 105 Toolik Lake papers and theses before 1987.

LTER Effects on Toolik Lake Research.

The coming of the LTER project has had a profound influence on the research at Toolik Lake. The element of long-term research has been added so that we now think quite differently about the questions that are possible to ask. These new questions about long-term changes have required that a data base be set up and that we be systematic in the collection of climate data. The computers and GIS purchased on the LTER technology supplementary grants have allowed us to do better modeling and begin to incorporate GIS technology into the mapping and modeling. The LTER network has meant that we now make comparative measurements of such things as litter decay across LTER sites and are able to plan comparative studies with several other LTER sites. Finally, the LTER project with the data base and whole-system manipulation experiments has made the site attractive to other projects so we now know much more about trace gas release (EPA projects) and toxic chemical accumulations (EPA project).

The goal of the Arctic LTER Project is:

To understand how tundra, streams and lakes function in the Arctic and to predict how they respond to human-induced changes including climate change.

To reach this objective the project will:

(1) Determine year-to-year ecological variability in these systems and measure long-term changes.
(2) Understand the extent of control by resources (bottom-up control) or by grazing and predation (top-down control).
(3) Measure rates and understand the controls of the exchange of nutrients between land and water.

Long-term Research, Long-Term Experiments.

In the pre-LTER research (1975-87) we made measurements of environmental variables such as summer climate and streamflow. There are data gaps in the years, e.g., 1983, when we were not funded. Now that the long-term funding is more secure, we have begun climate monitoring year-round and are taking steps to ensure better hydrology measurements. To ensure that the data are archived and available, we have set up a data management system and data base. The various sets being entered are given in table form in the section of the proposal titled "Long-term data sets in the Arctic LTER database". They include river data on discharge, nutrients, pH, alkalinity, temperature, conductivity, sestonic and epilithic chlorophyll, insects, and fish. Data on lakes includes oxygen, temperature, conductivity, pH, light, nutrients, chlorophyll, primary production, zooplankton, insects, and fish growth. Terrestrial data include flowering data along the haul road transect, nitrogen mineralization, plant biomass and production, and chemistry of rain water. Weather station data at several sites includes air temperature, wind, relative humidity, precipitation, PAR, soil temperature, and barometric pressure.

Before LTER we carried out experiments that mostly lasted one field season. Now we have long-term manipulation experiments that better reflect the long life spans of some of the keystone species such as lake trout and grayling (which live 50 and 15 years, respectively), chironomids (can live 7 years), and tundra sedges and shrubs. On the Kuparuk River we alter nutrients (begun in 1983), and fish density (started in 1985), on the Oksrukuyik River we do the same experiments and also will remove all of the black flies (base-line studies begun in 1990). Lake manipulations include measurements of lake recovery from 5 years of fertilization (begun in 1990), measurements of ecosystem response to slow (begun in 1975 and 1989) and rapid removal (begun in 1988) of the top predator, the lake trout, measurements of changes due to the introduction of lake trout (begun in 1988) and sculpin (began in 1991), and measurements of long-term response of the food web to eutrophication. Terrestrial manipulation experiments include response to an NP fertilization (started in 1980), response to greenhouse-caused warming, shade, and fertilizer (started in 1980 and 1988), and a herbivore exclosure experiment (began in 1989).

Research Highlights.

Terrestrial studies. The observations and experiments with the dominant sedge of the area, Eriophorum vaginatum, show that growth and flowering vary uniformly from year to year over most of northern Alaska, but these annual fluctuations are not clearly correlated with annual variation in any climatic variable. Our fertilizer experiments have revealed that it takes about 2 years for a growth response, and 3 years for a flowering response to develop after fertilizer addition. The probable reason for this slow response is the time it takes to develop and differentiate new vegetative and flowering meristems. The slow response is also the key to understanding the natural changes in growth and flowering for large changes should require two or more consecutive years of above- or below-average climatic conditions. The effects of smaller climatic changes from year to year may cancel each other out by this buffering process and produce no change in the plant growth and flowering.

Through the manipulations of temperature, light, and nutrients, we have found that direct effect of air temperature change on plants is slight even after 9 years of treatment. Added nutrients do elicit a large response, not surprising in this strongly nutrient-limited environment, with the tussock tundra initially dominated by sedges becoming dominated by deciduous shrubs (birch). There will likely be long-term response of the vegetation to climate warming which, at first, will be caused by a thicker layer of soil available to the roots as the permafrost melts slightly, and later by increased mineralization and availability of nutrients in the warmer soils. In laboratory tests of soil processes, we found that arctic soils had relatively high respiration rates compared with temperate soils; these rates did not change very much from 3° to 9°C but did show a rapid rise from 9° to 15° indicating both adaptation of the soil microbes to faster rates at low temperatures and a threshold above 9°. If soil temperatures were to rise above 9° during climatic warming, a rapid oxidation of the organic matter in these soils would ensue.

Lake studies. Some 16 years of data on primary productivity and its control show that the lakes are strongly limited by phosphorus availability. In fact, the overall level of algal biomass (chlorophyll) in the lakes can be predicted from the phosphorus inflow. Year-to-year variations in primary productivity correlate quite well with river flow but the exact mechanisms of this effect have not yet been sorted out.

We were able to carry out whole-system experiments on the mechanisms of nutrient cycling by dividing a 7 m deep lake with a curtain and treating half of the lake with nutrients. There was an immediate response of phytoplankton biomass, primary production, and snail numbers and growth to the added nutrients. But the zooplankton, fish, and most benthic organisms responded either after a 1 or 2 year lag or not at all. One reason for the lag was that much of the phosphorus added to the lake was tightly bound to the iron-rich sediments and was not recycled to overlying waters. This phenomena of strong nutrient binding in sediments should allow for a rapid recovery from lake eutrophication caused by the added nutrients.

One of the most interesting changes we have found is the long-term decrease to virtual extinction of two large-bodied species of zooplankton in Toolik Lake from 1975 to 1990. The abundance of Daphnia middendorffiana has decreased by a factor of 50 and Holopedium gibberum by a factor of 200. The cause seems to be the increased human fishing of lake trout. Between 1977 and 1986 the average lake trout size declined from 578 to 318 g. The decrease in the large lake trout allowed the zooplanktivorous grayling to increase in the open water of the lake with a resulting decline in the large-bodied forms of zooplankton.

To investigate the higher trophic levels and their controls on populations below them we have been both monitoring and experimentally manipulating a series of lakes. We obtained one unexpected result when we removed lake trout from a lake. The expectation was that sculpin, a common prey of lake trout, would move out from the rocky shallows and into the soft sediment areas where there was more food. Instead, sculpin became even more restricted in their distribution and even fewer were trapped away from the rocky shallows. The explanation was that the removal of the lake trout allowed another large and rare predator, the burbot, to move from deep in the lake to the nearshore zones. Apparently the control of sculpin by burbot predation is even stronger than was the control of sculpin by lake trout.

Stream studies. There are large year-to-year variations in the flow of water in the Kuparuk River. Over the last 8 years the mean summer discharge has varied from a low of 0.3 to a high of 3.8 m^{-3} sec^{-1}. These differences have been accompanied by equally large differences in primary production, insect abundance, and grayling growth but the causes of these changes are not completely known. We do know that primary production of eiplithic algae can be set back by the scrubbing of rocks that takes place during high discharge events, while black flies do well during high flow years because allochthonous organic matter fluxes are high. The low flow summers appear to be much better for larval grayling growth while adult grayling grow faster during high-flow summers.

The productivity of the river food chain from algae to grayling is closely tied to the supply of external nutrients. When phosphorus is added, epilithic algae grow much faster and provide food to the grazer insects as well as to filter feeders down stream when algal clumps slough off the rocks. Insects grow better and can exert top-down control on the algae but this took several years for enough grazer mass to develop. However, the productivity of the dominant insect, the black fly Prosimulium, decreased when nutrients were added. The explanation is that the caddis fly Brachycentrus increases when nutrients are abundant and competitively interacts with the black flies.

Land-water Interaction Studies. The pCO_2 in soil water, in streams, and in lakes is supersaturated. It appears that this excess CO_2 comes from decomposition in soils and moves via groundwater to the streams and lakes. We estimate that the release in this pathway is 20-50% of the estimates of tundra net primary productivity. This excess CO_2 was not accounted for in previous studies of tundra productivity.

We have begun developing a heirarchical GIS for the Toolik and Kuparuk River watersheds that will be used in scaling up our knowledge of tundra, lakes, and streams to an integrated model of land-water interactions at the level of whole, heterogeneous watersheds. Working with D. and M. Walker (Niwot Ridge LTER) the first steps involved production of a series of maps of soils, vegetation, geology, and topography at various scales.

Synthesis and Modeling Highlights.

Site data from the Arctic and Harvard Forest LTERs were used in the General Ecosystem Model developed by scientists from the Arctic LTER and Harvard Forest LTER. This model is an aggregated biogeochemical model of plant and soil processes, particularly of nitrogen and carbon fluxes and allocations. The model was first calibrated to simulate present stocks and turnovers of carbon and nitrogen at these two LTER sites. We then ran simulations to examine response over 50 years to a doubling of atmospheric CO_2, a 5^o C temperature rise, and an increase in N deposition. These two ecosystems have tremendous differences in the amount of wood in the system and in the distribution of carbon and nitrogen in the vegetation and in the soil. In terms of grams of organic carbon per square meter, the tundra contains 500 in the plant matter and 21,600 in soil organic matter while the temperate forest contains 9,000 in the plants and 8,000 in soil organic matter. Despite these basic differences, the two ecosystems have qualitatively similar responses. Both responded very little to increased CO_2 concentrations because of severe nitrogen limitation. Both responded to the combination of the increased temperature and increased CO_2 concentrations by increasing the carbon in the plants by about 1.5 times. The temperature effect is the result of the increased availability of soil nitrogen caused by increased microbial decomposition. The overall similarities in the response of thee two ecosystems are probably associated with the large stocks of soil organic matter in both, and the slow turnover of these stocks.

Relationship of Past Research to Proposed Research.

After 17 years of research and some 200 publications, we are now at the point where we feel we understand reasonably well the controls on structure, function, and rates of major processes in these ecosystems.

Over the next six years we plan to build on this understanding in three specific ways. First, by continuing and expanding our monitoring and survey program we expect to identify long-term trends and relationships.

Second, by continuing and expanding our whole-ecosystem manipulations we expect to identify long-term responses of processes and populations to human and climatic impacts, and feedbacks controlling those responses. Third, we are now at the point in our understanding where we are ready to carry out experiments and research to identify interactions between terrestrial, lake, and stream components of the landscape. This is an essential step toward our long-term goal of scaling up our understanding to the whole watershed and regional levels.

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Updated Jan. 22, 1992

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THE ARCTIC LTER PROJECT:

TERRESTRIAL AND FRESHWATER RESEARCH ON ECOLOGICAL CONTROLS

I. INTRODUCTION

A. Overview. Aquatic and terrestrial ecologists began work near Toolik Lake, a foothill site in the Alaskan Arctic, in 1975. In 1987, the Arctic LTER project was funded. After 17 years of research, we have documented the basic ecology of lakes, a river, and the tundra vegetation near Toolik Lake in nearly 200 published papers including several syntheses and reviews. We are now at the point where we feel we understand reasonably well the controls on structure, function, and rates of major processes in these ecosystems.

Over the next six years (1992-1998) we plan to build on this understanding in three specific ways. First, by continuing and expanding our monitoring and survey program we expect to identify long-term trends and relationships. Second, by continuing and expanding our whole-ecosystem manipulations we expect to identify long-term responses of processes and populations to human and climatic impacts, and to identify feedbacks controlling those responses. Third, we are now at the point in our understanding where we are ready to carry out experiments and research to identify interactions between terrestrial, lake, and stream components of the landscape. This is an essential step toward our long-term goal of scaling up our understanding of arctic ecosystems to the whole watershed and regional levels.

The broad goal of the Arctic LTER project is to understand and predict how arctic ecosystems function and how they respond to change. Three specific goals are:

(1) to determine year-to-year and long-term ecological variability and their correlations with environment,

(2) to understand the extent of control over ecosystem structure and function by resources (bottom-up control) versus control by grazing and predation (top-down control), and

(3) to measure rates and understand controls of the exchange of nutrients and organic matter between terrestrial and aquatic components of the landscape.

For management as well as scientific purposes the research is divided into lakes, streams, and terrestrial components. Each component includes research on each of the three specific goals.

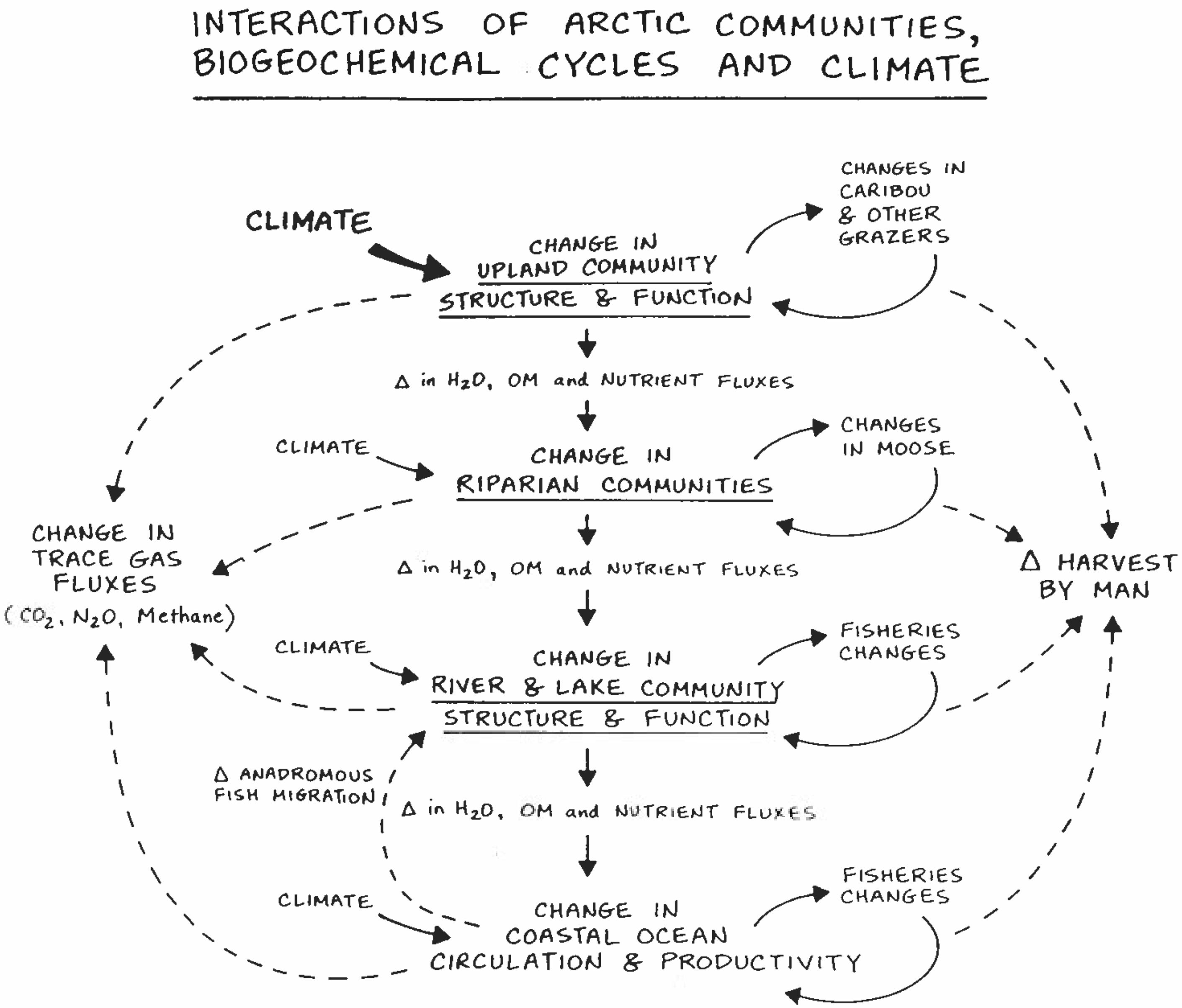


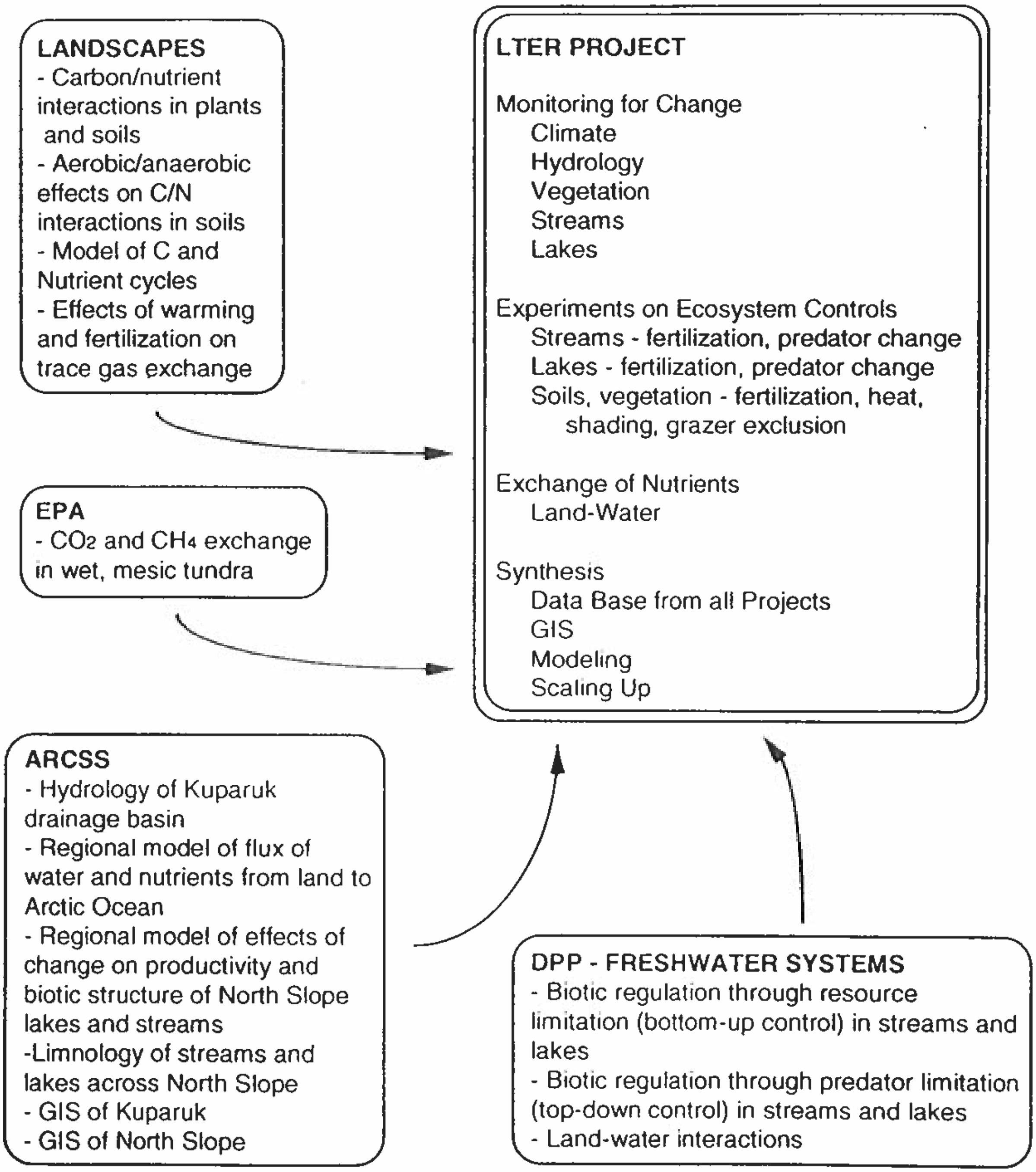
Fig. 1. Diagram of the interactions of arctic communities, their biogeochemical cycles, and climate. The diagram shows how terrestrial, riparian, stream, and lake communities are linked through the transport of water, nutrients, and organic matter between them, through their impacts on atmospheric trace gases, and through their relationships with human populations.

The first specific goal requires measurement of year-to-year variability and long-term changes. In lakes this includes measurements of temperature, chlorophyll, and primary productivity; in streams this includes nutrients, chlorophyll, insects and fish; and on the tundra this includes flowering, air temperature, solar radiation, and biomass. **The second goal (really the heart of the Arctic LTER program) requires study of factors controlling ecosystem structure and function.** We do this through measurement of response to disturbance in long-term experimental manipulations of tundra, lake, and stream ecosystems. The disturbances include fertilization of lakes and streams, addition and removal of lake trout from lakes, and shading, fertilizing, and heating of the tussock tundra. **The third goal requires measurements of soil-nutrient, water-nutrient, and land-water interactions.** The measurements are made in plots on the tundra, in streams and lakes, and in the watershed of a small, first-order stream. This work also requires development of a watershed model that will be interactive with geographically referenced data bases so the model and process information may be extrapolated to the larger region.

Over the next six years (1992-1998), we plan to continue with the same overall goals and management structure. The major new feature of the research is an emphasis on land-water interactions and the linkages between terrestrial, riparian, lake, and stream components of the arctic landscape (Fig. 1). To do this we particularly need to strengthen our research on the basic hydrology of our field sites, and to beef up our efforts to build a detailed, spatially heirarchical Geographic Information System (GIS) for the site. We also need to increase our modeling efforts, especially related to "scaling up" from small plots, sections of streams, or single lakes to larger watersheds. These needs were also identified by the site review team that visited Toolik Lake in the summer of 1991. One particular concern of the site review team, that soils processes and the role of terrestrial herbivores were not receiving adequate attention, will be addressed through a new, separately-funded project (NSF-BSR #9019055). Another concern, that we were not doing enough sampling outside the summer months, will be addressed in the next six years by expanding our sampling schedule into the spring thaw and fall freeze periods.

B. Cooperative research The goals, objectives, personnel and experimental sites of the Arctic LTER project overlap extensively with those of several other projects working cooperatively at Toolik Lake (Fig. 2). The

Toolik Lake Research Activities



LANDSCAPES
- Carbon/nutrient interactions in plants and soils
- Aerobic/anaerobic effects on C/N interactions in soils
- Model of C and Nutrient cycles
- Effects of warming and fertilization on trace gas exchange

EPA
- CO_2 and CH_4 exchange in wet, mesic tundra

ARCSS
- Hydrology of Kuparuk drainage basin
- Regional model of flux of water and nutrients from land to Arctic Ocean
- Regional model of effects of change on productivity and biotic structure of North Slope lakes and streams
- Limnology of streams and lakes across North Slope
- GIS of Kuparuk
- GIS of North Slope

LTER PROJECT

Monitoring for Change
  Climate
  Hydrology
  Vegetation
  Streams
  Lakes

Experiments on Ecosystem Controls
  Streams - fertilization, predator change
  Lakes - fertilization, predator change
  Soils, vegetation - fertilization, heat, shading, grazer exclusion

Exchange of Nutrients
  Land-Water

Synthesis
  Data Base from all Projects
  GIS
  Modeling
  Scaling Up

DPP - FRESHWATER SYSTEMS
- Biotic regulation through resource limitation (bottom-up control) in streams and lakes
- Biotic regulation through predator limitation (top-down control) in streams and lakes
- Land-water interactions

Fig. 2. Diagram showing the major cooperative research projects based at Toolik Lake and the specific activities associated with each project. The Arctic LTER project provides a management framework, maintains the field experiments and monitoring, supports the data base and core synthesis and modeling activities, and holds an annual workshop.

Arctic LTER Project provides a management framework and supports the collection of data to study long-term changes, the setup and maintenance of ecosystem-level experiments, synthethic activities such as a data base, GIS and modeling, and an annual workshop in Woods Hole. The Freshwater Systems project (NSF-DPP#9024188) supports research on the ecology of streams, lakes, and the exchanges between land and water. The Carbon Balance of Ecosystems or Landscapes project (NSF-BSR#9019055) supports research on carbon cycling in terrestrial ecosystems, and there is additional EPA support for research on trace gas emissions at Toolik Lake. In 1992, we also plan to apply to the NSF-DPP Arctic System Science (ARCSS) Program for funding to expand our watershed-level research and its extrapolation to regional and global biogeochemistry.

This tight linkage between related projects was strongly endorsed in the summary comments of the 1991 LTER site review team, with one reviewer saying, "In many respects this project is a model for what other LTER projects can be. The project serves as a core from which other research takes off - with funding from NSF and other sources." One major advantage of such linkage is the efficiency that results from sharing sites, personnel, and other resources. A second advantage is the intellectual "leverage" obtained when all data are collected from identical sites and experimental treatments. All together, funding for this group of projects will total $1.7 million in 1992. This includes shared support for 8 whole-lake and divided-lake experiments, 3 major stream experiments, and greenhouse, fertilizer, and shade experiments in 4 different tundra types. About 30-40 personnel are supported in the field each summer, including 16 principal investigators from 8 different institutions.

C. Why an Arctic Alaska Long-Term Ecological Program? There are three reasons: First, basic science -- the Arctic 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, and some questions and experiments need 5-10 years. Long-term studies are especially important 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 global warming may first manifest itself in the Arctic, so a long-term data base and appropriate experiments are needed. Third, efficiency and effectiveness -- ongoing projects provide a 16-year data base, experienced investigators, and already operative sites and experiments.

All fundamental ecosystem processes occur in the Arctic, yet these are relatively simple systems where the unraveling of the interactions of cycles and populations is often straightforward. For example, in streams there is little litter input and most of the particulate carbon comes from eroding 1000-year-old tundra peat. Here the ecosystem biota is microbes, four dominant species of insects and one species of fish. On land, light, temperature, and nutrients control the growth form, productivity, and biomass of the vegetation. Effects of these factors and their interactions can be sorted out by whole-system experimental manipulations because of the low stature of the vegetation and its relatively low species diversity. A greenhouse or shade experiment needs only a 1 m high structure -- simple, cheap, and effective.

Comparative studies within the LTER site network are also enhanced by an arctic site. The data from the arctic site fall at the extremes of most comparisons of ecosystem properties (e.g., primary productivity of lakes, decomposition rates in soils, species richness of communities).

Another basic research need arises from a global perspective on the Arctic. Global models require information on input and cycling of elements in all types of ecosystems including the Arctic. Current models also predict that the greenhouse warming will be greatest at high latitudes so long-term data sets are needed to assay ecosystem responses such as trace gas emissions from the soils. Arctic ecosystems will be the first to experience large climatic changes and adequate baseline data are urgently needed. Early studies here may be our best hope for predicting ecosystem responses elsewhere.

There is an immediate need for applications of science in northern Alaska. The only road to northern Alaska was opened to the public in 1991 and questions are being asked about effects of fishing and hunting pressure on as-yet undisturbed populations and ecosystems. Impact of wastes and construction activity on tundra and streams is also a major concern, and 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. 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 the kind of long-term measurements and large-scale experimental manipulations provided by the Arctic LTER program. Long-term experiments are already set up and have been running for several years, experienced investigators from a number of institutions are available, and we have an excellent field camp, allowing state-of-the-art research to be carried out.

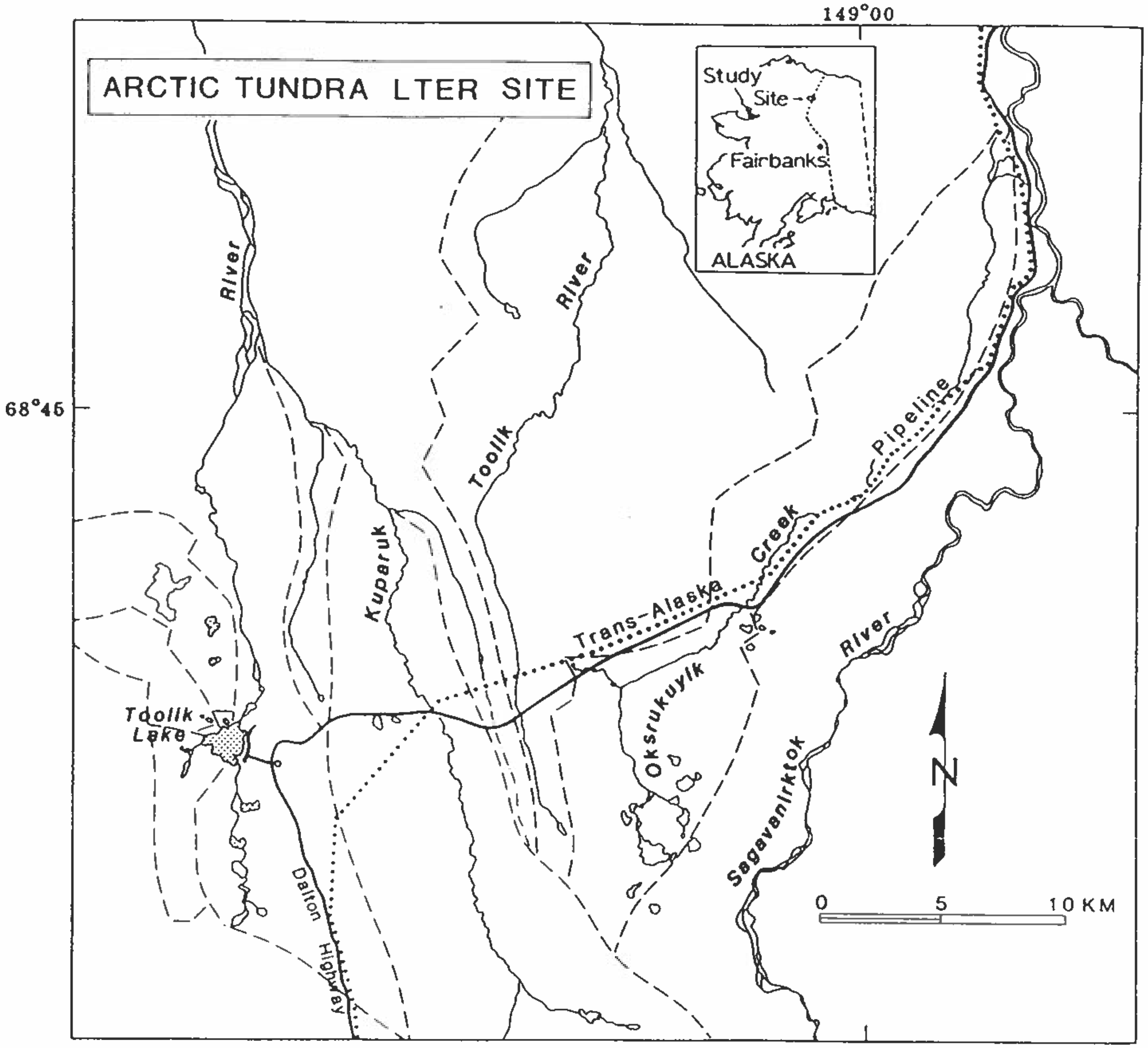


Fig. 3. Location of Arctic LTER research site at Toolik Lake, Alaska, showing the Toolik Lake, upper Kuparuk River, Toolik River, and Oksrukuyik Creek watersheds (outlined in dashes) and their locations along the Dalton Highway.

II. SITE LOCATION AND DESCRIPTION

The Arctic LTER research site is on the North Slope of Alaska and includes the entire Toolik Lake watershed and the adjacent watershed of the upper Kuparuk River, down to the confluence of these two watersheds (Fig. 3 and Frontispiece). This area is typical of the northern foothills of the Brooks Range, with continuous permafrost, no 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. 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). Between 1947 and 1977, most of the scientific research there took place on the Coastal Plain near Pt. Barrow (Brown et al. 1980, Hobbie 1980). After 1975 the Dalton Highway provided access to an 800 km transect from Fairbanks north to the Arctic Ocean and interest shifted to sites along the highway, including the foothills area around Toolik Lake.

The Toolik Lake Research Station (owned and managed by the University of Alaska) is located 16 km north of the Brooks Range in rolling foothills (68°38'N and 149°38'W, elevation 740 m). By road, the station is 210 km south of the airport at Prudhoe Bay and 570 km north of Fairbanks. Eleven km northeast of Toolik Lake the road crosses the Kuparuk River (the primary stream study site), and 22 km beyond that the road meets the Sagavanirktok (Sag) River, where another terrestrial research site is located and a second stream, Oksrukuyik Creek, is under study (Fig. 3).

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 averages -10°C and the total precipitation is 200-250 mm (Selkregg 1977). Despite the dry climate, the permafrost prevents deep water drainage, cold temperatures lower the evapotranspiration, and the soils are usually moist to soggy. The vegetation is a mosaic of types ranging from evergreen heaths on drier sites, to wet sedge tundra in flat lowlands, to riparian deciduous shrubs (Chapin and Shaver 1985a, Shaver et al. 1990, Giblin et al. 1991). The most abundant vegetation type is cottongrass-tussock tundra. Vegetation composition on any site depends upon time since glaciation, soil type, exposure, drainage, and topography (Walker et al. 1989).

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 18°C, and is ice-free from July through September. Lake trout and arctic grayling are the dominant fish, Heterocope, Daphnia, and Bosmina the zooplankton, and chironomids and snails the benthos (Hershey 1985b). In the surrounding moraines 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. Research so far has been concentrated on the upper 25 km of the River (Peterson et al. 1986 and submitted). 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, mayflies, chironomids, and a caddisfly. There is but one fish, the arctic grayling; the entire grayling population migrates to a lake in the headwaters each winter.

III. RESEARCH ACCOMPLISHED THUS FAR

Due to constraints on proposal format and length, we simply cannot discuss in detail the rich background of prior research on arctic ecosystems, or the general intellectual background for our interests in top-down versus bottom-up controls of ecosystems. Thus we confine our discussion here to research done by current LTER researchers working at and near Toolik Lake since 1975. In addition to our work, for several years another large, integrated ecosystem research program was also based at Toolik Lake, the DOE-funded "R4D" program. Research done by the "R4D" group was first summarized in a special issue of Holarctic Ecology (Oechel 1989), and a synthesis volume is now in press (Reynolds and Tenhunen in press).

Prior research on terrestrial ecosystems in the Arctic has been reviewed and summarized in several books and monographs over the past 25 years, including those by Billings and Mooney (1968), Bliss (1971, 1977), Wielgolaski et al. (1975a, 1975b), Brown et al. (1980), Bliss et al. (1981), Chapin and Shaver (1985), Chapin et al. (1991), and Shaver (in press). The role of animals in arctic terrestrial ecosystems (top-down controls) is reviewed in Jefferies et al. (1991), while resource controls (bottom-up) are a major theme of the book edited by Reynolds and Tenhunen (in press).

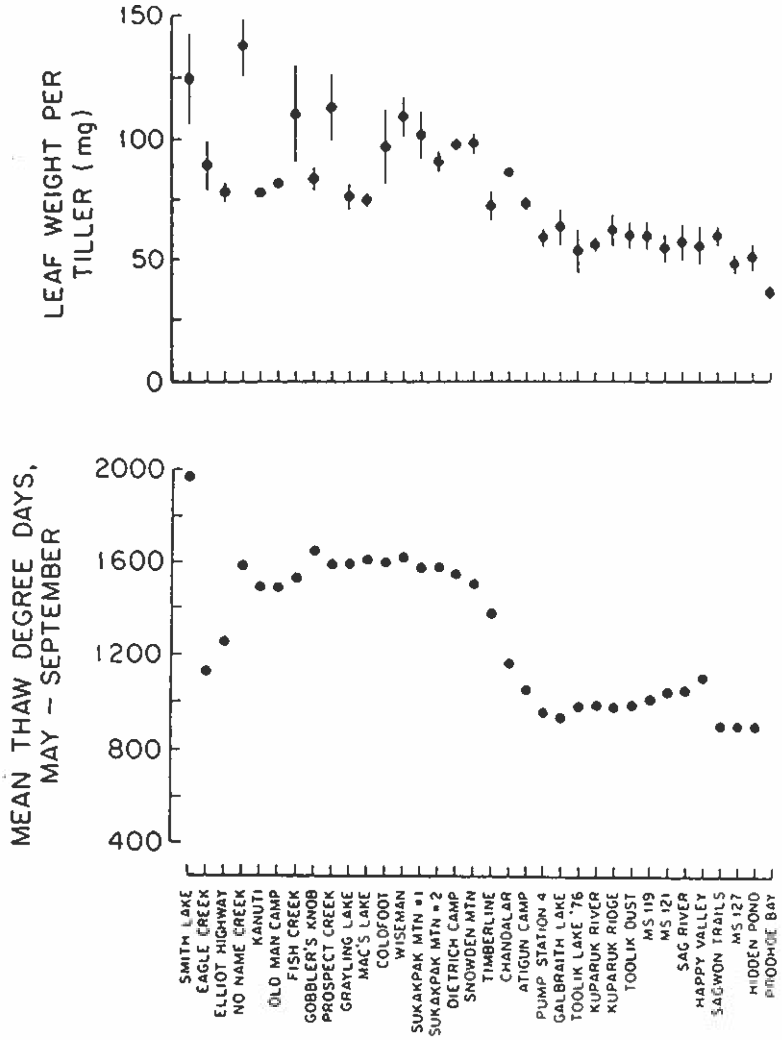


Fig. 4. TOP: Long-term mean (1980-1983) leaf weight per tiller of Eriophorum vaginatum along a latitudinal transect running from Fairbanks (= Smith Lake, in the University of Alaska arboretum) to Prudhoe Bay. BOTTOM: Estimated long-term average number of thawing degree-days between May and September along transect. Although leaf weight per tiller is correlated with degree-days, the correlation is due mainly to ecotypic variation in tiller size, and only secondarily to direct effects of current-year's climate on current-year's leaf growth (Shaver et al. 1986a).

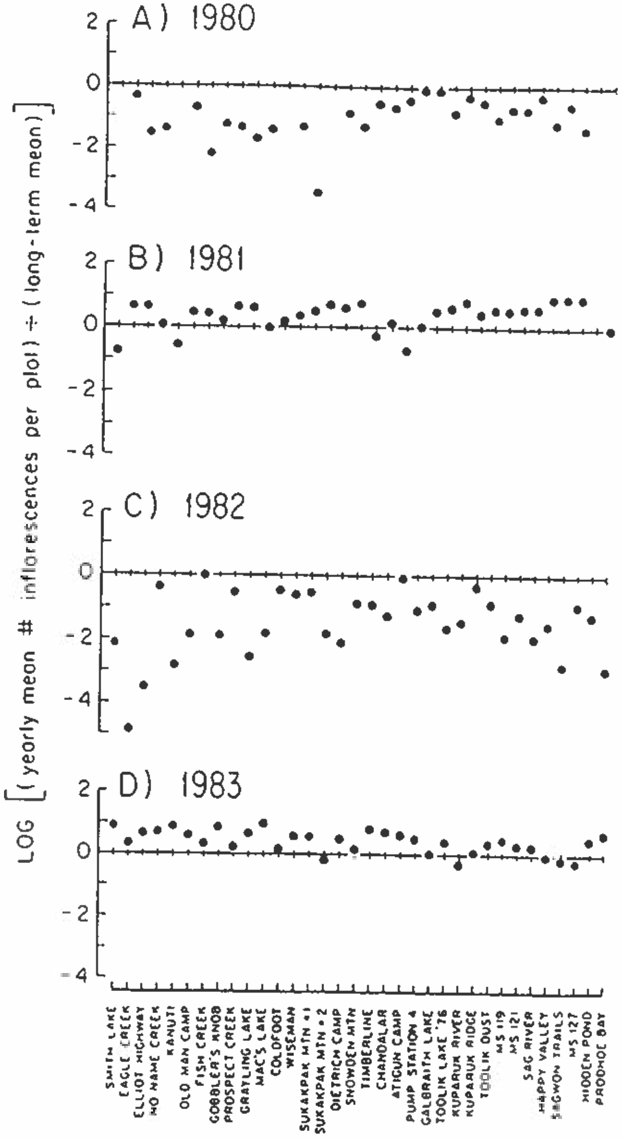


Fig. 5. Yearly mean inflorescence density relative to the long-term mean for Eriophorum vaginatum at 34 sites between Fairbanks (= Smith Lake) and Prudhoe Bay, 1980-1983. The years 1980 and 1982 were poor flowering years almost everywhere along the transect, while 1981 and 1983 were consistently high flowering years. (Shaver et al. 1986a)

Research on aquatic ecosystems has been summarized by Hobbie (1973, 1980). Up-to-date reviews are now in press (Hobbie et al. in press, O'Brien et al. in press) or submitted (Hershey et al. submitted, Peterson et al. submitted). Because these new reviews are not yet widely available, the general background of research on top-down/bottom-up controls in aquatic ecosystems is reviewed in Appendix I of this proposal.

A. LTER GOAL I: ECOLOGICAL VARIABILITY AND LONG-TERM CHANGES

Terrestrial research

Can we detect long-term changes in the Arctic climate? Are terrestrial ecosystems changing in response? This question is addressed through long-term monitoring and through manipulation of both climate (with small greenhouses and shade frames) and nutrient availability (with fertilizers). For example, growth and flowering of Eriophorum vaginatum, one of the most common and often dominant arctic plants, has been monitored at 34 sites along the climatic gradient between Fairbanks and Prudhoe Bay since 1976 (Shaver et al. 1986). At 14 sites factorial fertilizer experiments have also been established (Shaver and Chapin 1986), and at 6 sites reciprocal transplant gardens were set up (Fetcher and Shaver 1990).

The combination of these approaches has allowed us to distinguish the effects of annual variation in climate from broad regional differences in climate at two time scales: in the long-term, we have shown that ecotypic differences between populations account for much of the variation in plant size and growth rate that we observe in the field, and that this variation is correlated with long-term average growing-season temperatures (Fig. 4). In the short-term, we have shown that growth and especially flowering vary uniformly from year to year over most of Alaska, but these annual fluctuations are not clearly correlated with annual variation in any climatic variable (Fig. 5). Our results have led us to the conclusion that short-term plant responses to climate must be strongly "buffered", or constrained, by other limiting factors such as nutrient availability, and that longer-term responses are constrained genetically (Shaver et al. 1986). Detection and explanation of multi-year trends in plant growth in relation to climate, then, requires linking climatic changes to changes in soil nutrient cycling processes and nutrient availability (Shaver and Kummerow 1991). By now, our record of observations at some sites is long enough that effects of long-term, cyclic events such as El Nino-Southern oscillation phenomena should soon become evident.

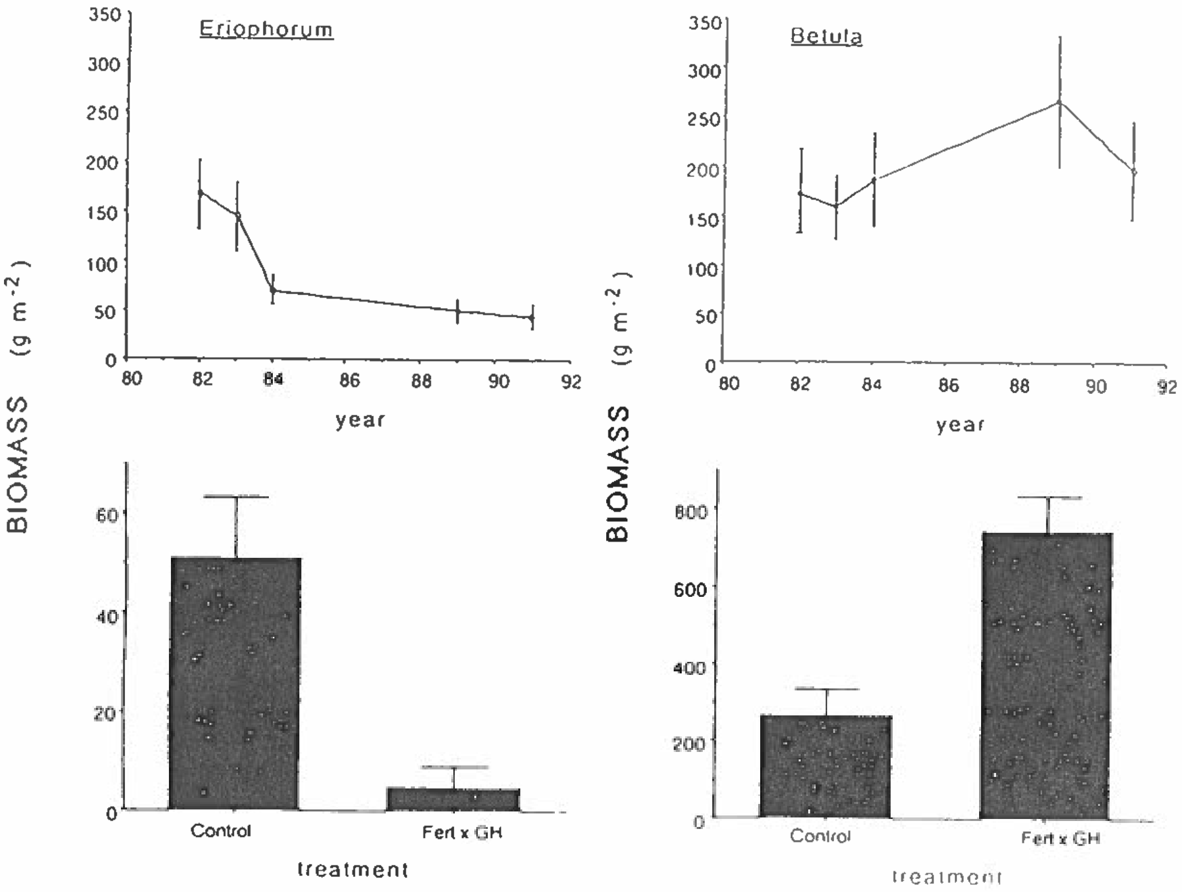


Fig. 6. TOP: Aboveground biomass of *Eriophorum vaginatum* and *Betula nana* in control plots of tussock tundra at Toolik Lake, 1982-1981. BOTTOM: Aboveground biomass of *Eriophorum* and *Betula* in control plots in 1989 and in plots recieving greenhouse plus fertilizer treatment from 1981 to 1989. (Chapin and Shaver in prep.)

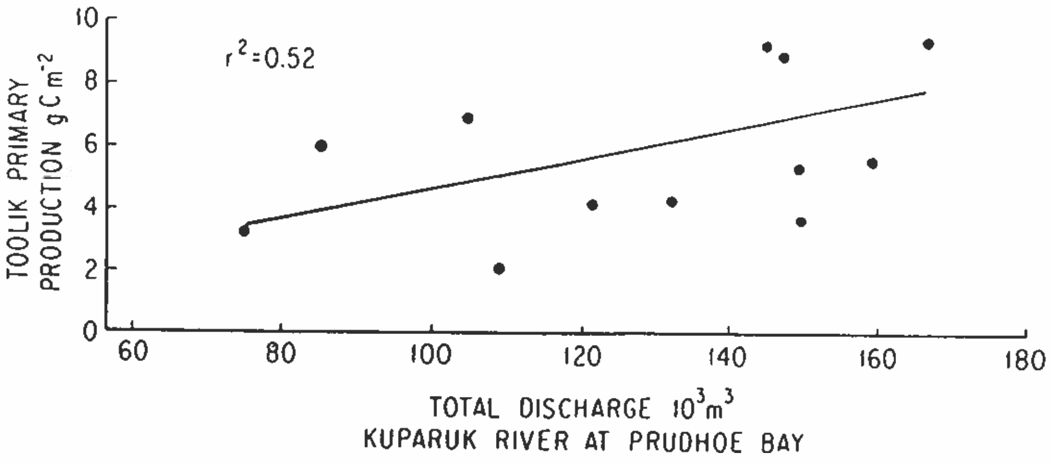


Fig. 7. Productivity of Toolik Lake is correlated with river flow. In this figure, primary productivity (summer) from 1975 to 1988 is plotted against the discharge of the Kuparuk River at Prudhoe Bay.

The consistent importance of nutrient limitation in determining both annual variation in productivity and long-term biomass accumulation of tundra plants has been shown clearly in our factorial fertilizer experiments (Shaver and Chapin 1980, 1986, Shaver et al. 1986). All tundra sites respond significantly to fertilizer addition, including both wet sedge tundra and moist tussock tundra. Intriguingly, however, the specific elements that caused the responses were different in each site, and the responses of wet sedge tundras were not consistently different from the responses of moist tussock tundras -- in both vegetation types, some sites are N-limited and some are P-limited (Shaver and Chapin in prep).

Our fertilizer experiments have also helped to reveal some of the mechanisms behind the complex relationship between annual climatic variation and annual variation in plant growth and flowering. Most importantly, it appears to take about 2-3 years for a growth response and 3 years for a flowering response to fertilizer addition (Shaver and Chapin in prep). The probable reason for this slow response is that it simply takes time to develop and differentiate new meristems that can act as sinks for increased resource availability. This suggests that annual fluctuations in climate may cancel each other out, and that large changes in growth and flowering may require two or more consecutive years of above- or below-average climatic conditions.

Changes in species composition, in response to both climatic change and direct experimental manipulation, take even longer to become clear. In this regard it is fortunate that our fertilizer and greenhouse experiments over the past decade have been performed in a period of unusually warm weather, especially during the last five to eight years. During this time we have noticed a significant decrease in biomass of the dominant sedge, Eriophorum vaginatum, on control plots of tussock tundra that we have harvested five times since 1982 (Fig. 6). During this time we have also found a significant increase in biomass of Betula nana, the dominant deciduous shrub. Could this dramatic change in relative abundances be due to the series of warm summers during the late 1980's? We think the answer to this question is YES, because it mimics exactly the kind of change in species abundances that we found in the first half of the 1980's in our fertilized greenhouse plots (Fig. 6). To us, these results represent an important validation of approach to this research, combining long-term observations with long-term experiments.

Lake Studies

What are the long term trends in primary productivity of arctic lakes and how are these trends related to potential climate changes? We are currently monitoring 7 lakes for primary productivity, temperature, light

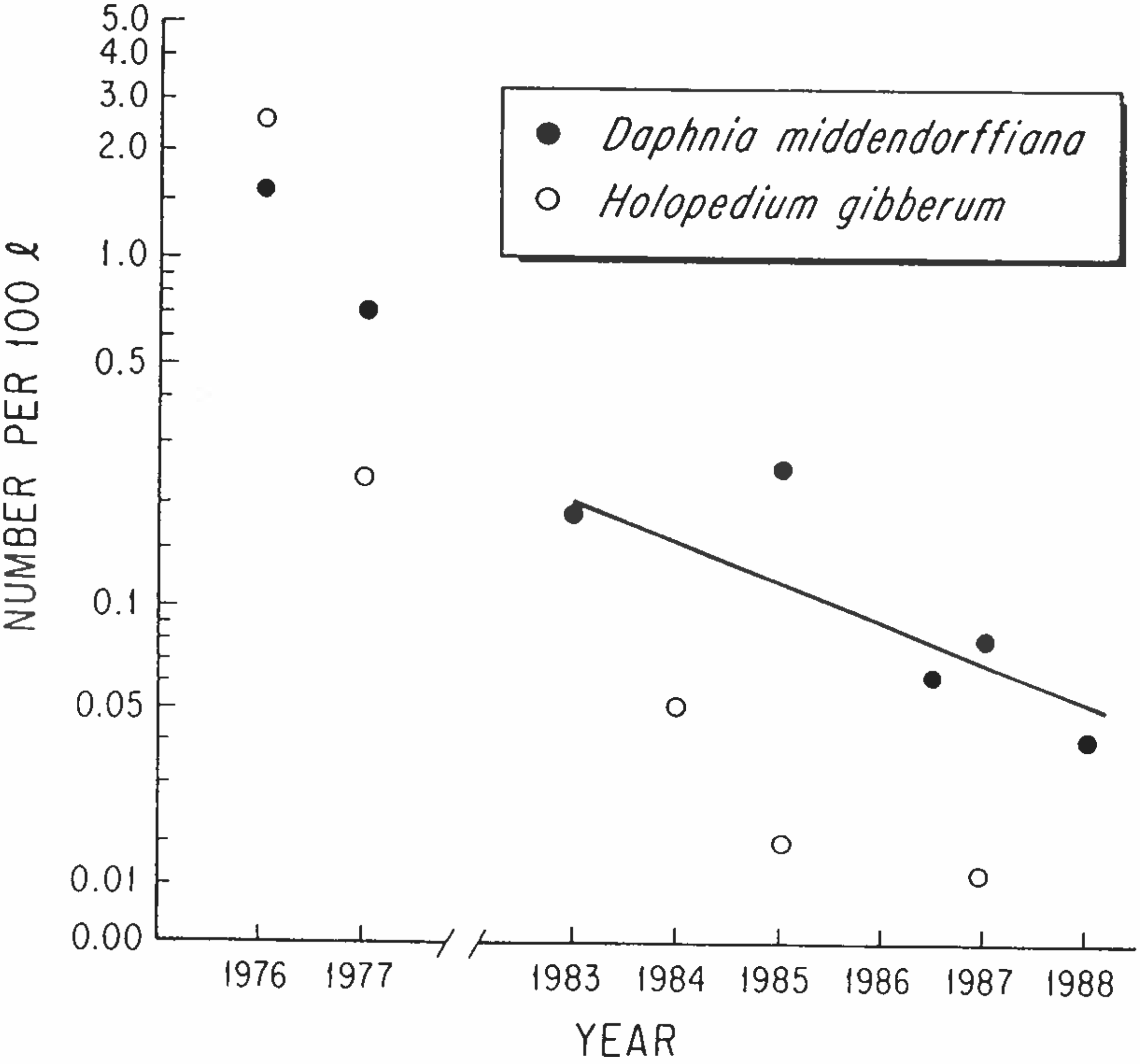


Fig. 8. Large-bodied zooplankton have declined in abundance in Toolik Lake in response to an increase in arctic grayling abundance. Data are the numbers per liter of two species of zooplankton in Toolik Lake, 1976-1988.

penetration, water chemistry, and species composition. For Toolik Lake we have a 15 year record of dissolved nutrients, temperature, algal biomass, and primary productivity (Miller et al. 1986). Our monitoring program over this time span indicates that the master variable for controlling productivity appears to be temperature. Temperature regulates weathering rates, decomposition, and the depth of thaw in terrestrial ecosystems, all of which alter the flux of nutrients through terrestrial landscapes and into lakes (Whalen and Cornwell 1985, Whalen et al. 1988). Temperature also regulates the strength and extent of thermal stratification and thus the zone of highest productivity in the lake.

Our best correlation so far is between annual primary productivity and annual water flow (Fig. 7). Under the present climatic regime, the amount of water flow controls the amount phosphorus entering the lake and it is the phosphorus quantity that limits algal primary productivity (Miller et al. 1986).

Are there long-term changes in species composition? Our longest record of changes in biota is from the zooplankton in Toolik Lake, where increased fishing pressure during the last 15 years has had dramatic effects on the size structure and composition of fish populations. The average lake trout size declined from 578 g in 1977 to 318 g in 1986, and grayling have moved away from shore into the open water because of reduced lake trout predation (McDonald and Hershey 1988). As a consequence of more zooplanktivorous grayling in the open water, large-bodied zooplankton species have declined dramatically, Heterocope septentrionalis by a factor of 2, Daphnia middendorffiana by a factor of 50, and Holopedium gibberum by a factor of 200 (Fig. 8). There is evidence that, in turn, the predatory Heterocope controls the abundance of small-bodied zooplankton (Luecke and O'Brien 1983). The smaller zooplankton in Toolik still seem to be facing severe predation pressure because Bosmina longirostis and Daphnia longiremis decrease in abundance throughout the summer whereas in other lakes in the area, which lack Heterocope, populations of these two species increase throughout the summer. Clearly we need to continue to monitor these populations in Toolik Lake.

Stream Studies

What is the variability in annual water discharge from the Kuparuk watershed and is there a discernible long-term trend in discharge possibly related to climatic change? The flow of water through the landscape affects many key biogeochemical processes that will potentially change if the hydrologic cycle is significantly altered by climatic change (Likens et al. 1977). For example, increased water flow will likely

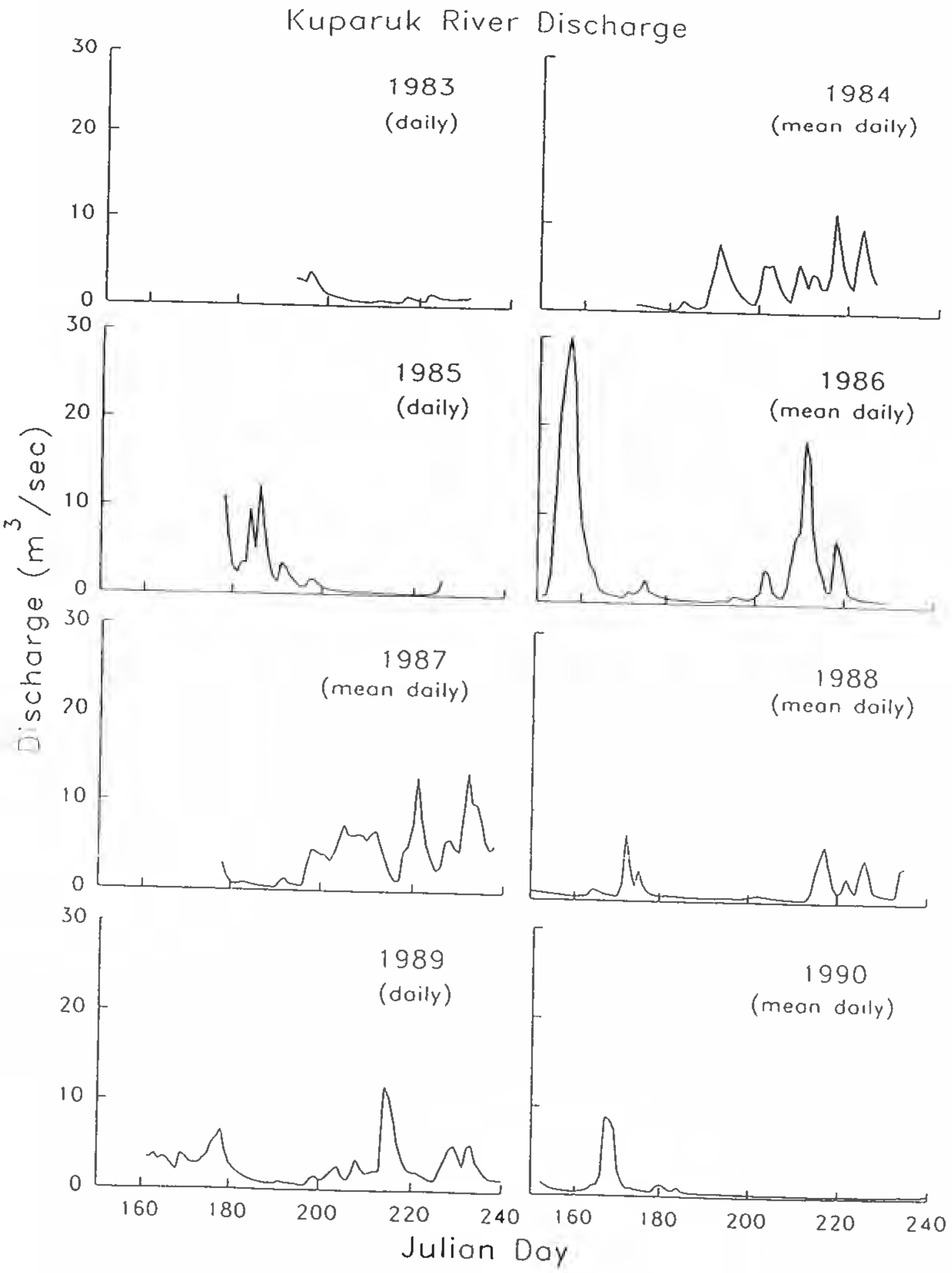


Fig. 9. River discharge is highly variable both within and between years. Data show mean daily discharge (m^3/sec) of the Kuparuk River for summers 1983-1990.

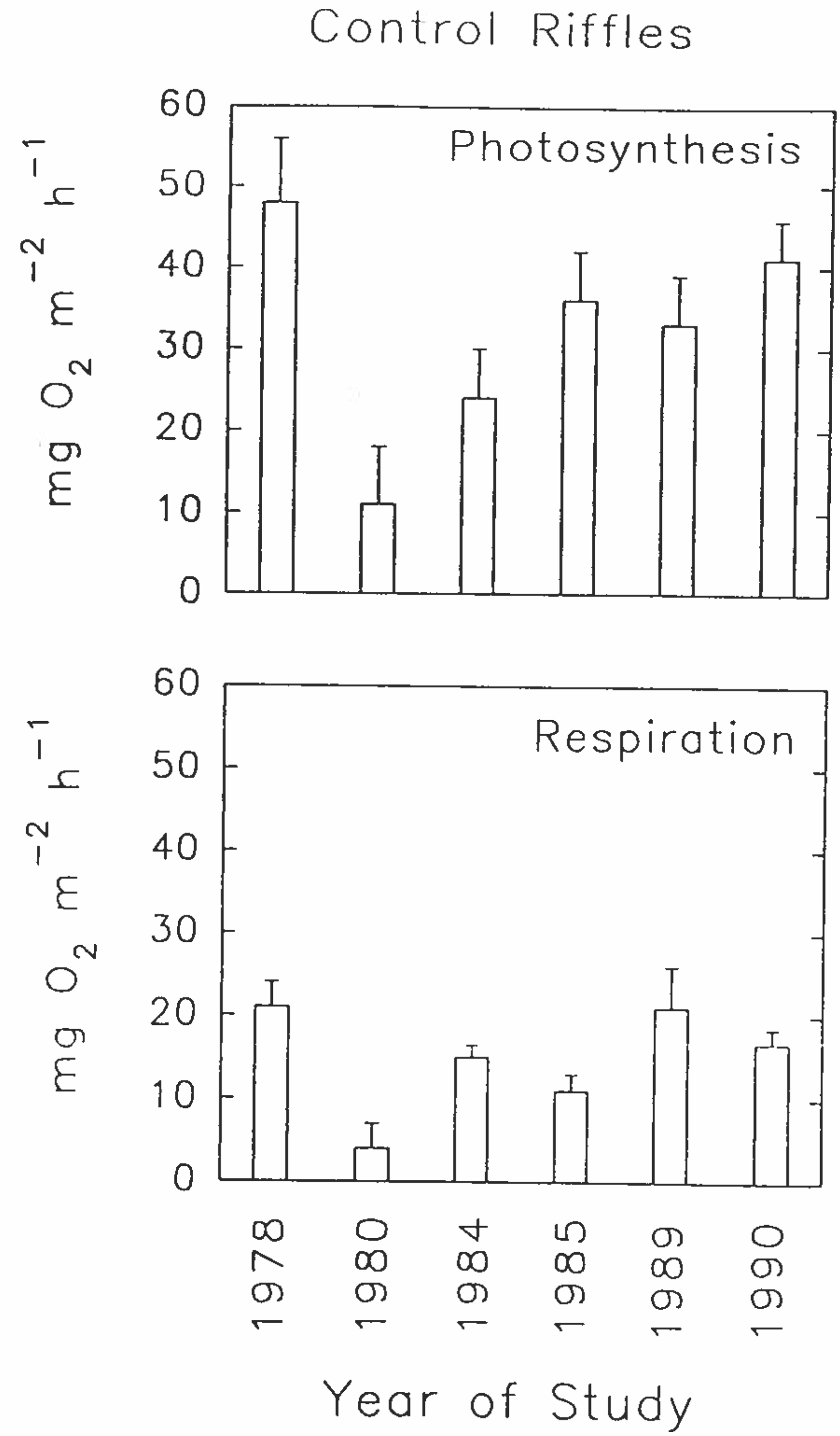


Fig. 10. Photosynthesis and respiration in the Kuparuk River. Values determined by oxygen change in enclosures of rocks from riffles in the control reach of the river.

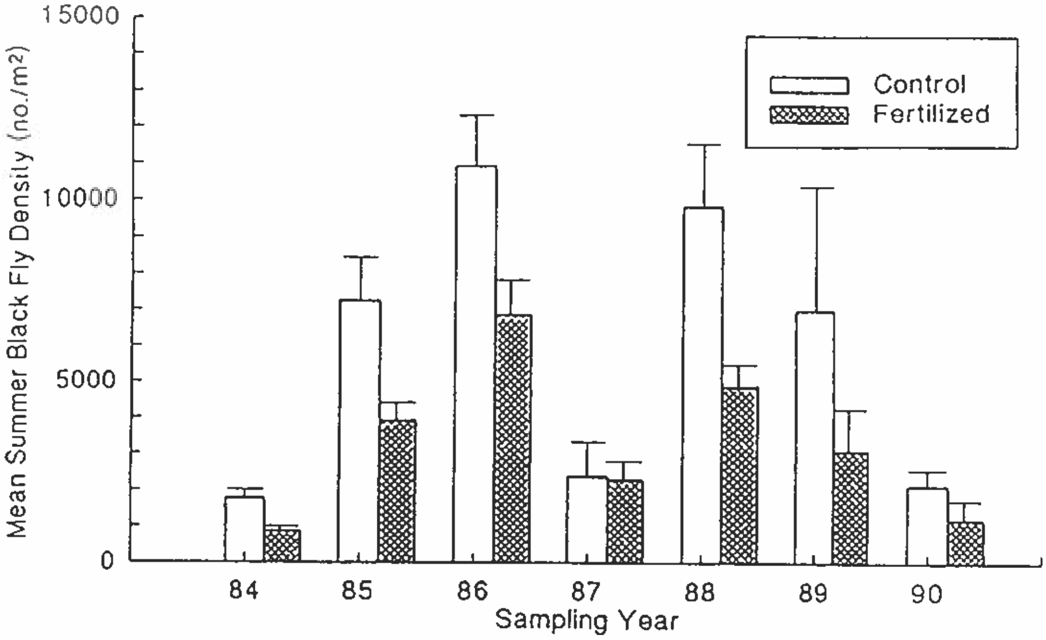


Fig. 11. Fertilization of the Kuparuk River resulted in a decline in black fly density. Data are mean density of black flies in control and fertilized reaches of the Kuparuk River for summers 1984-1990.

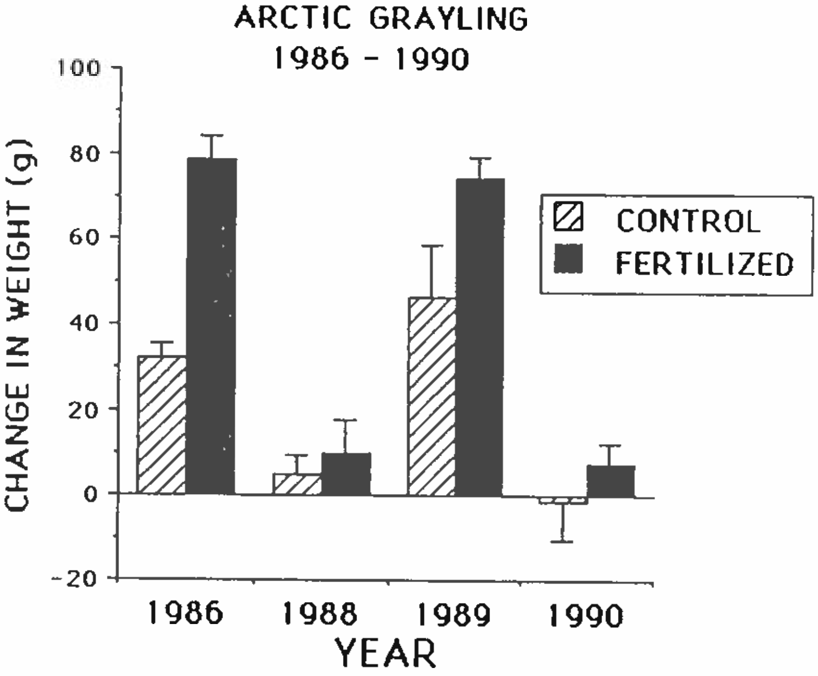


Fig. 12. Fertilization of the Kuparuk river resulted in increased growth of adult arctic grayling. Data are mean change in weight of arctic grayling in control and fertilized reaches of the Kuparuk River for summers 1986, 1988-1990.

increase weathering and leaching rates of soils in the watershed and increase the export of dissolved nutrients and organic materials from land to rivers and lakes. Higher discharge will also lead to greater streambank erosion which brings peat into the river. If climatic change results in lower discharge, the flux of materials from land to water would be decreased and the balance between autotrophic and heterotrophic processes in streams and lakes would shift. Climatic change will probably affect both the amount of water flow through arctic watersheds and the timing of these flows. We expect large changes in nutrient fluxes and in biotic activity in rivers, lakes, and estuaries to accompany such hydrologic changes.

Mean summer discharge of the upper Kuparuk River over the last 8 years has varied from a low of 0.32 m^{-3} sec^{-1} in 1990 to a high of 3.8 m^{-3} sec^{-1} in 1984 (Fig. 9). These differences have been accompanied by large differences in primary production, insect abundance and grayling growth. Primary production can be set back by removal of epilithic algae during high summer discharge events (Fig. 10), but black flies may do well during high flow years when allochthonous organic matter fluxes are high (Fig. 11). On the other hand larval fish growth is poor during high discharge summers while adult grayling do well (Fig. 12). These relationships are only beginning to emerge from our studies to date but it is clear that climatic factors are affecting all chemical fluxes and all trophic levels in the river.

B. LTER GOAL II: BIOTIC REGULATION THROUGH RESOURCE LIMITATION (BOTTOM-UP) VS. BIOTIC REGULATION THROUGH PREDATOR LIMITATION (TOP-DOWN)

Terrestrial Studies

What is the relative importance of changes in air temperature, light intensity, and soil nutrient availability on terrestrial ecosystems, and how might these changes interact? In a series of short- and long-term experiments that began in 1976, we have manipulated air temperature by building small greenhouses, light intensity by shading, and nutrient availability by fertilization (Shaver and Chapin 1986, Shaver et al. 1986). Thus far, we have shown that changes in nutrient availability have effects on both production and composition of tundra that are far greater than changes in either air temperature or light (Fig. 13). Production and biomass accumulation are closely tied to whole-plant nutrient content (Shaver and Chapin 1991, Shaver et al. 1992). The main effect of increased air temperature is to speed up the changes due to fertilizer alone. Without fertilizer

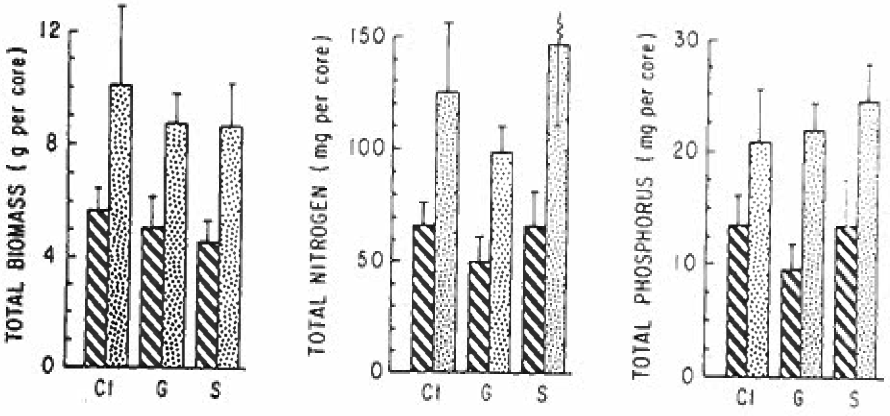


Fig. 13. Fertilizer increases biomass and N and P mass of Eriophorum vaginatum, while increased air temperature and light have no effect after two years. Data show the effect of two years of experimental treatment on biomass, N mass, and P mass of Eriophorum vaginatum in a field experiment in moist tundra at Toolik Lake, Alaska. Hatched bars represent unfertilized treatments; dotted bars represent treatments fertilized with both N and P. Ct = controls (no additional treatment); G = fertilized and unfertilized plots contained within a greenhouse that raised average air temperatures by 5° C during the growing season; S = plots covered by shade cloth that reduced light intensity by 50 per cent. Data are given as means standard errors. (Shaver et al. 1986b)

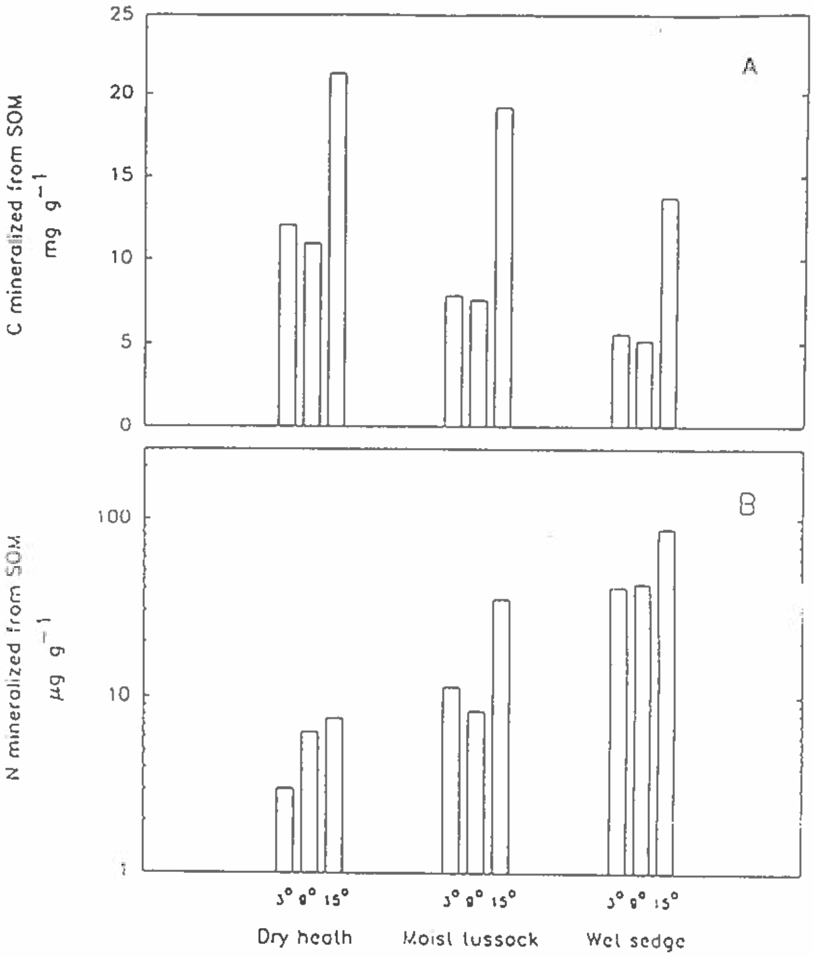


Fig 14 Respiration and N mimeralization of organic soils from dry heath, moist tussock, and wet sedge tundra ecosystems show no little or no temperature response below 9°C, but differ greatly among sites. Soils were incubated in the laboratory for 13 weeks at -0.06 MPa moisture tension and either 3^{0}, 9^{0}, or 15^{0} C Bars show (A) cumulative microbial respiration (CO_2-C production) and (B) cumulative nitrogen mineralized (NO_3-N plus NH_4-N leached). (Nadelhoffer et al. 1991).

the effect of increased temperatures on the vegetation is slight, and probably results from the effect of temperature on soil nutrient mineralization.

These results are consistent with our monitoring studies, and again lead to the prediction that effects of climate on nutrient cycling are the key to understanding long-term controls on productivity and total organic matter accumulation in the Arctic (Shaver et al. 1992). The Arctic is one of the few natural systems where such whole-ecosystem experiments are possible, due to the low stature and fine-grained heterogeneity of the tundra vegetation. Because the number of species is small, both the responses of individual species and the whole vegetation can be easily determined and compared.

Our field experiments have been complemented by laboratory experiments. For example, one experiment involved incubating soils from six contrasting tundra ecosystems at three temperatures to determine effects of temperature on soil respiration and N and P mineralization (Fig. 14, Nadelhoffer et al. 1991a). At a given temperature there was a threefold variation in respiration among soils from different ecosystems, and up to tenfold variation in N and P mineralization rates. These intersite differences were greater than the differences in respiration or mineralization rates due to temperature changes for a given soil. In comparison with temperate soils, our arctic soils had high respiration rates and low net N and P mineralization rates (Nadelhoffer et al. 1991b), suggesting high microbial demands for these elements and helping to explain the very low mineralization rates and strong nutrient limitation of plant growth that we have observed in the field.

Not only the total amounts of N and P made available to plants, but also their specific molecular forms, are critical to understanding vegetation patterns and productivity. In a survey of the N stable isotopic ratios ($\delta\,^{15}N$) in leaves of various tundra plant species, we found a remarkably wide range of $\delta\,^{15}N$ values among species, suggesting that N gets into these plants either by a number of different uptake pathways or in different forms (such as NH_4 versus NO_3). These differences between species are also consistent across sites. Graminoids like Eriophorum vaginatum and Carex Bigelowii are consistently enriched in ^{15}N, by about 4-6$^{o}/_{oo}$, relative to deciduous birch or willow species while ericads like Ledum palustre are consistently the most depleted in ^{15}N. Forb species are variable, with deep-rooted forbs more enriched in ^{15}N than shallow-rooted forbs. We can envisage several explanations for these patterns, involving at least three factors: (1) mycorrhizal versus nonmycorrhizal N uptake, (2) type of mycorrhizae responsible for uptake, and (3) rooting depth.

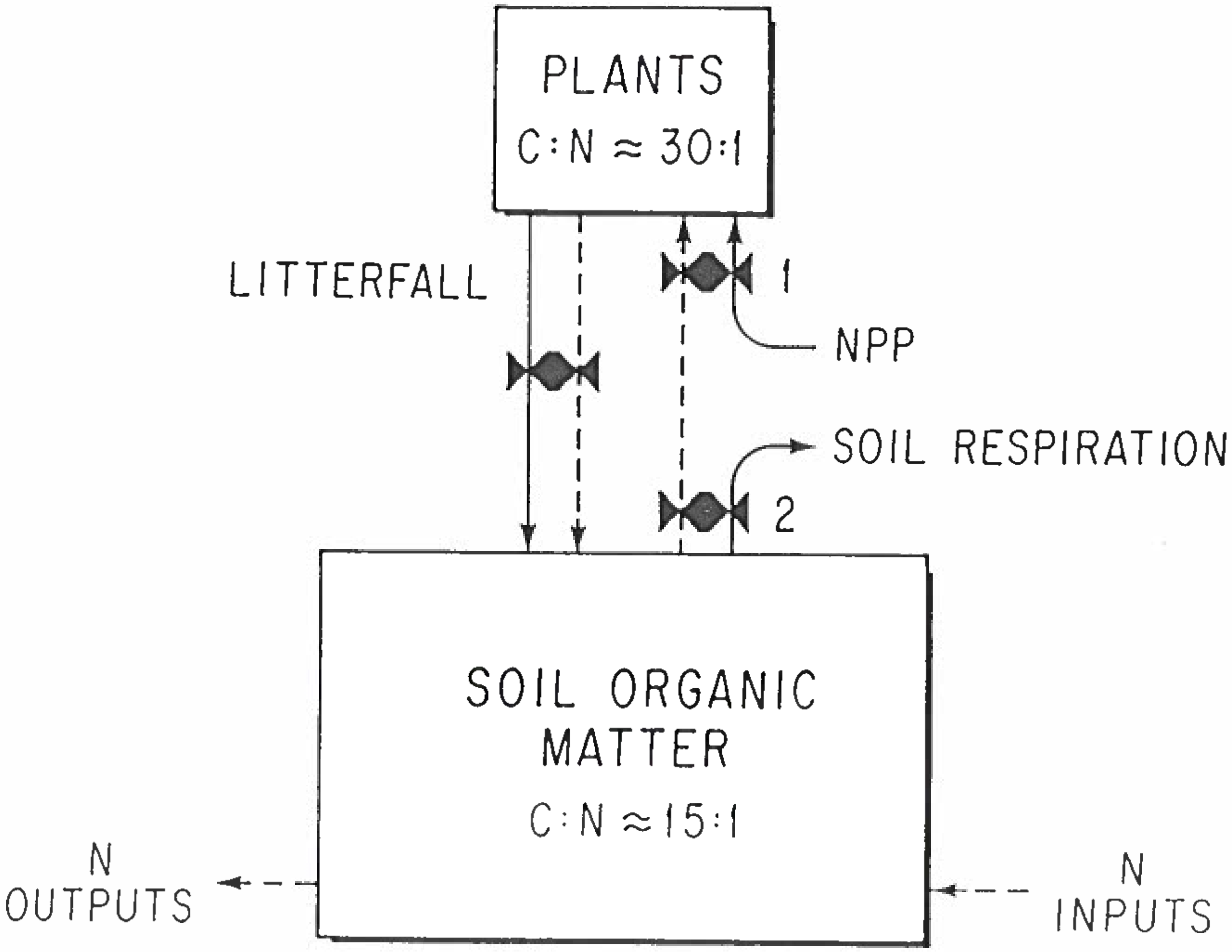


Fig. 15. A conceptual model of carbon and nutrient interactions in terrestrial ecosystems, using C and N as an example. There are two major pools of organic matter in the ecosystem, i.e., plants and soil organic matter. Carbon fluxes into and out of these pools are indicated by solid lines, and N fluxes by dashed lines. The "bow ties" are intended to suggest linkages between the C and N fluxes.

Bow tie #1 implies that net carbon uptake by plants (NPP) is constrained by the plant's ability to take up N, and vice versa. We suggest that in many nutrient-limited ecosystems, essentially all of the plant N supply comes from mineralization of soil organic matter (including recent litter), and that N mineralization is linked to the loss of C in soil respiration (Bow tie #2). Thus, at least in a proximate sense, the overall carbon balance of such ecosystems (i.e., the difference between NPP and soil respiration) is largely determined by carbon gains associated with N uptake balanced against carbon losses associated with N mineralization. (Shaver et al. 1992)

Our results have led us to an overall conceptual model (Fig. 15) of carbon and nutrient interactions at the whole ecosystem level which we are currently using to guide our research (Shaver et al. 1992, Rastetter and Shaver 1992). In the model, linkages between the C and N cycles occur through controls over the C:N ratios in plant and soil organic matter, and through controls over the ratios of the fluxes of C and N into and out of these pools (the "bow ties" in Fig. 15). The C:N ratios indicated in the boxes are typical of wet and moist tundra ecosystems but can have much higher values elsewhere, especially in forests where woody biomass may have a C:N ratio of 200 or more. The basic idea, however, is generally applicable; that is, all pools and fluxes of organic matter must contain both C and N, and the ratios of these elements are not infinitely flexible.

All the evidence reviewed above is consistent with the idea that large, long-term changes in tundra carbon cycling will be tightly constrained by changes in cycling of other elements (Shaver et al. 1992). Because plant C accumulation in the tundra at Toolik Lake is strongly N-limited, a sustainable increase in C accumulation requires a sustainable increase in N uptake (some other tundras are P-limited). Environmental changes, such as CO_2 increase, that do not directly affect the N cycle will be constrained in their effects on the C cycle by constraints on C:N ratios.

Lake Studies

How much is the structure and function of the lake ecosystem controlled by resources (bottom up control), such as the rate of nutrient input, and how much by grazing and predation (top down control)? To isolate the effects of nutrient availability on productivity,we initiated process oriented studies on the effects of lake fertilization. These studies began in 1983 using large limnocorrals (O'Brien et al. in press) and have been expanded to whole lakes in our current program (O'Brien et al. in prep). The summer of 1990 was the last of 6 years of nutrient fertilization in the divided Lake N-2. During this period there were large increases in phytoplankton biomass and snail numbers and growth in the fertilized side of the lake (Fig. 16). The zooplankton, grayling, and other benthos responded either with a 1 to 2 year time lag, or not at all, which is consistent with our previous results and with several other fertilization studies in arctic and temperate lakes. Much of the phosphorus added to the lake was tightly bound to the iron-rich sediments, and was not recycled to overlying waters under aerobic or anaerobic conditions (Kipphut 1988). This iron-bound PO_4 is apparently available only to benthic algae, and we measured a 2 to 3 fold increase of benthic algal productivity in the

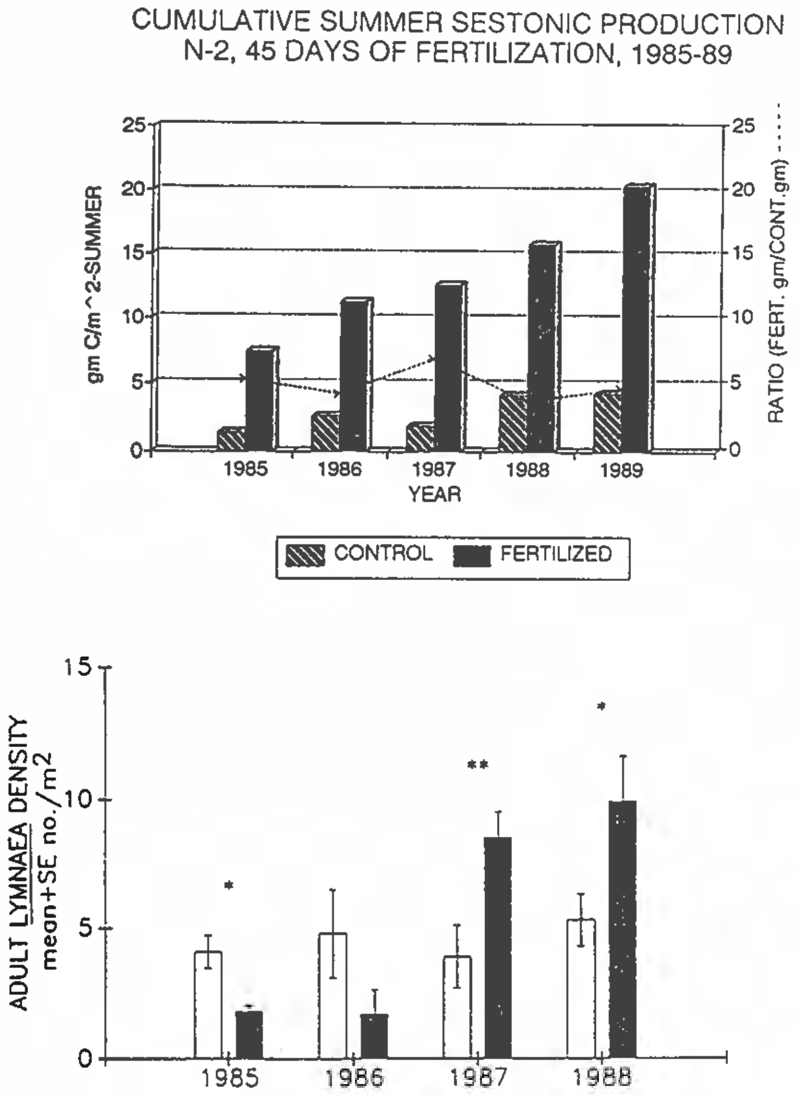


Fig. 16. **Fertilization of Lake N-2 affects the entire food web.** TOP: Response of planktonic primary production to fertilization during the summers of 1985-1989. BOTTOM: Numbers of the snail Lymnaea in the control (open bars) and fertilized (solid bars) sections of the lake. Data are given as means standard errors. Asterisks indicate significant differences between fertilized and control sections.

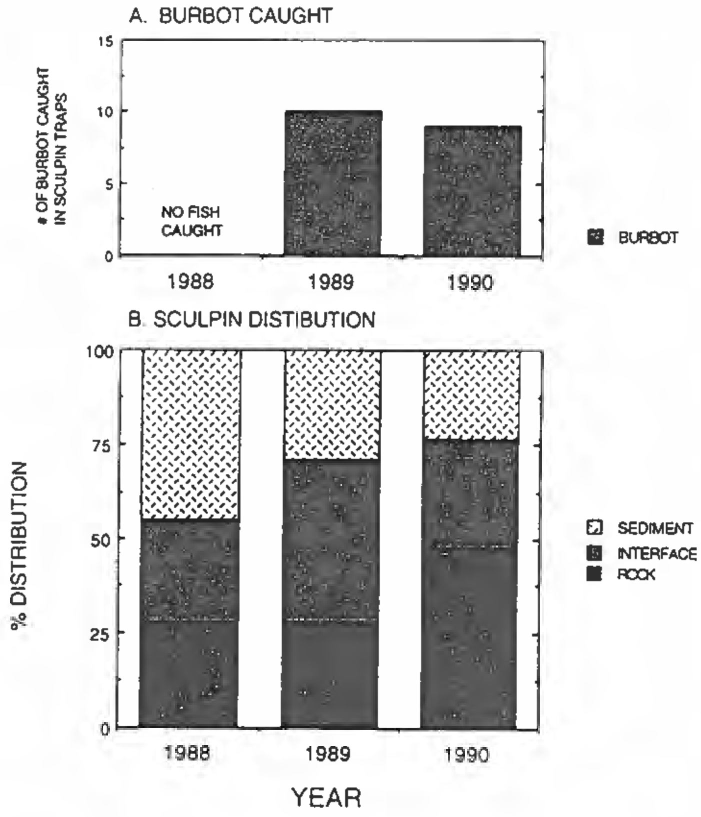


Fig. 17. Sculpin and burbot habitat selection is strongly affected by presence of lake trout. Data show changes in distribution in Lake NE-12 following removal of lake trout in 1988. TOP: Burbot appearance in sculpin traps indicates a shift in their distribution from deep water to nearshore zones after lake trout removal. BOTTOM: Changes in distribution of sculpin among sediment, interface, and rock habitats.

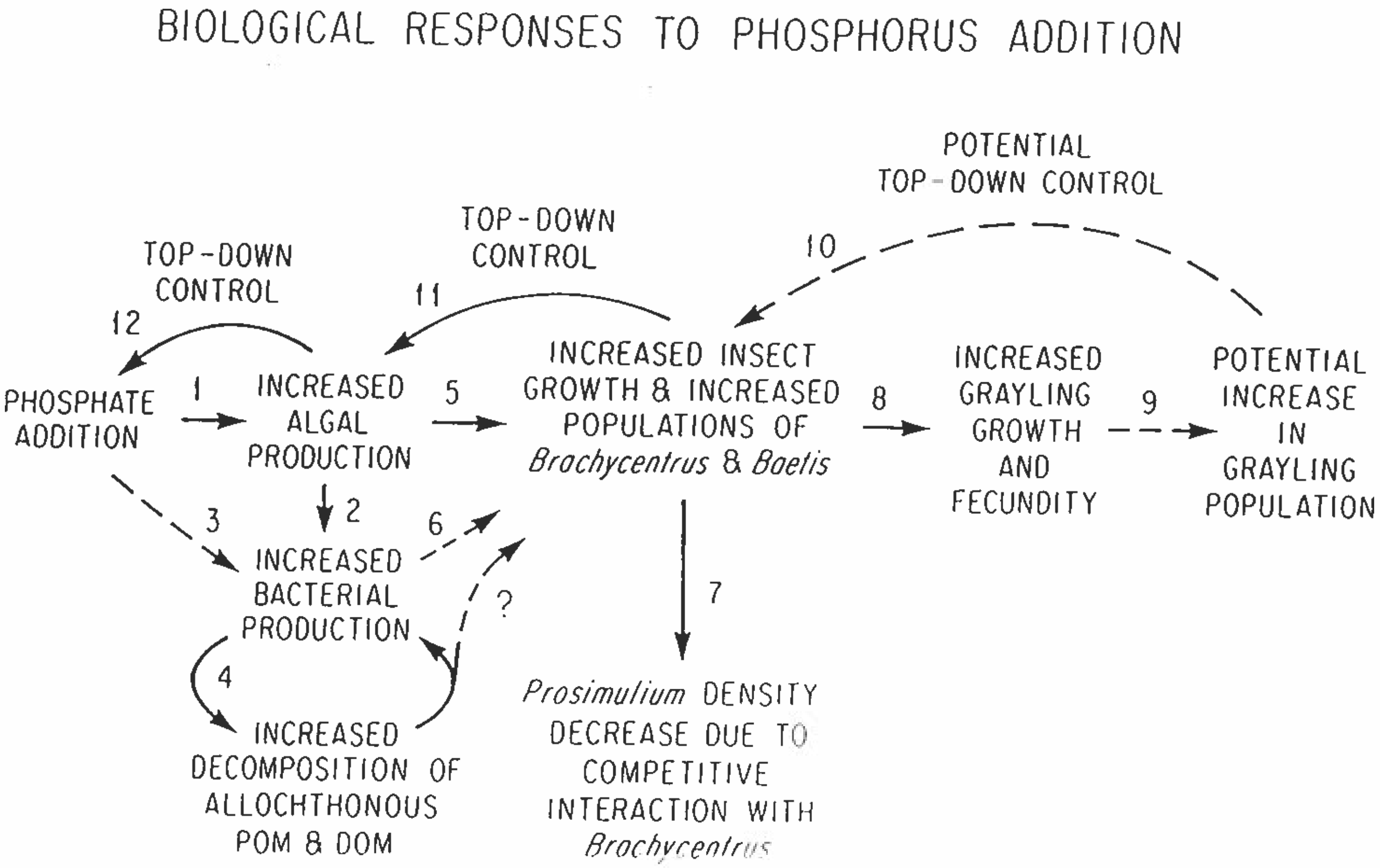


Fig. 18. Response of the Kuparuk River biota to the addition of phosphorus and to possible changes in predators. See text for explanation.

fertilized side of Lake N-2. This phenomenon of strong nutrient binding in sediments should allow for a rapid recovery from lake eutrophication caused by external nutrients. We will test this prediction by measuring the rate of recovery to the pre-fertilization conditions of water chemistry and biota in Lake N-2 since fertilization stopped in 1990.

A second whole-lake fertilization experiment was started in 1990 in nearby Lake N-1. One advantage of Lake N-1 is that it contains grayling as well as the top predator lake trout, whereas Lake N-2 contained only grayling. The addition of nutrients to Lake N-1 will thus allow us to look at the effects of fertilization on higher trophic levels when the top predator is present, and to better define the interaction between bottom-up and top-down controls. For example, predation by lake trout, in combination with resource competition, seems to limit snail populations in these lakes (Hershey 1990). When lake trout are absent, snails are very abundant and fertilization stimulates their growth and increases their numbers, as occurred in Lake N-2. In 1990 we also measured an increase in snail growth in cages that excluded lake trout in Lake N-1, but whether the population sizes of snails will increase as well in a fertilized lake containing lake trout can only be determined by continuing the long-term enrichment study.

To investigate the importance of top-down controls we have been both monitoring and experimentally manipulating a series of lakes. The experimental manipulations of top predator populations include a slow removal of lake trout from Lake I-8, a fast removal of lake trout from Lake NE-12, and the introduction of lake trout to Lake S-6. The most striking result so far is a change in the distribution of the bottom dwelling sculpin and predaceous burbot in response to complete removal of lake trout from Lake NE-12. We had expected that in the absence of predation pressure, sculpin would move away from the rocky shallows and out onto the soft sediment where food availability is higher. Instead, sculpin moved even more toward the rocky shallows after the lake trout were removed (Fig. 17). We also measured a large number of burbot moving from deep in the lake, where they can most easily avoid predation by lake trout, into the nearshore zones. This large increase in burbot in the shallows drove the sculpin away from the soft, exposed sediment, and apparently the control of sculpin by burbot predation is even stronger than was the control of sculpin by lake trout. We will continue to monitor these behavioral responses to changing predator populations.

Our experimental designs have allowed us to test the interaction of bottom-up and top-down controls at the ecosystem scale. For example, at the level of fertilization we applied to Lake N-2, chironomid density did not respond even after benthic algal productivity had more than doubled. We conclude that predation by sculpin is intense enough to maintain chironomid densities below the level at which they would be food or resource limited (Hershey 1985a). A corollary of this is that lake trout will not obtain extra food from sculpin during eutrophication of these lakes. This important finding requires more work and confirmation in other lakes. We will continue the fertilization of Lake N-1, which contains chironomids, sculpin, and lake trout, and beginning in 1991 we will add sculpin to Lake E-1 (no sculpin, abundant chironomids) and remove sculpin from Lake N-3 (sculpin, few chironomids) to test the intensity of the linkage and of the controls.

So far the results of our experiments indicate that both bottom-up and top-down controls operate simultaneously and are important in these ecosystems; rarely is there a single master variable that constrains the structure of all populations or the processes involving nutrient and carbon flow.

Stream Studies

How much is the ecosystem controlled by resources (bottom-up) vs. predation (top-down) control? If climate change accelerates chemical weathering and phosphorus export from the tundra, how will the life of streams and rivers be changed? An overview and synthesis of the response of the Kuparuk River biota to the addition of phosphorus is given in Fig. 18. The bottom-up effects of nutrients as they propagate through the ecosystem are diagrammed flowing from left to right. The top-down or feedback effects are diagrammed flowing from right to left. The steps are numbered and described in the following paragraph.

The sequence of responses that we have measured over the past seven years is as follows (numbers in parentheses refer to Fig. 18): dissolved phosphate added to river water stimulates the growth of epilithic algae (1). Increases in algal production lead to sloughing and export of algal biomass and increased excretion and mortality. Increased algal excretion and mortality stimulate bacterial activity which is also stimulated directly by phosphorus addition (2, 3). Increased bacterial activity and biomass make possible an increase in the rate of decomposition of refractory compounds such as lignocellulose and many components of the DOM pool (4). The increases in algal and bacterial biomass provide increased high quality food for filtering and grazing insects (5, 6). The insects respond with increased growth rate and, in the case of Baetis and Brachycentrus, with increases in density. However, Prosimulium density in the fertilized reach declines due to competitive interaction with Brachycentrus (7). The increases in insects other than Prosimulium increase the available food for grayling; both young-of-the-year and adult grayling grow faster and achieve better condition in the fertilized reach (8). In the long-term, if the experimental nutrient addition were expanded to include the whole river and barring other overriding but unknown fish population controls, we hypothesize that the fish population would increase (9). If so, it is possible that predation by fish would exert increased top-down control over insects such as Baetis or Brachycentrus which are vulnerable to fish predation when drifting and emerging (10). Experimental evidence from bioassays using insecticides indicates that grazing insects control algal biomass (11). Finally, increases in epilithic algae and bacteria are responsible in part for uptake of added phosphorus and ammonium and for uptake of naturally abundant nitrate (12). Thus, the bottom-up effects of added nutrients are paralleled by several top-down effects of fish on insects, insects on insects, insects on epilithic algae, and epilithic algae and bacteria on dissolved nutrient levels.

In summary, the entire biological system in the river is responsive to added phosphorus. The bottom-up effects propagate to all levels in the food web. Also both top-down effects and competitive interactions are clearly important in the response of the ecosystem to fertilization.

C. LTER GOAL III: RATES AND CONTROLS OF THE EXCHANGE OF NUTRIENTS AND ORGANIC MATTER BETWEEN LAND AND WATER

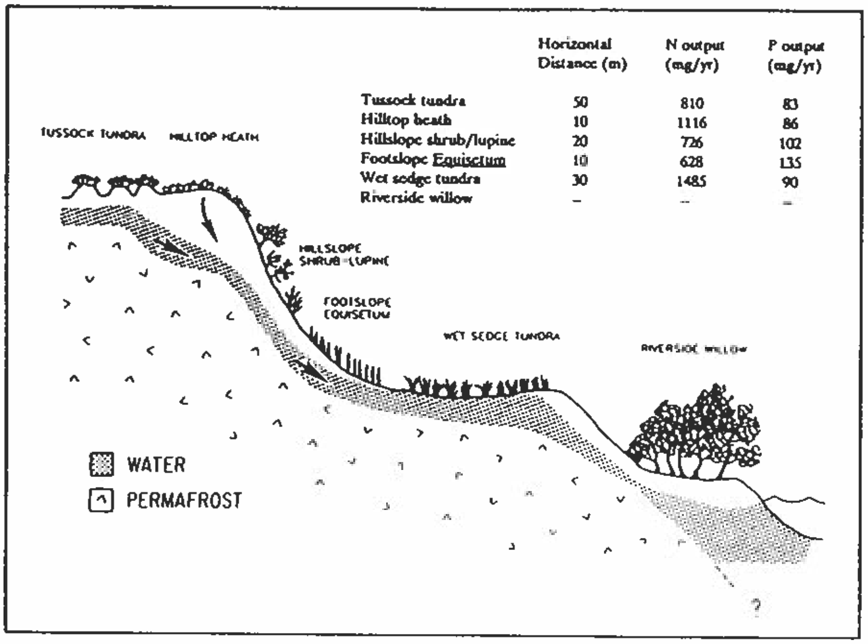
General. From the preceding discussions, it is evident that the quantity and type of externally supplied nutrient and organic matter play a central role in structuring both terrestrial and aquatic systems of the Arctic. In the Arctic, nutrients and organic matter enter streams mostly in the inflowing surface and ground water. The permafrost seals the soil below about 0.5 m depth so ground water does not percolate through nutrient-rich subsoil as in temperate watersheds. Accordingly, our knowledge of the entire system and its controls is incomplete until we understand what controls both the flow of water and the release of nutrients and organic matter from the land into the streams and lakes.

The flux of nutrients to streams and lakes is determined by surface and groundwater runoff, by chemical weathering, by plant uptake, and by the microbial reactions that influence groundwater composition. Dissolved and particulate carbon flux to streams is determined by these factors as well as by the erosion of peat, the leaching of tundra plant remains, and the quantity and quality of terrestrial litter in areas where there are well-developed trees. Eventually, we need to understand what controls the fluxes of nutrients and organic matter at the subwatershed and watershed level, i.e., in systems made up of many different slopes, soils, and vegetation types. Only then will we understand how the land-water interactions operate and be able to predict how they will operate in the future under changed land use and climate conditions.

The hydrological cycle of the Arctic has unique characteristics. First, it affects terrain that is relatively young - much of it formed since the last glaciation and in most areas without a completely developed drainage system. Second, infiltration and groundwater motion are blocked, in most areas, by the permafrost and related periglacial phenomena. Third, the seasonal regimes of rivers, soil moisture, and surface-groundwater interactions are dominated by freezing and thawing processes. Because of the uniform topography of extensive areas in the Arctic, moderate changes in hydrological conditions may lead to large changes in the area of surface water, in the amount of soil moisture, and in the amount of ground ice near the surface (Lachenbruch and Marshall 1986). These changes, in turn, will have important feedbacks to climate and vegetation. Unfortunately, baseline hydrologic data are few. Of all elements of the arctic environment, hydrology is one of the most pervasive in its influence but perhaps the least known.

One of the earliest studies of arctic hydrology was made at the Cape Thompson (western Alaska) site designed for an atomic blast. Here, Waller (1966) and Likes (1966) reported on the rainfall-runoff relations and on groundwater capacity. Most of the North Slope research has been carried out along the coast near Barrow (Brown et al. 1980, Hobbie 1980, Dingman et al. 1980) and on the runoff regime of the large rivers (Scott 1978). The Canadian Arctic has been quite well studied, mostly on the Arctic Archipelago, but the sites do not compare well with the foothills of the North Slope (see Woo and Steer 1986 for a review of permafrost hydrology, especially of the Canadian literature). Fortunately, a small watershed was intensively studied near Toolik Lake (Imnavait Creek, the R4D study of DOE) from 1985 through 1989 and the results are reported in the PhD thesis of L.D.Hinzman (1990) and in a number of associated papers (Hinzman et al. 1990, Kane et al. 1989, Kane and Hinzman 1988, Kane et al. 1990).

Precipitation in the Arctic is low, with the highest amounts normally occurring during late July, August, and September (Kane and Hinzman 1988). According to Haugen (1980), between 30 and 80% of the precipitation occurs as snow but it is very difficult to measure the snowfall exactly because of drifting and great



	Horizontal Distance (m)	N output (mg/yr)	P output (mg/yr)
Tussock tundra	50	810	83
Hilltop heath	10	1116	86
Hillslope shrub/lupine	20	726	102
Footslope Equisetum	10	628	135
Wet sedge tundra	30	1485	90
Riverside willow	–	–	–

Fig. 19. Inorganic N and P outputs from a one-meter wide toposequence leading down to the Sagavanirktok river, 40 km northeast of Toolik Lake (Shaver et al. 1990). Outputs from each ecosystem are the inputs to the ecosystem immediately downslope. Each of the six ecosystem types along the toposequence has major effects on the amounts of inorganic N and P that eventually reach the river.

variability of the snow density. Hinzman (1990) concludes that evaporation and sublimation is likely small during the winter but is the largest part of the water balance during the summer (Kane and Hinzman 1988).

The hydrologic regimes of arctic basins are determined mainly by the melting of snow and ice; most of the annual runoff and the peak flows occur during the spring snowmelt (Woo and Steer 1983). Permafrost prevents deep infiltration and maintains a perched water table within the active (annually thawed) layer (Hinzman 1990). Hinzman summarizes the annual cycle of a small basin near Toolik Lake as follows. On hillsides during the 10 days of snowmelt, water flow is either overland or through the organic layers at the soil surface depending upon the dryness of the upper layers of the active layer. Much of the overland flow occurs in water tracks (Kane et al. 1990), small drainage channels on slopes, which rapidly convey water down the slope to the streams. The active layer thaws throughout the summer and becomes up to 0.5 m thick in the foothills of the North Slope. After the snowmelt, water usually flows through the organic peat of the active layer but water tracks may channel water overland during unusually large rainfall events. About 1/2 to 2/3 of the annual precipitation occurs as rainfall. From 1986 through 1989, the centimeters of observed total precipitation and total runoff were, respectively, 27.2 and 11.9, 38.0 and 25.0, 33.0 and 11.1, 41.2 and 17.2. In 1989, the snowmelt for the basin went 61% to runoff, 10% to soil storage, and 30% to evaporation.

A process model reported in Hinzman (1990) and Kane et al. (1990) predicts that an annual temperature rise of 5°C would result in an increase of the thaw depth from the present 0.5 m to a maximum of 1.12 m after 30-40 years. A 20% increase in precipitation would result in wetter soils for longer periods, more evaporation, and more discharge.

What controls the flux of nutrients and water over the arctic landscape and into aquatic ecosystems? Our aim is to evaluate the magnitude and relative importance of nutrient and organic matter fluxes in soil water moving across the surface of the permafrost, between terrestrial ecosystems, and into aquatic systems. Our most intensive study site has been a toposequence of six contrasting ecosystem types in the Sagavanirktok River valley about 40 km northeast of Toolik (Fig. 19). To estimate N and P fluxes at this site we developed overall N and P budgets for all six ecosystems, and linked these budgets with a hydrologic model (Shaver et al. 1990).

Our results indicate that the net uptake of N and P from moving soil water is small relative to internal fluxes like annual plant uptake or N mineralization. However, each of the six ecosystem types has a very

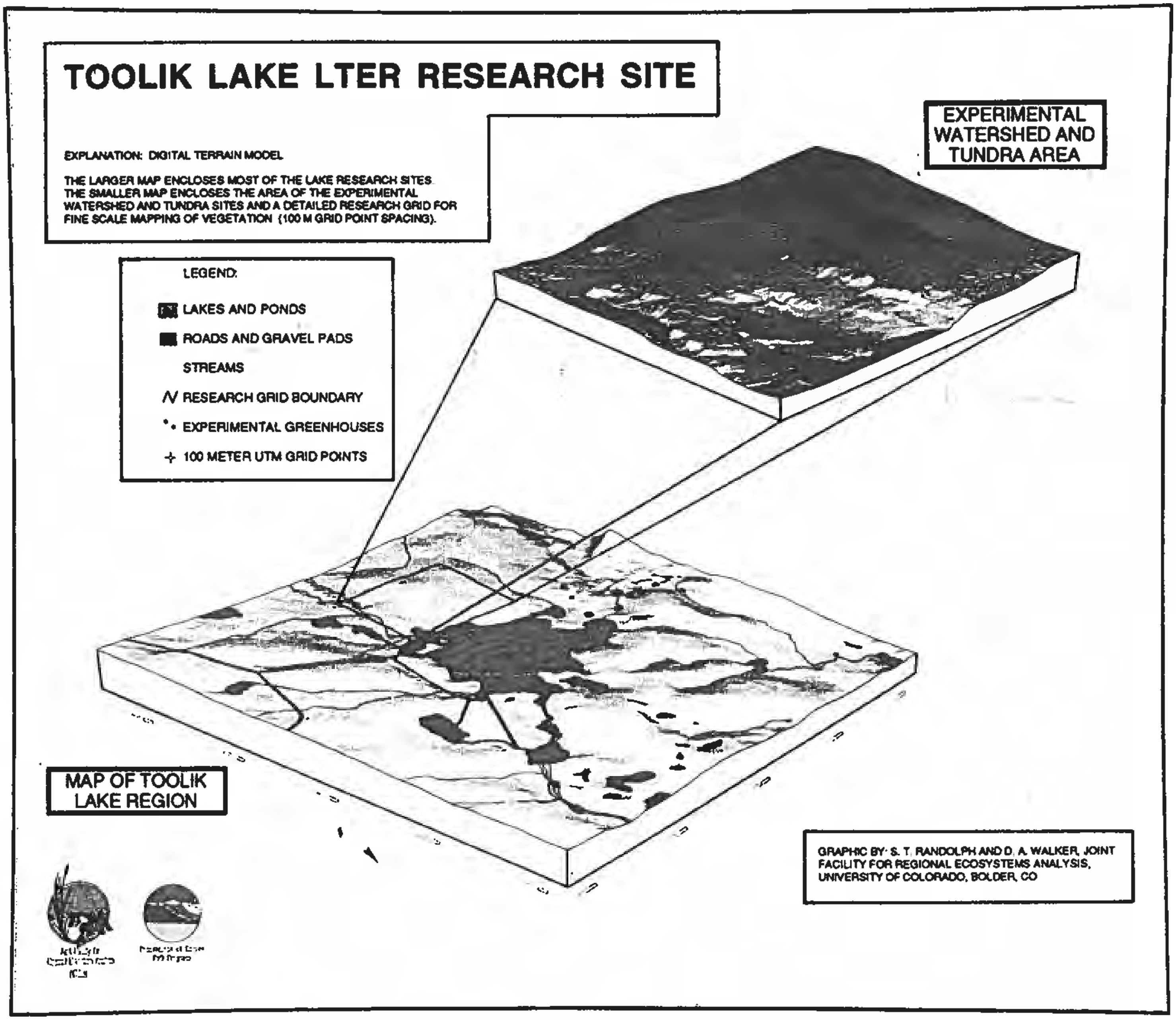


Fig. 20. Perspective view from the northeast of the intensive study areas in the Toolik Lake watershed at two scales (corresponding to the two rectangles shown in this watershed in the Frontispiece). The larger area is 5x5 km and the smaller area is 1x1 km (maps by D. Walker). In addition, nearly 100 1x1 m plots have been mapped at 1 cm resolution by M. Walker throughout the 1x1 km area. Parallel information and maps are available from the DOE-R4D intensive site within the Kuparuk River watershed (rectangles shown in Kuparuk watershed in Frontispiece). Several of the experimental lakes and all of the long-term terrestrial experiments are included within the large area shown here, and the experimental watershed and many of the terrestrial experimental plots (shown as dots) are included within the small area.

TOOLIK LAKE RESEARCH GRID

PRIMARY VEGETATION MAP

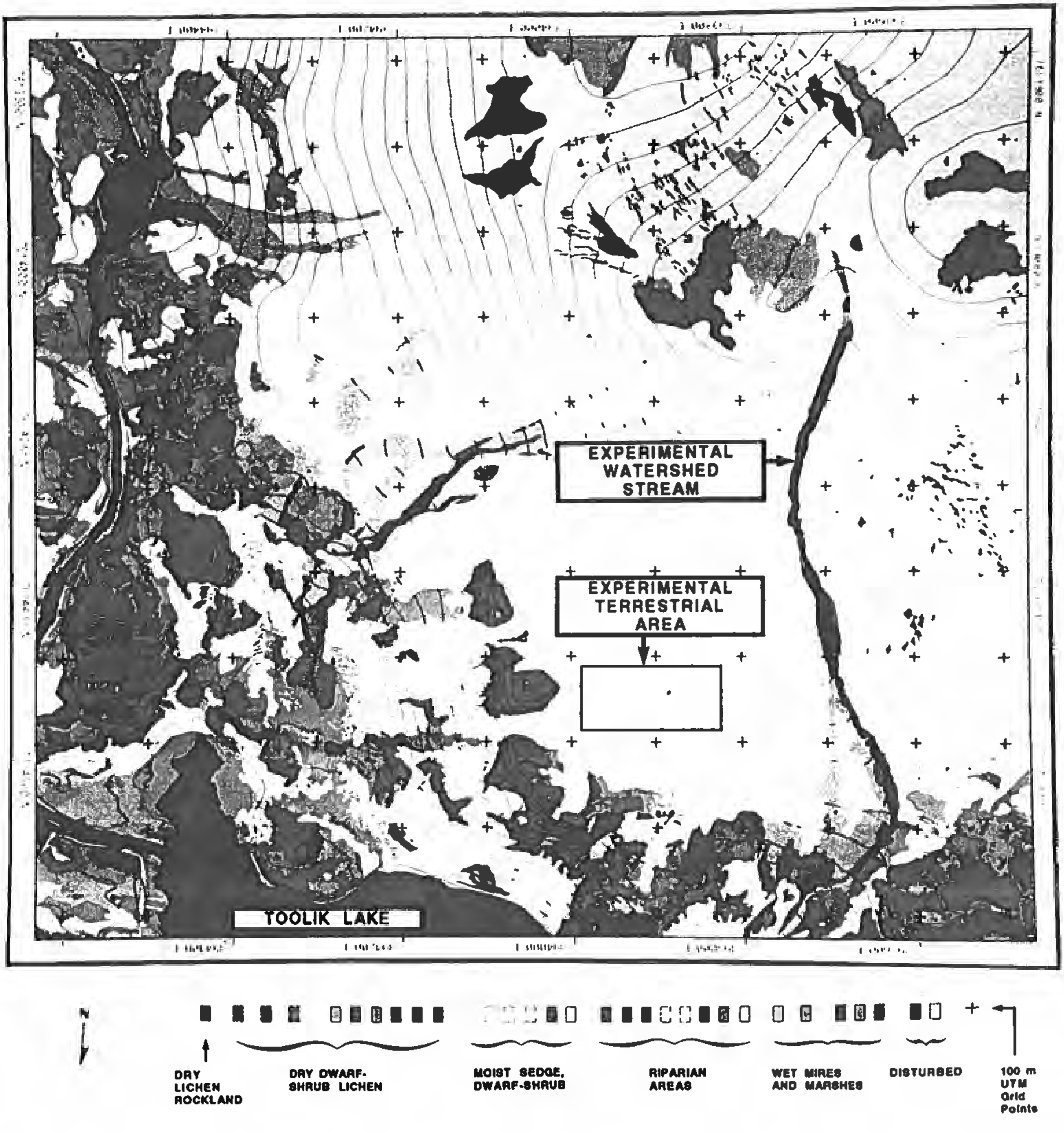


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Fig. 21. A vegetation map of the 1x1 km area in Fig. 20 (map by D. Walker), including our experimental primary watershed and terrestrial area. Maps of soils, surface geomorphology, glacial geology, and surface water have also been completed for both this area and the larger 5x5 km area.

different effect on the total amounts of NO_3, NH_4, and PO_4 in the soil water (Fig. 19). Thus, the specific arrangement of terrestrial ecosystem types near streams controls the amounts and forms of inputs to aquatic ecosystems. Some ecosystem types, like tussock tundra and dry heath, are strong sources of N to soil water. Others, particularly those occurring under or below late-lying snowbanks, are important N sinks and P sources to soil water. Poorly-drained wet sedge tundra is a P sink with a remarkably high N mineralization rate (Shaver et al. 1990, Giblin et al. 1991).

We have also learned a great deal about patterns and controls of N and P cycling along the toposequence (Giblin et al. 1991). One of our most important discoveries is that nitrification is much more important along the toposequence than we suspected based on earlier research, and many plant species show high nitrate reductase activity. We also have strong evidence from stable isotope analyses that different plant species are using isotopically different N sources, and that these species differences are maintained across sites. The relative amounts of different forms of organic and inorganic P in soils also vary dramatically across sites.

In summary, our work at the Sagavanirktok River site has shown that different terrestrial ecosystems differ strongly in their chemical interactions with the soil water, and thus have highly variable effects on the chemistry of water entering aquatic systems. This work is important in the context of environmental change, because if either the composition of the landscape mosaic changes, or the biogeochemistry of individual landscape units changes, the chemistry of inputs to aquatic systems will be altered.

In 1991 we began sampling a small experimental watershed close to Toolik Lake for further investigation of nutrient transformations as water moves from land to lakes and streams. This watershed has been mapped for vegetation, soils, topography, and landforms at the 1:500 and 1: 24,000 scales (Figs. 20, 21). By measuring nutrients in soil waters across a transect from upland tundra to the riparian zone, we have confirmed the pilot studies that suggested active nitrification occurred near the lake and streamedge. The lower part of the experimental watershed contains an area underlain by glacial material that is only about 15,000 years old, compared to the 100,000 year old material covering the upper watershed. Because the age of the land surface influences the extent of weathering, there are large differences between young and old areas in the amounts of major ions draining into surface waters. Our preliminary results indicate that nutrient export may be affected by landscape age as well. In addition to this spatial variability in nutrient concentrations and forms, we have also detected strong seasonal trends in the concentrations of nutrients draining from tundra soils. All of this information, along with the results from the monitoring of soil water chemistry and flow, will be incorporated into our modeling approach and the GIS system we have developed for the Toolik LTER.

What are the effects of riparian zones on nutrients? Our focus here has been on nutrient transformations as water flows through the riparian zone and into streams and lakes. The hyporheic (deep-flowing) zone beneath streams also plays a role in delivering and transforming the nutrients. Pilot studies have shown that there is frequently active nitrification in the deeply thawed creekbank willow zone. Water seeping downslope is high in ammonium entering the willow zone but the ammonium is rapidly converted to nitrate in the last few meters before seeping into the river. We know from our whole river ammonium addition that nitrification is also very active in the river channel. Preliminary data from the hyporheic zone suggest that water in this layer is derived from lateral seepage and is not simply river water. There may be some nitrification as well as water with high ammonium concentrations moves from the hyporheic zone upward and closer to the river channel.

How does the flux of dissolved inorganic and organic carbon from lakes to rivers affect changing carbon balance in the Arctic? We have shown that the flux of inorganic carbon from tundra to lakes and streams is much greater than anyone had anticipated (Kling et al. 1991). The arctic lakes and streams we examined are consistently supersaturated with CO_2 and thus continuously release CO_2 to the atmosphere. Measurements of the pCO_2 of soil waters in our experimental watershed and selected sites in the Kuparuk watershed showed even greater supersaturation, which leads us to believe that the excess CO_2 comes from decomposition in tundra soils and moves into streams and lakes in groundwater. The magnitude of CO_2 release from lakes and streams to the atmosphere is 20-50% of the estimated value for terrestrial net primary productivity. The implications of this finding are that first, previous net primary productivity numbers based on CO_2 exchange in terrestrial sites were too high because of the loss of terrestrially fixed carbon to aquatic systems. Second, the large release of carbon gases to the atmosphere that is projected under a scenario of temperature increases in the Arctic will be augmented by CO_2 evasion from lakes and streams. We do not know, however, how much of the release from lakes and streams actually comes from CO_2 in soil water and how much comes from in-lake decomposition of organic matter originating from the land. In 1992-1998 we will

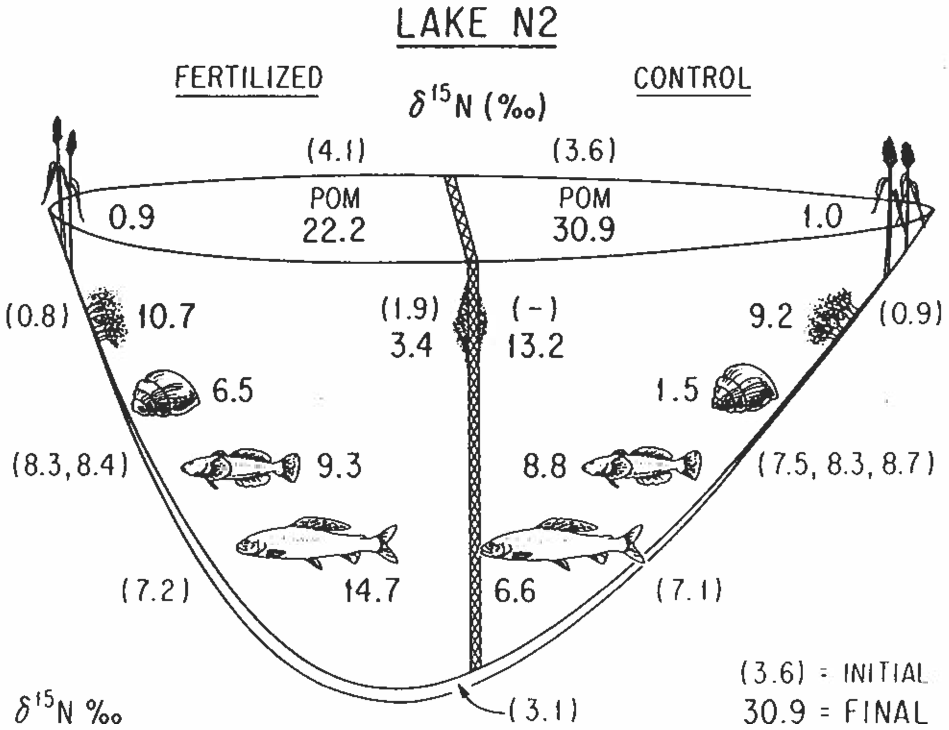

Fig. 22. The delta ^{15}N values for particulate organic matter (POM, mostly phytoplankton) and for three genera of zooplankton in the control and fertilized sides of Lake N-2. The ^{15}N was added continuously as trace amounts of NH_4Cl starting on 1 July 1988.

gauge the export of water from the experimental watershed, and measure how much dissolved organic matter (DOC and DON) from soils enters the lakes and streams.

While the response of aquatic organisms to inputs of dissolved inorganic nutrients is well understood, the response to dissolved organic and particulate material washed in from the tundra is less clear. In some high latitude lakes, for example, the zooplankton make their living directly from inputs of terrestrial detritus rather than from the phytoplankton in the water column. We tested the importance of this linkage between lake organisms and inputs of particulate material from the tundra by adding tracer amounts of $^{15}NH_4Cl$ to Lake N-2 in order to label the phytoplankton. The terrestrial detritus remained unlabeled with ^{15}N . The ^{15}N label appeared in the algae almost immediately, and their ^{15}N content increased steadily over the summer. By the end of the summer, the ^{15}N content of zooplankton was similar to that of phytoplankton in both sides of the lake (Fig. 22). This similarity in ^{15}N content shows that the pelagic food web is dependent on algal production within the lake rather than on terrestrial detritus washed into the lake. We need to continue this work to elucidate the details of the benthic food web.

D. COMPARATIVE STUDIES

Lake and Stream Survey on North Slope Transect. To extrapolate our data and understanding to the regional scale, we have measured physical, chemical, and biological variables at a variety of aquatic sites on the North Slope. In 1990 we completed a survey of 45 lakes and 7 streams along a 230 km transect from the Brooks Range north to the Arctic Ocean (Kling et al. in prep). Variations in water chemistry among the sites were related to differences in bedrock and the age of associated glacial drift, while variations in species composition were related mostly to biotic interactions (Kling et al. in press). These surveys will continue in 1992-1998, and will concentrate on determining how widespread is the phenomenon of strong nutrient binding by the sediments that we observed in the Lake N-2 fertilization experiment.

Comparisons Among LTER Sites. We are actively involved in a number of intersite comparisons and have hosted several workshops leading to such comparisons. In 1989, Brian Fry hosted a workshop on stable isotopes in ecosystems that resulted in a publication (Fry 1991) comparing C and N isotope distributions in 11 LTER sites. A second project involving all sites in the LTER network is currently underway to test the effect of

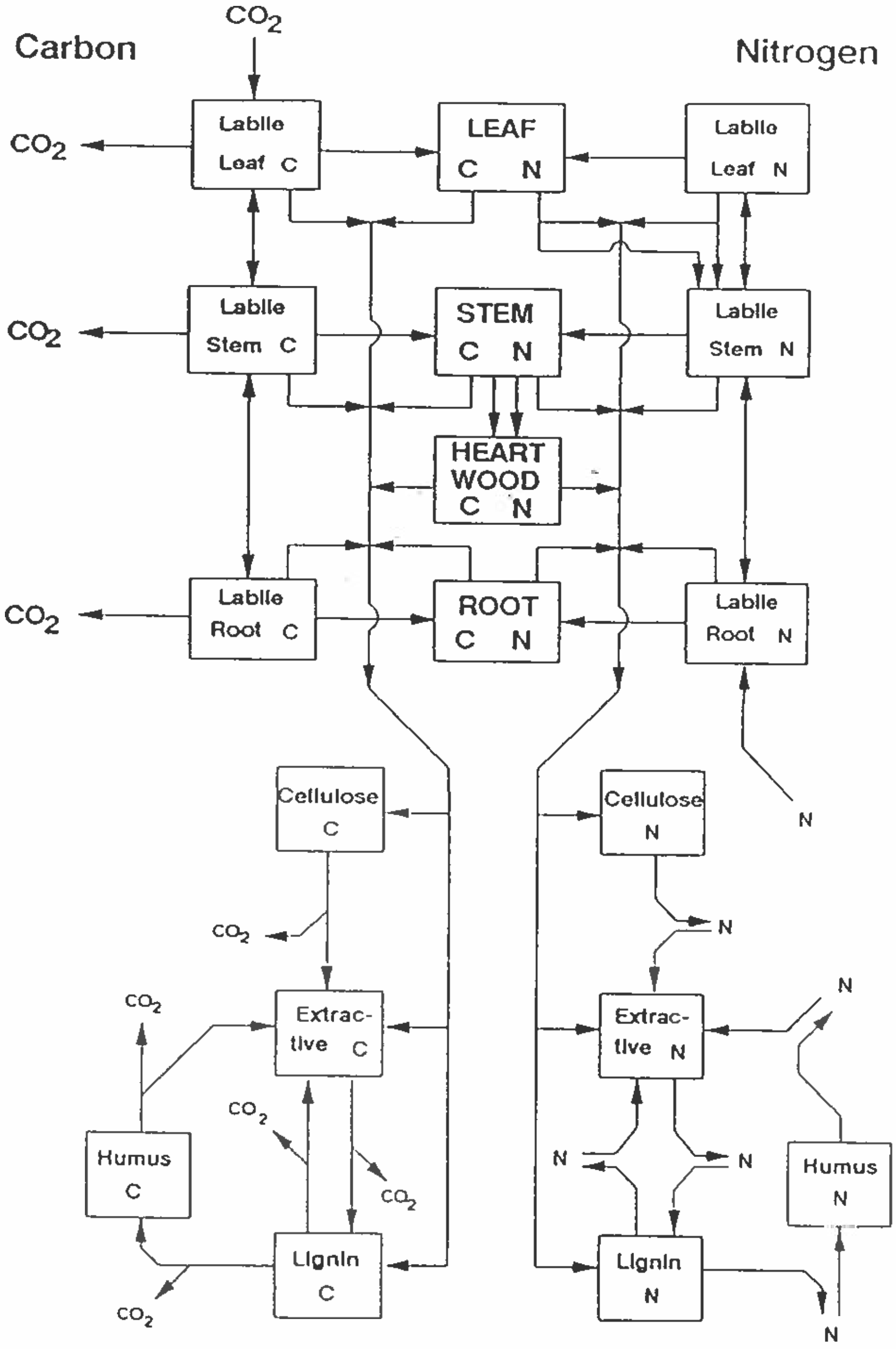

Fig. 23. Schematic diagram of a general model of carbon and nitrogen cycles within terrestrial ecosystems (GEM; Rastetter et al. 1991).

manipulation of litter inputs on long term accumulation and cycling of soil organic matter (M. Harmon et al.). The Arctic site is actively involved in both litter bag studies and the planning for the long-term soil organic matter study. The Arctic and Harvard Forest sites also hosted the original workshop in Woods Hole at which much of the early planning for this project was done. A third LTER workshop, organized by Bill Schlesinger, was held in Woods Hole in September, 1991, on soil warming experiments. The aim of the workshop was to discuss the possible effects of soil warming at contrasting LTER sites, and perhaps to develop another intersite experiment. We will be active participants, and in fact carried out some preliminary soil warming studies in the field in 1991.

An EPA project (J. Schimel and K. Nadelhoffer) measuring CO_2, CH_4 and N_2O emissions at both the Arctic LTER and the Bonanza Creek LTER sites will use the long-term LTER manipulations of nutrients, shade, and warming.

Finally, one of the goals of our modeling program is to use our models to predict and compare the possible responses of contrasting ecosystem types to disturbances including global climatic change. We have already completed one paper comparing Harvard Forest stands with tussock tundra at Toolik Lake (Rastetter et al. 1991), and have succeeded in parameterizing our GEM model for several other LTER sites and comparing their responses to changes in CO_2, temperature changes, and N deposition (Rastetter et al. in prep, McKane et al. in prep).

E. MODELING

<u>Modeling of Tundra Biogeochemistry</u>. With funding from NSF-BSR, a group at the Ecosystems Center has developed a General Ecosystem Model (GEM) of the responses of terrestrial ecosystems to changes in atmospheric CO_2 concentration, climate, and nutrient inputs (Rastetter et al. 1991). This highly-aggregated, process-based, biogeochemical model is designed to examine changes in the fluxes and allocation of carbon and nitrogen among foliage, fine roots, stems, and soils in response to changes in atmospheric CO_2 concentration, temperature, soil moisture, irradiance, and inorganic nitrogen inputs (Fig. 23). GEM was developed on the principle that the responses of terrestrial ecosystems to changes in CO_2, climate, and N deposition will encompass kinetic responses of enzymes, stoichiometric shifts in tissue C to N ratios, changes in the allocation

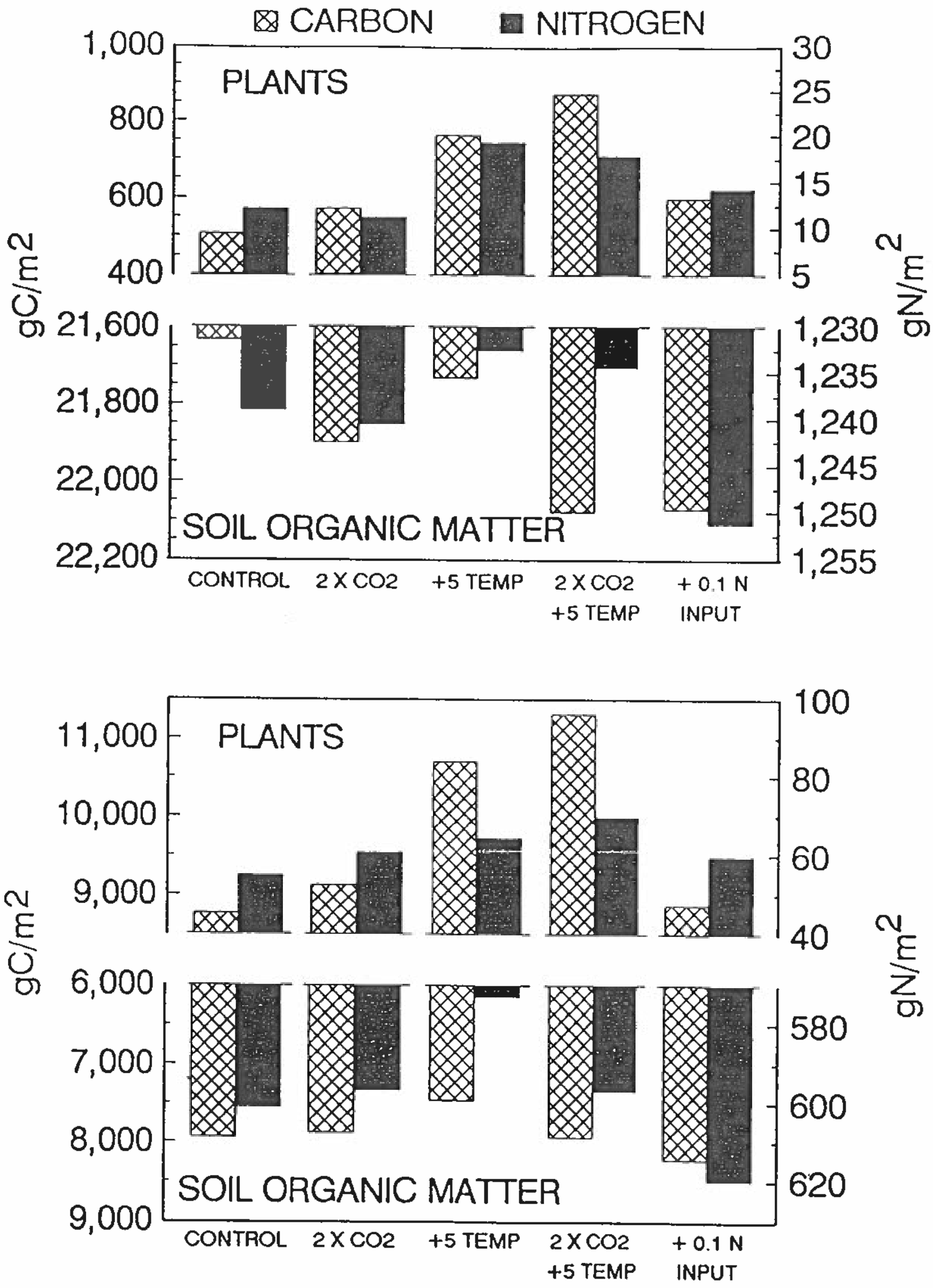

Fig. 24. Modeled plant and soil stocks of carbon and nitrogen in tundra at the Arctic LTER site (upper graph) and northern hardwoods at the Harvard Forest LTER site (lower graph) after 50 years of exposure to a doubling of CO_2 concentration, a 5 C increase in temperature, a combined CO_2 and temperature increase, and a 0.1 g N m^{-2} mo^{-1} increase in nitrogen deposition.

of plant biomass among tissues, altered rates of soil organic matter turnover and N mineralization, and ultimately a redistribution of C and N between vegetation and soils.

The model simulates changes in the amounts of C and N in several vegetation tissues and in four soil organic fractions, as well as the amount of soil inorganic nitrogen. Within the vegetation, both labile (readily mobilized) and structural (including enzymatic machinery and structural framework) components of foliage, stems, and fine roots are represented. For woody vegetation, the amounts of C and N in heartwood is also simulated. Younger soil organic matter including litter is divided into "extractives", "cellulose", and "lignin". Older organic matter is converted to humus.

The model was first calibrated to simulate present stocks and turnovers of carbon and nitrogen at the Arctic and Harvard Forest LTER sites (Fig. 24). We then ran simulations to examine responses to a doubling of atmospheric CO_2, a 5°C temperature rise, and an increase in N deposition. The two ecosystems had qualitatively similar responses. The small quantitative differences can be attributed to differences in the initial distribution of carbon and nitrogen between plants and soil organic matter and to differences in the amounts of wood in these two ecosystems. These simulations indicated that sustainable responses in production and biomass accumulation to any of these changes are strongly bounded by rates of nutrient recycling through soils.

In both ecosystems, linkages between the carbon and nitrogen cycles constrain responses to perturbation. Because the amounts of nitrogen imported from outside, both of these ecosystems are small relative to the nitrogen recycled internally, both ecosystems are limited in their ability to respond to perturbations by their ability to redistribute existing nitrogen within the ecosystem. The ability of these ecosystems to sequester carbon is therefore limited by their ability to move nitrogen from components with low ratios of carbon to nitrogen, such as soils and leaves, to components with high ratios of carbon to nitrogen, such as wood.

After a 50-year simulation, the sustained responses to increased CO_2 are relatively minor because of nitrogen limitation. Sustained responses to increased temperature are much larger. They lead to an increase in the nitrogen cycling rate through soils and a shift in nitrogen from the soil into the plants. When both CO_2 and temperature are increased, the responses are dominated by the temperature effect on nitrogen cycling. Responses of vegetation to nitrogen fertilization are constrained by the immobilization of nitrogen in soil organic matter.

The overall similarities in the responses of these two ecosystems are probably associated with the large stocks of soil organic matter in both, the slow turnover of these stocks, and their dependence on the internal distribution of nitrogen.

Modeling population structure and behavior of aquatic organisms. We have developed two models of aquatic organisms to help evaluate our experimental and survey results. Our bioenergetics model predicts the growth of lake trout feeding on snails and other fish. This model, applied to our arctic lakes, accurately simulates the change in growth pattern that occurs in some individuals as they shift from feeding on snails to piscivory. This shift is not universal, however, and some individual lake trout feed on snails throughout their lives. Our model results indicate that there are severe constraints to lake trout growth unless there is an adequate forage fish available. We plan to test this prediction by adding a forage fish such as cisco to a lake with lake trout.

We have also developed models of the feeding of arctic grayling on zooplankton in lakes and drifting insects in streams. The zooplankton feeding model predicts quite accurately the decline of large-bodied zooplankton that we have measured in Toolik Lake. By using the stream model, we can determine the favored distribution of grayling in the stream depending on stream velocity, and these distributions are consistent with observations in the arctic as well as in other systems. We are also using this model to help understand the impact of predation on population regulation of drifiting insects. Depending upon assumptions of drift distance and frequency, there may be either very little or very great impact of predation on drifting insects.

IV. PROPOSED RESEARCH

We propose no drastic changes in research direction for the LTER research. The data from the long-term monitoring part of the research increase in value each year. Research on the ecosystem controls by resources vs. by grazing and predation depends, to a large degree, upon long-term manipulation experiments and we do not intend to change these. Land-water interaction research is comparatively new for the Arctic LTER and will be increased.

We also plan to do more work outside of the warm summer months, as recommended by the site review team. Most of our LTER work has been done in the summers, but there is good reason to extend the season of our observations into the early-spring periods of snowmelt and soil thaw, and the late-fall period of freezeup. We have begun this by measuring stream flow and weather year-round, and by monitoring fish populations during migration at thaw and freezeup. Highest priority for future spring and fall sampling activities is soilwater and stream chemistry as well as flow. Past research at other North Slope sites (Hobbie 1963 and others) suggests that additional research in midwinter is a low priority.

A. TERRESTRIAL RESEARCH

A major goal for the future is to integrate the terrestrial research more closely with the aquatic studies through the land/water interactions research described in section IV-D below. We also plan to continue our monitoring of annual variation of plant growth and flowering between Fairbanks and Prudhoe Bay, and monitoring of long-term changes in vegetation biomass, productivity, and species composition of tussock tundra. Our highest priority will be experimental research on top down/bottom up controls of tundra structure and function, with a particular emphasis on (1) processes affecting or dependent on element transport over the tundra landscape, and (2) carbon/nutrient interactions as controls on terrestrial carbon budgets (Fig. 15). All of these efforts are essential if we are to scale up our results to predict both nutrient inputs to aquatic systems and CO_2 and methane exchange of complex landscapes.

Ecological variability and long-term changes in terrestrial vegetation. In 1992-1998 we plan to continue the monitoring of Eriophorum vaginatum at 34 sites between Fairbanks and Prudhoe Bay, as we have done since 1976. The aim of the work is to distinguish the roles of annual climatic variation, multi-year climatic sequences, and long-term climatic averages in regulating growth and flowering of this important and often dominant arctic plant species. Our first two papers (Shaver et al. 1986, Fetcher and Shaver 1990) were focused on the shortest and longest of these three temporal scales, mainly because the length of our observations did not allow us to distinguish, for example, the effects of two or three years of exceptionally warm or cold weather. Over the next six years, we plan to focus on analysis of plant responses to such multi-year climatic sequences. We expect that the longer period of observation (by the end of 1998 we will have a 22 year-record at some sites) will explain why there is very little relationship between the current-year's weather and plant growth in many arctic species (Shaver and Kummerow 1991).

Also in 1992-1998, we plan at least one major harvest of the series of the 6 reciprocal transplant gardens we set up in 1979 and 1980, between Fairbanks and Prudhoe Bay. We have already shown (1) that ecotypic variation in leaf size is far more important than the direct effects of climate on leaf growth in Eriophorum vaginatum (Shaver et al. 1986), and (2) that ecotypes from different parts of Alaska also differ in their responsiveness to climate (Fetcher and Shaver 1990). Our next harvest will focus on ecotypic variation and responses to climate of leaf and tiller turnover patterns. The long-term goal here is to understand how genotype and environment interact to determine effects of climate on arctic plant growth.

Finally, at least twice during the next six years we plan complete harvests of vegetation biomass, production, and species composition in the same tussock tundra plots we have harvested five times since 1981. These harvests will allow us to relate the changes we observe in climate and in Eriophorum vaginatum growth and flowering to longer-term, whole-community and ecosystem-level changes. At least once we will also do complete vegetation N and P budgets, for comparison with data from 1981 (Shaver and Chapin 1991) and from 1983 and 1989 (Chapin and Shaver in prep.).

Biotic regulation by resources (bottom-up) versus regulation by herbivores/predators (top-down) in terrestrial ecosystems. We have maintained a long-term fertilizer experiment in tussock tundra at Toolik Lake since 1980 (Shaver et al. 1986), and similar experiments in six contrasting ecosystem types at our Sagavanirktok River toposequence (Shaver et al. 1990, Giblin et al. 1991) since 1986. In 1988 we established factorial fertilizer, shade, and greenhouse experiments in four major, contrasting tundra types (Shaver and Chapin 1991) at Toolik Lake. All of these experiments will be maintained in 1992-1998, with the most intensive research being done in the four-tundra comparison at Toolik Lake. Additionally, we hope to develop a soil warming experiment, at least in tussock tundra, if appropriate methods can be worked out. This work will be tightly integrated with that done under NSF grant #BSR-9019055 (Shaver, Giblin, Nadelhoffer, and Rastetter).

The aim of all of these experiments is to understand the "bottom-up" controls over production, biomass, and species composition of tundra vegetation by light, temperature, and soil nutrient availability. Our broad focus is on C/N/P resource interactions in relation to these environmental factors (Shaver et al. 1992, Fig. 15). Over the next few years, our particular focus will be on interactions between these elements in soils processes. We will maintain all of the current field experiments, including climatic and microclimatic monitoring,

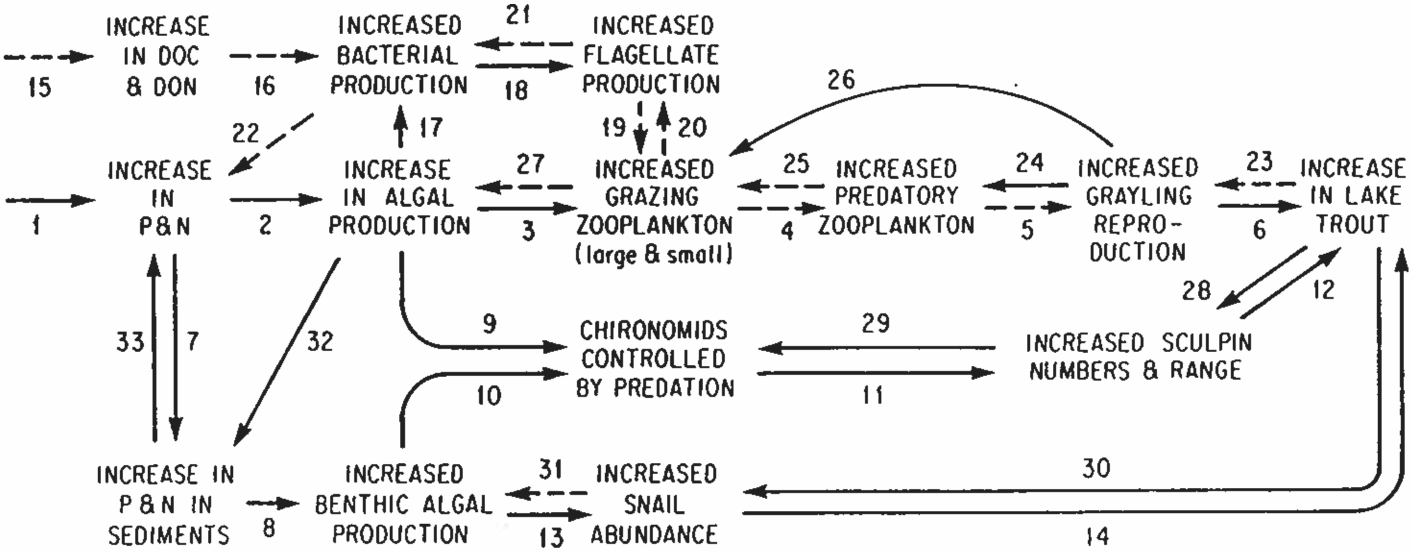

Fig. 25. Predicted responses of the Toolik Lake ecosystem to fertilization (left-to-right arrows) and to altered abundance of top predators (right-to-left arrows). Numbers beside each arrow refer to interactions under investigation in the proposed research.

monitoring of soil chemical characteristics using lysimeters, annual and seasonal KCl extracts, "buried bag" studies, and ion-exchange resin methods (Giblin et al. 1991). We will also perform two or three annual biomass/NPP harvests of these experiments over the next six years (Shaver and Chapin 1991), and measure net CO_2 and methane emissions on the experimental plots. In addition, the NSF "Landscapes" grant will support laboratory incubation studies of C/N/P interactions, using both soils alone and whole soil-plant microcosms (Nadelhoffer et al. 1991.).

The "top-down" controls of tundra ecosystems by herbivores have received little attention at Toolik Lake so far, except for a three-year study of microtines by George Batzli in the mid-1980's (Batzli and Hentonnen 1990). We plan to increase our efforts in this area in the next six years. We have already set out a number of nested, 10x10 m herbivore exclosures in tussock and heath tundra, designed to exclude sequentially microtines, ground squirrels, and caribou. We will continue monitoring these exclosures for long-term effects of herbivore exclosure on tundra vegetation. Our main goal, however, is to attract another, independently-funded research project, focused on herbivory and its effects, to Toolik Lake. To do this we have already invited Dr. J. Bryant of the Bonanza Creek LTER site to help us plan such an effort. In the summer of 1992, Bryant, Shaver, and Dr. John Pastor will lead a visit to Toolik Lake and Bonanza Creek by a group of invited experts, with the aim of developing a set of research priorities on the role of herbivory in northern ecosystems. By the spring of 1993, we hope to obtain funding for a workshop on this topic, resulting in a published review paper. Most importantly, Shaver, Bryant, and Pastor have begun discussions for a separate proposal on herbivory in northern ecosystems, including work at both Toolik Lake and Bonanza Creek.

Land/water interactions. Our primary experimental site is located immediately adjacent to our primary experimental watershed for land/water interactions studies (Figs. 20, 21). Our terrestrial research will contribute to the studies of land/water interactions by obtaining basic data on C, N, and P cycling processes and budgets in four contrasting tundra types. Details are provided in section IV-D below.

Modelling. Modelling has played and will continue to play an important role in synthesis of our terrestrial studies. The model we have been using for this purpose is a general model of carbon-nitrogen interactions (GEM) that can be used to examine the responses of terrestrial ecosystems to changes in atmospheric CO_2 concentration, irradiance, temperature, soil moisture, and inorganic nitrogen inputs

(Rastetter et al. 1991). In the next six years, this model will be modified to include interactions of the phosphorus cycle with the carbon and nitrogen cycles, to address anaerobic soil processes like methanogenesis, and to examine the consequences of a changing depth of thaw. These modifications will be guided largely by our field experiments and will in turn help to define further field studies that will be needed to understand the biogeochemistry of arctic tundra. Thus far, our analysis of GEM has suggested three key characteristics of terrestrial ecosystems that largely determine their response to disturbance: 1) Their relative dependence on internally recycled versus external sources of nitrogen and other vital elements, 2) the distribution of carbon, nitrogen, and other vital elements between vegetation and soils, and 3) the flexibility of element ratios in vegetation and soils. These three characteristics are the basis of the conceptual model (Fig. 15; Shaver et al. 1992) around which we are developing a synthesis of our 15 years of biogeochemical research in terrestrial arctic ecosystems and around which we have planned our research design for the next six years.

Because of the synthesis role of models in our LTER, they form the perfect basis from which to make comparisons between LTER sites. We have already used our GEM model to compare the responses of arctic tundra (our LTER) and northern hardwood (Harvard Forest LTER) to a doubling of CO_2, to a 5°C increase in temperature, and to N fertilization (Rastetter et al. 1991). We have also used GEM, calibrated to data from nine LTER sites, to reconstruct changes in carbon storage resulting from changes in CO_2, temperature, and N deposition over the last 250 years (Rastetter et al. in prep, McKane et al. in prep.). The decomposition part of GEM will be used to analyze the results of a cross-LTER litter decomposition study being coordinated by Mark Harmon of Oregon State University (NSF BSR91-08329).

B. LAKES RESEARCH

Overview: Our hypotheses about interactions controlling lake ecosystems are summarized in Figure 25; each interaction is numbered, and interaction numbers cited below refer to this Figure.

The continuing lake research will consist of: (1) measurements in Toolik Lake to examine the long-term changes and correlations of biota and biotic processes with physics and chemistry; (2) observations of biotic and chemical recovery from fertilization of the divided lake N-2; (3) observations of the effects of fertilization of a whole lake (Lake N-1) containing lake trout as the top predator; (4) observations of the effect of lake trout fast removal (Lake NE-12), slow removal (Lake I-8), no removal (Lake I-6), and addition (Lake S-6) on the trophic structure and dynamics.

The new lake research has four parts: (1) determine the importance of DOC and DON entering Toolik Lake (water budget, DOC+DON budget); (2) experiments to test utilization of organics and to examine control of microbial food webs; (3) demonstrate the value of a strong-interaction plankton feeder in the transference of energy to higher trophic levels (transplant least cisco (Coregonis sardinella) into a lake trout lake); and (4) test the importance of sculpin as an intermediate predator (add and remove sculpin).

Finally, to extrapolate the Toolik Lake insights to other lakes on the North Slope, we will survey other systems using a variety of methods including stable isotopes (^{13}C and ^{15}N) to determine feeding interactions and patterns of trophic structure.

Continuing research: Toolik Lake (Interactions #2, 22-26, 28-31 of Fig. 25) We will continue monitoring the aquatic organisms in Toolik Lake, the reference lake that we began studying in 1975. As described earlier, the lake is undergoing significant changes caused, we believe, by the steady removal of the top predator (lake trout) by angling. Some changes, such as the change in the size structure of the fish population and the virtual extinction of two species of large-bodied zooplankton, have been documented but need to be followed over time to see if the changes and trends continue. Eventually, the small-bodied zooplankton and even phytoplankton species, biomass, and productivity may be affected; these populations must be measured several times each year. Toolik snail and chironmid communities may also change. We also will continue to sample grayling, lake trout, and round whitefish populations, for comparison with the 1976 and 1986 surveys to understand the effect of continued sport fishing.

Lake N-2 (Interactions #7, 13, 27): Lake N-2 was divided in 1985 and has been fertilized with inorganic N+P through 1990. In 1991, we stopped fertilizing and began observing the characteristics of arctic lake recovery from eutrophication. We expect that the nutrients will continue to be regenerated from the sediments for several years. As the nutrient concentration decreases on the fertilized side, phytoplankton biomass and productivity will quickly drop to control-side levels and zooplankton numbers will return more slowly to the control-side values. Also, the abundance and growth rate of Lymnaea will decline but the response must be measured for several years because this snail is long-lived. We will continue to measure growth of tagged grayling in fertilized and control sides.

Lake N-1 (Interactions #9, 13, 20, 23, 24, 25, 31): Lake N-1 contains lake trout; fertilization began in the summer of 1990 and will continue throughout this research period. Studies on this system will answer questions about the impact of eutrophication on a lake trout lake (previous fertilization experiments were carried out on lakes with grayling only). We predict that there will be a different response from that of Lake N-2. That is, lake trout will exert such a stong top-down control that the alleviation of the resource limitation will be unimportant at the mid-levels of the food web. In lake N-1 we will measure the response of primary producers, zooplankton, benthos, and fish in the presence of lake trout. We will measure snail growth as well as density and relative abundance of species. Chironomid density is predicted to remain constant. When the zooplankton finally respond to the fertilization (probably after two years) there should be increased lake trout and grayling recruitment. Eventually, about year 3, this will give large lake trout an added food supply and increase their growth rate.

Other experimental lakes (Interactions #24, 25): We will continue to make observations in the four experimental lakes where lake trout have been added and removed. When trout are removed, we predict that grayling will move into the open water and reduce the numbers of large-bodied zooplankton and the larger snail, Lymnaea will increase at the expense of the smaller snail Valvata. Chironomids will decrease in abundance as sculpin move out on the open sediments. There will be increased recruitment of small lake trout and of grayling.

Control of the microbial food web (Interactions #16-20, 30): We will carry out more field experiments on the use of externally supplied DOC by the bacteria in the lake. These will be 2-3 week experiments in large, translucent polyethylene bags containing 10 m^3 of lake water. This water will be collected near the inlet of the lake so that it contains land-derived DOC with a delta ^{13}C of -28 o/oo. We will add $H^{13}CO_3$ so that the DOC produced from algae is labelled (delta ^{13}C of +200 o/oo) and every 5 days will analyze the ^{13}C of the bacteria to find out if the bacteria are using the fresh algal photosynthate or the incoming DOC or both. There will be fertilized and unfertilized, dark and light bags.

This experiment will also quantify the other interactions of the microbial food web. In the bags, we will make measurements each day of the bacteria and algal biomass and production, of DOC concentrations, and of numbers and feeding rates of the flagellates and their predators (ciliates, rotifers). A similar experiment has

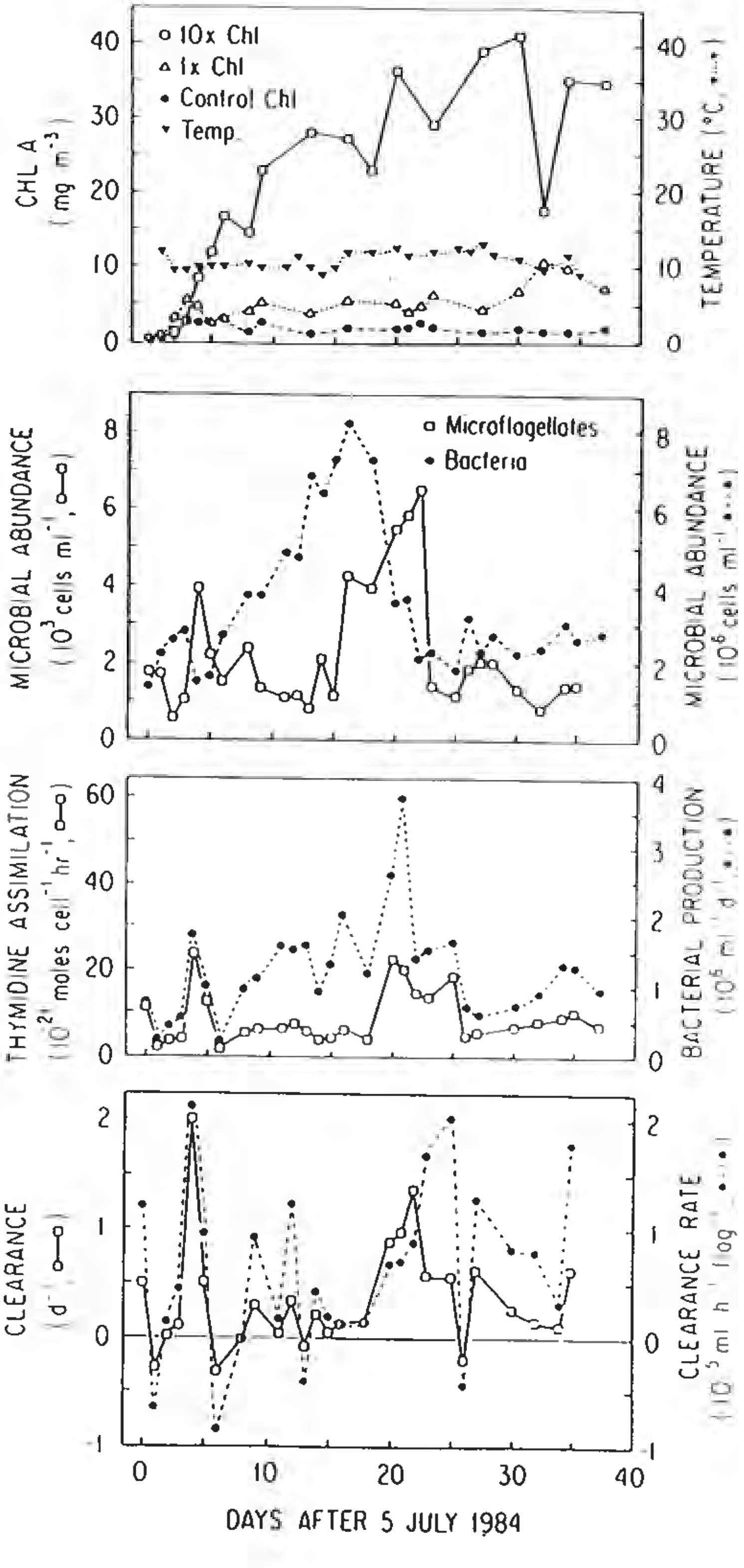

Fig. 26. Mesocosm experiments trace the effects of added nutrients. Top panel shows the concentration of chlorophyll a in limnocorrals placed in Toolik Lake in 1984. The corrals were fertilized at 1 and 10 times the rate of nutrient loading to Toolik Lake (on a square meter basis). Lower panels show changes in bacterial and flagellate numbers, thymidine assimilation, and bacterial productivity (Hobbie and Helfrich, 1988).

already been run in a different system (Fig. 26). However, arctic lakes are better systems because their lower temperatures permit a less intensive sampling schedule of once a day.

New Research: DOC+DON entering Toolik Lake (Interaction #15, 16) The overall goal is to determine the importance to the lake ecosystem of the DOC+DON entering Toolik Lake in stream water. First, we have to determine the quantity of DOC and DON entering the lake. For this we will adapt for Toolik waters a new method for determining the DOC and DON of natural waters. The technique was developed for ocean studies by Sugimura and Suzuki (1988), and summarized in Williams and Druffel (1988). In the ocean, the method has resulted in the increase of the known amounts of DOC by 500%; we do not expect errors of this size in freshwaters but there will likely be increases of 20-50%. After the new techniques have been tested for Toolik waters, we will conduct a year-round sampling for DOC and DON concentrations to determine the extent of the differences from previous measures of Whalen and Cornwell (1985).

Second, we will measure continuously the water flow in and out of Toolik Lake. In 1991 we installed a flow-stabilizing weir which allows us to calibrate the principal inflow of Toolik Lake so that an adequate rating curve can be obtained of stage height vs. flow. The water depth in Toolik Lake is already being measured continuously with a pressure transducer and a data logger. The rating curves, stage heights, and concentrations of DOC+DON will allow us to construct an annual budget of inflow and outflow (Interaction #15). This will give us some quantification of the expected loss of DOC and DON during the passage of water through the lake.

Interaction of a plankton feeding fish with zooplankton and lake trout (Interactions #31 and 6). In this study, we will move least cisco (white fish already found in northern Alaska (Morrow 1980)) into Lake NE-14 which contains lake trout and measure the responses in the zooplankton, fish, and benthic communities. This effort will be coordinated with the Alaskan Department of Fish and Game. We predict that large-bodied zooplankton will be eliminated. Because the cisco is a very efficient zooplankton feeder, juvenile grayling will show a reduction in numbers and growth rate due to competition for food. The cisco is an excellent food for the lake trout so lake trout growth will increase. This cisco/lake trout interactions is strong and contrasts to the apparently weak interaction of lake trout feeding on grayling, snails, and young lake trout (Lake N-1 experiment). As predicted by the bioenergetics model (Fig. 27), lake trout should grow faster when feeding on

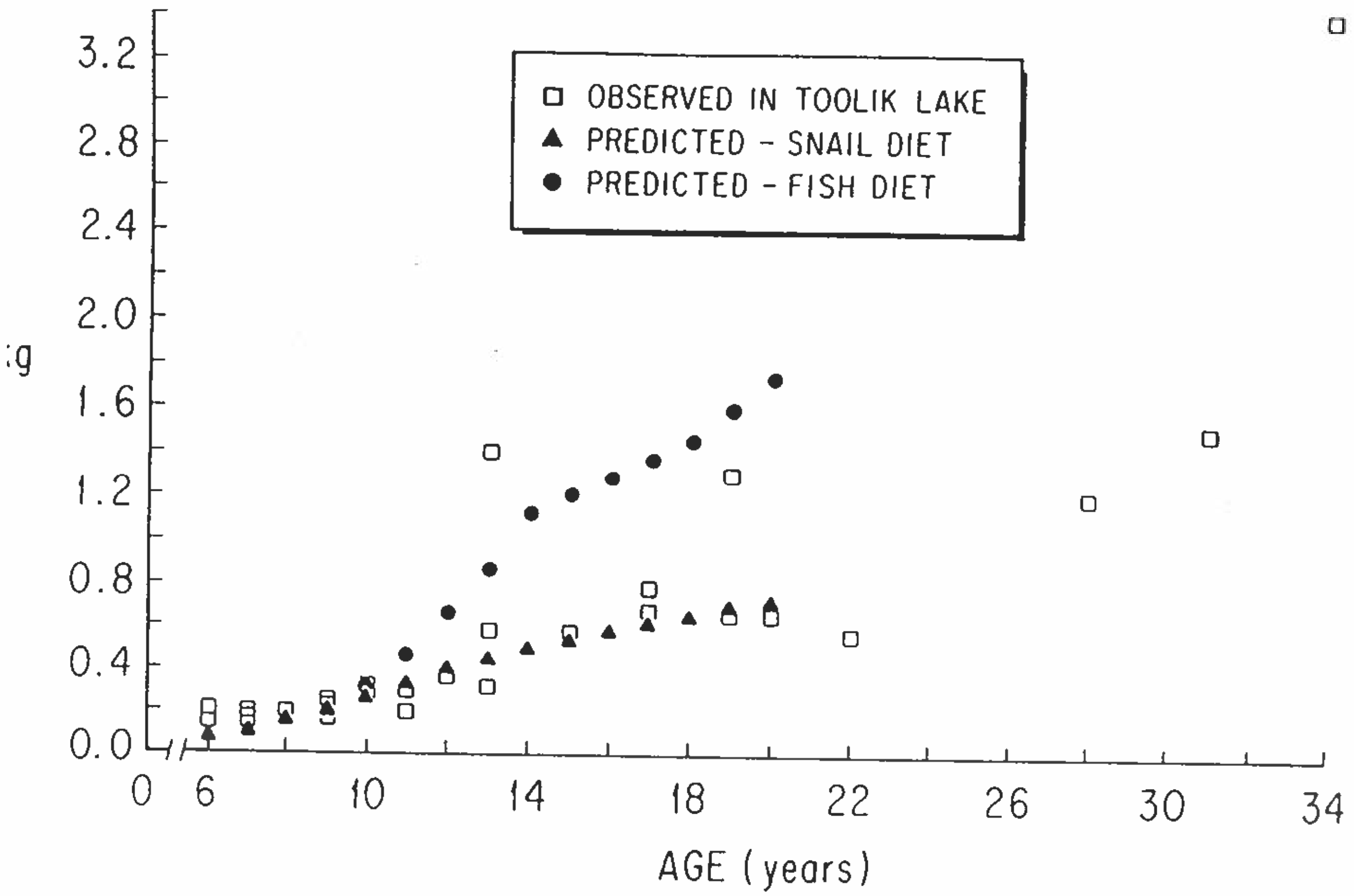

Fig. 27. Growth and condition of lake trout is highly dependent on availability of a fish forage base. Data are the weight of lake trout in Toolik Lake at various ages (squares) and the predicted weight from a bioenergetic model of lake trout growth when feeding on fish (triangles) and on snails (crosses) for the critical period from age 6 to age 20.

a fish diet than on a snail diet. As lake trout switch from feeding on snails to feeding on cisco, we also expect to see a release of Lymnaea from predation, a higher density of large snails on bare sediments, a larger body size of snails, and fewer Valvata on bare sediments due to competition with Lymnaea. Sculpin may also be released from predation and become more abundant on bare sediments.

Sculpin as an intermediate predator (Interaction #24). The sculpin control of chironomid density has been experimentally demonstrated in exclusion cages (Hershey 1985a) and in studies in lakes comparing the relative densities of chironomids and sculpin (Goyke 1990). We now need to confirm the experimental results at a larger scale. We propose to test the sculpin control of chironomids by both removing sculpin from one lake (Lake N-3) and by introducing sculpin into a sculpin-free lake with high densities of chironomids (Lake E-1).

We predict that in Lake N-3 chironomid density will increase initially. The longer lived predatory chironomids will increase in importance in two years and then chironomid density will decline. In Lake E-1, the introduced sculpin will have faster growth rates than sculpin in other lakes. Chironomid larval density will decline in the first year and there will be a lower proportion of predatory chironomids, and chironomid emergence will decline.

C. STREAMS RESEARCH

The streams research will consist of (1) continuing monitoring of the Kuparuk River to examine long-term variability and to study the pattern of recovery from long-term fertilization; (2) observations of the pattern of biotic responses to fertilization of a second river, Oksrukuyik Creek; (3) a study of the ecosystem effects of experimental removal of the dominant component of the insect community, black flies, (4) studies of the role of invertebrate and vertebrate predators in arctic rivers and (5) a studies of the flow of nutrient and organic matter in rivers.

Kuparuk River Basic Observations and Fertilization. We plan to initiate a study of recovery from fertilization in the Kuparuk in 1992. The river has been fertilized every summer for the past 9 years. In 1992 and beyond no nutrient would be added to the Kuparuk but our standard observations would continue at transects of stations in both control and recovery reaches. Investigation of the causes of year to year variability in algal, insect and fish production as related to factors independent of fertilization will go on through continued sampling in the control reach.

The standard sets of measurements to be continued in both control and fertilized reaches include nutrient concentrations, chlorophyll, organic carbon and organic nitrogen in the epilithon, primary productivity and nitrogen uptake, insect abundance and production, and both young-of-the-year and adult grayling growth. In addition to these sets of observations, stream stage (later converted to flow) is monitored with a pressure sensor and temperature is recorded year-round. Samples are taken weekly for pH, alkalinity, chlorophyll, major cations and anions, iron, aluminum, DOC, DON, POC and PON to monitor export from the entire watershed.

Fertilization of a Second River, Oksrukuyik Creek. Oksrukuyik Creek is our second river for experimental fertilization. This stream is 3rd rather than 4th order with discharge about half as great as the Kuparuk. Oksrukuyik Creek also drains a watershed dominated by lakes rather than stream channels and in consequence the variation in discharge is damped and water quality modified by lake passage. It has a similar set of dominant fishes and insects, but it also has an abundant and large invertebrate predator, Ryacophila, which may affect the response of the insect community to fertilization. For these reasons, we view Oksrukuyik Creek as representative of a somewhat different class of tundra river from the Kuparuk.

We began adding phosphorus (as phosphoric acid) to Oksrukuyik Creek in 1991 and propose to continue this fertilization at a mean concentration of $10 \mu g \ P \ l^{-1}$ above ambient for the next six years. We expect the pattern of responses to be broadly similar to those we have observed in the Kuparuk. Specifically we predict: (1) epilithic algal biomass will increase in years 1 and 2 but may be controlled by grazing in years 3 and beyond; (2) insect growth will be stimulated for all species, but total secondary production will not increase because an increase in Brachycentrus will cause a decline in black fly abundance; (3) growth of young-of-the-year and adult grayling will be increased, lipid stores will be increased in adults, and swimming speeds of young-of-the-year grayling will be increased.

Black fly removal. We propose to remove black flies from a river reach in the Oksrukuyik Creek (10 km below the fertilized site). Because black flies may significantly reduce seston concentrations in the water (Maciolek and Tunzi 1968, Merritt et al. 1984, Hart 1986, Morrin et al. 1988) and interact with other grazing and filtering invertebrates (e.g., Hart 1986), removal of black flies may have major implications for downstream transport of nutrients and utilization of limiting food within the invertebrate community.

Black flies will be removed by treating a reach with the bacteria Bacillus thuringiensis var. israefensis (BTI). BTI is highly specific for simulid larvae and mosquitoes and should not affect any other insects (Lynch and Hobbie 1988). We predict (1) that black fly removal will result in higher seston concentration during periods of low discharge; (2) that removal of black flies will result in higher density of small chironomids, Orthocladius, and Baetis but no change in Brachycentrus density; (3) that black fly removal will increase growth of both young-of-the-year and adult grayling.

We will monitor a control reach consisting of 3 pool/riffle areas upstream of the BTI addition point, and 3 pool/riffle areas downstream as the treatment. Control and treatment reaches will be monitored for nutrients, epilithic chlorophyll, primary production, insects, young-of-the-year grayling and adult grayling growth as in the Kuparuk.

Testing the role of invertebrate predation in arctic streams. The Kuparuk River does not have an abundant invertebrate predator although a few Ryacophila have been collected. In contrast, Oksrukuyik Creek has a much higher abundance of Ryacophila. We propose an experimental approach to define the role of this potentially key species in the riverine food web. We will measure predation rates and prey preferences in stream microcosms. We predict (1) that Ryacophila will eat relatively more Orthocladius and black flies than Baetis, and (2) that Baetis will effectively avoid Ryacophila by drifting. We also will estimate the predation on Ryacophila by fish by comparing gut contents of grayling in Oksrukuyik Creek and the Kuparuk River. As a further test we will experimentally increase grayling abundance 5-fold in sections of both the fertilized and control reaches in Oksrukuyik Creek. We predict that Ryacophila and Orthocladius density will decline in the reach with increased grayling abundance.

Testing the role of fish predation. Adult grayling in the stream are primarily insect drift feeders, although they also forage on pool bottoms. Young-of-the-year (YOY) grayling feed first on small chironomids in pool margins then move out into gentle currents where they take larger drifting prey. We propose a combination of field and laboratory work to evaluate the importance of fish predation in arctic streams. We will increase the density of adult grayling to 5 times ambient density in short sections of both the control and fertilized reaches of Oksrukuyik Creek and compare the drift community in the ambient and high density reaches. We predict that Baetis and Orthocladius will decline in abundance in the drift in the high density zone. We will also do short-term caging experiments with YOY grayling in the shallow margins of pools to determine if they control densities of small chironomids. We predict that small chironomid abundance will be reduced in

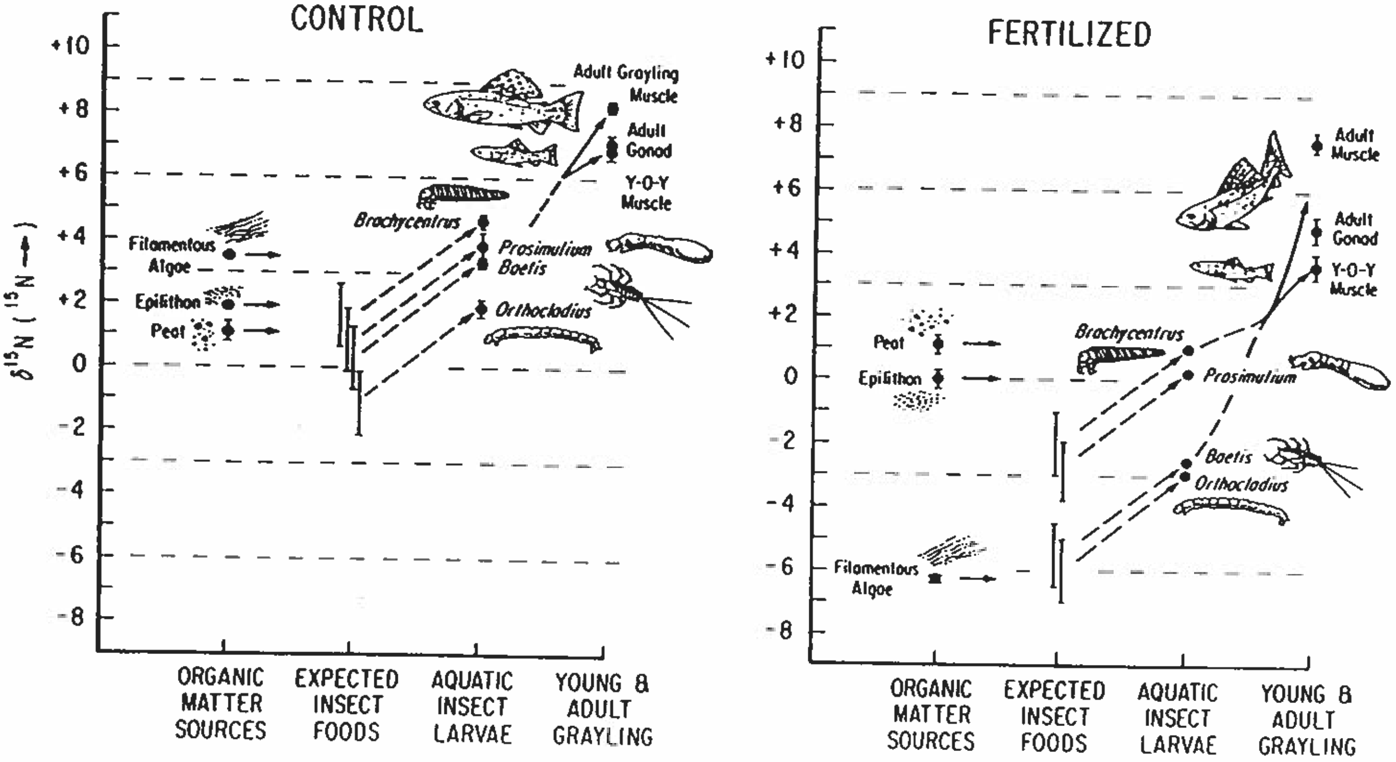

Fig. 28. Changes in nitrogen isotope composition of organisms in the Kuparuk river following nutrient fertilization. The mayfly Baetis was observed to strongly graze new algal production in the fertilized stream reach. This was confirmed by shifts in $\delta\ ^{15}N$ of Baetis and indirectly because the chironomid Orthocladius has similar $\delta\ ^{15}N$ values and is known to feed on diatoms. This also shows that the dependence of Baetis on nitrogen from peat or detritus is weak. In the control reach the $\delta\ ^{15}N$ values of the insects are closely grouped and similar to several potential nitrogen sources. We propose to label the algae with N^{15} in the control reach to determine the pathways of nitrogen flow for comparison with the pathways of nitrogen flow for comparison with the pathways in the fertilized reach.

the pool margins by YOY grayling. As a test of the impact of YOY on drift, later in the summer, we will remove all the YOY from pool/riffle areas and measure the immediate effects this removal has on drift. We predict that YOY consume a significant fraction of drifting Baetis and chironomids and the drift will immmediately increase following their removal.

Determining the fluxes of C and N with isotopic tracers. We propose to examine with isotope tracers the important trophic interactions among organisms in arctic rivers. The food of Brachycentrus and the black fly Prosimulium in the fertilized reach consists of a mixture of algae and peat (Fig. 28). The chironomid Orthocladius has as its main food the diatom Hannae arcus that grows on the chironomid tube. Because algal growth is strongly stimulated by fertilization, we predict a greater relative dependence on algae in the fertilized reach compared to the control reach of the river. In order to test this prediction we will analyze and compare these insects for ^{15}N, ^{13}C, and ^{14}C content in the control and fertilized reaches.

In the control reach, however, the naturally occurring stable isotope values do not provide a powerful tracer because the isotope compositions of the potential foods are very similar to each other (Fig. 28). In order to resolve this problem, in 1991 we added NH_4- ^{15}N at a tracer level (not a fertilization) to the control reach of the Kuparuk River in order to determine trophic interactions in the control reach (Fig. 29). By adding a label of ^{15}N to the river we traced the uptake of ammonium by algae and the fate of algal production. We found (1) a large ^{15}N enrichment in epilithic filamentous algae, (2) a rapid subsequent enrichment in the grazers Baetis and Orthocladius, (3) a much smaller ^{15}N enrichment in Prosimulium and Brachycentrus, and (4) a significant ^{15}N enrichment in YOY and adult grayling.

This experiment has allowed us to model the flow of N in the control reach and to compare the trophic structure in the control reach to that determined previously with natural abundance isotopic tracers for the fertilized reach. We propose to apply a similar approach to determining nitrogen transport, spiralling, and trophic structure in the control and fertilized reaches of Oksrukuyik Creek. We surveyed the Oksrukuyik Creek biota in 1991 for stable isotope distributions upstream and downstream of the P addition site. In 1992, we will add ^{15}N enriched ammonium at a tracer level to Oksrukuyik Creek to determine the flow of this added N downstream and through the food web.

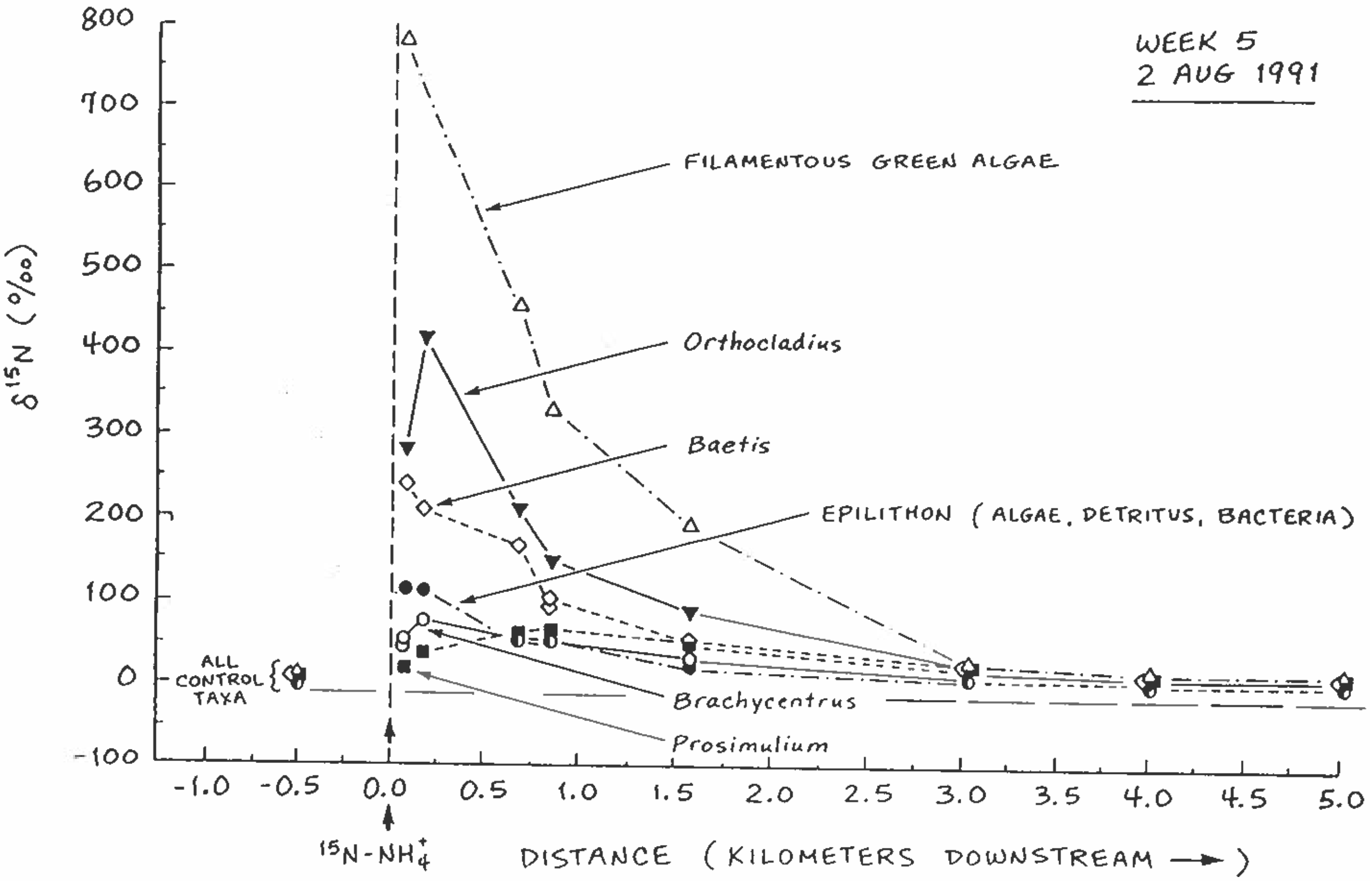

Fig. 29. The downstream distributions of $\delta\ ^{15}N$ values for algae, epilithon and insects after 5 weeks of continuous addition of trace level $^{15}N-NH_4$. By this time all taxa were uniformly labelled. The shapes of the distributions for autotrophs reflect the travel distance of added ^{15}N. Grazers of diatoms and epilithon show similar profiles but with different ^{15}N content reflecting their different diets. Baetis and Brachycentrus have different downstream $\delta\ ^{15}N$ distribution reflecting a filtering rather than grazing mode of feeding and lower ^{15}N contents reflecting a dependence unlabelled food (imported as fine particulate matter) from upstream. The tracer is easily detectable in all taxa 5 km downstream although the scale here obscures that fact.

D. LAND-WATER INTERACTIONS RESEARCH

Overview: To achieve one of our major long-term objectives of understanding controls of water and nutrient flux at the whole watershed and regional levels, we must strengthen our research on land-water interactions. To achieve this objective, we will need a simulation model that incorporates hydrological factors, soil and terrestrial ecology factors, and aquatic ecology factors. We planning on cooperation with arctic hydrologists such as D. Kane and L. Hinzman who have worked in the Toolik Lake area and are expected to play a role in the upcoming ARCSS program. A preliminary meeting on research coordination was held in Boulder, Colorada in January 1991; attendees included Hobbie, Peterson, Rastetter, and Shaver of the Arctic LTER, D. Kane, D. and M. Walker, and G. Hornberger.

The research we propose here addresses five major questions:

1. What is the basic hydrologic budget of our study site and its watersheds?
2. What is the role of various landscape units in determining the amount and chemistry of water flowing from land to rivers and lakes?
3. What is the specific role of the riparian zone in modifying the chemistry of water and the amount of allochthonous organic matter entering rivers and lakes?
4. What is the role of rivers and lakes in retaining and transforming organic matter and nutrients as they move downstream through a drainage?
5. How do landscape units, the riparian zone, rivers, and lakes interact to determine the structure and function of downstream aquatic ecosystems?

From our history of experiments of nutrient fertilization of lakes and rivers, we know that lake and stream biota are very responsive to both short and long term changes in phosphorus and nitrogen supply. Thus we have a large amount of information on the last question (#5). Our previous work on the chemistry of soil and soil water and the nitrogen and phosphorus turnover in soils gives a good starting point for expecting that different terrestrial ecosystems will yield very different quality runoff water. In the next 6 years of research, we need to determine the relationships between larger landscape units (up to say 0.1 to 1 km^2) and water quality of runoff, the role of the riparian zone, and the role of river reaches and lakes in processing water, organic matter, and nutrient inputs from terrestrial systems. Thus we plan to focus on questions 1, 2, 3 and 4.

(1) Tundra hydrology. To pursue our goal of understanding land-water interactions, we must quantify water movement across the tundra. We will do this with a combination of field monitoring, field experiments, and modelling. Much of this work will be done with consultation from Dr. Doug Kane of the University of Alaska who has separate funding to build a highly detailed, soil-process hydrological model for Imnaviat creek, a tributary of the Kuparuk within our study area. We will be using Dr. Kane's model and data to evaluate our own models and to guide our field efforts.

Discharge following snow melt in the spring is the largest single hydrologic event on the tundra and contributes most of the annual P input to lake ecosystems. However, soils are generally frozen during this event and rainfall later in the growing season is probably more important from the perspective of nutrient movement through terrestrial ecosystems. We will measure waterflow and its chemistry during both the spring thaw and the summer growing season, through to the fall freezup.

Snow depth are being surveyed by D. Kane and D. Walker for the Imnavait creek area, and have been since 1985 by Carl Benson and colleagues. We will use these data, in conjunction with the topographic maps being developed by D. Walker of the University of Colorado (Frontispiece, Figs. 20, 21) to develop a statistical model relating snow depth to topography. With this model we can extrapolate snow fall measurements from the small Imnaviat Creek watershed to the scale of the Toolik and Kuparuk watersheds.

We already monitor rainfall at two sites near Toolik lake and at three sites within the Kuparuk watershed. Because most rainfall on the tundra is associated with weather fronts and not with convective storms, the spatial heterogeneity of rainfall is less problematic than snow redistribution.

To quantify the movement of water, nutrients and dissolved organic matter through the soils we plan to modify the TOPMODEL of Beven and Kirkby (1979) to accommodate solute transport. This is a highly aggregated, topographically-based model that is **calibrated** based on discharge. We already have the digital elevation model (DEM) and record of stream flow needed to implement TOPMODEL. We plan to make extensive comparisons between this model and the more detailed, process-based model being developed by Dr. Kane. To validate our model, we will use groundwater wells and suction lysimeters already installed in our experimental watersheds. As described below, we also will be using an inert tracer (SF_6) and stable isotope measurements to assay nutrient and organic matter sources and flows.

The flow of water in streams and rivers has been monitored for several years. We have stream gauges in place at the inlet to Toolik Lake, in the Kuparuk River where it passes under the haul road, at the discharge of one of the headwater lakes on the Kuparuk, on the Oksrukuyik River, and in our primary experimental watershed feeding Toolik Lake. For several streams we already have cross-sectional flow diagrams in pools and riffles, estimates of downstream travel time for particles, estimates of mixing between hyporheic and stream water, and estimates of lateral seepage and base flow. More gauges will be added as needed to calibrate and test our models.

Finally, the hydrology of lakes will need to be quantified. We already monitor the chemistry and thermal structure of Toolik Lake on a weekly basis during the spring and summer, and lake height and temperature at 2 m depth hourly through the entire year. From previous years we have estimates of total water inflow and outflow, water turnover time, thermal stratification, thaw and freezeup, and annual nutrient budgets. We need to partition the total inflow into different sources (streams, seepage, watertracks) and increase the spatial detail on the path of water movement through the lake. We will further quantify water movement and chemistry in Toolik Lake by developing a simple stratification model based on the DYRESM model of Imberger and Patterson (1981).

(2) Determinants of the chemistry of water entering streams and lakes. We will test our expectation that time since glaciation, soil type, slope, aspect, and vegetation cover affect stream water chemistry by sampling selected lower order streams in the Toolik Lake, Kuparuk River and Oksrukuyik Creek watersheds. Pilot studies have demonstrated that the chemistry of different tributaries is similar for phosphorus but very different for nitrate and ammonium. For the Toolik Lake and the Kuparuk watersheds, Skip Walker et al. are developing GIS-based maps of terrain, soil, and vegetation (Frontispiece, Figs. 20, 21). These maps will allow us to obtain quantitative slope, aspect, soil, geologic substrate, and vegetation cover type estimates for small tributary watersheds. The development of the maps will allow us to take the next step by relating water chemistry to characteristics of the tributary watershed. From previous surveys (Kling et al. in press), we will select 20 tributaries for monitoring (3 times/summer). Water chemistry will include pH, alkalinity, CO_2, SRP, NO_3, and NH_4. We also will determine soil minerals on each site, with special reference to carbonates to determine their potential importance as carbon inputs to soil water. On selected samples major ions, aluminum, iron, TDP, TDN, and DOC will be analyzed as well. Special sites near Atigun Pass in the mountains, near Sagwon on very old glaciated surfaces, and on the coastal plain with and without loess (high vs. low pH) will be added to supplement our intensive studies of small watersheds in the Toolik area.

Our second area of proposed research on the controls of water chemistry focuses on the transport and transformation of nutrients and dissolved carbon at the watershed level. We know, for example, that nitrogen mineralization and transformations such as nitrification are dependent on vegetation type and topographic location. In addition, there is evidence of preferential uptake of NH_4, NO_3, or DON by different plant species. We will test how these controls on nitrogen chemistry interact across vegetation types and landscape positions by adding tracer amounts of $^{15}NH_4$ to our small experimental watershed. We will measure the uptake of ^{15}N by vegetation, its chemical transformation, and its net flux from upland soils into the primary stream in this gauged watershed. At the same time we will add a biologically inert chemical tracer (Sulfur hexafloride, SF_6) as a dissolved gas to the upper watershed. Although we have previously determined the approximate magnitude of excess CO_2 and CH_4 flux from surface waters to the atmosphere across the North Slope, we have a poor understanding of the processes controlling the rates of lateral transport of these gases from land to water. The SF_6 will function as a conservative indicator of the partitioning of dissolved gases between downslope transport in soil water and vertical flux into the unsaturated zone and subsequently to the atmosphere. From this information on transport pathways we will determine how the balance of nutrient and carbon production, transformation, and loss affects the chemistry of waters delivered to aquatic systems.

(3) Riparian dynamics. We propose to examine the specific influence of the riparian zone on nutrient dynamics and transport by installing wells and lysimeters along transects through distinct riparian communities (e.g., high cut banks without riparian vegetation, low flat banks with moss-sedge communities, birch-willow communities, and bare gravel-cobble). We will measure NH_4, NO_3, DON, N_2O, SRP, TDP, DIC, and DOC three times each summer. At least a portion of the samples will be analyzed more completely, including pH, alkalinity, major ions, iron, and manganese to provide information for future biogeochemical modeling.

We also hypothesize that important chemical changes occur in the hyporheic zone of the river. To test this we will continue and expand our sampling of the hyporheic zone in a series of riffle and pool bottoms. We also propose to measure winter temperatures beneath pools and riffles with a series of thermistors. This is

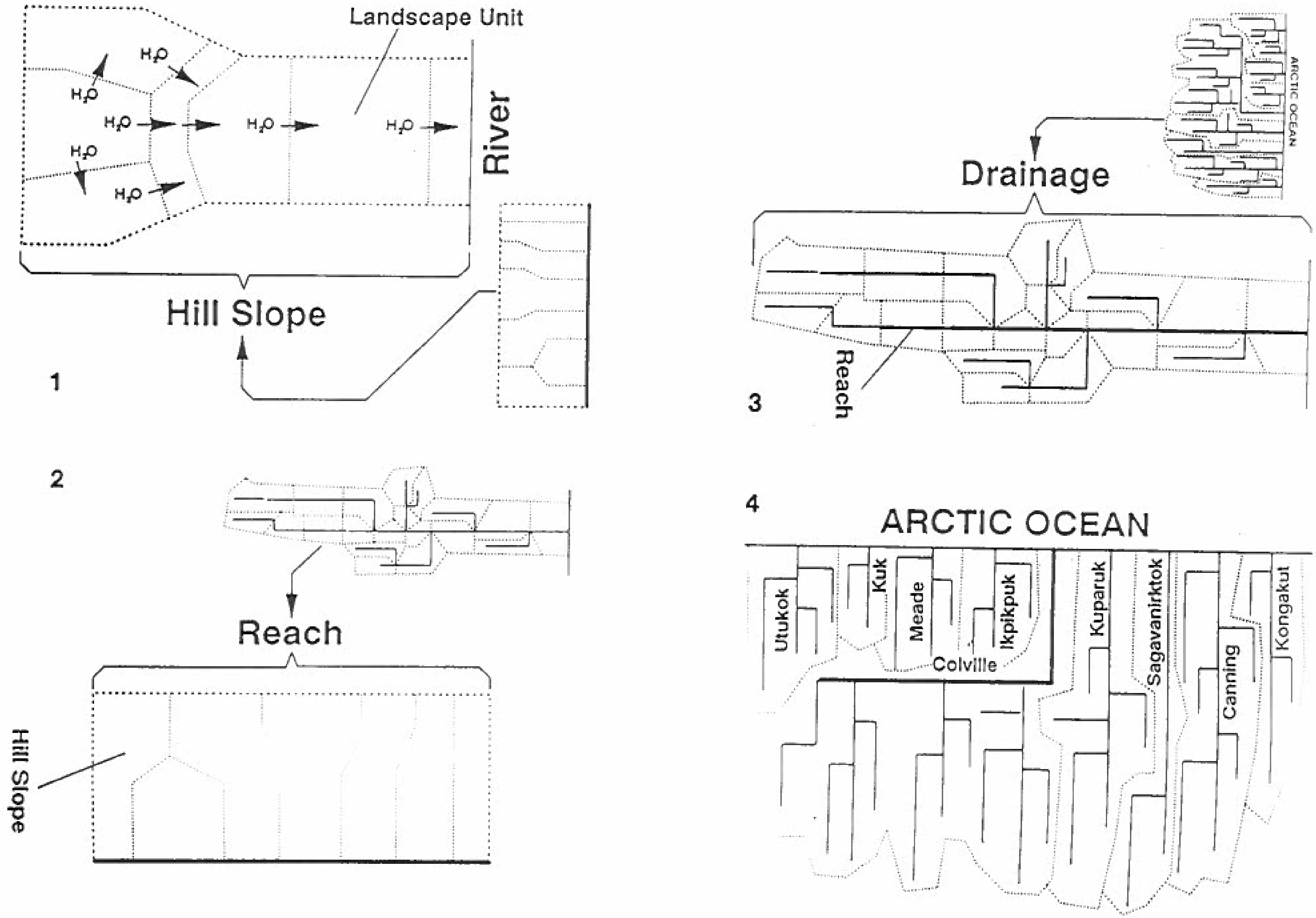

Figure 30. Conceptual framework for development of a nested series of hillslope-to-large watershed models of the biogeochemistry of the North Slope of Alaska. (1) Hillslope model; (2) River reach model; (3) Large river drainage model (e.g., the entire Kuparuk); (4) Multiple-drainage, regional model.

needed to define the seasonal extent of water seepage beneath the river channel and to determine the temperature regime experienced by overwintering insects. We already have in place data loggers used for meteorological studies that can record this information.

__(4) The role of lakes in modifying catchment inputs__. Our intensive study watersheds contain several natural experiments on the role of lakes in controlling and modifying organic matter and nutrient flow in drainages. The Toolik Lake watershed consists of a series of lakes, and most stream reaches in that drainage receive water processed by one to several lake passages. By comparing input and output of organic matter and nutrients in this series of lakes, we can determine the net effect of these lakes on stream water chemistry. The watershed of Oksrukuyik Creek is even more dominated by lakes than the Toolik Lake watershed. In contrast, the Kuparuk River study site is little influenced by lakes as less than 20% of the water exiting the drainage at the Haul Road has passed through lakes. By comparing the discharge, water chemistry, morphology and biological characteristics of these watersheds and river reaches we will gain an understanding of the effect that lakes have on downstream chemistry and biology.

These observations on the processing of organic matter and nutrients by lakes will be combined with experiments to determine the in-lake biotic use of terrestrially derived organic matter. For example, we know that the abundance of bacteria in Toolik Lake is far higher than expected based on the low primary production. We propose a series of bag experiments in which we will determine the within-lake use of terrestrial DOC and DON (see section on Lake Research).

__Modeling__: Modeling will play a central role in the synthesis of our research on land-water interactions. The modelling effort will proceed in parallel with the experimental research on the major questions described in detail above. The centerpiece of this modelling effort will be a hill-slope model that will simulate the downslope movement of water, nutrients, and dissolved organic matter through the various vegetation zones (units of the landscape), including the riparian zone, and into rivers and lakes (Figs. 19, 30). To build this hill-slope model, we will use our general ecosystem model (GEM) to simulate the biogeochemistry of each unit of the landscape and tie these units together with a soil-hydrological model that will move water, nutrients, and dissolved organic matter down slope (based on the TOPMODEL of Beven and Kirkby 1979). The hill-slope model will not only be able to simulate the delivery of nutrients and organic matter from terrestrial ecosystems

Table A. Research on five LTER research areas at the Arctic LTER site.

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1. Primary production, pattern and control

Tundra: primary production - biomass control by nutrients, light, temperature; exclosures to test effects of herbivores; annual and regional variation in growth and flowering; comparisons of vegetation types and sites

Streams: production control by nutrients, grazers; natural variations, seasonal, yearly, and between streams

Lakes: primary production natural variation measured seasonally, yearly, and between lakes; control of production by nutrients, grazers

2. Populations representing trophic structure, spatial and temporal distribution

Streams: trophic insights by populations of algae (chlorophyll), insects, fish; ^{15}N gives trophic level, ^{13}C gives food resources; isotope comparisons with other LTER's

Lakes: phytoplankton and benthic algae (species, chlorophyll); zooplankton, insects, molluscs, fish; ^{15}N distribution gives trophic level, ^{13}C gives food resources; isotope comparisons with other LTER's

3. Organic matter accumulation in soils and sediments, pattern and control

Tundra: organic accumulation by ^{14}C dating; decomposition in lab and field; comparative decomposition with other LTER's; effects of fertilizer and greenhouse treatments on decomposition

Lakes: sediment accumulation by ^{14}C; sediment trap studies; benthic respiration in chambers; nutrient addition effects on sedimentation and respiration; controls of sulfur accumulation, sediment cores

4. Nutrients, inorganic inputs and movement through soils and ground and surface waters

Tundra: nutrient budgets of contrasting sites; water and nutrient transport between systems on a toposequence; export of nutrients and dissolved organic matter from watershed

Streams and Lakes: output budget Kuparuk, Toolik Inlet; seasonal and yearly variations in nutrients; transformations in riparian and hyporheic zone; flux of CO_2 and CH_4 from surface waters to atmosphere; ^{18}O distributions in precip., surface waters

5. Disturbance at site, pattern and frequency

Tundra: disturbance-caused community shifts due to climate change; disturbance by road dust; species population responses; nutrient addition - short and long term effects

Streams: eutrophication responses; fishing pressure and trophic effects; extreme variations in snowmelt, discharge

Lakes: eutrophication responses; disturbance of trophic structure caused by lake trout removal; variations in discharge and resulting changes in nutrient input affect primary production

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to rivers and lakes, but will also simulate the dependence of down-slope terrestrial ecosystems on the biogeochemistry of ecosystems further up hill. We already have begun discussions with Drs. Doug Kane (U. Alaska) and George Hornberger (U. Virginia) with the aim of formulating the soil hydrology model. We hope to attract a PH.D student from Dr. Hornberger's lab to help us in developing this model.

To examine the transformation of nutrients and organic matter as they move downstream through a drainage, a model will need to be developed that ties river reaches and lakes together in a way similar to the way vegetation zones are tied together in the hill-slope model. This model will be built from three components. The first is a water-routing model, which will tie the drainage system together in much the same way as the soil-hydrological model tied the landscape units together in the hill-slope model. The second is a much simplified version of the hill-slope model to deliver water, nutrients, and organic matter to each reach of the river and each segment of lake shoreline. The final component is a model of the biogeochemistry of the aquatic systems themselves. We hope to follow the same principle of general applicability for this aquatic model as we have for our terrestrial model. This general applicability means that the same aquatic model, with different parameters, can be used to simulate the biogeochemistry of contrasting river reaches and lakes.

TWELVE TOPIC DESCRIPTION

I. RESEARCH ON FIVE CORE AREAS COMMON TO LTER SITES

The Arctic LTER project is very broad, encompassing terrestrial, stream, and lake habitats. This breadth means that all five LTER core research areas are an integral part of the research (Table A). Primary production, organic matter, and nutrients (Core areas 1, 3, and 4) are studied in all habitats. Populations (Core area 2) are examined in streams and lakes, and our plans to build up terrestrial research in this area are described in section IV-A of the main body of the proposal. Disturbances (Core area 5) due to road dust, construction-related disturbances, eutrophication, year-to-year climatic and river flow variations, and overfishing are examined in all habitats.

Table B. Long-term, whole-ecosystem experiments in tundra, streams, and lakes at the Arctic LTER site.

Terrestrial

- NP fertilizer in tussock tundra (started 1980)
- greenhouse warming, shade, fertilizer factorial (1980-1989; restarted in tussock, wet sedge, heath, and riparian tundras 1988)
- herbivore exclosure in tussock and heath tundras (started 1989)

Rivers

- P addition (Kuparuk R. started 1983, Oksrukuyik Creek started 1991)
- grayling density (Kuparuk R. started 1985, Oks. Creek started 1990)
- black fly removal (Oks. Creek planned to start in 1992)

Lakes

- Recovery from 5 years of fertilization (Lk. N-2 started in 1990)
- N + P addition in lake with lake trout (Lk. N-1 started in 1990)
- Density of lake trout
    - Slow removal in Toolik Lk. started in 1975
    - Slow removal in Lk. I-8 started in 1989
    - Fast removal in Lk. NE-12 started in 1988
    - Introduction of lake trout in Lk. S-6 started in 1988
- Density of sculpin
    - Introduction in Lk. E-1 started in 1991
    - Removal in Lk. N-3 started in 1991

II. LONG-TERM EXPERIMENTS

Experimental manipulations have been at the heart of the research approach of the Arctic LTER. The results have been presented earlier and published in a number of papers. The ongoing and planned experiments are listed in Table B.

III. LONG-TERM DATA SETS IN THE ARCTIC LTER DATABASE.

Long-term data sets are listed in Table C.

IV. DATA MANAGEMENT

Management Structure: The data manager reports to the Principal Investigator. For the past several years B.Moller (a senior research assistant with M.S.) has held this position and has been assisted by J.Pallant (programmer, half-time). A replacement for Moller is currently being sought at the same level.

Hardware. The data are stored on a 200 Megabyte hard drive in an IBM compatible computer located at the field station during the summer and in Woods Hole during the winter. Each data file is accompanied by a documentation file in a standard format. The data and documentation files are backed up on both floppy disks and the Sun Sparc Unix system in Woods Hole. The Sun Sparc machine can be accessed by Telnet. As of January 1992, there were 160 data files from 16 principal investigators entered into the database. Additional backup is done on a tape drive (40 mB). Optical disk drives for storage and transferring data are also available (CD ROM read-only, 600 MB optical disk drive read and write).

Procedures. (1) When each data and documentation file is received at the main office (MBL), it is first copied to the hard drive of the main computer. The documentation and the data are then compared to make sure they correspond. Minor changes are made only to the copy on the hard drive (leaving the original unaltered). The changes to the data file are made using a spreadsheet program (Quattro Pro) and changes to the ASCII documentation file using a word processing program (XyWrite). (2) If there are any major changes or discrepancies between the data and the documentation, the data manager contacts the principal investigator (PI). The data managers do not validate the accuracy or precision of the data (but they do try to note any large discrepancies). The PI's are responsible for making sure that the data submitted into the database is accurate.

Table C. Long-term data sets in the Arctic LTER data base

Rivers:	**Kuparuk River**	
	Discharge	1983-1991
	Nutrients	1987-1991, 1983-86
	Physics and Chemistry (pH, alkalinity, temperature, conductivity, cations and anions)	1983-87, 1988-1991
	Sestonic and epilithic chlorophyll	1983-91
	Fish growth, length and weight	1985-1991
	Insects	1989, 1988, 1990
	Isotopes	1988
	Oksrukuyik River	
	Discharge	1988-1991
	Nutrients	1991, 1989-91
	Physics and Chemistry(pH, alkalinity, temperature, conductivity, cations and anions)	1989-91
	Sestonic and epilithic chlorophyll	1989-91
	Fish growth, length and weight	1989-1991
	Insects	1989, 1991
	Isotopes	
Lakes:	**Toolik Lake**	
	Physics and Chemistry (oxygen, temperature, conductivity, pH, alkalinity, light, secchi depth, cations and anions)	1975-1981, 1983-1991
	Nutrients	1975-1981, 1983-1991
	Sestonic chlorophyll	1975-1981, 1983-1991
	Primary production	1975-1981, 1983-1991
	Zooplankton	1989, 1975-1991
	Insects	1988-1991
	Fish growth, length and weight	1986-1989
	Toolik Lake inlet discharge	
	Isotopes	1987-1989
	Lake N-2	
	Physics and Chemistry (oxygen, temperature, conductivity, pH, alkalinity, light,secchi depth, cations and anions)	1986-1989, 1991
	Nutrients	1986-1991
	Sestonic chlorophyll	1986-1989, 1990-1991
	Primary production	1986, 1988-1991
	Zooplankton	1983-1991
	Insects	1988-1991
	Fish growth, length and weight	1987-1989, 1985-87, 1990-1991
	Isotopes	1987-1989
	Lake I-8	
	Physics and Chemistry (oxygen, temperature, conductivity, pH, alkalinity, light, secchi depth, cations and anions)	1989-91, 1986
	Nutrients	1986, 1989-91
	Sestonic chlorophyll	1986, 1989-91
	Primary production	1986, 1989-91
	Zooplankton	1986, 1989-91
	Insects	1986, 1989-91
	Fish growth, length and weight	1989, 1986, 1990

(continued)

(3) After all corrections are made, the data file is translated into Paradox 3.5 (a relational database program) and locked so that no further editing can be performed on the file. (4) After the final versions of the data files are archived in the computer, they are separated according to their availability status. (5) Each scientist receives an annual update disk of the data they have entered into the databank.

Availability Status. The philosophy is that all data are available as soon as practicable. The timing of availability does vary as follows:

Type 1: Published data and "meta-data" (data about data) are available upon request

Type 2: Collective data of LTER site (usually routine measurements). Available within 1 year after data are generated.

Type 3: Data from individual investigators (experimental data). Available 1 year after the termination of the grant or earlier with permission of the investigator.

Type 4: Unusual long-term data collected by individual investigators. Available with permission of the investigator.

Procedures for Access. Upon application to the data manager, a scientist receives the files in hard copy or on disk. Files have even been successfully transferred via Internet to a Swiss project on airborne dust (data on wind speed and direction).

GIS. A new Sparc workstation is being acquired so that one station will run the GIS exclusively (ARC/INFO). The GIS is being used in two ways. First, it is used to build the data base on the distribution of vegetation (a joint DOE-R4D/LTER project carried out by D.Walker of the University of Colorado) and to build a spatial model of water flow and nutrient transfer within two drainage basins. So far Walker has completed a 1:500 GIS data base for small watersheds in the Toolik Lake and Kuparuk River watersheds and a 1:5000 GIS data base for larger sections of these watersheds (Frontispiece, Figs. 20, 21). The data bases include elevation, vegetation, and soils information.

A second use of the GIS has been in collaborations between the LTER and two other projects at the MBL that are modeling at the continental scale. Data from the LTER project have been used to calibrate the processes modeled in a terrestrial ecosystem model (TEM; Raich et al. 1991). The model interacts with the cells of a GIS of the entire Arctic at the 1/2° 1/2° scale, to predict NPP (Fig. 31). This GIS data base, which covers the globe, has been developed jointly by UNH and MBL.

Table C. (continued)

Terrestrial: mesic tussock tundra, heath, wet sedge, salix shrub sites	
Flowering data along the haul road transect	1976-1991
Nitrogen mineralization	1988-1991, 1986-1991
Weight per tiller (*Eriophorum vaginatum*)	1976-1991
Plant biomass	1982-1985, 1989, 1991
Rain chemistry (pH, nutrients)	1986-91
Weather Stations:	
Toolik Lake, Toolik mesic tussock tundra, Kuparuk crossing, Kuparuk headwaters, Sagavanirktok river heath	
Air temperature (max, min and average)	1988-1991
Wind (speed, direction)	1988-1991
Relative humidity	1988-1991
Precipitation	1988-1991
Photosynthetic active radiation (par)	1988-1991
Net radiation	1988-1991
Solar radiation	1988-1991
Soil temperature (different depths)	1988-1991
Barometric pressure	1990-1991
Toolik lake temperature	1988-1991
Toolik lake water level	1988-1991
Kuparuk river level	1988-1991

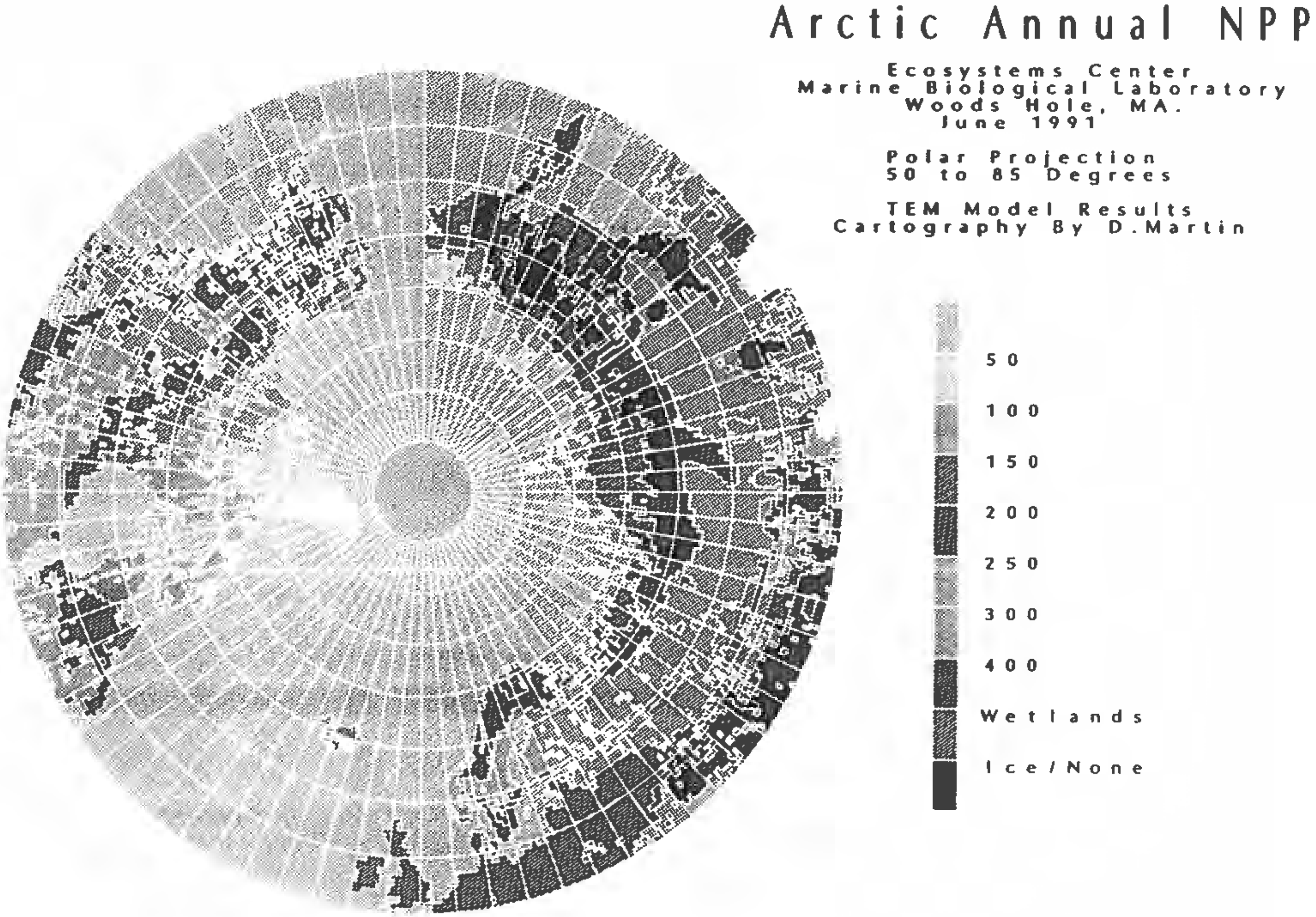

Fig. 31. Map of predicted annual net primary production of the arctic region (excepting Greenland) at a resolution of 1/2° latitude by 1/2° longitude. Predictions were developed using the TEM model (Raich et al. 1991), parameterized with data on climate, vegetation, and soils from a global data base maintained at the Marine Biological Laboratory and the University of New Hampshire.

V. SYNTHESIS AND MODELING

Synthetic activities. The LTER terrestrial research has been synthesized in a number of journal articles and chapters in books. Shaver (in press) reviewed the history of integrated ecosystem research in northern Alaska, and also edited a book on Arctic Ecosystems in a Changing Climate (Chapin et al. 1991). In the book, Shaver and Kummerow (1991) summarized phenology, resource allocation, and growth of arctic vascular plants, and Nadelhoffer et al. (1992) reviewed microbial processes and plant nutrient availability in arctic soils. Arctic data was placed in a landscape context by Shaver, Nadelhoffer, and Giblin (1991) and by Giblin et al. (1991). A paper in BioScience (Shaver et al. 1992) deals with global change and the carbon balance of arctic ecosystems.

The LTER aquatic research has been summarized by Hobbie et al. (in press). More details are given in a series of papers that will make up a special issue of Hydrobiologia (O'Brien, ed.), including 15 papers on the freshwaters around Toolik Lake. One paper (O'Brien et al. in press) summarizes control mechanisms of arctic lake ecosystems, as revealed in a multiyear limnocorral experiment in Toolik Lake. Mark Oswood of the University of Alaska is editing a book titled Alaskan Limnology. There will be chapters by O'Brien on the lakes, Hershey on the streams, and Hobbie on the history.

Finally, Hobbie, Shaver, Peterson, and O'Brien took part in an NSF-sponsored workshop in Boulder in October 1989 that synthesized current knowledge about arctic systems and suggested future research directions and led to development of a research plan for a new program sponsored by NSF, called Arctic Systems Science (ARCSS).

Modeling. Computer simulations have been developed for planktivorous fish feeding (O'Brien and Evans in press), piscivorous fish energetics (McDonald), and drift feeding (under development by O'Brien and Hershey). A simulation model of terrestrial productivity and biogeochemistry (General Ecosystem Model) has been published using an example of the Arctic LTER site and predicting changes in biomass and nutrients after 50 years of fertilization, temperature change, and CO_2 doubling (Rastetter et al. 1991). The terrestrial ecosystem model (TEM) of Raich et al. (1991), a dynamic model that interacts with a GIS, has been calibrated and run for the Arctic LTER site as a part of a project on primary productivity of North America (Fig. 31). A more general model of multiple element limitation for acclimating vegetation by Rastetter and Shaver is in press in Ecology.

We are currently beginning development of a model of land-water interactions (nutrient and water movement) in the upper Kuparuk watershed. This model will be eventually scaled-up to simulate the flow of water and nutrients in the entire river and perhaps over the entire North Slope.

VI. INTERSITE AND NETWORK ACTIVITIES

Comparative research with other LTER projects. The design for the stream fertilization manipulation of the Arctic LTER is being duplicated at the H.J. Andrews Forest LTER site. The data for stable isotope distribution in the two sites indicates that the trophic structures of the two sites are quite different so it will be informative to find out if the Andrews stream responds to fertilization in the same way as the arctic stream.

A comparison of the Arctic LTER and Harvard Forest LTER plant and soil carbon and nutrient cycling was carried out by a simulation model (GEM, Rastetter et al. 1991). The pattern of the 50 year response to changed temperature, CO_2 concentration, and nitrogen deposition was similar in the two systems despite tremendous differences in the carbon storage characteristics of the two sites (Arctic has low above-ground biomass, high amounts of soil organic matter while Harvard Forest has high above-ground biomass and low amounts of soil organic matter). The same model was used to reconstruct historical patterns (from 1750 to present) of carbon sequestration in a number of North American ecosystems including eight LTER sites (McKane and Rastetter, 1991 and in prep.).

A comparison is underway of trace gas (CO_2, CH_4 and N_2O) release from soils in the Arctic and Bonanza Creek LTER sites (K.Nadelhoffer and Joshua Schimel, funded by EPA). The study makes use of the experimental manipulations at the Arctic LTER site to examine effects of added nutrients and changed soil temperatures.

Intersite Research: Network Activities. The Arctic LTER has been the host site for three LTER workshops held at the MBL: Stable Isotopes, Soil Decomposition, and Soil Warming. The workshop on Soil Decomposition led directly to a proposal (now funded by NSF) on litter decomposition that includes about 20 sites in North and Central America. The aim of the project is to compare decomposition of standard litter types that have been distributed to all sites. A second, longer-term intersite project, on the effect of manipulation of litter inputs on long term accumulation and cycling of soil organic matter, is now in the planning stages. We are actively involved in both the litter bag study and the planning for the long-term soil organic matter study.

Our workshop on stable isotopes was also quite successful; it has led to a sharp increase in the use of stable isotopes at LTER sites and a paper (Fry 1991) detailing the stable isotope comparisons of trophic structure in LTER sites.

The Arctic LTER project also has links with research in Canada where a strong arctic limnology program is underway. During 1991, H.Kling visited Toolik Lake for a week to make comparative studies. She is the algal ecologist and taxonomic expert responsible for most of the species research in the Canadian arctic.

VII. RELATED RESEARCH PROJECTS

The Arctic LTER research is closely integrated with two separately-funded research programs (NSF-DPP, NSF-Landscapes) also based at Toolik Lake, and collaborates to various degrees with several others. This integration and collaboration includes the joint design, maintenance, and sampling of large, long-term experiments, the sharing of data, equipment, laboratories, and personnel, and the writing of books and scientific papers. In effect, LTER provides the integration, the framework, and the support for setting up and maintaining the experimental manipulations. The other projects provide salaries for principal investigators and for the detailed scientific activity such as the workup of the samples.

DPP Project on Freshwater Processes. A current project on streams and lakes, funded by NSF's Division of Polar Programs, was refunded for 3 years beginning in May 1991 ($2.5 million). The 11 P.I.'s are the same as the LTER P.I.'s excepting Giblin, Nadelhoffer, Schell, Shaver, and Fry. The goals of this project overlap with the LTER goals and it is combined with the LTER for joint administration (financially) under OPAS. The goals of the research include studies of the regulation of processes and populations by resource limitation (bottom-up control) and by predation (top-down control). A second goal is to understand the controls of the nutrient release from land to streams and lakes as well as to understand the transformations of nutrients and carbon in these waters. Experimental manipulations include nutrient addition to rivers and to lakes, the changes in numbers of fish, and removal of black flies from a stream. We will measure the quantity of nutrients entering the river from different types of tundra vegetation and the role of the riparian zone and the upstream lakes in modifying stream chemistry.

NSF-Ecosystems Project on Terrestrial Biogeochemistry. Since 1985, Shaver, Giblin, Nadelhoffer, and Rastetter have been working on an NSF-Ecosystem Studies project called "Landscapes". This group has recently been renewed (November 1991) for three years ($1.2M). The focus of their research is carbon and nutrient interactions in contrasting tundra ecosystem types, specifically in the context of global climate change. Their research will be done in close collaboration with fertilizer, greenhouse, and shade experiments established and maintained by the LTER. The work will also include controlled-environment experiments on soils, plants, and soil-plant microcosms; these experiments are designed to be complementary to the LTER field experiments.

The original focus of this group was on quantifying element transport over the tundra landscape in soil water, and on the importance of that transport to element cycling along a toposequence of contrasting ecosystem types. Since the bottom of their toposequence ended in a stream, their work has been useful in development of our current thoughts on land-water interactions and the varying importance of different terrestrial ecosystem types in regulating element inputs to aquatic systems. This group's currently-planned research on carbon and nutrient interactions includes a strong interest in controls on carbon and element losses from terrestrial to aquatic ecosystems.

EPA trace gas projects. For the next two years Knute Nadelhoffer and Josh Schimel, with funding from EPA, will be measuring CO_2, CH_4 and N_2O emissions from a variety of sites at both the Toolik Lake and the Bonanza Creek LTER sites. Results from our field experiments and our planned soil incubation experiments will help to explain the broader patterns they observe, and their results will help us greatly in extrapolating our results to other tundra and boreal forest sites. Bill Reeburgh and Steve Whalen (University of Alaska) are continuing their EPA-funded work on trace gases along the Alyeska oil pipeline, including sites near Toolik Lake and the Kuparuk River.

Mellon Project on Arctic Modeling. The Andrew W. Mellon Foundation provided partial support for a postdoctoral fellow, George Kling, to work on the LTER project during 1990-91. Dr. Kling paid special attention to the land-water interactions part of the project and carried out measurements on the movement of CO_2 and CH_4 from soils to lakes and streams and on nutrient movement through soils. The goal of this research is to lay the groundwork for modeling of the land-water interactions.

The DOE R4D Project. The scientists funded by the DOE-R4D program, also based at Toolik Lake since 1984, have now completed their research. One scientist, D.Walker, was funded both by the R4D project and by the Arctic LTER project. As part of a book synthesizing their results so far, Gus Shaver has written a review chapter on the history of integrated ecosystem research in Alaska up to 1990 (Shaver in press). More importantly we have developed a plan to apply our data to a separate series of simulation models developed by the R4D group. This will provide an independent test of conclusions based on our General Ecosystem Model (GEM). Field data, produced by the R4D group, strongly support our earlier ideas about nutrient limitation and the importance of nutrient transport between landscape units, but their data and models also suggest a more important role of soil moisture in determining landscape patterns. Soil moisture and its relationship to soil oxygen availability and respiration/mineralization linkages may provide an explanation for this contrast between their results and ours.

Arctic Systems Science (ARCSS). The ARCSS program of NSF's Division of Polar Programs is designed to investigate the interactions of global change with the processes of the whole arctic system, that is, atmosphere, ocean, and land (including freshwaters). Proposals for the Land-Atmosphere-Ice Interactions (LAII) component of ARCSS are due in March 1992. Principal investigators of the Arctic LTER have helped design the LAII-ARCSS and Hobbie and Shaver currently serve on the organizing committee. The LAII Science Plan (November 1991) identifies Toolik Lake as one of the three sites for intensive research over the next decade.

The stategy of the Arctic LTER investigators is to propose to use an ARCSS-LAII funded project to extend the findings and models of the LTER project to a regional level. The topics would be effects of change on water and nutrient flux, effects of change on aquatic communities, and effects of change on terrestrial ecosystems. In order to do this, some of the funds would go to expansion of the hydrology measurements and modeling, some funds would go to expansion of the spatial mapping (GIS) of vegetation and soils, and some would go to scaling up the LTER models to whole watersheds, whole rivers, whole regions, and perhaps to the whole Arctic. There would be additional research on hydrology and on distribution of vegetation, soils, and plants and animals over the entire North Slope. Remote sensing would be an important tool.

VIII. ARCHIVES AND INVENTORIES

Inventories and Surveys. A detailed inventory of plant species and soils on two 1 km x 1 km grids, one at the R4D site in the Kuparuk drainage and at the LTER site in the Toolik Lake drainage, has been carried out by D.Walker and M.Walker (Frontispiece, Figs. 20, 21). Some funds were provided by the LTER project for the surveying, mapping, and placement of the permanent UTM markers (every 100 m) at the Toolik site.

There have also been a large number of studies of the distribution of plants and animals and chemical factors at the LTER site. For example, O'Brien has a series of papers on the zooplankton of the area's lakes and ponds. Kling et al. (1991) report details of inorganic carbon chemistry for lakes and streams in the area. These papers are recorded in a bibliography of Toolik area papers available from the Arctic LTER office (see RESULTS FROM PRIOR NSF SUPPORT and Appendix II).

IX. LEADERSHIP, MANAGEMENT, AND ORGANIZATION

Organization of the LTER Project. Hobbie is the overall director while Shaver, Peterson, O'Brien, and Kling form an executive committee and direct the tundra, streams, lakes, and land-water interaction sections, respectively. Dr. Kling has recently been added to the executive committee both to expand the leadership and to provide training for younger scientists towards longer term leadership of the project. Interactions among the scientists are accomplished in two ways. First, all of the scientists are present at the field site for a number of weeks each summer; the small size of the camp and the isolation fosters interactions. Second, we will hold weekly seminars during the summer, we will continue to hold an annual meeting of all the scientists and staff at a central location in February or March, and the various sections will meet at least once during the year at a central location or at a scientific meeting. All P.I.'s use LTERNET.

The general philosophy of management is collegial with major decisions, such as the experiments to be carried out, being made by the entire group. The executive group of five make the day-to-day decisions. The large experiments are maintained and basic monitoring is carried out by technicians under LTER funding. Individual scientists and their students are responsible for other measurements of the results of the experiments. There is also the opportunity for individual scientists to carry out other related research along their own lines of interest.

X. NEW PROJECTS AND TECHNOLOGIES

New Projects. During the next 6 years of the Arctic LTER project, we will greatly expand the project's use of GIS. The first task is expansion of the present GIS of the upper Kuparuk drainage basin, which now includes only elevations, to include vegetation, soils, and other information needed for a watershed water and nutrient flow model. We have set the stage for this step through the continued funding of D.Walker to carry out ground-truth studies of vegetation and aerial photography in the Kuparuk and Toolik Lake basins. Some of the ARCSS project funding will go to accomplish this GIS/mapping work.

There will also be greater emphasis on hydrologic measurements needed to support the upper Kuparuk flow model and the entire watershed models. This will be accomplished mostly through the related ARCSS research proposed by the LTER investigators or through a separately funded ARCSS hydrology project. Finally, during the next 6 years we hope to promote new research on the role of terrestrial herbivores in tundra ecosystems. During the summer of 1992, in collaboration with Dr. John Bryant of the Bonanza Creek LTER, we will invite a group of experts to Toolik Lake to discuss possible new research on plant-animal interactions. Also with Dr. Bryant, we plan to develop a proposal for a workshop on "The Role of Animals in Northern Ecosystems" to be held in the spring of 1993.

New Technologies. One research area where new techniques are urgently needed is in the ecology of microbes. We propose to work to further develop the ideas of R. Coffin, now at the Gulf Breeze EPA Laboratory, on the measurement of bacterial stable isotopes through extraction of bacterial DNA/RNA and subsequent mass spectrometry. If successful, this technique would allow us to measure how much of the bacterial production in Toolik Lake is due to the input of allochthonous DOC from land and how much from autochthonous algal processes in the lake. This question of the amount of utilization of the DOC from land in aquatic systems is unanswered in any aquatic system. Drs. Peterson and Fry, investigators on this Arctic LTER project, have carried out extensive research on this method through other grants.

For any scaling up, and indeed for our whole-watershed GIS and models, we need remote sensing. Satellite data are available but the extensive cloud cover and the limited field season create many difficulties. In 1991, for example, neither the Thematic Mapper nor SPOT was able to give us a useful image. Radar is independent of cloud cover and a new tool, Synthetic Aperture Radar (SAR), has recently become available to the Arctic LTER. A ground station is now operative at Fairbanks that receives SAR data from the First European Remote Sensing Satellite, ERS-1. This particular satellite has no on-board data recorders so data will be taken only while the spacecraft is within about 3000 km of Fairbanks. Initially, the satellite will pass Toolik Lake every three days. The microwave instrument operates in the C band, illuminates a swath of about 99 km, and has a resolution of about 30 m. While the extent of usefulness to ecological studies is yet to be determined, we do know that the image is excellent for separating ice and water. Therefore, we should be able to follow the thawing of lakes in the Toolik area, and potentially of all the lakes on the North Slope, and separate deep lakes from shallow lakes through differences in the timing of the thaw. Another use will be in soil moisture and vegetation surveys although the later satellites with L band radar will be better for this. Investigators from the Arctic LTER project have applied to become investigators at the Alaska SAR Facility and the director, Dr. W.Weeks, says that there will be no difficulty in obtaining the designation or the data.

XI. DISSEMINATION OF INFORMATION

The Arctic LTER project keeps in close contact with state and federal agencies carrying out research on the North Slope. Investigators regularly visit and brief the Alaska Fish and Game agency and the U.S. Bureau of Land Management in Fairbanks. Representatives of the U.S.G.S., U.S.Park Service, and EPA attend our spring LTER meeting. We cooperate with a large EPA project on the North Slope monitoring toxic chemicals and heavy metals. We have provided U.S.G.S. scientists with Toolik information to enable them to make a proposal to add the Kuparuk River to their research network, and we measure stream discharge of Oks Creek to calibrate their stream stage recorder there. In addition, we keep in contact with the North Slope Borough through their visits to Toolik Lake and with science managers of ARCO, EXXON, and BP (several have attended our spring meeting).

We also are involved with other national and international projects. Hobbie is a scientific advisor to the U.S. Arctic Research Commission (the commissioners were briefed at Toolik by L. Deegan in August 1991). Shaver participated in an international meeting in Leningrad that led to the formation of the International Arctic Science Council. The responsible body for the IASC in the U.S. is the NAS Polar Research Board of which Hobbie is a member.

Several years ago Bruce Peterson and Linda Deegan of the Arctic LTER participated in the making of a video for Alaska Public Broadcasting (paid for by NSF). The stream research at Toolik occupied about half of the production.

XII. SUPPLEMENTAL SUPPORT

The Arctic LTER has made use of a special NSF program to establish the "Minimum Standard Installation (MSI)" for communications and data storage, to include undergraduate in the research, and to bring other NSF-funded research projects to the site. The MSI, as recommended by a subcommittee of the LTER Coordinating Committee, has been attained through three Technology Supplement grants. These have provided two Sun Workstation equivalents, a 486 computer for data storage and field use, communications packages, tape and optical storage readers and backup, and software for GIS. With these, the Arctic LTER has set up its database, has joined the Marine Biological Laboratory (MBL) and the LTERnet communication network, and has run dynamic models linked with continental-scale GIS's. The MSI has also been used extensively by three MBL investigators at the Harvard Forest LTER (Melillo, Steudler, Nadelhoffer).

The Research Education for Undergraduates program has also been used at Toolik Lake through the DPP project. Drs. Anne Hershey and Breck Bowden have both had undergraduates included in their projects to learn field and laboratory techniques. Dr. Parke Rublee of the University of North Carolina Greensboro has used the Research at Undergraduate Institutions Program of NSF to carry out cooperative research at Toolik Lake with the Arctic LTER project. His specialty is the ecology of microzooplankton.

Finally, we have encouraged several researchers to apply to the Expanded Research Opportunities at LTER sites (EROL). One group of moss taxonomists from the University of Georgia spent several weeks at Toolik in the summer of 1990. The information they provided is a valuable addition to the species distribution information for the Toolik Lake site. A second group, form the University of Washington, studied the ecophysiology of ground squirrel reproduction.

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APPENDIX 1. REVIEW OF BIOTIC REGULATION THROUGH RESOURCE LIMITATION (BOTTOM-UP) VERSUS PREDATOR LIMITATION (TOP DOWN).

The following appendix is a review of two of the major themes, top down versus bottom-up control, guiding the research in the aquatic portion of the LTER. We include this appendix because our recent reviews of this material are not yet generally available to reviewers (O'Brien, ed., in press, Peterson et al. in press, Peterson et al. submitted).

MAJOR THEME: BIOTIC REGULATION THROUGH RESOURCE LIMITATION (BOTTOM-UP)

General. Ecologists have long studied the mechanisms regulating population densities and community structure (Hairston et al. 1960, Brooks and Dodson 1965, Paine 1966). In freshwaters, regulation is mostly through resource limitation (bottom-up control) or through predator limitation (top-down control).

Lakes. The concept of bottom-up regulation of lake ecosystems began with Thienemann (1928), who first used the word "eutrophic" to describe lakes rich in plant nutrients and algae. As humans added more and more nutrients to temperate lakes through sewage and detergents, eutrophication became a management issue and the correlations were developed between nutrient supply measured as input of total phosphorus and algal growth measured as chlorophyll (Dillon and Rigler 1974, Prepas and Trew 1983). Similar, but not identical, relationships have been observed by Shortreed and Stockner (1986) and Ostrofsky and Rigler (1987) for lakes in the subarctic. While algae certainly respond to added phosphorus, a question remains about how much of the increased primary productivity is passed up the food chain.

In most lakes, the secondary production of grazers and detritivores increases with primary production. In natural lakes, a number of workers have, for example, correlated chironomid productivity with lake trophic level (Jonasson 1972, Aagaard 1978, Moore 1978). Clearer relationships have emerged from experiments such as the fertilization of Great Central Lake in British Columbia (LeBrasseur and Kennedy 1972) where increased primary productivity rates resulted and zooplankton biomass increased 10-fold. At the Cornell fertilized ponds, O'Brien and deNoyelles (1972) found that both phytoplankton production and cladoceran biomass greatly increased with added nutrients. In a similar experiment, Hall et al. (1970) found that zooplankton increased and fish production was enhanced. Yet, these relationships are not always so clear. Stockner (1984, 1986) observed in deep fertilized lakes in British Columbia that the growth of salmon fry increased without any increase in phytoplankton biomass. Smith et al. (1984) found that several lakes in the subarctic of eastern Canada did not respond at all to a doubling of the total phosphorus; they attributed this to an induced nitrogen limitation and did not examine higher trophic levels.

Arctic and subarctic lakes respond predictably to added nutrients with increased phytoplankton productivity and biomass. Meretta Lake, in the high Canadian Arctic, received sewage during ice melt and developed 10 times more chlorophyll than did nearby Char Lake (Schindler et al. 1974, Kalff and Welch 1974, Kalff et al. 1975). This eventually resulted in the disappearance of the major zooplankter. McCoy (1983) added nutrients to two shallow tundra lakes near Umiat, Alaska, and found that nitrogen alone had no effect on chlorophyll levels, phosphorus alone increased chlorophyll 10-fold, and the two nutrients together increased chlorophyll another 10-fold. Several small lakes around Saqvaqjuac near Hudson Bay were fertilized (Welch 1985, Welch et al. 1989) and showed similar responses in the phytoplankton; adding phosphorus and nitrogen together resulted in large and sustained increases in primary productivity. In a major subarctic study in northern Sweden (Persson et al. 1977, Holmgren 1984, Jansson 1978), phosphorus but not nitrogen stimulated both algal productivity and biomass. The zooplankter Bosmina responded to the fertilization but only after a lag of two years.

In some lakes, biomass at the higher trophic levels does not increase when nutrients are added. Bare Lake in Alaska, for example, received fertilizer which stimulated phytoplankton but gave no corresponding zooplankton increase (Nelson and Edmondson 1955). In the same way, fertilization of ELA Lake 226 stimulated phytoplankton but resulted in no increase in zooplankton biomass; whitefish growth rates increased and their condition and fecundity increased (Malley et al. 1977).

When studied in detail, the interactions of fish with their food become intertwined with the complex behavior and life cycles of these higher organisms. For example, most young fishes first feed upon zooplankton; for this reason the successful recruitment of a cohort may depend upon the availability of the appropriate sizes and types of zooplankton. As fish increase in size, they routinely shift up the size preference of the prey they consume (Hunter 1981) and optimal diets will include progressively larger prey (Werner 1974, 1977). A limited density of size of prey will constrain fish growth and even increase size-dependent mortality (see Crowder et al. 1987).

Streams and Rivers. In rivers, the flow of energy and especially the controls of energy flow are not as well studied as they are in lakes but in large part the same general principles apply. Productivity and community structure in rivers can be controlled from below, as for example, by supplies of available nutrient for algal growth (Stockner and Shortreed 1978, Elwood et al. 1981, Hart and Robinson 1990), or from above, as for example, when snails control algal biomass by grazing. The situation in rivers has additional complications such as the control of epilithic algae by physical factors such as scouring during high water periods. Also, in rivers allochthonous organic matter often serves as the dominant energy source for bacteria, fungi and many insects (Cummins 1974, Vannote et al. 1980, Peterson et al. 1986).

Many rivers respond to increases in nutrient loading with increases in algal biomass and in primary production, but the response varies depending on the characteristics of the system. Rivers with high sediment load or dense shading may have little algal production because of light limitation, scouring or both. Rivers with very high current velocity or highly variable discharge may have low algal biomass because of scouring or drying of rock surfaces. Primary production in temperate streams may be limited by phosphorus, by nitrogen, or by light (see review in Peterson et al. 1983). Less frequently, trace element or bicarbonate additions stimulate algal production (Dickman 1973; Wuhrmann and Eichenberger 1975; Crawford 1979). Often when nutrient additions have no stimulatory effect, it is because nutrients have already been added by man's activities in the watershed (Patrick 1966; Rodgers 1977). There are also examples of interactions between limiting factors. In several cases nitrogen has been shown to stimulate algal production only after shading vegetation has been removed (Gregory 1980, Busch 1978). Recently, Lamberti et al. (1989) determined that for a given amount of nutrient, light levels determined the productive capacity of periphyton and altered the outcome of plant-herbivore interactions. When either nitrogen or phosphorus is the primary limiting element, adding the other element can frequently result in additional growth stimulation (Stockner and Shortreed 1978, Crawford 1979, Peterson et al. 1983). Thus there is ample evidence that in many rivers nutrient supply plays a key role in limiting primary production at some time during the year.

Our knowledge of the controls of energy transfers farther up the food web is much less certain. Detritivorous insects in streams appear to be limited by food quality and temperature, rather than food quantity (Ward and Cummins 1979; Merritt et al. 1982). Stimulation of primary production can enhance growth of these insects (Peterson et al. 1985) apparently because algae are high quality food. Grazing insects in streams are also likely to be limited by the quantity of their food; for example, both Hershey et al. (1988) and Hart and Robinson (1990) found that nutrients added to a stream stimulated the growth rate of grazers. The control of the ultimate biomass of insects often depends upon the interactions of several factors including food quality and quantity, biotic interactions such as the effect of caddisflies on black fly density (Hershey and Hiltner 1988) or fish predation (Northcote 1988, Cooper et al. 1990), and abiotic factors such as flash floods (Grimm and Fisher 1989).

There are several lines of evidence which indicate that fish production in streams may be limited by food availability. Studies comparing the biomass of prey consumed to the biomass of prey available suggest that fish should be food limited in streams. For example, Allen (1951) estimated that trout consumed annually 40-150x the standing crop of invertebrates in the Horokiwi stream in New Zealand. Other investigators have made similar comparisons and found that measures of prey consumption equal or exceed prey production (e.g., Allan 1983, Mann 1965). These apparent discrepancies, known as Allen's paradox, could be explained in part by either an overestimate of fish consumption or an underestimate of prey production, but they still suggest that fish populations in some streams may be food limited. Certainly laboratory experiments on the relationship of fish growth to ration (or food availability) have indicated that increasing food supply, while holding everything else constant, will increase fish production (Hoar et al. 1979). In addition, several experimental field studies support this observation. Warren et al. (1964) observed that a 4-fold increase in invertebrate production, induced by adding sucrose to a stream, resulted in a 7-fold increase in fish production (measured as increase in weight of young-of-the-year). Mason (1976) increased the growth of young-of-the-year salmonids by supplemental feeding in a natural stream. Fish production in ponds and lakes frequently increases when nutrients are added (Hall et al. 1970, Mills 1985, LeBrasseur and Kennedy 1972), but there is little evidence for rivers. A recent experimental river fertilization of a coastal stream in British Columbia (Slaney et al. 1986) provides an interesting comparison with our Kuparuk River study. The Keough River, a steelhead and coho salmon stream, was fertilized with inorganic nutrients at five sites over two years. There was a strong response of the epilithic algae MDUL MDNM to nutrient additions especially in the shallower upstream reaches with clearer less organically-stained water. Drift samples revealed little response of the insect community to enrichment. Nonetheless, after two years, the growth of the juvenile salmonids was sharply stimulated by the fertilization.

Although fish generally grow better when given more and better quality food, physical and other factors may play a key role. Kreutzweiser (1990) found no difference in fish growth or mortality between a control stream and a stream where insects had been greatly reduced with insecticide and suggested that temperature was of overriding importance. Recent experiments with white suckers by Ahlgren (1990a) showed that fish supplemented their invertebrate diet with detritus when invertebrates became rarer. The detritus did not support growth but did prevent weight loss.

MAJOR THEME: BIOTIC REGULATION THROUGH PREDATOR LIMITATION (TOP-DOWN)

Lakes. The concept that lake ecosystems are regulated through top-down control was first put forth for plankton systems by Hrbacek (1962) and Brooks and Dodson (1965). They noted that the introduction of planktivorous fish into lakes dramatically altered the size and species composition of the zooplankton; most large zooplankton species were eliminated and replaced by small sized species. Hall et al. (1970) showed similar effects on benthic food webs in experimental ponds. Many subsequent investigators have noted the strong correlation between the presence of planktivorous fish and small size zooplankton (Nilsson and Pejler, 1973; O'Brien et al. 1979b; Post and McQueen 1987) but closer study by Dodson (1979) revealed numerous plankton communities that did not appear to be regulated by food or by predation. Recently the idea has been suggested that the cascading effect from manipulating piscivorous and planktivorous fish could reach lower trophic levels (Shapiro and Wright 1984, Carpenter et al. 1985) and even reduce algal blooms (the conceptual "saw tooth" model is that every other trophic level will be reduced). One example is that of Lake Michigan where changes in the piscivorous fish population (Stewart et al. 1981, Kitchell and Crowder 1986, Kitchell et al. 1988) likely caused changes in the forage fish community (Crowder 1986, Crowder et al. 1987), in the zooplankton community (Evans 1986, Evans and Jude 1986), in water quality (Scavia et al. 1986), and in the macrobenthos (McDonald et al. 1990).

The next step after the recognition of the effect was to determine the mechanism. Brooks and Dodson (1965) suggested that, in the absence of fish, competition was the force acting to maintain large sized species (see Hall et al. 1976 for a review to that date). But Dodson (1974) later suggested that predation from invertebrates might be more important than competition. Subsequent study has shown that invertebrate planktivores may indeed exclude small bodied zooplankton from lakes and ponds where such predators can become abundant (Neill and Peacock 1980, Kerfoot 1977, Luecke and O'Brien 1983). Thus, there is strong evidence that both vertebrate visual planktivores and invertebrate tactile planktivores can exert sufficient predation pressure on plankton food webs to eliminate vulnerable species and sizes of prey.

There is evidence that arctic plankton communities are also structured by predation. Nilsson and Pejler (1973) examined Swedish lakes and found that when very planktivorous fish species were stocked, small sized zooplankton communities developed. In the Alaskan subarctic, O'Brien (1975) found clearly delineated zooplankton communities; in most of the deep lakes planktivorous whitefish were abundant and only a small sized zooplankton community existed. In ponds where no fish occurred, however, only the predaceous copepod Heterocope and other large bodied zooplankton were found. More recently, it has been well documented that Heterocope predation is fully intense enough to exclude small bodied species (Dodson 1979, 1984, Luecke and O'Brien 1983, 1990).

It is less clear, however, to what extent these changes in zooplankton community structure and density actually cascade downward and affect phytoplankton and microbial community structures. In several studies (Hrbacek 1962, Hurlbert et al. 1972, Losos and Hetesa 1973, and Lynch and Shapiro 1981) in which high densities of planktivorous fish have been added to ponds or to enclosures in ponds, zooplankton were severely reduced and phytoplankton generally stimulated. Hrbacek et al. (1978) pointed out that reservoirs with low fish stock have much lower chlorophyll concentrations than would be predicted from the phosphorus to chlorophyll correlations of Dillon and Rigler (1974). They suggested that resulting high zooplankton densities reduced chlorophyll concentrations. In contrast, reservoirs with more normal fish stocks and zooplankton densities fit the correlation well.

Only a few studies have investigated the effects of fish removal on the entire pelagic food chain. Stenson et al. (1978) removed fish from a small Swedish lake and found that large zooplankton soon dominated the zooplankton community, that primary productivity declined by 90%, and that large phytoplankton increased in importance. In a more natural experiment, Benndorf et al. (1984) reduced planktivorous fish abundance in a small quarry pond by the addition of piscivorous fish and a definite cascading effect was seen throughout the food chain. Zooplankton biomass increased 400% with large daphnids appearing for the first time. While phytoplankton biomass in the pond remained the same, the composition of the phytoplankton community shifted predominantly to small species or to species with gelatinous coating such as Oocystis. A similar shift in phytoplankton community structure was also found by Porter (1976) who studied high densities of zooplankton in small enclosures in a pond.

Experimental work on lake benthic communities has implicated predation as an important control mechanism. When fish are removed from ponds there is generally an increase in biomass of benthic insects (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), but for infaunal chironomid communities the effect is greater on smaller-bodied individuals (Werner et al. 1983, Hershey 1985a). Susceptibility to fish predation may be determined mainly by habitat structure on lake bottoms; thus fish are not effective predators on benthic invertebrates in communities with dense macrophyte stands (Thorpe and Bergey 1981, Crowder and Cooper 1982, Gilinsky 1984, Hershey 1985a).

Fish predation on snails does appear to be important in controlling size-frequency distribution and community structure (Brown and DeVries 1985, Hershey 1990). However, fish predation may affect snail community structure without affecting biomass by causing shifts in the relative abundance of species. For example, fish which crush snails select prey based on shell strength (Stein et al. 1975, 1984, Vermeij and Covich 1978). Snail recruitment has been shown to be controlled by the feeding of mudminnows on snail eggs and juveniles (Brown and DeVries 1985). Trout also eat snails (Macan 1966, Smith 1972, Johnson 1972, Ware 1973, Tippets and Moyle 1978, O'Brien et al. 1979b, Hershey 1990), especially when a pelagic forage fish is absent (Nilsson 1972).

Streams and Rivers. For stream communities, there is good evidence for top down control of algal communities, however, evidence for control of stream insect communities by predation is mixed. Experimental evidence (reviewed below) thus far suggests that predators often do not control stream invertebrate community structure, due at least in part to the highly mobile nature of many prey species.

Both invertebrate and vertebrate grazers can control the biomass and community structure of the epilithon. Experimental manipulations of stream caddisflies have shown that these dominant grazers control not only microspatial distribution patterns (Hart 1985, 1987) but also abundance of other grazers through competition for space (Lamberti and Resh 1983; McAuliffe 1984, Lamberti et al. 1987). Grazing caddisflies aggregate in areas of high periphyton standing crop until they reduce the resource to background levels and control primary productivity by maintaining low algal standing crop and high turnover rates (Lamberti and Resh 1983, Hershey and Hiltner 1988). This control by grazing caddisflies may occur whether the stream is dominated by heterotrophic (Cummins 1974) or by autotrophic processes (Minshall 1978, Naiman 1976). Algal biomass can also be reduced by snails as has been shown for laboratory streams (Earnest 1967, McIntire 1973) and in field studies (Jacoby 1985). Where grazing fish occur, they also can control epilithic standing stock (Powers and Matthews 1983, Powers et al. 1985, Stewart 1987), while the distribution of grazing fish may be in turn controlled by predators (Powers 1984). In the Kuparuk, we have found strong effects of insect grazers on algal biomass (see below).

The importance of fish predation on the composition of aquatic invertebrate communities has been demonstrated in lakes (e.g., Brooks and Dodson 1965, O'Brien et al. 1979b, Hershey 1985a, Northcote 1988), however, in running waters the influence of fish predation is less clear. Some researchers who have experimentally examined the role of fish predation in the field (Allan 1982, Reice 1983, Flecker and Allan 1984) have shown that although fish feed heavily on stream insects, they play a minor role in determining insect abundance and diversity. Although trout (Allan 1982; Newman and Waters 1984) and sculpin (Newman and Waters 1984) are size-selective predators 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 that fish did not affect insect abundance, Bowlby and Roff (pers. comm.) found strong evidence for top-down control of benthic invertebrates in an Ontario stream. When piscivorous brown trout were present, the biomass of invertebrate feeding fish was significantly lower and the abundance of benthic invertebrates was higher than when trout were absent. Also in contrast to Allan (1982), Griffiths (1981) increased the density of trout by 3-4 fold over normal densities and found that some insect species increased in abundance, while others decreased.

In pools, significant effects of fish predation on invertebrates have been observed. Flecker (1984) found in cage experiments that fish reduced abundance of chironomids and of the stonefly Leuctra, but did not observe an effect on other invertebrates. The overall density of invertebrates was best correlated with levels of coarse particulate organic matter. Similarly, Flecker and Allan (1984) found an increase in large invertebrates when predators were absent but these large taxa were rare and so the overall impact of fish was small. Predatory invertebrates are particularly vulnerable to trout predation; trout can reduce the numbers of hemipterans and odonates (Cooper and Hemphill 1983) and gerrids (Cooper 1984). Wilzback et al. (1986), in an experiment on forested and logged stream pools, demonstrated a significant increase in drift density in pools from which trout were removed. In an experimental pool, Gilliam et al. (1989) demonstrated that juvenile creek chubs caused up to a 90% reduction in the volume of invertebrates, mostly isopods and oligochaetes. Thus, it seems fish can effect stream insect communities in pools.

Fish predation in some streams might be unimportant for several reasons. In a recent synthesis, Cooper et al. (1990) stated that predator effectiveness is inversely correlated with prey mobility in freshwater benthic communities. Their hypothesis is consistent with observations of greater effect of predators in standing rather than in moving waters and within moving waters a greater effect in pools rather than riffles. Similarly, the common observation that fish are effective predators on chironomids (Flecker 1984) and on invertebrate predators (Cooper and Hemphill 1983, Cooper 1984) is also consistent with their model because aquatic invertebrate predators tend to be less mobile than their prey. Insect drift or recolonization could compensate rapidly for local depletion due to predation (Sheldon 1984, Gilliam et al. 1989). It is also possible that fish may be feeding primarily on excess production above the invertebrate carrying capacity (Waters 1972). Fish often feed primarily on drift, and several investigators have suggested that drift rates are density-dependent indicating a benthic substrate carrying capacity that must be attained before drift will occur (Sheldon 1984). Drift rates are also higher after depletion of insect food resources or in areas with lower food availability (Kohler 1985, Sheldon 1984). Thus the impact of fish predation may only be detectable through a change in the drift community which could then influence recolonization. One explanation for the lack of effect on invertebrates is that the diel periodicity of invertebrate drift (high at night, lower during the day) serves as a temporal refuge (Waters 1972, Muller 1974) and prevents visually feeding predators from significantly depressing the abundance of prey.

Fish predation in arctic rivers is not fully understood, but temperate models may not apply due to differences in prey and physical constraints. In both the Kuparuk River and Oksrukuyik Creek, predominantly drift feeding arctic grayling is the only fish species present. Thus, temperate studies suggesting that bottom feeding fish control some prey types in pools do not apply. Unlike the situation in temperate rivers, drifting insects in arctic rivers have no refuge of darkness (Hinterleitner (1990) found no diel periodicity in the Kuparuk drift). For this reason, drift feeding fish may have more impact in the arctic than in temperate regions.

There is also an interaction between the trophic state of a stream and the importance of predation. When the Kuparuk was fertilized, there was a decrease in the drift rates of Baetis, the most abundant drifter and a key component of grayling diets. The caddis fly Brachycentrus, the other important item in the grayling diet, is not abundant in the drift except early in the summer. Because it is a large organism, it is probably disproportionately selected by grayling. Because both Baetis and Brachycentrus are more abundant in the fertilized reach, and Baetis grows larger, grayling may be feeding on more and larger insects in the drift. It is clear that grayling growth is enhanced in the fertilized reach (see Fig. 10).

In summary, the processes of resource limitation, predation, and competition are known to control both community composition and species distribution in lakes and streams. There may also be interactive effects that cascade across two or more trophic levels. These processes may operate singly or in combination. Even though these processes and the cascade effects have been identified in freshwaters, they have rarely been studied in entire ecosystems. Arctic lakes and rivers offer the advantages for study of simplicity of trophic structure and ease of manipulation.

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