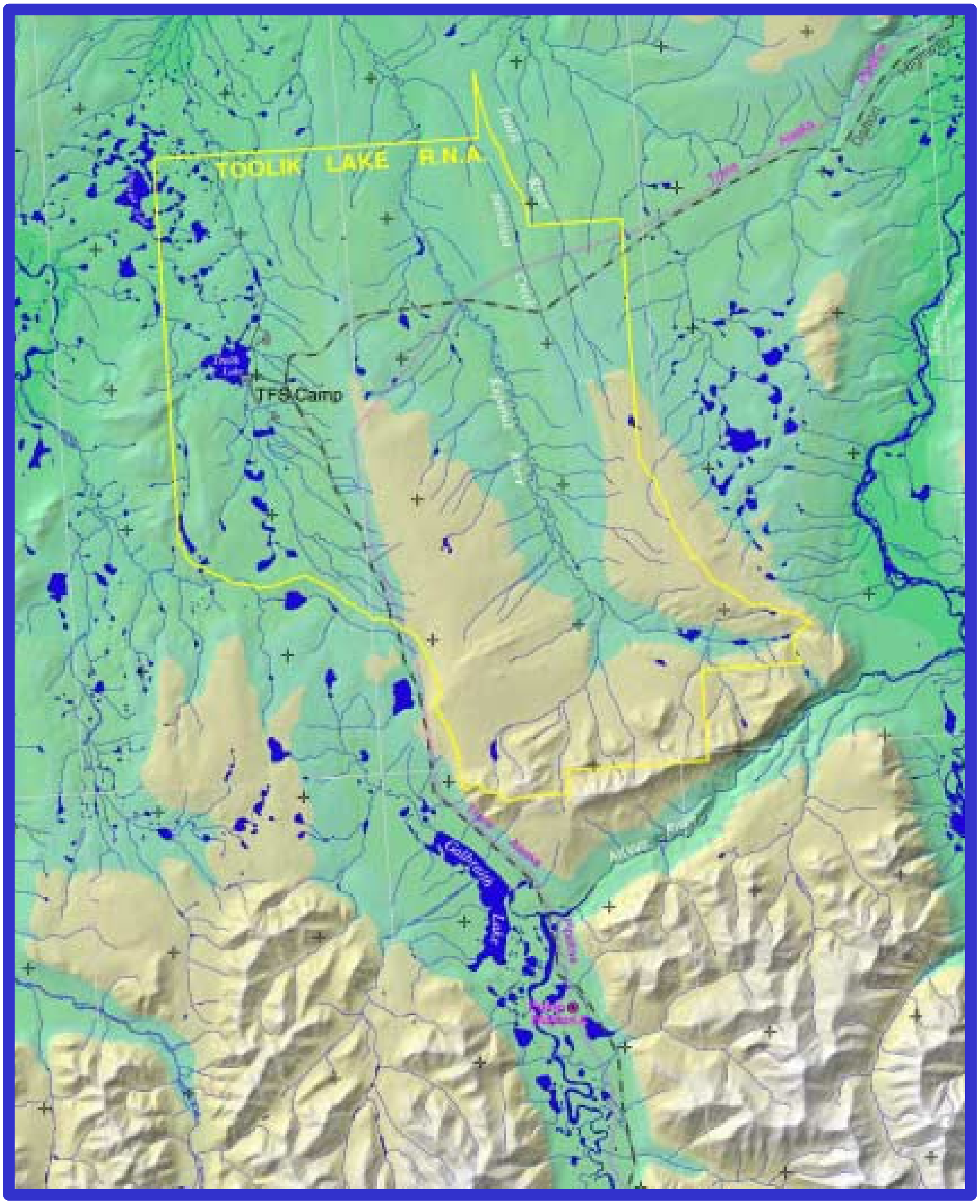


Arctic LTER 2001 Site Review

Cover: Map of Toolik Lake Research Natural Area developed from base data adapted from USGS digital data and from base data collected at Toolik Field Station by various investigators. Map layout by Andrew Balser, Toolik Field Station GIS, Institute of Arctic Biology, University of Alaska, Fairbanks.

History of Project

Immediately after World War II, the Office of Naval Research began in 1947 to sponsor research at Pt. Barrow, Alaska, in a variety of natural science fields. Eventually a large research laboratory, the Naval Arctic Research Laboratory was built (1968). Later, at the end of the 1970's, ONR ended their support and gave the laboratory buildings to the North Slope Borough, the city of Barrow, and a local college. During the more than 25 years that the laboratory existed, every conceivable aspect of the arctic environment was investigated from permafrost to the physiology of polar bears. Ecology was a major field. Dan Livingston and John Hobbie carried out Ph.D. projects on the limnology of mountain lakes in the Brooks Range; others worked on coastal ponds (e.g., Jacob Kalff). Plant ecology was investigated by Larry Bliss, Dwight Billings, and Larry Tieszen. From 1971 through 1974 one of the five U.S. IBP (International Biological Program) biome projects was carried out at Barrow under the leadership of Jerry Brown. John Hobbie led an intensive IBP project on tundra ponds (see the 1980 book on the Limnology of Tundra Ponds edited by Hobbie), Gus Shaver and Terry Chapin were graduate students on the IBP.

In 1975 NSF/Office of Polar Programs made funds available for further integrated ecological research in the Arctic. The aquatic group decided to extend their research beyond the coastal plain and mountains to lakes and rivers of the foothills; Toolik Lake was chosen as the primary site because of the size and depth of the lake and because of accessibility. The pipeline road had just opened – oil began to flow in 1976. John Hobbie, John O'Brien, and Bruce Peterson took part in this first project, based in tents and one trailer. A history of Alaskan limnology is given in Hobbie (1998) and Toolik papers were published in an issue of Hydrobiologia (O'Brien 1992). Terrestrial scientists, including Terry Chapin and Gus Shaver, began research based at the developing camp in 1979 (see history of research at Toolik Lake by Shaver (1996). The University of Alaska took over the camp management from the aquatic project in the early 1980's; the Arctic LTER project was funded in 1987. Serious NSF buildup of the camp facilities began in 1994 and continues.

The aquatic research funded by NSF's Office of Polar Programs (Arctic Natural Sciences or ANS and Arctic System Science or ARCSS), has continued since 1975 in a series of competitive grants (with the exception of two years in the early 1980's). There have also been projects funded by NSF's Division of Environmental Biology (DEB), and DOE. The terrestrial research has been funded by grants from DEB, ARCSS, and EPA.

Another large, integrated, multi-investigator project was the DOE-supported "R4D" of Response, Resistance, Resilience, and Recovery from Disturbance of tundra ecosystems, sited at a first-order watershed at Imnavait Creek, about 10 km northeast of Toolik Lake. An overall synthesis of the R4D project was published in a book (Reynolds and Tenhunen 1995). The geographic information system and landscape classification and mapping schemes developed in the R4D project (Walker, Walker and Auerbach 1994) laid the foundation for the GIS maps of the Toolik area.

Goals of the Arctic LTER

To predict the future ecological characteristics of the site based on our knowledge of the controls of ecosystem structure and function as exerted by physical setting and geologic factors, climatic factors, biotic factors, and the changes in fluxes of water and materials from land to water.

Secondary goals:

1. To describe in detail the physical, chemical, and biological environment of the Toolik Lake region
2. To monitor for change
3. To study LTER themes of primary production, nutrient fluxes, disturbance, organic matter accumulation and decomposition, organisms at higher trophic levels

The Arctic LTER Project

Organization. The LTER project has a director, John Hobbie, and five members of the Executive Committee who assume responsibility for research planning and reporting in their subject areas (Shaver, terrestrial; Kling, land/water; Peterson, streams; O'Brien, lakes; Giblin, "at large"). The "at large" position rotates. Note that it is unusual that an LTER project covers the entire landscape with four subject areas. The whole LTER meets each March; the Executive Committee more frequently. Most of the scientists take part in field meetings at Toolik Lake in early July.

Research assistants in the four subject areas are responsible for taking the field samples, making the measurements in the laboratory, and maintaining the large-scale experiments. They also oversee summer research assistants and, some times REU's. Jim Laundre, the R.A. for terrestrial ecology, also collects the climate data and serves as project data manager. The LTER budget (NSF DEB) is spent on salaries for the R.A.'s and a few months for administration, for meeting costs and travel, and for per diem costs at the Toolik Field Station (current cost is $40/day). Thus, the LTER project provides the structure of organization, experiments, monitoring measurements, and data base that facilitates the work of other projects for work at Toolik Lake.

Cooperative projects. The OPP project (ANS) titled "Aquatic Ecosystem Responses to Changes in the Environment of an Arctic Drainage Basin" is closely tied to the LTER aquatic research goals of determining the controls of processes and assembling the information into predictive models of land/water interactions, streams, and lakes. The P.I.'s at the MBL are Hobbie, Peterson, Deegan, Giblin, Vallino. Other P.I.'s receive subcontracts (O'Brien, Luecke, Kling, Huryn, Bowden, Stieglitz). These funds from OPP pay for some months of P.I. salary, for graduate students, for postdocs, and for research technicians. In actuality, these OPP funds pay for persons who carry out the modeling, data analysis, and publishing of scientific papers.

The ARCSS program of NSF OPP funds some projects that interact closely with the LTER project. Ed Rastetter and John Hobbie (MBL) use LTER data to calibrate the MBL General Ecosystem Model of terrestrial carbon cycling and storage over the entire Kuparuk River basin (~10,000 km^2) and over the next 100 years. Knute Nadelhoffer (MBL) has a project on below-ground carbon cycling and storage. Gus Shaver also has ARCSS-ITEX funding to analyze vegetation response to climate change. Marc Stieglitz is constructing a large-scale hydrology model of the Kuparuk River basin. Bruce Peterson and Charley Vörösmarty (University of New Hampshire) are studying the water and material transport in all the rivers of the pan-arctic watershed.

Shaver is lead on a cooperative project with Swedish scientists that will compare processes at Toolik with those at Abisko, Sweden (same latitude, sub-arctic birch forest).

Data Base. The web site http://ecosystems.mbl.edu/arc/. We archive data collected each year on the climate of the site and on natural and experimental systems including, lakes, streams, and terrestrial ecosystems. The 1,297 data files extend back to 1975. All these files are available to outside users -- most files without restrictions. The user should always discuss use with the provider and should acknowledge the source.

Ecology of the Toolik Region

Climate impacts The Arctic LTER site is located near Toolik Lake (68° N and 149° W) and consists of the upper Kuparuk River basin including the Toolik Lake drainage (Fig. 1). Only the three summer months have air temperatures above freezing (Fig. 2) and the precipitation is low – the summer average (three months is 188 mm) and the yearly total is ~300-400 mm. The sun is above the horizon continuously from May through most of August, which means that the there is nearly the same amount of annual solar radiation as in temperate regions.

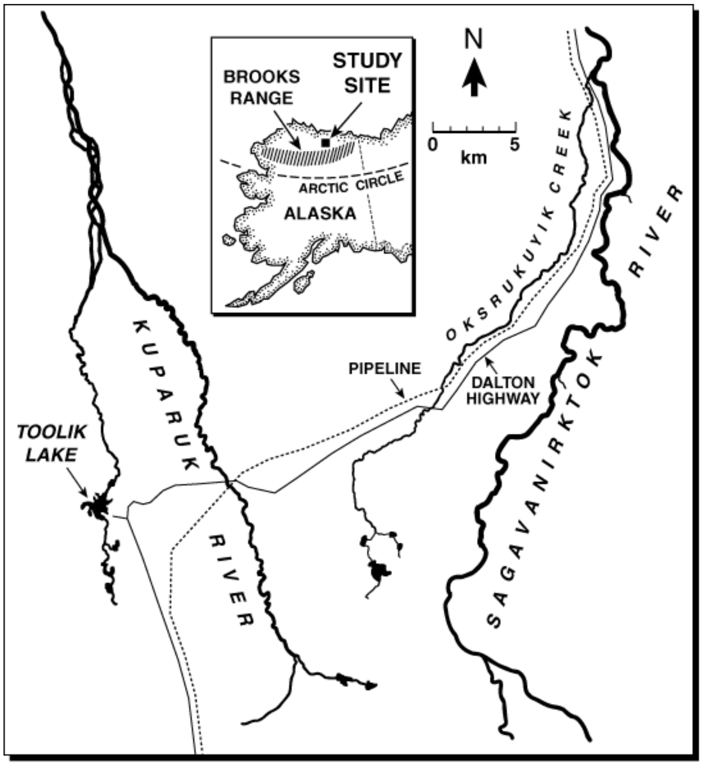
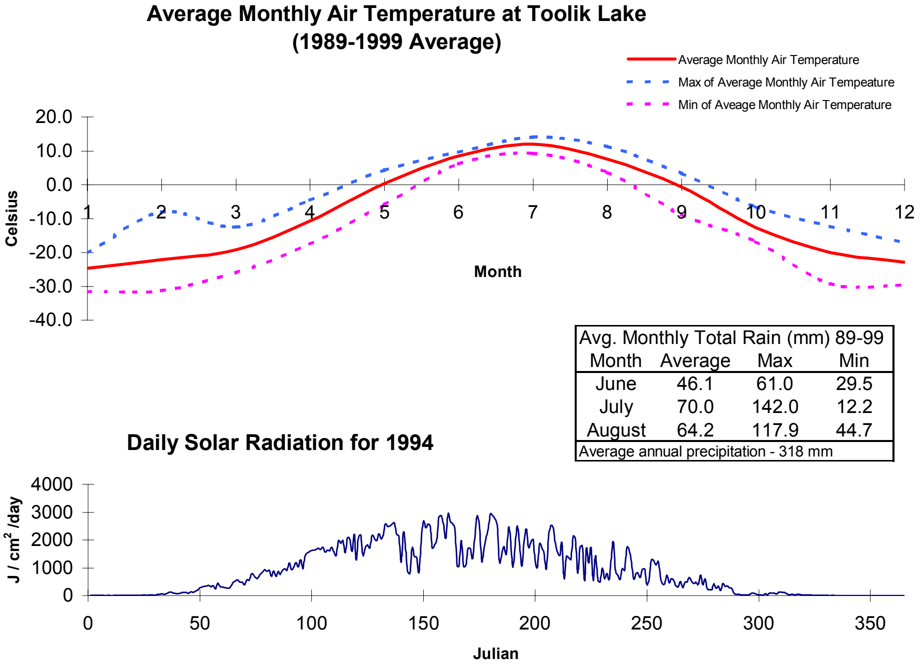


Fig. 1. The Arctic LTER site encompasses the upper Kuparuk Basin including that of the river draining Toolik Lake.



Avg. Monthly Total Rain (mm) 89-99			
Month	Average	Max	Min
June	46.1	61.0	29.5
July	70.0	142.0	12.2
August	64.2	117.9	44.7
Average annual precipitation - 318 mm			

Fig. 2. Mean monthly temperatures and summer precipitation (yearly mean is -8.6° C) and the summer total precipitation averages 188 mm (three summer months).

Effects of the arctic climate on the ecology include a shortened growing season for plants. As noted in Fig. 3, the long-lasting snow cover (9 months) means that nearly 50% of the solar radiation is unavailable to the plants. Cool temperatures in late summer lead to a cessation of photosynthesis in mid August. The streams stop flowing and the pools are frozen from mid September until mid May. Lakes are frozen from late September until June. One consequence is that only one species of fish, the arctic grayling, is found in the Kuparuk River. Cold soil temperatures reduce decomposition although respiration of soil microbes continues down to -7.5^{o}C and nearly half of the yearly total soil respiration takes place beneath the snow cover.

There has been a pronounced warming over the past 30 years in arctic Alaska. Chapman and Walsh (1993) state that this warming has been as much as 2^{o} in the winter and 1^{o} in the winter. Over the same period, the plant communities in the acidic tussock tundra at Toolik show a shift towards dominance of woody plants, especially the dwarf birch (*Betula nana).* Pollen from the sediments of lakes near Toolik show that the plant communities have been stable for some 6,500 years and that there was a peak of birch pollen abundance before that time. The last glacial advance that reached Toolik was around 10,000 years ago.

Permafrost and glacier impact Permafrost, defined as any material with a temperature continuously below the freezing point, has a depth of ~200 m at Toolik. There is warming but no melting expected of the permafrost. It is more likely that the active layer will deepen (this is the 28-46 cm of surface vegetation and soil that thaws annually). Toolik is a member of the Circum-Polar Active Layer Monitoring (CALM) network of sites where the depth of thaw is monitored every summer; variability is large from meter to meter over the Toolik transect so change is difficult to detect. Permafrost and the active layer have the following ecological impacts: plants roots have limited depth of penetration; soils have limited water holding capacity – runoff is immediate and flashy; and soils are cold and wet – decomposition is inhibited.

The Pleistocene was marked by several northward advances of mountain glaciers from the Brooks Range into the foothills. The coastal plain was never glaciated. The existing glacial tills that cover the hills near Toolik have three different ages, >300,000 years, 60,000 years, and 10,000 years (see Fig. 4). Lakes in these different landscapes differ in their chemistry with the oldest lakes being very dilute with low amounts of inorganic ions and alkalinity. Soils are acidic in the 60,000 year surface and less acidic in the 10,000 year surface because of less leaching of the carbonate-rich glacial till. One consequence is a different vegetation covers these two surfaces (for example, there is no birch in the non-acidic tundra).

Controls of Ecosystem Structure and Function

Generalized plan of relationships controlling structure and function To reach our goal of a predictive understanding of the ecology, we continue to study the controls of structure and function. These controls are listed in Fig. 5 under the general headings of physical setting, climate, biota, and fluxes. Structure of the ecosystem is defined by stocks of biomass, carbon, and nutrients as well as by the biodiversity and trophic relationships. Function includes the processes of production (primary and secondary), respiration, decomposition, grazing, predation, nutrient cycling, and evapotranspiration. The controls of terrestrial, land/water, stream, and lake systems will be described in detail in the following pages. Each section is organized into the following sections:

1. observations – biota, physics, chemistry, short-term and long-term changes
2. experiments to understand process and controls.
3. synthesis – integration to a whole system, scaling in space and time

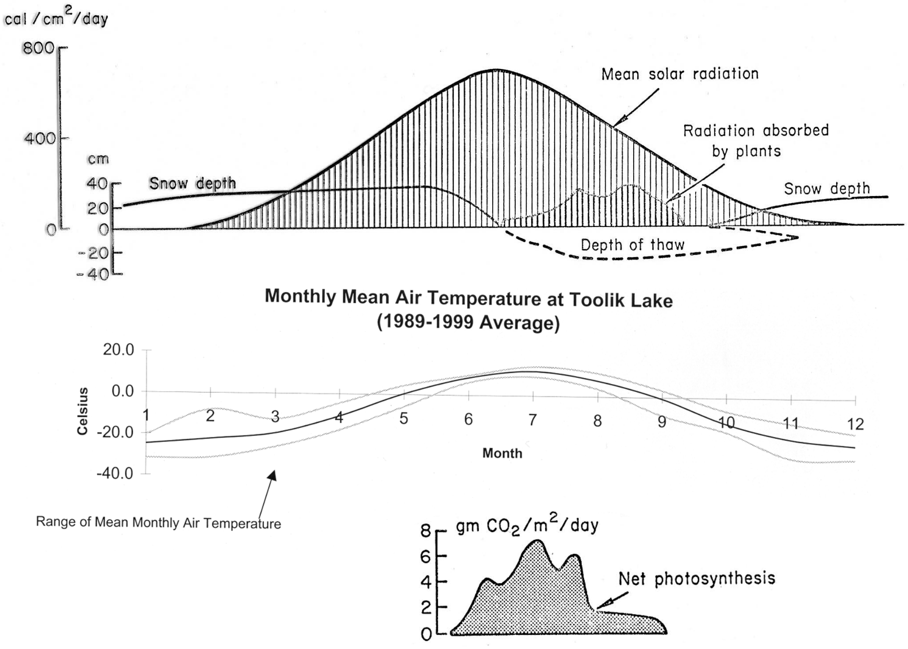


Fig. 3. A schematic of spring, summer, and fall solar radiation, plant photosynthesis, snow cover, and soil temperatures at Toolik Lake, Alaska. Note that the annual temperature data include the entire year.

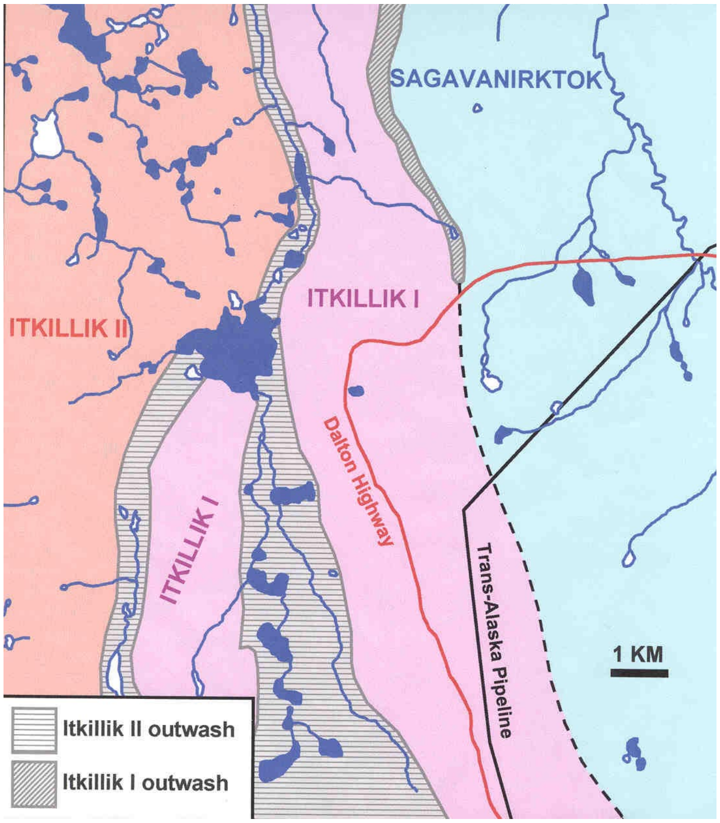


Fig. 4. Three glacial ages of till at Toolik Lake. Note that the glaciers advanced from south (bottom of figure) to north and that the older Itkillik material lies on the south side of the lake.

Observations There are a large number of routine measurements made at regular intervals. With these measurements, we expect to identify long-term changes and have already noted a change in the alkalinity of streams and changes in the dominant vegetation types. The year-to-year variation also gives information on the controls of plant flowering and grayling growth. For example, we found that adult grayling grow best in summers with cold temperatures and high water flow.

These measurements include year-round climate measurements at several sites, stream and lake temperatures, the transparency and oxygen content of lakes, primary productivity of tundra, streams, and lakes, nutrient content of streams and lakes, stream flow, the algal biomass (chlorophyll *a*) of stream rocks and lake waters, zooplankton abundance and species, and fish abundance and growth. Nearly 12,000 grayling are tagged in the Kuparuk River.

Questions include the following:

- What is the seasonal, annual, and long-term variability in elements of the arctic system?
- Is long term change occurring?
- What are the carbon and nutrient budgets in these systems and do they differ from other arctic and temperate systems?
- How do biota, physics, and chemistry differ across a catchment and a river basin with changes in age of soils, a toposequence, the stream order, and the climate.
- What processing of material takes place across a landscape?

Experiments Large-scale experiments, that is, larger than plot level, are an important tool for developing and testing our ecological understanding. Response is often slow; we found that the results of greenhouse-heating of tundra was different after 9 years than after 3 or 6 years. Furthermore, response is often unexpected: mosses in a fertilized reach of stream came to dominate plant biomass but only after a decade of low-level fertilization. Some of the large-scale experiments of the Arctic LTER were begun before the start of the LTER project. For example stream fertilization began in 1983.

- Tundra: heat soil, reduce light, fertilize, exclude grazers
- Land/water: increase soil moisture
- Stream: fertilize, add or remove predators
- Lake: fertilize, add or remove top predator (lake trout), add predator (sculpin)

Questions include the following:

- What is the importance of bottom-up and top-down control of ecosystem properties in the Arctic? (Note that properties include structure (species, biomass) and function).
- What differences do increases in trophic status (increasing primary production) make in lake microbial food webs.
- What are the controls of the rates of transfer of CO_2 from the land to the atmosphere?
- How does tundra carbon cycling change with temperature and nutrient changes?
- Are the higher trophic levels of lakes linked to benthic or planktonic productivity?

Synthesis In this step we bring together process information to describe fluxes and cycles in ecosystems, catchments, and river basins. Information is needed on linkages within an ecosystem, on how an ecosystem varies with differences across a landscape, catchment, or whole river basin. Modeling of single ecosystems, of ecosystems linked within a catchment, and of entire river basins will be used.

Questions include the following:

- What is the future status of an arctic system under a scenario of climate change? Under a scenario of increased direct human impact?
- How do ecosystems differ across a heterogeneous landscape?
- What are the key connections among aquatic ecosystems?

- How are environmental impacts transmitted or propagated within a series of linked systems such as stream reaches or a topographic sequence in the tundra?
- How will an increase in precipitation in the future affect carbon storage in an entire river basin?
- What will happen to the organic carbon in arctic soils when the upper layers of permafrost melt and soil microbes are stimulated by easily used organic material from photosynthesis?
- Is there a process-based model of the transfer of organic and inorganic carbon and of nutrients from soil to streams?

One example of how a model can synthesize data and predict rates for an entire watershed is Williams et al. (in press) in which net ecosystem productivity of tundra was modeled at an hourly time step for the whole summer for each square kilometer of the ~9,000 km^2 Kuparuk River basin. The model is based on fundamental physiology of plants including responses to temperature, light, CO_2 and water. Remote sensing gave NDVI; this was related to leaf area index and, in this system, nitrogen content of leaves. A simplified version was developed for the arctic system. The results were tested against eddy correlation studies of net carbon flux at a number of sites in the basin (Fig. 6) and a map developed of the spatial distribution of gross primary production (Fig. 7). This modeling effort was funded by the ARCSS program and much of the data provided by the Arctic LTER project.

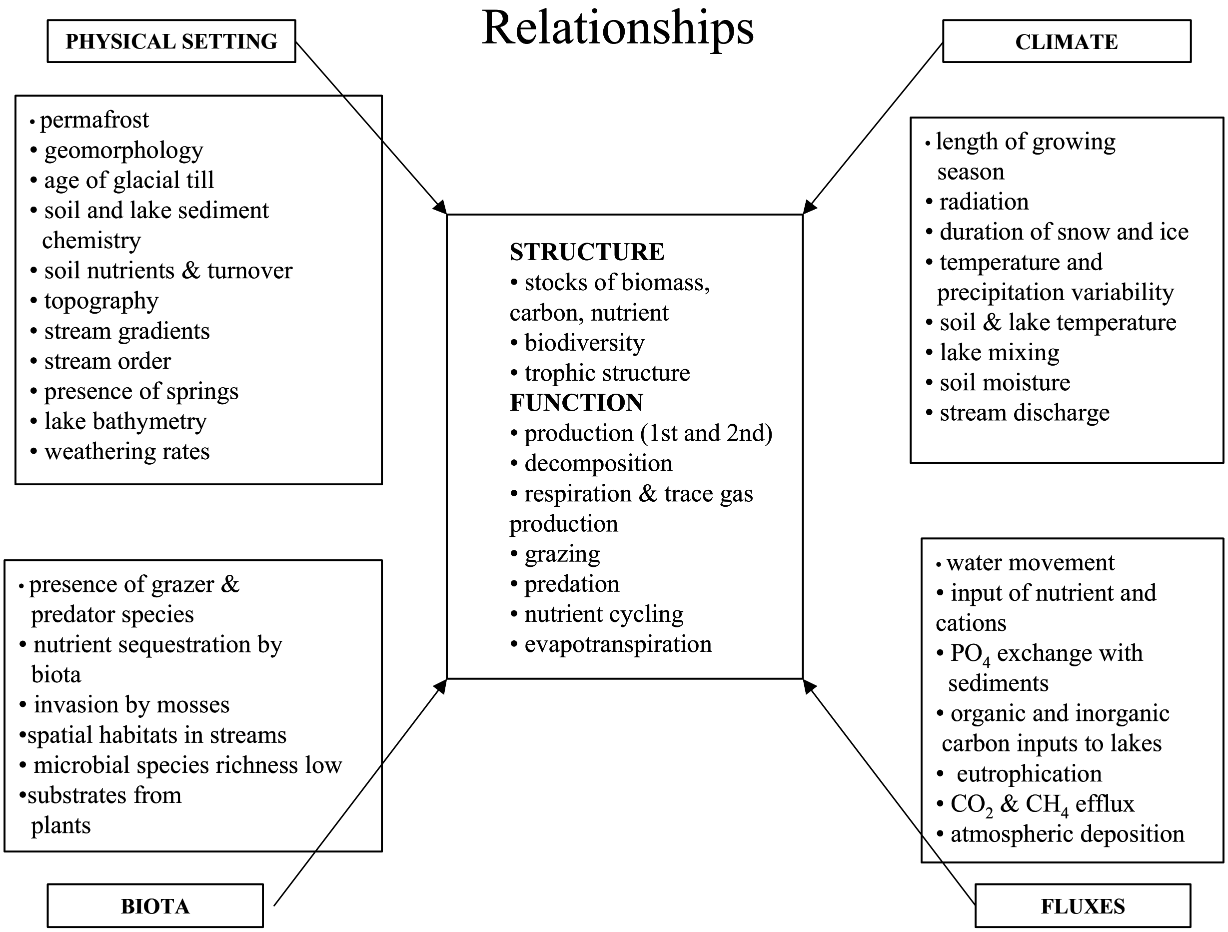


Fig. 5. Ecological relationships showing the four primary factors (physical setting, climate, biota, and fluxes that control the structure and function of the ecosystems in the Arctic LTER.

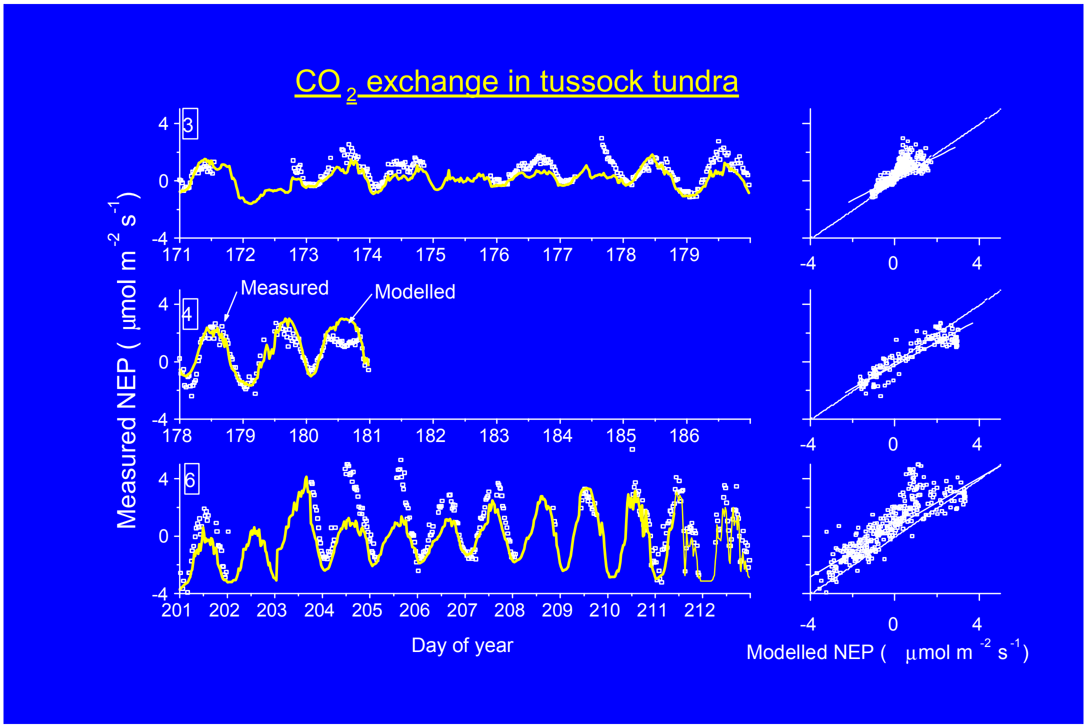


Fig. 6. The CO_2 exchange in tussock tundra measured with eddy diffusivity towers at three sites within the Kuparuk River basin and modeled as described in Williams et al. (2000).

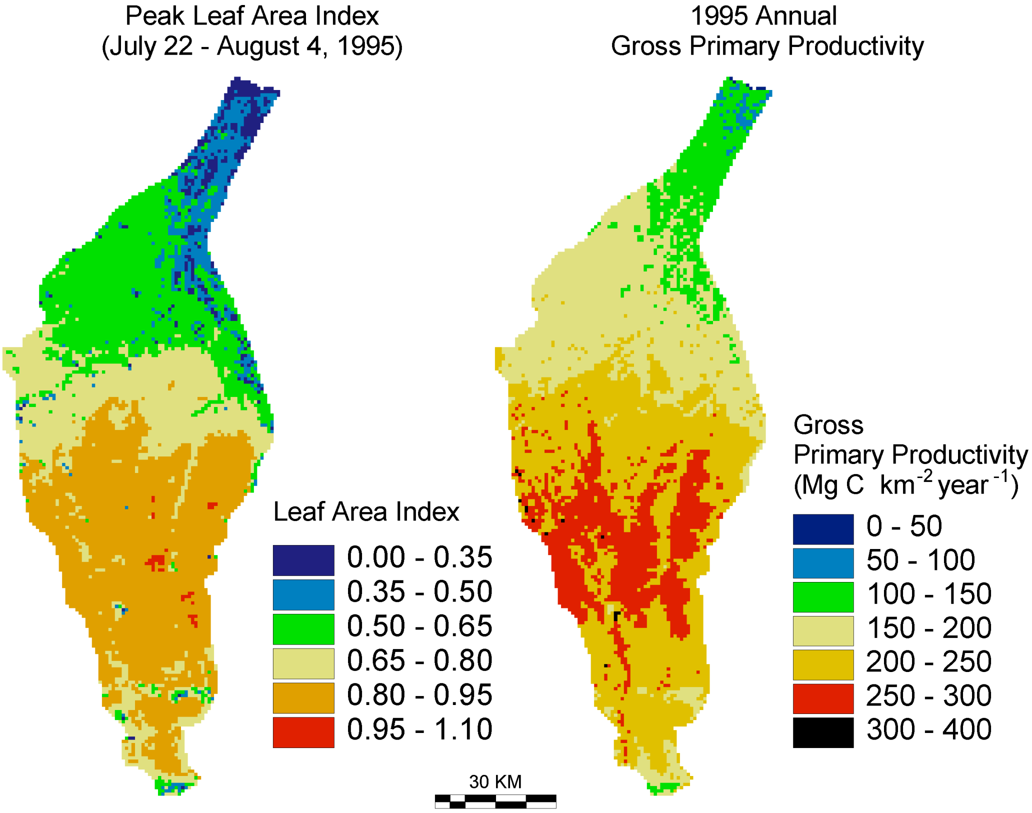


Fig. 7. The NDVI-derived leaf area index and the modeled gross primary productivity for the Kuparuk River basin (from Williams et al. in press).

ARCTIC LTER TERRESTRIAL COMPONENT

Overall Design

There are three major components to the terrestrial research of the Arctic LTER, including: *(1) Observations and Monitoring, (2) Long-term, Whole-Ecosystem Experiments,* and *(3) Process, Species, and Community-level Studies.* These components are linked through additional, separately funded *(4) Synthesis and Scaling* efforts that aim to apply our results to long-term, large-area predictions of stability and change in the arctic landscape. Finally, within the last 5 years we have begun an active program of *(5) Cross-Site Comparisons* in which we seek to test the generality of our results by direct comparisons with data from other sites, both in the Arctic and at lower latitudes.

The design of our terrestrial research incorporates a combination of comparisons among sites that differ in their physical setting (e.g., topography and geologic history) and biota (plant functional types) with long-term manipulations of climate and nutrient inputs in each of these different sites (Table 1). Since 1988 we have maintained a series of observations and experiments in which contrasting tundras, dominated by different mixes of plant functional types, are subjected to identical manipulations of nutrient inputs, air temperature, and shading (light reduction). Comparisons among treatments within each tundra type have taught us a great deal about the roles and interactions of climate and biogeochemistry (e.g., Chapin et al. 1995, Shaver et al. 1998, Gough et al. submitted). Additional comparisons of the responses of contrasting plant species and functional types to a common suite of manipulations in different sites have taught us how differences in species function affect overall ecosystem characteristics (e.g., Bret-Harte et al. 2001, submitted, Shaver et al. in press, Gough et al. submitted.)

A simple, general conceptual model of climate/carbon/nutrient interactions in arctic terrestrial ecosystems (Shaver et al. 1992; Fig. 1) helps us to integrate our work on contrasting tundra types and plant functional types. This model also serves as a conceptual starting point for much of our simulation modeling (e.g., McKane et al. 1997a, 1997b, Rastetter et al. 1997a, Herbert et al. 1999) and for our cross-site comparisons and syntheses (e.g., Shaver and Jonasson 1999, Shaver et al. 2000, Jonasson et al. 2000, 2001). Our work is also linked conceptually to the lakes, streams, and land/water components of the Arctic LTER, viewing terrestrial ecosystems as sources and controls on water and element inputs to aquatic systems (e.g., Kling et al. 1991, 1992, 1995).

(1) Observations and Monitoring: Terrestrial ecosystem research at Toolik Lake began in 1976, and by the time the LTER project was funded in 1987 an extensive background of data on tundra biogeochemistry and ecophysiology was already in place (Shaver 1996a, 1996b). Our descriptive data base grows yearly as a result of annual, intensive harvests of one or more tundra types in the Toolik Lake region. These harvests allow development of detailed descriptions of species composition, plant biomass allocation, primary production, and biomass turnover in a wide range of tundras dominated by different plant forms and varying at least 10-fold in productivity. Over the past 20 years, we have gradually described C, N, and P budgets and standing stocks for all the major vegetation and soils types in the study area (e.g., Shaver and Chapin 1991, Giblin et al. 1991, Chapin et al. 1995, Shaver et al. 1998, Gough et al. 2000, submitted). These data sets are all stored in the Arctic LTER data base and are widely used both in our own modeling and synthesis efforts and in cross-site comparisons (described below).

Repeated intensive harvests over the past 20 years have also allowed us to define the "normal" range of annual variation in aboveground production and biomass in moist tussock tundra, the dominant ecosystem type at our study site, and to determine whether the vegetation is changing as a result of the general warming that has occurred over this period. For example, total aboveground biomass in 2000 was the highest we have ever measured and it also included a higher proportion of the deciduous shrub, *Betula nana* than in any previous harvest (Fig. 2). Both of these changes are expected to occur as a result of climatic warming (e.g., Chapin et al. 1995). However, for both total biomass and *Betula* biomass the most similar year to 2000 was 1982, the earliest year of our record, leading us to the conclusion that if the vegetation is changing in response to climate the magnitude of the change is small relative to typical year-to-year variation.

Table 1. Experimental Designs for Terrestrial Research of the Arctic LTER Project.

Location	**Year Started**	**Ecosystem Type**	**Treatments**	**Major Harvests, sampling**
Toolik Lake	1981	Moist Tussock	N+P Fert	1982, 1983, 1984, 1989, 1995, 2000, 2005
	1988	Moist Tussock Wet Sedge Dry Heath Riparian Shrub	N, P, N+P, Greenhouse, Shade, Greenhouse+N+P, Shade +N+P	Tussock: 1995, 1996, 2002 Wet: 1992, 1993, 1994, 2001 Heath: 1992, 1993, 1996 Riparian:
	1989	Moist Tussock Dry Heath	Herbivore Exclosure	Annual monitoring of flowering only
	1992	Moist Tussock	15N Addition	1992, 1993, 1998
	1996	Moist Tussock Dry Heath	Herbivore Exclosure, N+P, Exclosure+N+P	Tussock: 1999, 2000 (CT only), 2001 (CT only), 2003
	1997	Nonacidic Tussock Nonacidic Nontussock	N, P, N+P, Greenhouse, Greenhouse+N+P	Tussock: 1999, 2000, 2001
	1997	Moist Tussock	Species removal, N+P Fert	2003 or 2004
	1998	Moist Tussock Nonacidic Tussock Nonacidic Nontussock	Lime, Sulfur	?
Sag River Topo-sequence	1984	Moist Tussock Dry Heath Snowbed Equisetum/Forb Wet Sedge Riparian Shrub	N, P, N+P, Labile C (starch, sawdust), Lime	1984-1989, 1994

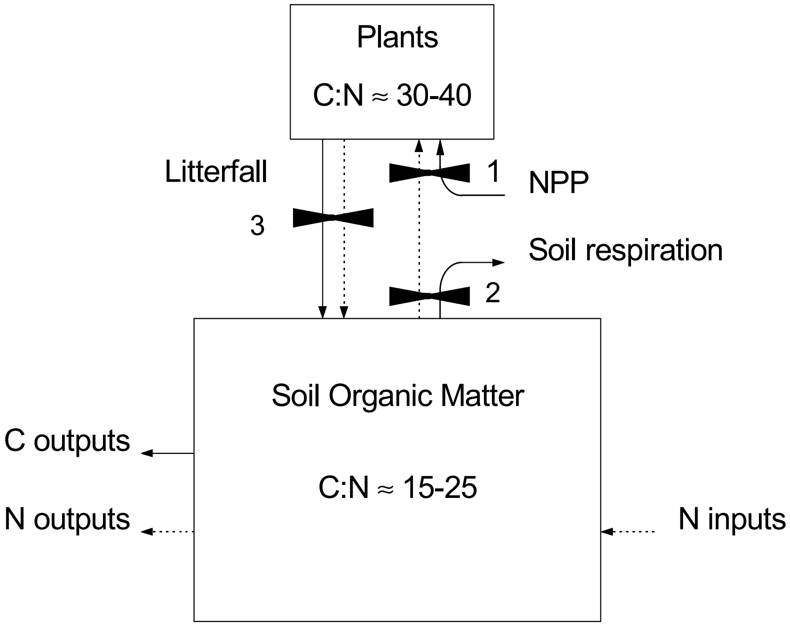


Fig. 1. The Simple Arctic Model (SAM; Shaver et al. 1992). This model contains two major organic matter pools, plants and soil. Carbon fluxes into and out of these pools are indicated by solid lines and N fluxes by dashed lines. Bow ties show links between fluxes. In the past we have assumed that in tundra ecosystems essentially all plant-available N comes from the mineralization of soil organic matter (including litter), that N mineralization is linked to soil respiration, and that dissolved C losses indicated by the arrow at lower left, are small relative to gaseous exchanges. Thus, at least in a proximate sense, the overall C balance of such ecosystems (i.e., the difference between NPP and soil respiration) is largely determined by C gains linked to plant N uptake, balanced against C losses linked to N mineralization. In future research we plan to test these assumptions at a watershed scale, especially about the small size of N inputs and outputs, about the importance of spatial heterogeneity in inputs and outputs, and about transport of N downslope along a watershed toposequence.

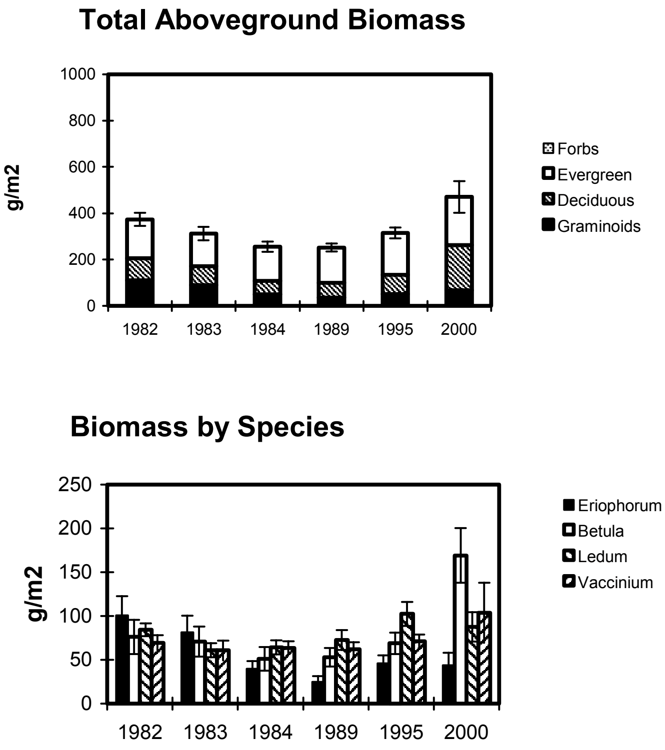


Fig. 2. Total aboveground biomass of the vegetation (top) and biomass of the four most abundant species (bottom) in moist tussock tundra at Toolik Lake, 1982-2000

Yearly monitoring of key biological variables in relation to weather allows further insights into long- and short-term climatic controls. For example, year-to-year variation in flowering of the arctic cottongrass, *Eriophorum vaginatum*, is a spectacular event on the North Slope of Alaska, but early work showed that this variation is not at all related to the current year's weather (Shaver et al. 1986). After more than 20 years of monitoring, we are now able to show that it takes two warm years *before* the year of flowering to increase flowering in the year of observation (Fig. 3, top). Furthermore, we are beginning to see that increased flowering in a given year is also related to increased N mineralization in the previous year, which is also predicted by soil temperatures over two years (Fig. 3, bottom)

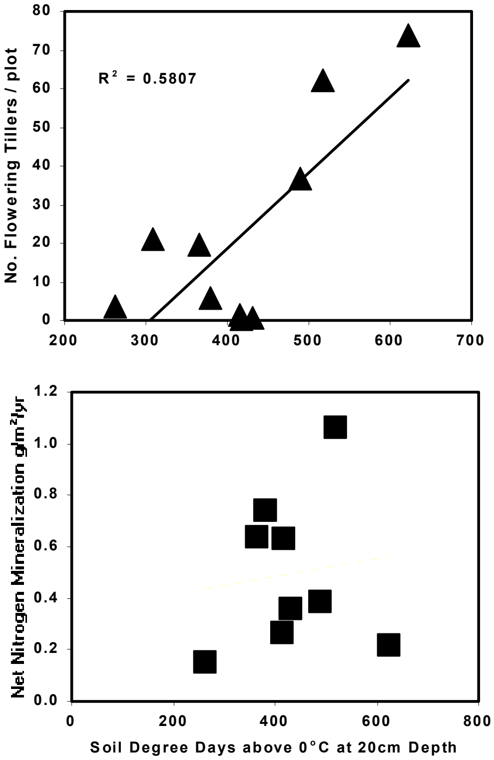


Fig. 3. (Top) Density of flowering tillers of Eriophorum vaginatum in 2x2 m plots at Toolik Lake over the years 1990-1999, plotted against soil temperature sum (degree-days above zero C) during the spring and midsummer (June and July) of the previous year, plus the the temperature sum during the fall months (August-September) two years previously. (Bottom) Net nitrogen mineralization at the same site, plotted against soil temperature sum during June and July of the current year, plus the the temperature sum during August and September) of the previous year.

(2) Whole-Ecosystem Experiments: In the current funding period (1999-2004) we maintain nine long-term experiments, the earliest of which began in 1981 (Table 1). Because these ecosystems continue to respond to our treatments, we gain new insights about ecosystem regulation with each harvest (e.g., Shaver et al. in press). Our principal efforts, however, have shifted to a new series of long-term experiments, specifically focused on effects of herbivory (biota) and variation in soil acidity (geology/geomorphology). We also have assumed responsibility for maintaining a set of long-term species removal experiments in which vegetation composition is controlled directly.

Each summer we complete a major harvest of one or more of our experiments (Table 1). The general aim is to harvest each experiment at least once every 3-6 years, but the schedule is kept flexible to allow coordination of our harvests with collaborating, independently-funded projects. These independent projects also use our experiments for more intensive, focused research at the process, species, or community level. By coordinating our ecosystem-level production, biomass, and nutrient budget harvests with detailed process research on the same plots we try to maximize the potential for integration of data collected at different scales.

Herbivore exclosures: The central hypothesis of this experiment is that herbivores play an important role in controlling tundra plant species composition, but are less important as direct controls on productivity or nutrient turnover at 1-10 year scales. We also hypothesize that herbivores induce changes in species composition more rapidly under fertilization, but that fertilized plots with or without herbivores will converge to similar species composition after about 10 years. In July 1996 we set up herbivore exclosures in acidic tussock and dry heath tundras. These exclosures were established within the existing LTER experimental areas, set up in 1987, on plots that had been randomly located as part of the original design but left unused for future treatments (*n*=4 in tussock tundra and *n*=3 in dry heath). There were two nested levels of exclosure (microtine exclosures nested within caribou exclosures), combined factorially with NP fertilizer addition. We harvested these plots in 1999 and currently plan to repeat the harvest in

2003. Results of our first harvest, in 1999 (Fig. 4), indicate that after three years of treatment there is greater productivity in the unfertilized plots where herbivores were excluded, and that most of the increase in productivity is by graminoids, the favored food of the local microtine rodents. This is a more rapid change than we initially predicted. Later harvests (the next is scheduled for 2003) will determine whether this trend continues.

Non-acidic versus acidic tundra: The broad aim of these experiments is to determine whether sites differing in pH but with similar production, biomass, and functional type composition to the acidic sites we studied previously, will differ in response to the same set of manipulations. A particular focus is on the importance of initial species composition to the overall ecosystem response, because many of the species most responsive to our manipulations of acidic tundra do not occur in nonacidic tundra (Gough et al. 2000). In July 1997, we established new experiments in non-acidic tussock tundra on the northwest shore of Toolik Lake. The new experiments are identical in design to the existing experiments in acidic tussock tundra and other sites that have been maintained since the start of the LTER project (Chapin et al. 1995, Shaver et al. 1998; Table 1). Three experimental blocks were set out at each non-acidic site. In both sites, factorial NxP fertilizer treatments were applied, using the same fertilizers and rates of application as in the existing sites. In the non-acidic tussock site, we also set up a factorial greenhouse x N+P fertilizer experiment identical to earlier experiments in other sites. A major harvest of the non-acidic tussock tundra experiment was completed in the summer of 2000. This harvest occurred in the third year of treatment and is thus directly comparable with our 1999 harvest of the exclosure experiment (Fig. 2) and with our 1983 harvest of our original greenhouse/shade/fertilizer experiment (Chapin et al. 1995).

Response to Liming/Acidification: This experiment focuses on links between soil acidity and ecosystem characteristics such as species diversity, productivity, decomposition, and N and P cycling. In 1998 we set up a new experiment in both acidic and nonacidic tussock tundra in which we are attempting to manipulate soil acidity directly by adding lime and elemental sulfur. We have not yet harvested the experiment but we continue to monitor it for obvious changes and view it as an important opportunity for future process-oriented research. Any harvest will be coordinated with a harvest of another long-term liming experiment at the Sagavanirktok River toposequence, begun in 1985 (Table 1).

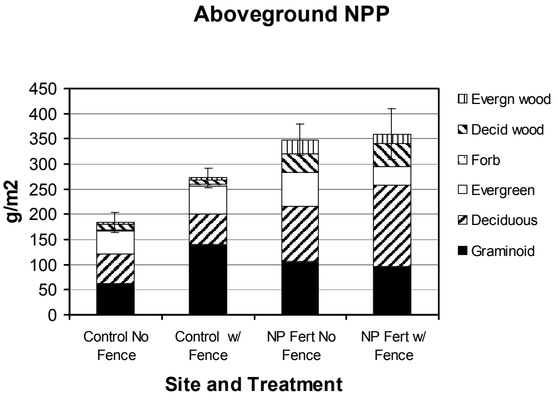
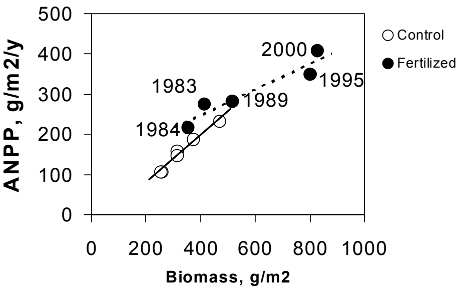


Fig. 4. Aboveground NPP in the 1999 harvest (third treatment year) of our herbivore exclosure x NP fertilizer experiment in moist acidic tussock tundra at Toolik Lake.

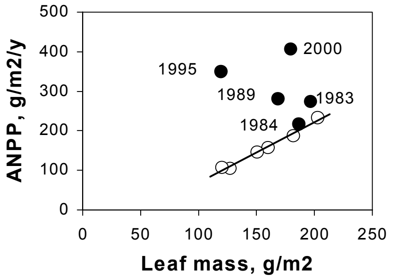
Species Removal Experiment: The aim of this experiment is to isolate the effects of individual plant species or functional types on ecosystem productivity, biomass, and element cycling by selective removal of target plants. The experiment was established in 1997 by our colleagues M.S. Bret-Harte and F.S. Chapin, III, and gradually we have assumed responsibility for its maintenance because it complements nicely our manipulations of light, temperature, and nutrient resources. Because species removal treatments are crossed with a NP fertilizer addition that is identical to our other experiments, this experiment also provides us with the opportunity to isolate fertilizer effects from species effects on biogeochemistry. A major harvest of this experiment is planned for 2003 or 2004, depending on when additional funding is obtained for detailed process studies on these plots. Thus far, annual monitoring has shown that removal of individual species often has consequences for other species, indicating that the tussock tundra community is tightly integrated through a wide range of direct competitive interactions (e.g., competition for soil N) and species effects on microenvironment (shading, soil temperature). The response to fertilizer in these plots is similar that we observed on our long-term fertilizer experiment (only about 50 m away downhill), but in these plots we also have a significant grass component, which is much more rapidly responsive.

Ongoing Experiments: Repeated observation and sampling of long-running experiments allows us to determine whether the initial magnitude and trajectory of ecosystem response to environmental change is sustained over the long term, and to examine interactions among slow- and fast-responding components of overall ecosystem change. Repeated observation also allows us to interpret long-term change in response to our manipulations in the context of long-term "normal" or "background" variation in ecosystem states and processes. For example, in the summer of 2000 we completed our fifth harvest of a 20-year old fertilizer experiment (the 6th harvest of control plots for this experiment). After 20 years it was clear that fertilized plots were distinctly different from control plots, not only in terms of their total production and biomass, but that they also differed functionally in terms of the relationships between productivity, leaf mass, and leaf area (Fig. 5). Remarkably, leaf mass in the fertilized plots was significantly *lower* than in the controls in both 1995 and 2000, while productivity in the fertilized plots was more than double that of controls. How is this possible? The main reason for this result is that the fertilized plots are not strongly dominated by dwarf birch, *Betula nana*, which has much thinner leaves (i.e., a much higher specific leaf area). Because birch has thin leaves, it can produce more than twice the leaf area of controls with a lower total leaf mass. This leads also to very different overall pattern of canopy and aboveground N allocation, with a much more efficient photosynthetic return per unit canopy N (Shaver et al. in press). It also allows much greater proportional allocation to woody stem growth, greatly increasing both the height of the canopy and the total aboveground biomass (Bret-Harte et al. 2001, submitted). This interpretation of the causes and implications of a change in plant functional type composition is radically different from earlier hypotheses (e.g., Chapin and Shaver 1985) and would not have been possible without long-term experimental evidence.

A. ANPP vs biomass



B. ANPP vs leaf mass



C. ANPP vs. estimated leaf area

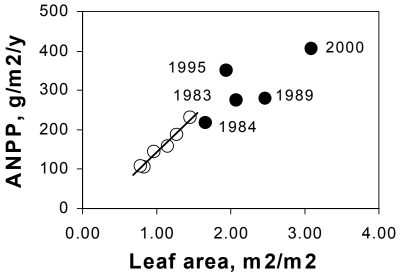


Fig. 5. Aboveground net primary production in fertilized and control plots in moist acidic tussock tundra at Toolik Lake, 1982-2000.

(3) Process, Species, and Community-level Studies. Several independently-funded projects coordinate their data gathering with LTER-supported research, usually by additional sampling of LTER experiments. The LTER experiments are designed to accommodate this additional sampling, mainly by setting up and manipulating much larger plots than would otherwise be needed, and by incorporating extra untreated plots for additional sampling or future treatments. Typically, the LTER-supported harvests provide the ecosystem-level budgets that provide context for evaluation of more focused process- and species-level data collection. The LTER funds are also used to support small, focused pilot studies that are intended to expand the overall scope of research and to fill gaps in the research program. Current efforts include the following:

International Tundra Experiment (ITEX): This project, supported by NSF-OPP, began in 1995 and will continue at least through 2004. By sampling LTER experimental plots, the aim is to understand and isolate the role of species in controlling ecosystem function and response to disturbance. An initial hypothesis was that RESOURCES (element stocks and cycling rates) control long-term NPP and organic matter accumulation; but species composition is not important to average NPP and turnover along large gradients of resource availability. However, SPECIES do determine the RATE of response to changes in resources, especially the initial response. Examples of this work are Donie Bret-Harte's work on shrub growth (Bret-Harte et al. 2001, in review) and Laura Gough's work on diversity/productivity relationships (Gough et al. 2000).

Soil-plant interactions: An ongoing theme of our research has been the constraints on C cycling imposed by C/N interactions, and variation in those constraints with topography (geology/geomorphology), species composition (biota) and nutrient inputs (fluxes). Current foci are: (1) C respiration/N mineralization interactions, and (2) below-ground C inputs, as root production and root exudation (NSF OPP 96 15563). In collaboration with other NSF-DEB and NSF-OPP projects, harvests of our plots provide biomass and production measures that complement process-level measurements of soil respiration, N mineralization, and the distribution and movement of stable isotopic tracers (^{13}C and ^{15}N) through plants and soils (Giblin et al. 1991, Nadelhoffer et al. 1991, Nadelhoffer et al. 1995, Shaver et al. 1998, Johnson et al. 1996 and submitted). During the summer of 2001, we will begin a major study of the movement of C from plants into the soil, using a ^{14}C labeling approach, in control and fertilized plots of wet sedge tundra. In 2002, we will continue the work in moist acidic tussock tundra. This work is under the direction of Dr. Knute Nadelhoffer, with George Kling and Loretta Johnson.

Soil biota and community structure: A new community-oriented initiative for 1999-2004 is to determine effects of our long-term experiments on soil invertebrate and microbial communities. For the past three summers Dr. John Moore and students have come to Toolik Lake to help develop techniques for sampling and describing invertebrate communities across the full suite of sites and experimental manipulations. In 2001, we will extend these descriptive studies to include bacteria and fungi, with NSF Postdoctoral Fellow Laura Broughton. This work is also being used by Moore and collaborators as part of their multibiome comparison of soil trophic structure and diversity.

(4) Modeling, Synthesis, and Scaling up in Space and Time: The LTER project and its data management/data archive capabilities are used to facilitate synthesis of terrestrial research in several ways. One way is by direct integration of diverse data sets, all collected from the same sites and experiments. We have used this approach successfully in the past to construct and compare C, N, and P budgets for vegetation and whole ecosystems (e.g., Shaver and Chapin 1991, Shaver et al. 1998). A second approach is to use simulation models, both as a means of gaining insight into process interactions and their implications for overall ecosystem function, and as a means of developing long-term and large-area predictions of change in the arctic landscape. We have used the MBL-GEM model, for example, to

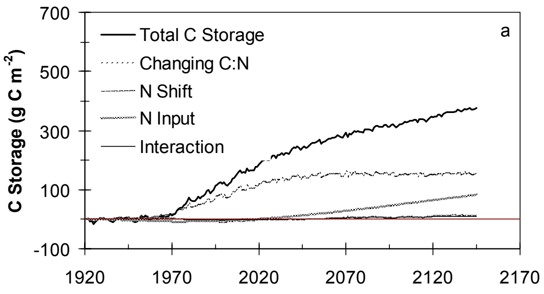


Fig. 6. Cumulative changes in carbon storage at Toolik Lake (from Hobbie et al., 1998). The changes are given as the total and also partitioned into changes caused by a change in the ratio of C:N in plants and soils, by a shift in N from low C:N organic matter to high C:N organic matter, by a change in the retention of N added in input, and by the interaction of all three of these changes. Fig. 6a is carbon storage for the GEM simulation in which percent water-filled pore space varied directly with the temperature changes. Fig. 6b is carbon storage for the GEM simulation in which percent water-filled pore space varied inversely with the temperature changes

evaluate the hypotheses in our general conceptual model of C-N interactions (Fig. 1) and their relative importance in regulating the changes we see in our experimental plots (McKane et al. 1997a). These insights have then been used to develop longer-term predictions of changes in tundra C stocks and C-N interactions in response to climate change (McKane et al. 1997b, Rastetter et al. 1997, Hobbie et al. 1998; Fig. 6). Several models have used the LTER data base in the development of large-area predictions of arctic C cycling at various scales ranging from the Kuparuk River drainage to the entire terrestrial arctic (e.g., Hobbie et al. 1998, Williams et al. 2000, Clein et al. 2000, McGuire et al. 2000). Finally, our data on plant functional types have been used to test theory of species effects on element cycling, using the MEL model developed by Ed Rastetter (Rastetter and Shaver 1994, Herbert et al. 1999, submitted).

(5) Cross-Site comparisons: Within the Arctic, the ITEX project involves comparative analysis of plant growth in response to experimental warming at over 25 sites throughout the Arctic. A recent metaanalysis including our data from Toolik Lake (Arft et al. 1999) showed that the responses to warming by individual species at Toolik Lake are similar to those at other arctic sites; this is a key step towards understanding the limits to extrapolation of site-specific results to the entire Arctic. Current ITEX research is focused on analysis of multi-year changes in community composition in response to experimental manipulations at ITEX sites, including Toolik Lake (M. Walker in preparation).

More recently, we have begun a detailed analysis and comparison of results of greenhouse/shade/fertilizer experiments similar to ours at Abisko, Sweden, and on Svalbard. Qualitative comparisons indicate that C-N interactions operate in similar ways at Toolik and Abisko (Shaver and Jonasson 1999, Jonasson et al. 2001). We have completed two detailed comparisons of Toolik and Abisko, one focused on plant secondary chemistry (Graglia et al. in press) and one on soil organic matter, microbial biomass, and soil N turnover (Schmidt et al. in press). With recent funding from the NSF Cross-site competition, we plan a series of reciprocal site visits and modeling analyses to further extend these comparisons; this will start with a visit to Toolik Lake by European ecologists in August 2001, followed by a second workshop at Abisko, Sweden, in 2002. Working with our Scandinavian and British colleagues, we also plan to develop a new model of climate-nutrient interactions and especially the role of temperature in regulating the response of arctic ecosystems to global warming.

Finally, we collaborate with several global networks and organizations to place our research in the context of global patterns of regulation of ecosystem processes and structure. Within the US LTER network, we were active participants in the recent synthesis of productivity-diversity relationships at LTER sites (Waide et al. 1999, Gross et al. 2000, Gough et al. 2000b) and also contributed data to the synthesis of temporal dynamics of primary production at LTER sites (Knapp and Smith 2001). We are active participants in the IGBP-GCTE Network of Ecosystem Warming Studies (NEWS), and helped organize a recent synthesis of ecosystem warming responses (Canadell et al. 2000, Shaver et al. 2000, Rustad et al. 2001; Fig. 7). These activities will continue with annual workshops over the next five years.

Summary

Terrestrial research of the Arctic LTER project contributes to overall project goals through a combination of long-term observations, long term experiments, and focused research on key processes, species, and communities. Together, these activities have produced an increasingly integrated and continuously growing data base that is used to explain and to predict the relative sensitivity and responses of contrasting arctic tundra ecosystems to climate change and other disturbances. The LTER data base is used in a wide range of modeling activities, at multiple spatial and temporal scales, and also in multisite comparative research both within and outside the Arctic.

Within the current funding period our broad priorities include the development of a new overall conceptual model of carbon and nutrient cycling in tundra ecosystems that considers more explicitly the importance and variability of N inputs and outputs in tundra ecosystems including the major forms of organic and inorganic N. Opening up the N cycle (and its links to the water cycle) will also strengthen our links to the land-water and aquatic components of the Arctic LTER program. Within the terrestrial systems, we need to strengthen and expand our research on the role of herbivores and soil invertebrate communities in biogeochemical cycles. All of this work is designed eventually to lead to better predictions of change in arctic ecosystems based on fundamental knowledge of controls on ecosystem structure and function as exerted by physical setting and geology, climate, biota, and biogeochemical fluxes.

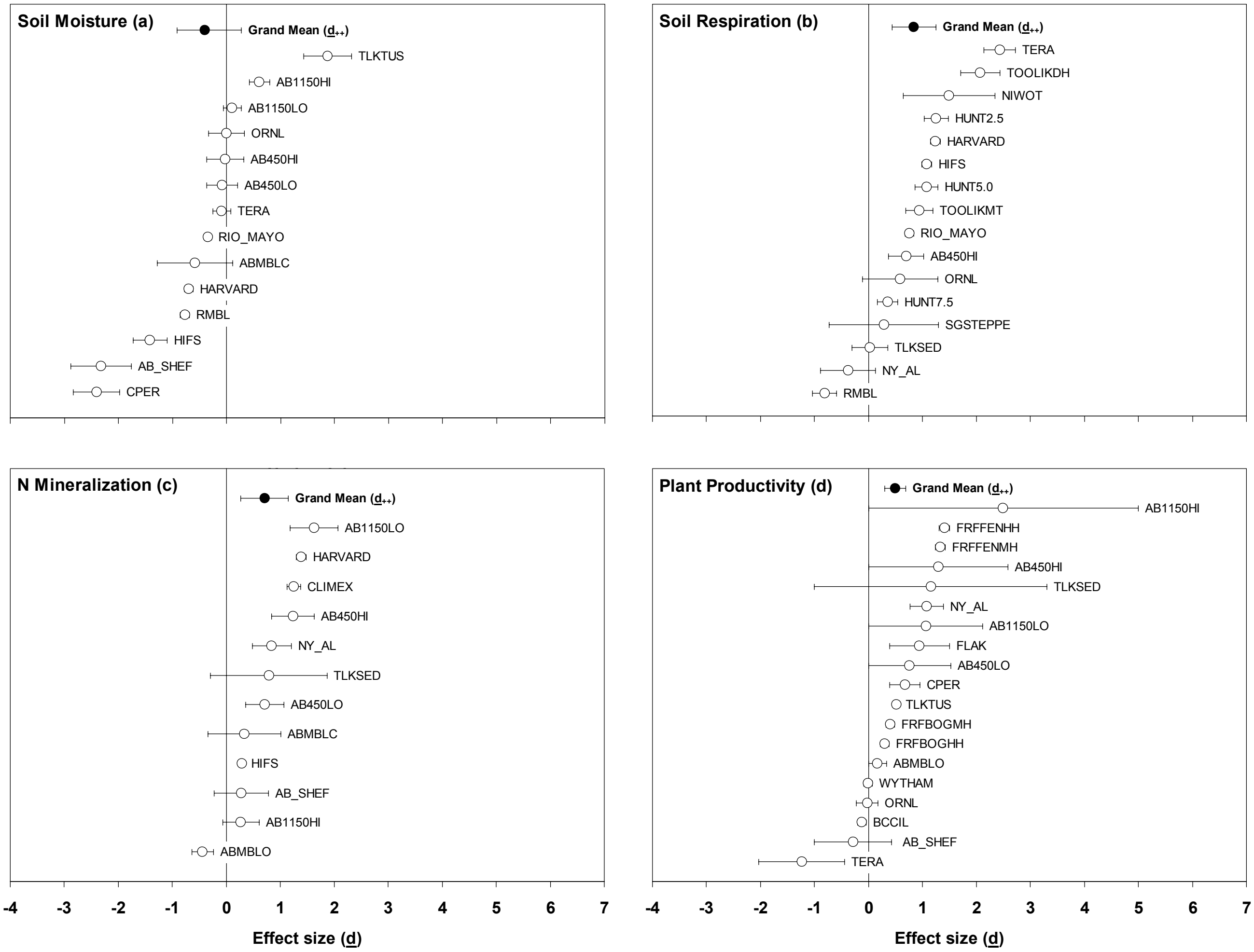


Fig. 7. Results of a metaanalysis comparing responses to experimental warming at a wide range of forest, grassland, and arctic sites. Data from the Toolik Lake tussock (TLKTUS), wet sedge (TLKSED), and dry heath (TOOLIKDH) sites are included, as are several Abisko sites (codes beginning with "AB"). With the exception of aboveground plant productivity, which showed a greater positive response to warming in colder, drier ecosystems, the magnitude of the response of these variables to experimental warming was not generally significantly related to the geographic, climatic, or environmental variables evaluated in this analysis.

ARCTIC LTER LAND-WATER INTERACTIONS COMPONENT

Summary

A program of measurements and process studies has been used to study the important controls on land-water-atmosphere interactions in the Arctic, and how these interactions influence ecosystem structure and function. The major research findings are:

(1) Experimental manipulation of plant-soil mesocosms showed that hydrologic flushing and vegetation type are the dominant controls on the production and export of dissolved carbon from soil waters to lakes and streams.

(2) Addition of $^{14}CO_2$ to plant-soil mesocosms showed that carbon fixed by photosynthesis was rapidly transferred to soil waters as DOC, dissolved CO_2, and dissolved CH_4, indicating that recent photosynthates are important substrates for dissolved carbon production in soils.

(3) Measurements in soil waters, lakes, and streams indicated a major pathway of dissolved carbon and trace gases from land to surface waters which is important from small (<0.1 km^2) to large (>9000 km^2) basin scales. Enough of this carbon that is lost from land to water is eventually released to the atmosphere or the ocean to account for ~20-80% of the net terrestrial carbon exchange with the atmosphere.

(4) A series of LTER cross-site workshops determined that this land to water to atmosphere cycling of carbon at landscape-level scales is a common phenomenon throughout the world, and is not confined to arctic or wetland regions.

(5) Experiments showed that differences in the quality of the organic carbon exported from land were related to its place of origin on the landscape and to the time of season, and this controlled the microbial metabolism of organic carbon to CO_2 in lakes.

(6) Measurements in a connected series of lakes and streams illustrate that over small geographic areas, and somewhat independent of lake or stream morphometry, consistent and directional (downslope) processing of materials helps produce spatial patterns that are coherent over time for many limnological variables. These results highlight that the integration of material processing in both lakes and rivers is critical for understanding the structure and function of surface waters, especially in a landscape perspective.

(7) We developed a process model that combines a soil-energy column and water balance routine with topographic statistics of the watershed. The model predicts the surface runoff, soil temperatures and respiration, and carbon and nitrogen residence times for a small watershed near Toolik Lake.

(8) Future research will concentrate on **(a)** determining the rates of soil production of dissolved C and nutrients and their transfer to and impacts on surface waters; **(b)** quantifying the interactions between different ecosystems across the landscape; and **(c)** mechanistic modeling of the transport of materials from land to water with the goal of predicting the impacts of future perturbations or global change.

Rationale for Research

The arctic ecological system includes the interactions among land, freshwaters, and the atmosphere. These interactions are illustrated in a conceptual model in Fig. LW-1. The dominant forms of interaction between ecosystems are the flux of materials and the flux of energy through climate forcing. For example, carbon moves from land to water and from water to the atmosphere, while the land and atmosphere exchange carbon in both directions.

Although we have made advances in understanding the role of land-water-atmosphere interactions in the Arctic, there are several missing keys to our ability to make rigorous predictions of how arctic system functioning is controlled. These keys are shown in the bottom part of Fig. LW-1, and are highlighted for the controls on C exchanges. For example, it appears that the ***land-atmosphere connection*** is governed by soil moisture, landscape age and geological substrate, and vegetation. Differences in parent material and soil age result in landscapes with varying soil pH and vegetation composition, identified in the Arctic as acidic, nonacidic, and shrub tundra. The acidic and nonacidic landscapes appear to have very different energy and carbon fluxes, and we know little about the shrub tundra. The ***land-water connection*** appears to be governed by belowground processes such as decomposition and the production rates of dissolved carbon species, quality of the carbon produced, and soil water movement as driven by hydrological processes. Finally, the ***water-atmosphere connection*** is driven by the spatial extent of water, carbon loading from land, and by the meteorological forcings of precipitation, net radiation, and wind. Although this conceptual model is somewhat generalized, it does summarize our current knowledge of the key processes involved in controlling the major interactions between terrestrial, aquatic, and atmospheric systems in the Arctic. The Land-Water component of the LTER focuses on the interactions between water and land and between water and the atmosphere.

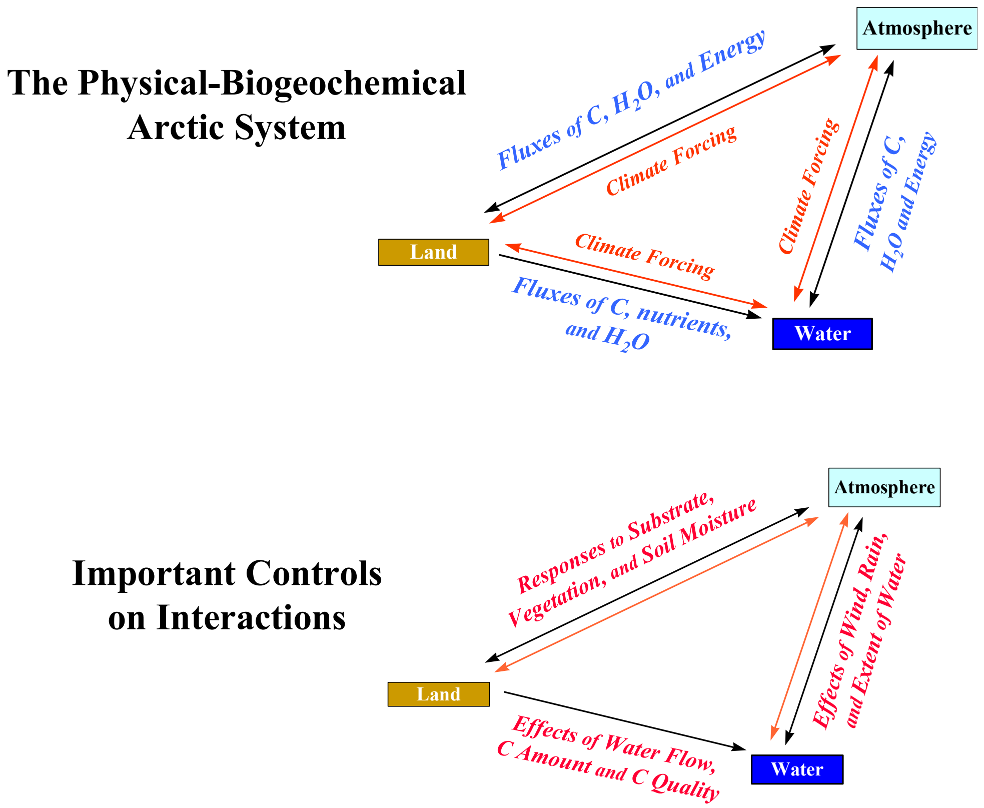


Fig. LW-1. **Linkages and important controls in the land-water-atmosphere system.**

We study these interactions between systems to better understand ecosystem structure and function. The relationship between system interactions, ecosystem structure and function, and the key processes and measurements that we make can be illustrated in three ways. The first way is shown by the ***Generalized Plan*** of relationships controlling structure and function given in Fig. 5 of this document's Introductory section. The second way is the organization of research approaches into ***Observations, Experiments, and Synthesis***, which is outlined for the Land-Water section in the Table below. The third way, somewhat specific for the Land-Water section, is to place the individual research projects within the logical framework of what controls the connections between land and water. A conceptual model of these controls is shown in Fig. LW-2. This model illustrates that (a) climate, vegetation, and physical setting act as controlling factors on the production of materials such as carbon and nutrients in soil waters, (b) hydrology in turn controls the material export from soils to surface waters, and that (c) these exported materials impact the receiving waterbodies. We are asking research questions about each of these controls, and synthesizing our observations in part by determining how these processes scale in space and time across landscapes. We have, however, only begun to incorporate these concepts and measurements into mathematical models; these models are necessary for extrapolations and predictions of how the arctic system operates and how it will respond to change. The sections below outline some of the background and highlights of our major research questions within the framework of land-water-atmosphere interactions summarized in Figs. 1 and 2.

Table of Observations, Experiments, and Synthesis Activities

Land-Water Interactions Research		**Observations** **Experiments** **Synthesis**
Location	***Ecosystem Type***	***Measurements***
Terrestrial Experimental plots	Moist Acidic Tussock, Wet Sedge, Nonacidic Tussock	Soil water chemistry, C and nutrient production Water additions to tundra $^{14}CO_2$ labeling
Tussock Watershed	Moist Acidic Tussock, Primary Stream	Stream flow and chemistry, rain events Soil water chemistry Hydrology and biogeochemistry model
Inlet Series of Lakes in the Toolik Basin	Lakes and Streams	Lake and stream chemistry Lake mixing and primary production Integration of ecosystems across the landscape Hydrology and biogeochemistry model
Toolik Lake, Lake E5	Lakes and their inlet streams	Ecological and chemical impacts of storm events (major inflows) on lakes

Table LW-1. This table illustrates the characteristics of research locations and the research approaches used to gather information on land-water interactions. Each of these approaches, and the resulting data, relates back to a major research question and the conceptual model of the important controls on land-water interactions shown in Figs. LW 1 and 2. Below we briefly describe three of the major research questions that these approaches address.

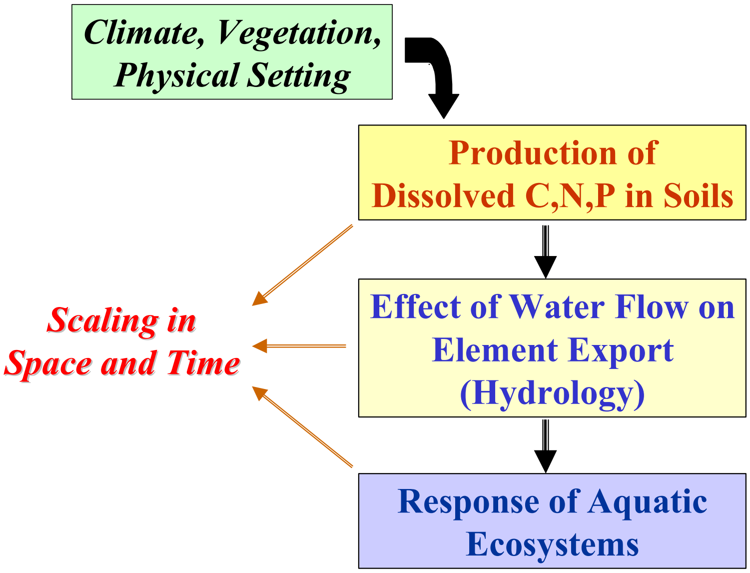


Fig. LW-2. Conceptual model showing the major controls and responses of land-water interactions. This model provides a framework for our major research questions.

Major Research Questions

Question #1: What controls the export of materials from land to water?
The general topic of land-water linkages, and specifically the movement of C and nutrients from arctic terrestrial ecosystems to the oceans, is of critical importance to understanding how the arctic system functions. Although the amounts, forms, and timing of terrestrial exports have been studied extensively (e.g., Swank and Crossley 1988; Lewis and Saunders 1989), we understand little about the specific plant and soil origins of these materials or the controls on their production and delivery. Previous work in the arctic (Shaver et al. 1990; Giblin et al. 1991) along a toposequence of tundra soils showed that different vegetation types and locations differed strongly in the inorganic nutrient chemistry of their soil waters. In addition to the inorganic nutrients, what little information exists for temperate systems on dissolved organic N, P, and C in soil waters (e.g., Sollins and McCorison 1981; McDowell and Likens 1988; Binkley et al. 1992) suggests that vegetation type and soil composition control the concentrations.

We have approached this problem by making measurements of soil water chemistry under different vegetation types and at different locations within catchments. In addition we have manipulated plant-soil mesocosms by adding water (to determine the impact of hydrological flushing) and by adding ^{14}C tracers to determine the origins and rates of production of C in soil waters (Judd & Kling submitted). We also developed a coupled hydrological-biogeochemical model that is capable of simulating the flow of water from the hillslope to the river network, and that incorporates biological processes so as to predict the fixation and respiration of CO_2 and its flux between land and the atmosphere (Stieglitz et al. 1999, 2000). Finally, we investigated the water-atmosphere interaction in terms of the flux of carbon gases as it relates to overall terrestrial carbon budgets.

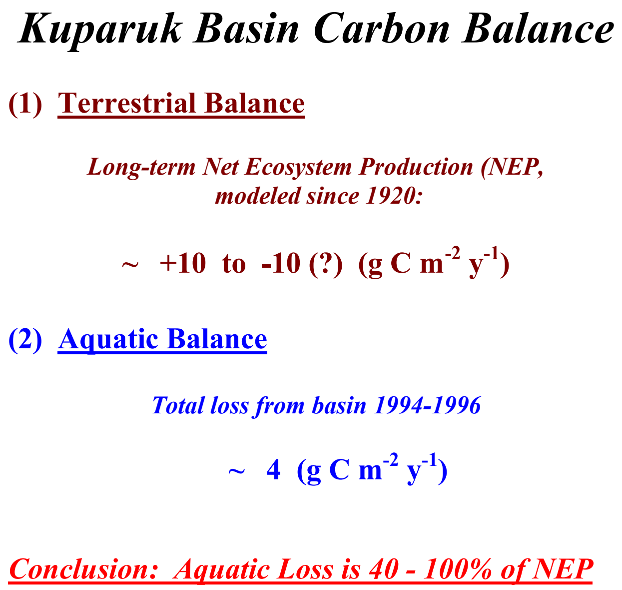
Highlights and Future Research. Two major findings from this research are that there is a substantial lateral flux of carbon from land to water; the amount that is exported from land and released to the atmosphere directly from surface waters, or transported to the Arctic Ocean in rivers, is in the range of the net ecosystem productivity of the entire Kuparuk basin (Fig. LW-3; Kling et al. 1991, 1992, 1996; Kling 1995; Reeburgh et al. 1998). Data assembled from cross-site studies and workshops indicate that this water-atmosphere flux operates worldwide, and is equal to ~20% of the total C flux from continents to the ocean (Fig. LW-4). Second, we have shown that the overlying vegetation and the flushing frequency of water through tundra soils controls the export of carbon (Judd & Kling submitted; Figs. LW-5 & 6).

We will continue studying the rates of production of dissolved nutrients and carbon in soil waters by looking at a broader range of ecosystem types. In addition we will improve our existing plant-soil hydrology model to incorporate processes controlling the delivery of water, of inorganic nitrogen and carbon, and of the gases carbon dioxide and methane to the stream network.

Question #2 -- What are the impacts of material exported from land on aquatic ecosystems?

One of the fundamental questions in ecology is how do systems respond to external influences, whether the influence is due to climate forcing or to species immigration or to inputs of nutrients and organic matter. We have extended our land-water research somewhat to examine specifically how inputs of C and nutrients impact lake metabolism.

Highlights and Future Research. One set of experimental results indicated that differences in the quality of the organic carbon were related to its place of origin on the landscape and to the time of season, and this controlled the rate of conversion of DOC carbon to CO_2 (Michaelson et al. 1998). We have also shown, using mesocosms, bioassays, and monitoring of inflow events, that this DOC is accessible to lake bacteria and that the use by bacteria depends on DOC concentration and the time of year (Kling 1995). A second set of measurements taken in 1999 showed the surprisingly persistent impact of a storm inflow event on the functioning of Toolik Lake. Fig. LW-7 shows changes in Chlorophyll a, NH_4^+, and productivity related to the inflow, and illustrates how these periodic forcing events can rapidly change the trajectory of system functioning, and can have long-lasting affects. Future research in this area will be coordinated with the Lakes component, and will expand measurements to other lakes with different morphometry and residence



Kuparuk Basin Carbon Balance

(1) Terrestrial Balance

Long-term Net Ecosystem Production (NEP, modeled since 1920:

~ +10 to -10 (?) (g C m^{-2} y^{-1})

(2) Aquatic Balance

Total loss from basin 1994-1996

~ 4 (g C m^{-2} y^{-1})

Conclusion: Aquatic Loss is 40 - 100% of NEP

Fig. LW-3 The Kuparuk Basin Carbon Balance

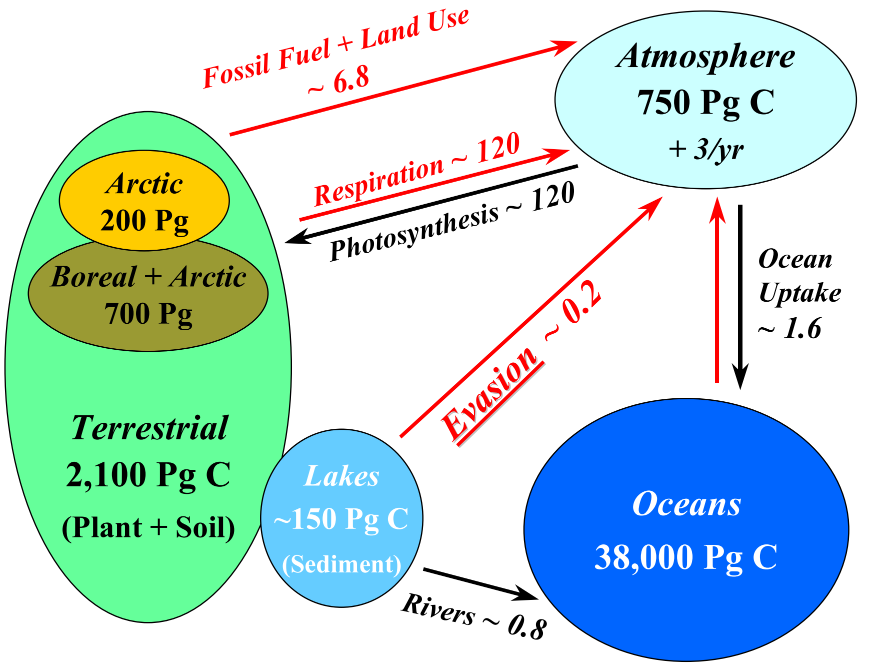


Fig. LW-4. Global carbon cycle with the “Evasion” term as a novel contribution (Pg/yr).

times in order to develop an understanding of the patterns of response of lake ecosystems to these periodic external forcing events.

Question #3 -- What are the relative magnitudes of interaction between ecosystems (land, lakes, streams) on the landscape?

One of the principles of ecological studies is that most descriptors of a system vary with the spatial or temporal scale of measurement. In biological studies, the spatial and temporal heterogeneity of organisms is a central component of several theories (e.g., evolution, succession), and new advances in understanding the consequences of environmental heterogeneity on biological systems have been made in the last ~20 years (Cliff and Ord 1973; Turner and Gardner 1991; Kratz et al. 1991; Levin et al. 1993; Fisher 1994; Powell and Steele 1995; Cooper et al. 1998). In addition to the importance of spatial distribution or patchiness of resources and organisms, the movement of organisms and the "connectivity" among patches is critical to system functioning (Hansen and di Castri 1992; Taylor et al. 1993). In studies of temporal dynamics, organisms are considered to adapt and evolve, and characteristics of the environment (e.g., soil properties) are considered to change from one time period to another. However, in studies of system function across spatial scales, the environmental characteristics and organisms of interest are usually considered to be static. In other words, the rates of movement of organisms or materials may be affected by the boundaries or ecotones that separate different environmental patches, but there is little or no change or “processing” that occurs as materials and organisms move across the landscape.

There are two exceptions to this generalization of an assumed lack of processing of materials moving across a landscape, one derived from concepts in stream ecology (the “river continuum”, “resource spiraling”, and “serial discontinuity” concepts), and one from studies of landscape position of lakes (Magnuson et al. 1990; Soranno et al. 2000; Kling et al. 2000). While these ideas about spatially dependent processes in rivers and lakes have had great utility in aquatic ecology, there has been very little empirical or conceptual integration of lakes and rivers at a landscape level. The result is that we can describe the functioning of individual systems, but there remains a large amount of residual variation among lakes and among streams that may only be explained through an understanding of ecosystem interactions at a landscape scale.

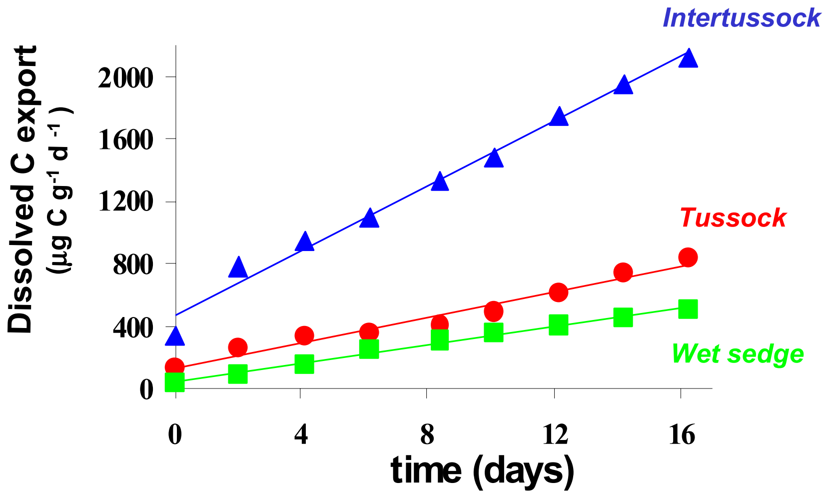
Our LTER research has led us to propose that current concepts related to the functioning of aquatic ecosystems within a landscape can be placed in a broader context by including the spatially dependent processing of materials in both lakes and streams taken together. The foundation of this idea is the concept of a “mass balance budget”, which allows determination of the changes in mass of substances (or the number of organisms) in a defined space and time, and requires only information on “pools” of variables such as populations or standing stocks of materials, and on processes that control the flows, production, consumption, and transformation of the variables. Each of the important processes defined by the ecological concepts described above may be represented in a mass balance format. For example, an ecotone such as a riparian zone is a pool considered to have inputs from other pools of material in the model, such as an upland area; specific production or consumption processes affect those inputs and contribute to a flow or output into an adjoining pool of material such as a stream.

Highlights and Future Research**.** Studies of the series of eight connected lakes that flow into Toolik Lake (the “Inlet Series”) have shown that there are distinct spatial patterns in chemical variables. These observed spatial patterns include mean concentrations of variables that increase, decrease, or remain constant along the lake chain from high to low altitude in the catchment (data for stream sites as yet show no strong spatial patterns with any variables). These patterns are determined in part by the effect of increasing catchment area feeding into lakes further downslope, and in part by the systematic processing of materials in lakes and in the stream segments between lakes. Table LW-2 presents the magnitude of this processing in lakes and streams for selected variables over several years of study. For example, lakes tend to “consume” alkalinity and calcium, while the stream segments produce these materials. These results, plus the more detailed analysis presented in Kling et al. (2000), illustrate that over small geographic areas, and somewhat independent of lake or stream morphometry, the consistent and directional (downslope) processing of materials helps produce spatial patterns that are coherent over time for many limnological variables.

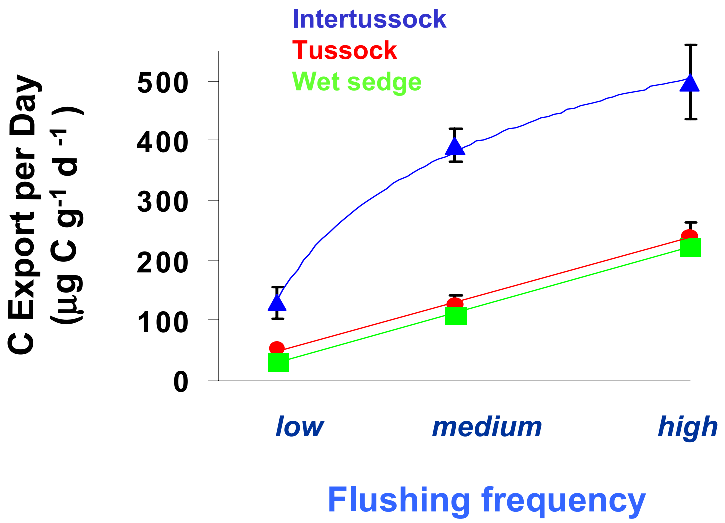
Future research in this area will concentrate on quantifying the inputs and outputs of chemical and biological variables from several stream and lake segments within the Inlet Series of Toolik Lake. In addition, we will continue the development of the lake, stream, and land-water models (described in this document) with the purpose of linking these models to help understand and predict how ecosystems interact across the landscape.

Conclusions

As mentioned earlier in this document, the goal of the Arctic LTER is to "predict the future ecological characteristics of the site given our knowledge of the controls of ecosystem structure and function". The Land-Water component focuses on three major controls, which are (1) how climate, vegetation, and physical setting act as controlling factors on the production of materials such as carbon and nutrients in soil waters, (2) how hydrology in turn controls the material exported from soils to surface waters, and (3) how exported materials impact the receiving waterbodies. Our specific research questions relate to these controls, and we are synthesizing our observations in part by determining how these processes scale in space and time across landscapes. As we improve our understanding of the ecosystem controls we are better able to predict the consequences of future ecological or climate change. Our hydrology-biogeochemical model is being developed to make such predictions, and our final goal is to assemble and link the Lake, Stream, Terrestrial, and Land-Water models that we are developing in order to make extrapolations and predictions of how the arctic system as a whole operates and how it will respond to change.

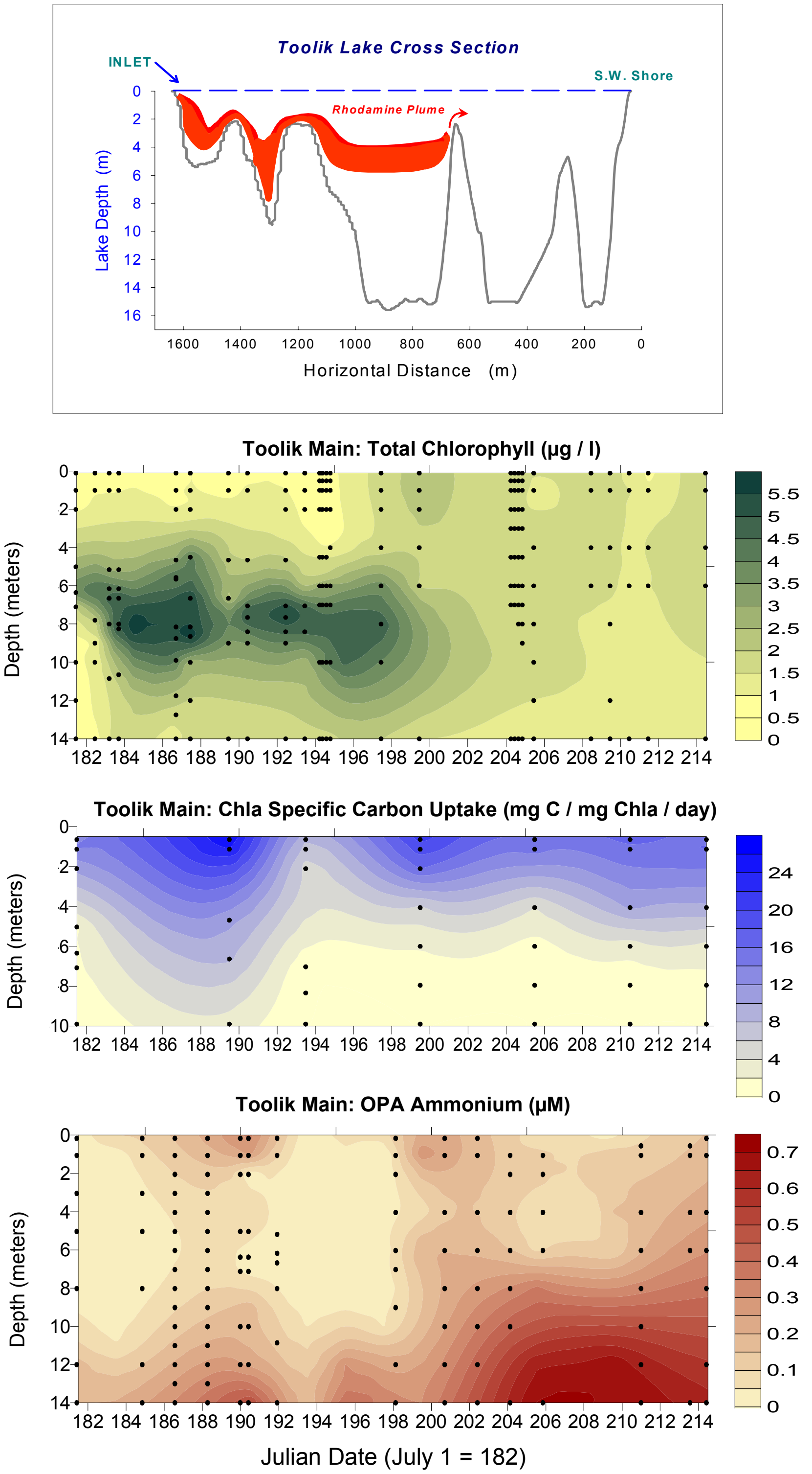


Cumulative export of total dissolved C



C Export Increases with Flushing

Figs. LW-5 & 6. Results showing how the C export from land is controlled by the overlying vegetation (top panel), and also the influence of hydrologic flushing frequency (bottom panel).



Interpolation Method: Kriging

data4/toolik99/lake_chemistry/TM1.srf

Fig. LW-7. Illustration of a storm-driven inflow event and its long-term impact on Toolik lake. The top figure shows the path of the inflow water traced by rhodamine. The bottom 3 panels show the impact of the storm event which occurred on Julian Day 199. Chla concentrations were diluted dramatically (top), but the rate of C uptake per unit Chla stayed the same (middle), probably due to the increase in ammonium concentrations in surface waters brought in by the storm (bottom).

Table LW-2. Effects of lake and stream processing by variable for all sites of the Inlet Series (~10 years of data for a series of 8 lakes connected by stream segments of varying length). Mean values (± SE) of limnological parameters are calculated for lakes by subtracting the inlet values from the outlet values, and for streams by subtracting the upstream values (at the lake outlet) from the downstream values (at the next lake's inlet). Positive values (blue) indicate production of materials and negative values (red) indicate consumption either in the lake or in the stream reach between adjacent lakes in the chain. Variables are sorted by decreasing consumption in lakes. "N" is the number of individual difference comparisons. "P" indicates the significance level of a T-Test (unequal variances) that the mean value is significantly different from zero; ** $P<0.01$ and * $P<0.05$. The results show that there is a consistent difference in processing of materials between lakes and streams; these differences contribute to the spatial and temporal patterns of concentrations of materials that are found in the lakes (Kling et al. 2000).

Red = Consumption **Blue = Production**

LAKES (Out-In)						**STREAMS (Down-Up)**				
	Mean	**SE**	**N**	**P**			**Mean**	**SE**	**N**	**P**
PCO$_2$ (µatm)	-374	60	86	**		PCO$_2$	338	60	139	**
PCH$_4$ (µatm)	-92	40	86	*		PCH$_4$	50	28	139	*
Alk (µEq/L)	-35	9.9	102	**		Alk	35	7.6	136	**
DIC (µM)	-24	6.9	48	**		DIC	28	3.2	96	**
Ca^{2+} (µM)	-11	4.3	69	**		Ca^{2+}	9.9	2.7	75	**
PC (µM)	-5.7	4.4	54			PC	5.8	3.6	80	
DOC (µM)	17	12	103	**		DOC	-8.1	8.0	145	
NH$_4^+$ (µM)	0.11	0.04	88	**		NH$_4^+$	-0.12	0.05	128	**
Chla (µg/L)	0.17	0.08	93			Chla	-0.06	0.08	111	

ARCTIC LTER STREAMS COMPONENT

Introduction

The streams of the foothills region of the North Slope of Alaska are strongly shaped by the physical setting and the climate of the Toolik region. Proximity to the Brooks Range, the divide between north and south flowing rivers, contributes to the relatively small size of the tundra watersheds and their streams near Toolik (Fig. 1). The mountains also add to the diversity of stream types near the arctic LTER site by providing the physical setting for glacial streams, mountain stream and many spring streams.

The cold climate greatly shortens the flowing water season and maintains a layer of virtually continuous permafrost beneath the catchments of these headwater streams. The snow that accumulates during the long winter melts and runs off abruptly during May and early June, often while the streambed is still encased in ice. The biota must adapt to the short flowing water season, the relatively cool water temperatures (Fig. 2) and the winter freeze through special adaptations for survival such as a tolerance for below-zero temperatures for insects and the fishes' ability to migrate to lakes where they overwinter. In spite of having a compressed season of biotic activity, the carbon and nutrient cycles of arctic streams are in many respects similar to cycles in temperate and tropical streams. These studies of arctic streams provide data on ecology at the low temperature and low productivity ends of the spectrum. Streams research at the Arctic LTER site currently blends long-term observations and monitoring, studies of populations, stream surveys, long-term experiments, nitrogen cycle tracer studies, cross-site studies, and scaling-up activities. Here we provide a brief introduction.

Fig. 1. The Brooks Range, Alaska, showing the uppermost reaches of the Kuparuk River watershed.

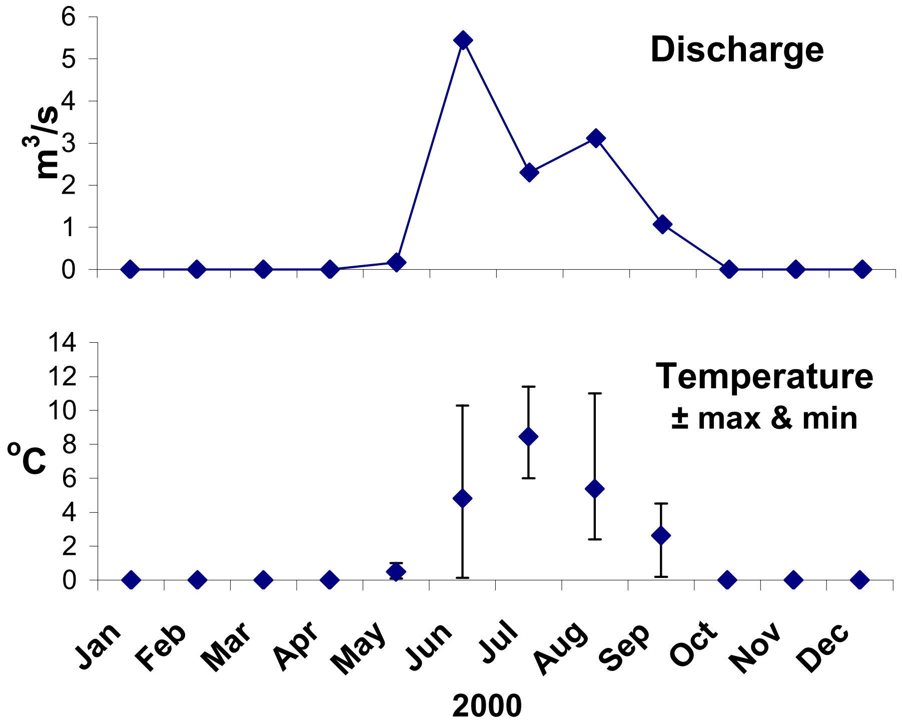


Fig. 2. Mean monthly discharge and water temperature of the Kuparuk River for 2000.

Observations

Long-Term Variability. Stream studies at Toolik started in 1978 with several years of baseline studies focused upon the carbon and nutrient cycles of the Kuparuk River (Peterson et al.1986, Peterson et al.1992). The Kuparuk was chosen because it was accessible by truck, had perennial flow, and supported all trophic levels including fish. The major initial findings were that the inorganic nutrient levels were virtually undetectable and productivity was quite low; about 10 g C m^{-2} yr^{-1}.

Since these early studies the long-term monitoring has documented the great variability in summer discharge regime (Fig. 3) and has confirmed the low ambient nutrient levels described previously. In several years summer storm peak discharge exceeded snowmelt discharge but snowmelt is always of longer duration. But other summers have had very few rains large enough to affect stream discharge. The Kuparuk has also been monitored for temperature, conductivity, major ions, epilithic (rock surface) chlorophyll, insect abundance and fish growth every year (Hershey et al. 1997). Most of these parameters have shown a high degree of interannual variability (Fig. 4) and we now know that much of this variability is related to seasonal and annual variation in discharge that depend on the amount of winter snow accumulation as well as summer storms (Slavik et al. in prep., Deegan et al. 1999). Without long-term systematic monitoring the relationships between discharge and algal biomass, insect abundance, and fish growth would have remained undetected. Parallel observations in a second tundra stream, Oksrukuyik Creek, confirm the high interannual variability in physical and biological factors in North Slope streams.

Long-Term Study of a Grayling Population. The arctic grayling is the only fish species in the Upper Kuparuk River and in most tundra rivers that have fish populations. The Kuparuk River grayling make an annual migration to deep-water habitat dictated by the fall freeze-up of the tundra streams. Most adult

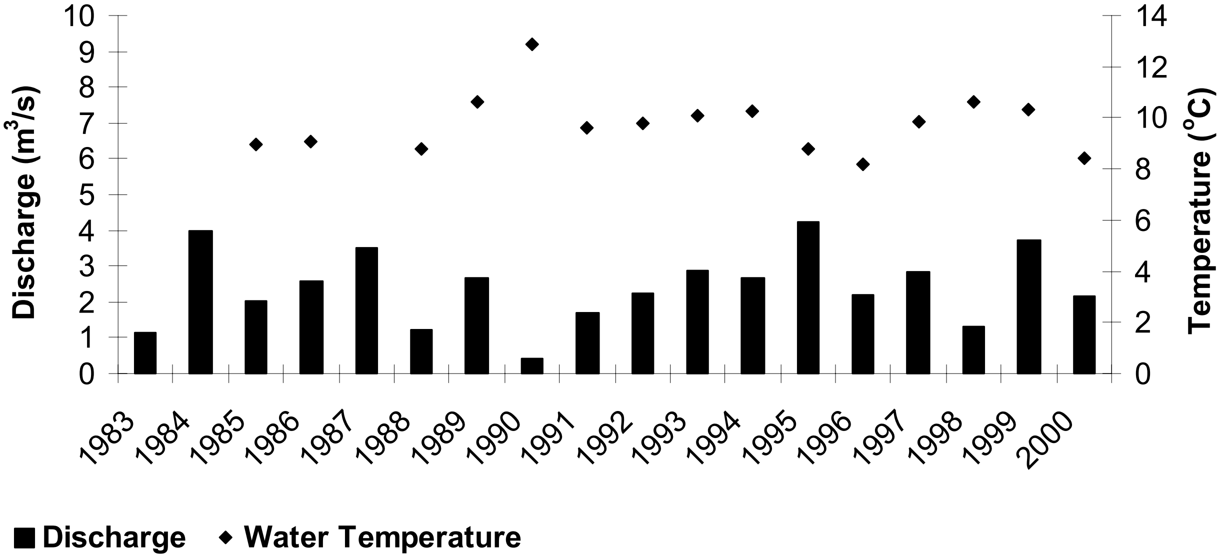


Fig. 3. Mean discharge and water temperature of the Kuparuk River during phosphorus fertilization.

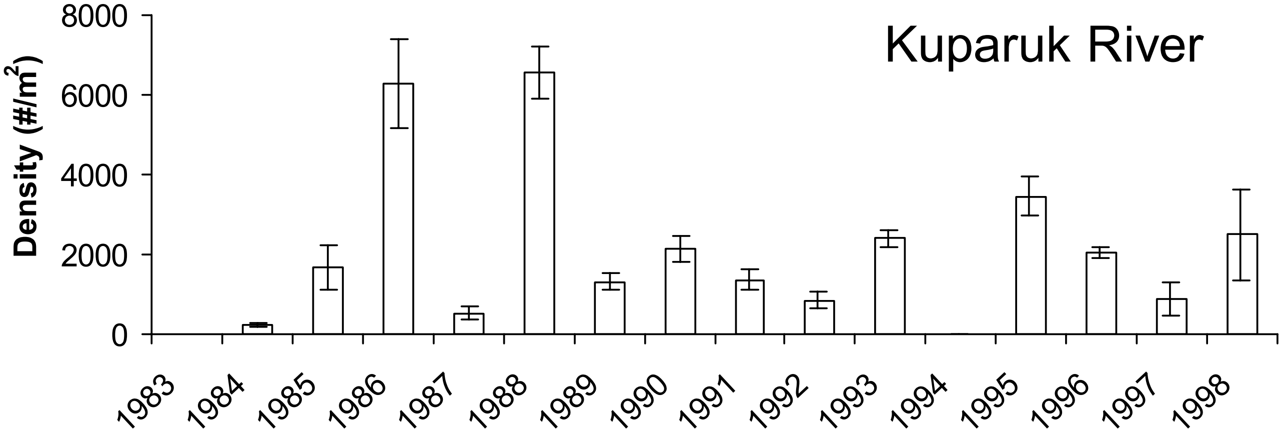


Fig. 4. Natural variability in the mean densities of *Baetis*, the dominant mayfly, in the reference and fertilized reaches of the Kuparuk R., 1984-1998. Data was not available for 1994.

graying in the Kuparuk travel upstream in August to Green Cabin Lake where they live under the ice until the spring runoff begins. In late May they reenter the river, spawn within several weeks and then establish summer territories that they defend against other grayling. Within a short two months of feeding on insects they must obtain enough energy to grow, migrate, over winter and spawn the following spring.

This annual migration has provided an opportunity to sample this population very efficiently as individuals move into the lake and has revealed a characteristic of the Kuparuk grayling population that is similar to what has been described for arctic lake trout populations. We have observed cycles of small and large-size grayling as strong cohorts enter and leave the population (Fig. 5). In 1989 the Kuparuk grayling population was comprised of predominantly of 36+ cm fish that declined and were quickly replaced by recruitment of smaller 29 to 33 cm fish that have subsequently grown to large size and just recently declined as they complete their life cycle. We are now studying the annual data to determine what controls the patterns of annual mortality for adult grayling.

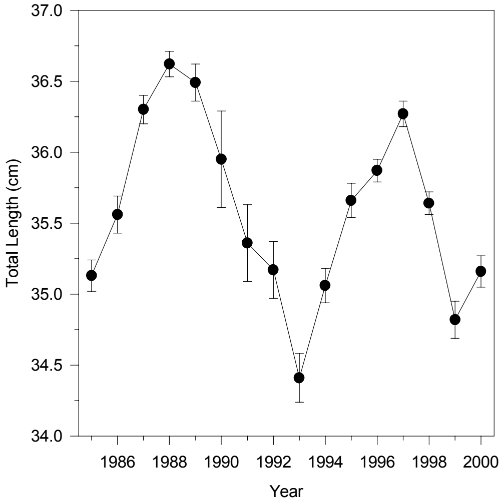


Fig. 5. The cyclical patterns in mean lengths (± SE) of Arctic grayling (1985-2000).

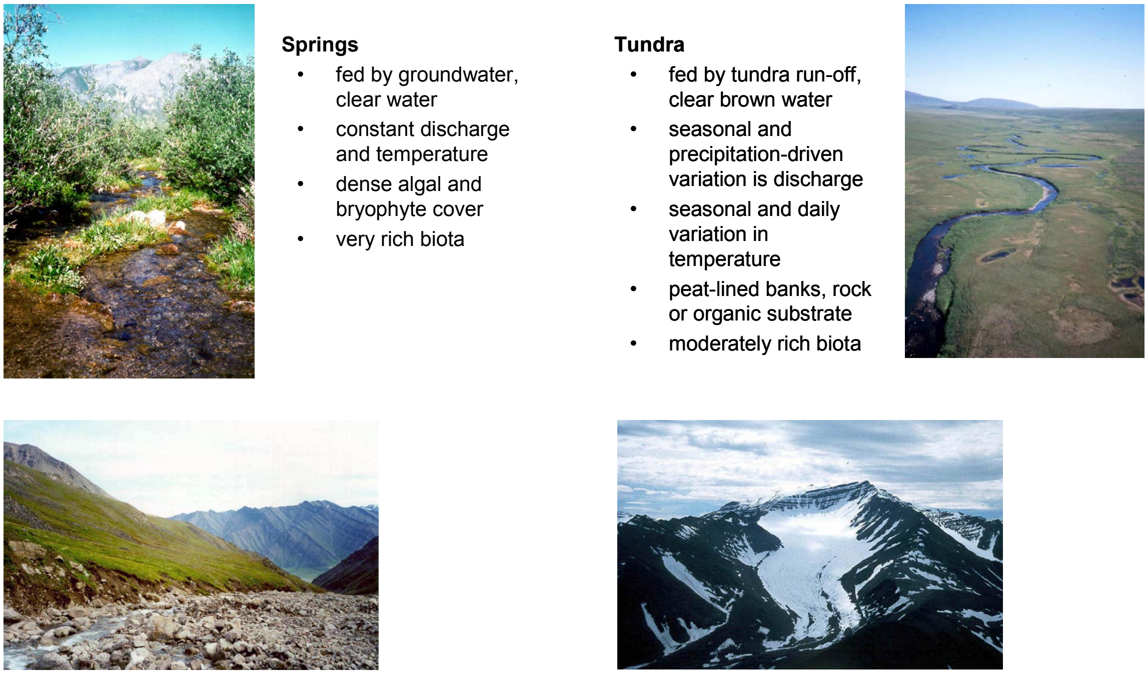
<u>*Surveys of stream types in the Toolik Region.*</u> The need to generalize our knowledge of arctic streams and to predict the response of arctic stream to change has given urgency to our surveys of stream types on the North Slope. Until recently our studies have focused on tundra streams accessible by truck from Toolik camp. However, within a 100-mile radius of Toolik, there are many mountain, glacial and spring streams with very different chemistry, productivity and community composition. Mountain and glacial streams have steep gradients, unstable substrata, high conductivity, moderate nutrient levels and low productivity (Fig. 6). The glacial streams have suspended sediment loads that scour and cover the rocky bottom, thus contributing to a low diversity of organisms. Springs, both hot and cold, are arrayed along the base of the Brooks Range Mountains with additional springs emerging between the foothills and the coastal plain. Spring streams have constant year around flow and temperature, high nutrient levels and elevated conductivity. Springs have the highest primary and insect productivity of all arctic streams. They serve as an obligate nursery for the fall spawning sea-run arctic char. Finally tundra streams are lowest in inorganic nutrients and have low primary productivity but receive the highest organic matter inputs from the surrounding terrain. The majority of the streams near Toolik are tundra streams.

Experiments to understand controls of steam ecosystem processes and structure

In order to test the hypothesis that the low productivity of the Kupark was due to lack of nutrients rather than harsh winter conditions, cold temperatures and physical scouring of the rocky stream bottom, we started in 1983 a long-term experimental fertilization study of the Kuparuk River. Even in the first summer of the fertilization it was apparent that phosphorus addition during the summer stimulated biotic activity of all types in the river (Peterson et al.1985). Bacterial activity on both labile and refractory substrates was increased by phosphorus addition (Hullar and Vestal 1989). Diatoms on the rocks responded within a few days to the added phosphorus and within a few years insect abundance and fish growth were measurably affected by the addition (Peterson et al. 1993). Some insects such as black flies declined but others including *Baetis* and *Brachycentrus* increased (Hershey and Hiltner 1988, Hershey et al.1988), contributing to accelerated fish growth (Deegan and Peterson 1992).

After several more years of fertilization we debated stopping the experiment because we thought we might have already observed the full response. However we were wrong and to our surprise moss began to proliferate on rocks in riffles after 8 or 9 years of continuous summer fertilization (Bowden et al. 1992). Over the next several years a dense mat of the moss *Hygrohypnum* covered the majority of what had previously been bare rock habitat covered by a thin biofilm of bacteria and diatoms. Again the insect populations underwent dramatic changes with increases in chironomids and *Ephemerella* and declines in *Orthocladius* and *Baetis* (Slavik et al. in prep). The effect of this recent transition in community structure on grayling is still unknown although surprisingly it does not yet appear to be large.

A second stream fertilization was performed in Oksrukuyik Creek starting in 1991. The pattern of response was similar to that observed in the Kuparuk with the exception that filamentous algae were more abundant in the fertilized reach than was observed in the Kuparuk (Harvey et al. 1998)



Springs

- fed by groundwater, clear water
- constant discharge and temperature
- dense algal and bryophyte cover
- very rich biota

Tundra

- fed by tundra run-off, clear brown water
- seasonal and precipitation-driven variation is discharge
- seasonal and daily variation in temperature
- peat-lined banks, rock or organic substrate
- moderately rich biota

Mountain

- fed by mountain run-off
- variable discharge and temperature
- unstable substrate and scoured channels
- sparse biota

Glacial

- fed by glacial run-off
- high suspended sediment
- high daily variation in discharge
- unstable substrate and scoured channels
- sparse biota

Fig. 6. Physical and biological characteristics of the four major stream types of the North Slope of Alaska: spring, tundra, mountain and glacial.

Nitrogen transformations in tundra streams- tracer studies. The fertilization experiments have shown us many dynamics of the tundra stream ecosystem but there remained several questions about the reference reach and other undisturbed streams that we could not answer. For example, how are nutrients transported downstream and what is the structure of steam foodweb? We knew something about the taxa in different streams but not much about how they were connected in foodwebs. A stable N isotopic tracer helped us answer these questions. In 1991 we performed a tracer-level ^{15}N-NH$_4$ continuous addition to the reference zone of the Kuparuk River. The experiment revealed many aspects of the nitrogen cycle and of energy flow through the food web (Fig. 7). For example, we found that ammonium molecules traveled downstream about 700 m before removal, mayflies travel 2 km upstream to oviposit (Hershey et al. 1993) and that detrital and long-lived insects retained measurable ^{15}N for over 2 years (Peterson et al. 1997). The results of this experiment stimulated the development of the Stable Isotope Stream Tracer Model (SISTM) in order to test hypotheses about N flow pathways in streams (Wollheim et al. 1999). In subsequent years we have studied the N cycle in various types and sizes of tundra streams (Wollheim et al. 2000).

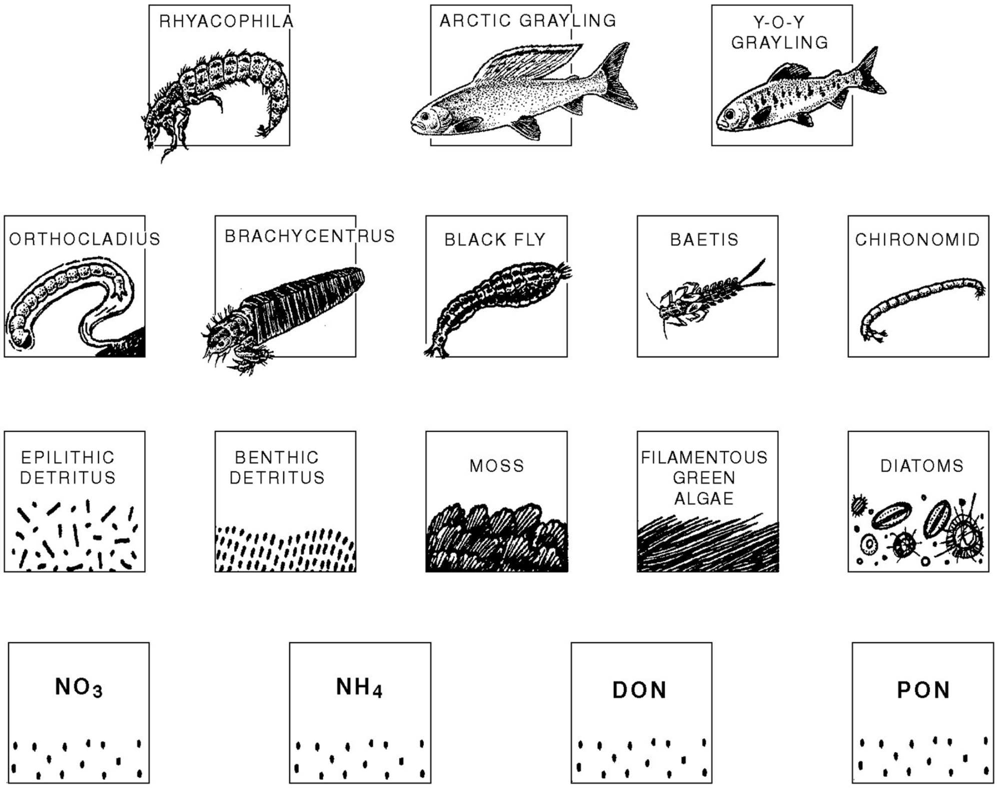


Fig. 7. Major components of the Nitrogen cycle of the Kuparuk River.

Synthesis

Scaling Up- modeling, watersheds and arctic synthesis. The fact that the arctic climate is already warming has prompted a focus on the task of scaling-up our knowledge of streams to the whole-catchment level. In order to predict the future status of arctic streams we must have knowledge of how inputs from land to streams will change. Marc Stieglitz and others have taken the first steps by developing a simplified version of TOPMODEL that can be applied on both local and regional scales. The model relies upon an aggregated statistical representation of catchment topography combined with a land surface model to simulate the energy balance and water cycle of the relatively dry upland and wetter lowland portions of catchments. The aggregation is what allows the model to be applied over large regions because it greatly reduces the number of computations needed to represent soil temperatures and discharge from catchments. After several years of work to adapt the model to arctic conditions, acceptable predictions of soil temperatures and stream hydrographs have been achieved (Fig. 8). Some of the future work will focus on biogeochemistry with the objective of predicting fluxes of C, N, and P from the landscape to streams and lakes. Since discharge regime and nutrient levels are primary determinants of stream ecosystem structure and function, these predictions are needed to predict how arctic streams will respond to regional or global change.

Since 1994 we have been performing intensive single summer studies of tundra stream reaches of different sizes and characteristics to develop a watershed-level database of stream biogeochemistry and trophic structure. In a recent synthesis paper Wollheim et al. (2001) have shown how stream size and trophic status of the tundra streams of the Kuparuk watershed influence the downstream transport of inorganic nitrogen and particulate organic matter. This data will be used to calibrate the stream network process model we plan to start this year. The model will be based upon a biogeochemical process model that tracks C, N and ^{15}N developed by Joe Vallino to simulate N cycling in tidal rivers at Plum Island Sound.

At the pan-arctic scale our efforts to understand water and constituent transport in rivers have focused on data rescue and synthesis. With funding from OPP-ARCSS we have developed a discharge database for the pan-Arctic watershed. This data set includes the monthly discharge for the period of record for over 3600 stream and river gauging stations and is available at http://www.R-ArcticNET.sr.unh.edu/ or on CD-ROM or from NSIDC, Denver. The data has been analyzed for trends in runoff for the entire drainage of the Arctic Ocean and Hudson's Bay (Lammers et al. 2001). We have used hydrological data from Imnavait Creek, a small watershed near Toolik, to calibrate the Permafrost Water Balance Model (PWBM) for prediction of runoff from ungauged arctic river basins under prescribed climatic conditions. We emphasize the fact that research at Toolik provides the core calibration and testing data for most of our global-scale model applications. The pan-arctic river network developed on this project will be needed to scale-up our understanding and models of stream transport and processing to the circumpolar level (Lammers et al. in prep.).

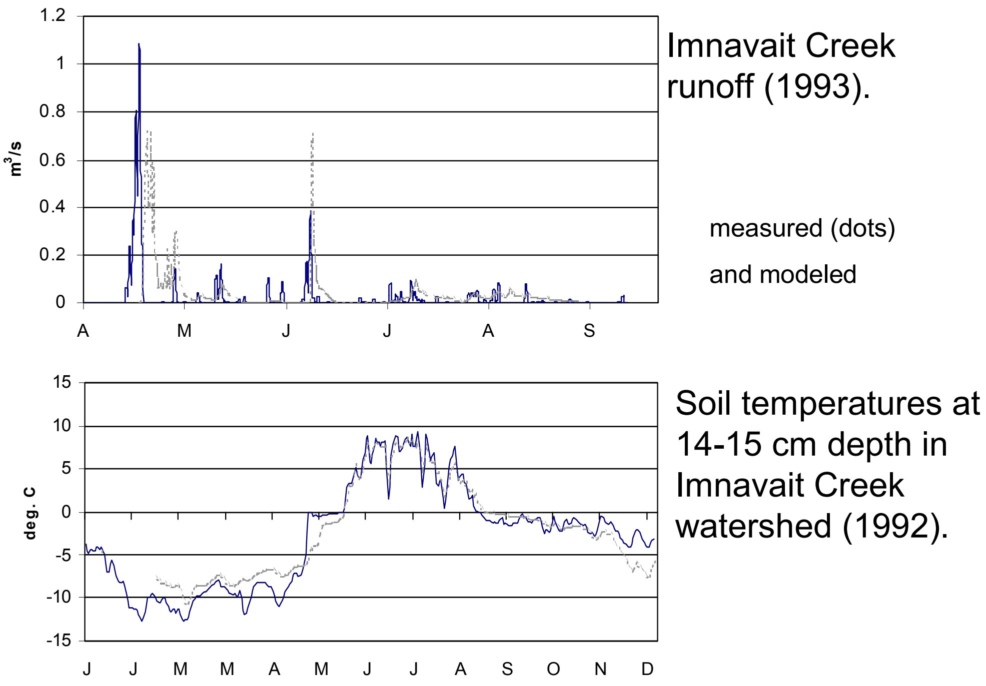


Fig. 8. Top: 1993 Imnavait Creek runoff (measured (dots) and modeled. Bottom: 1992 soil temperatures at 14-15 cm depth in Imnavait Creek watershed (measured (dots) and modeled). From Stieglitz et al., 1997.

A companion pan-arctic data set on river biogeochemical fluxes is under development but the amount of information and quality of the data is limited (Holmes et al. 2000, 2001). Experience with low levels of nutrients in streams at Toolik have made it possible to locate errors and repair gaps in these global databases. The current status of the biogeochemical synthesis can be viewed at htpp://ecosystems.mbl.edu/partners. The dimensions of the problem can be highlighted by simply noting that neither the Yukon River nor the Mackenzie River is now monitored for continent to ocean fluxes. Russian and Canada both have experienced a 30% decline in gauge sites in the last decade and the farthest downstream gauge of the USGS Pilot Station on the Yukon has been closed for the past 5 years. The possibilities for detecting change or validating models for the land to ocean river fluxes of the Arctic are rapidly diminishing.

Cross-site studies: Organic Matter Budgets, Bryophytes and ^{15}N Tracers. Stream ecologists have a particularly strong tradition of cross-site studies as demonstrated by LTER PUBLICATION 15: Stream Research in the LTER Network (1993). Stream ecologists from around the world came together at the North American Benthological Society (NABS) meetings for an extra day for several years to synthesize information on the organic matter cycle of streams (Webster and Meyer 1997). The Kuparuk was the only tundra stream in the comparison and was on the low end of the spectrum for detrital organic matter stocks and gross primary production (Harvey et al.1997).

The rapid invasion of moss in the Kuparuk fertilization experiment prompted a review of the role of mosses in a special session organized by Breck Bowden at the 1996 NABS meeting. The Stream Bryophyte Group subsequently published a large review documenting the effects of bryophytes on the biogeochemistry and food web structure of rivers (Stream Bryophyte Group 1999) (Fig. 9). In summary, bryophytes are much more widespread and important in streams than commonly assumed. Even a low percent cover of moss may dominate stream productivity because of their large biomass per unit area compared to epilithic algae. Bryophytes compete with algae for space and for nutrients while altering the habitat for insects and fish. Once moss cover reaches the dimensions achieved in the Kuparuk fertilization, moss production outpaces algal production by an order of magnitude. And once moss is well established it can persist for years even after nutrient addition has stopped (Bowden, unpublished data).

LTER cross-site experiments involving whole-ecosystems are unusual but of great potential value in testing the generality of our understanding of stream ecosystems. An LTER workshop grant provided the means to bring stream researches from across the network to Coweeta Hydrological Station to plan a comparison of nitrogen cycles in streams and to test the SISTM model (Hall et al. 1998). Subsequently, the NSF Ecosystems program funded a 12-site study of N cycling in headwater streams of North America (Fig. 10). Major findings were that inorganic N transport is predictable across biomes from information on stream size, gross primary productivity and total respiration. Even in these small headwater streams the concentrations of nitrate and ammonium were as strongly controlled by in-stream processes as by inputs from land, a finding that surprised many proponents of small watershed studies (Peterson et al. 2001).

This stable isotope tracer approach developed at the Arctic LTER site is already being employed in a variety of additional settings. In New Zealand the ^{15}N tracer is being used to study the impact of introduced brown trout on streams previously dominated by native galaxid fishes. In Iceland the link between steam insect production and riparian spider populations has been established with ^{15}N tracer. At the Plum Island Sound LTER site ^{15}N-nitrate has been added to estuaries to trace the fate of nitrate discharged from rapidly developing watersheds (Holmes et al. 2000, Hughes et al. 2000). New applications of the approach are being discovered every year.

Plans for Future Research

Observations

1. Continue the long-term monitoring of the Kuparuk River
2. Continue long-term study of the grayling population
3. Continue surveys of selected stream types

Experiments

4. Continue the fertilization of the Kuparuk River
    a. Special focus: the succession of bryophyte species
5. Initiate a fertilization study of a very small tundra stream
6. Continue intensive process studies of stream reaches
    a. Special focus: hyporheic metabolism and whole-stream productivity.

Synthesis

7. Start development of a stream reach simulation model of biogeochemical processing and food web dynamics; scale-up to the stream network of a drainage basin.

Conclusions

The LTER research on streams and their response to perturbation is contributing to our understanding of controls of stream processes and to the prediction of how stream ecosystems will respond to global change. We now know some of the ways that variations in discharge and in nutrient loading interact to change the structure and function of tundra streams. Our next initiative will be to more strongly link land, stream and lake in our field research and in our modeling. The rationale is that changes in vegetation and hydrology on the land surface will alter the inputs of water, nutrients and organic matter to streams and to lakes. To predict change in aquatic ecosystems, we must view the landscape as a mosaic of interacting units rather than as independent patches of the landscape.

The Arctic LTER streams group has made strong contributions to syntheses and experimental studies of how streams function throughout the world. Research at Toolik has stimulated efforts to scale-up reach studies to entire drainages and has contributed to the development of pan-Arctic watershed-scale databases and models of global change impacts on rivers. The incorporation of our process level and community structure understanding into what currently are mass balance models of stream and river networks of the Arctic remains a long-term goal. This goal appears more attainable now than it was even 6 years ago at our last LTER site review. It appears likely that a combination of strong hydrological forcing and relatively simple community structure in Arctic streams will contribute to rapid progress in modeling.

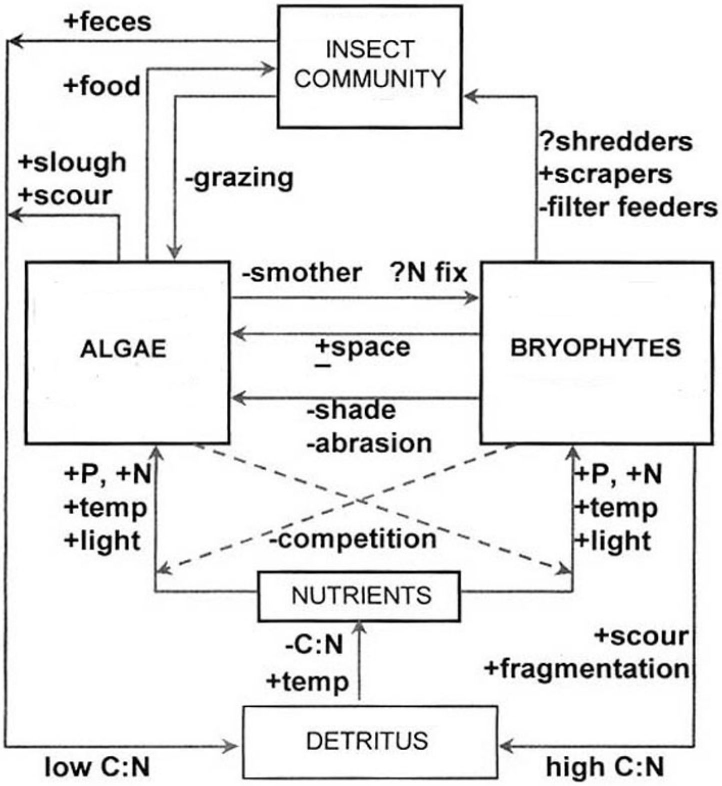


Fig. 9. Conceptual model of the role of bryophytes in streams.
Stream Bryophyte Group, 1999.

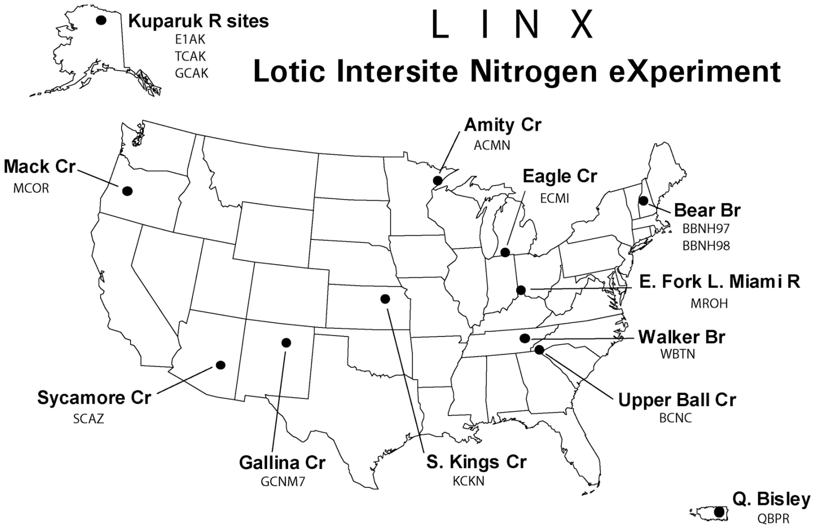


Fig. 10. Locations of the study sites in the Lotic Intersite Nitrogen Experiment (LINX). From Peterson et al. 2001.

ARCTIC LTER LAKES COMPONENT

Introduction

The first research undertaken, at what is now the Arctic LTER, was the study of the structure and function of the Toolik Lake ecosystem beginning in the summer of 1975. There were six principal investigators with the study organized along a food chain model, i.e., nutrients, phytoplankton, zooplankton etc. (Hobbie et al. 1991). This approach and organization continued until 1983 when we undertook a major limnocorral study adding plant nutrients and fish to some limnocorrals and leaving others as reference systems. This research was organized around the theme of the control of arctic lakes as being either from fluxes of nutrients entering the base of the ecosystem and food chain (bottom up) or top predators regulating the system from the top (top down). These themes were incorporated into our initial LTER research in 1985 (Hobbie et al. 1991). We have subsequently broadened our thinking about control mechanisms of arctic ecosystems to include aspects of the landscape and climate, as well as continuing with the idea of biota control (top down) and control by fluxes of nutrients (bottom up). To study and understand these control mechanisms we have used three general approaches. These are long-term observations by monitoring a series of lakes and through surveys that trade space for time. We also measure rates and controls of lake ecosystems through experiments where we manipulated limnocorrals, changed whole or divided lakes by adding nutrients, or added or removed various predators. Lastly we are synthesizing our knowledge of lake ecosystems through the use of simulation models.

Observations

Far and away the longest monitored lake is Toolik Lake, which was first studied in 1975 (Fig. 1). (O'Brien et al. 1997). We have noted a variety of long-term trends in Toolik Lake. One is the warming of the mean July water temperature at 1 m for each year (Fig. 2); the overall trend is statically significant with the regression having a *p* value of 0.025. The "y" intercepts for 1975 versus 2000 indicate that, on average, the lake is 2° C warmer now than at the beginning of the study. (Hobbie et al. 1999). While even 25 years is too short a time to confirm arctic warming, these data are certainly consistent with such a warming trend. We have also noticed that the alkalinity of Toolik Lake water has increased (Fig. 3). This increase has not been linear but shows two spurts one early in our study of the lake and then one much more recently with a cubic equation fitting the data with a remarkably low *p* value. Analysis of the precipitation chemistry shows that this increase is not due to increased salinity in the precipitation but is mostly likely coming out of the Toolik watershed, possibly due to deepening of the thaw layer above the permafrost. Another long-term trend in Toolik Lake we have noted is the reduction in size of lake trout. Early in the study in 1977, the median weight of lake trout was 578 g and by 1986 this was reduced to almost one-half (McDonald and Hershey 1989) of what it was (Fig. 4). By 1997 the median weight of lake trout was still 60% of the 1977 weight. This reduction in the size is doubtless due to the fairly heavy fishing pressure Toolik Lake has received and the very slow growth of lake trout. Our estimates of lake trout growth rate averages less than 5% increase yr^{-1} for adult fish.

We have also used surveys to extend our observations to more of the North Slope of Alaska. Early surveys were constrained to lakes that could be reached by walking in one day from the TLRS or accessible from the Dalton Highway (Luecke and O'Brien 1983; Kling et al. 1992). In recent years we have had helicopter support which helps tremendously in survey work. Early surveys were of zooplankton community composition and these indicated that the presence of fish strongly determined the type of zooplankton community present. Fish may be absent from a lake for two general reasons. If the lake or pond is shallow, fish will be excluded because the lake will freeze solid and kill the fish. Secondly a stretch of the outlet stream of a lake may be too steep for fish to negotiate. During our recent Geomorphic-Trophic Hypothesis (GTH) survey of 115 lakes we found that outlet aspect was more a filter than an absolute gate often allowing one or two species of fish into a lake while restricting others (Hershey et al. 1999). Sculpin and grayling are the best pioneers while lake trout and arctic charr are the poorest. The absence of fish profoundly affects the zooplankton community. Without fish one often finds very large zooplankton such as fairy shrimp and *Chaoborus* (Fig. 5). But with only arctic grayling one finds a very small crustacean zooplankton community made up of only four species of crustacean zooplankton (*Daphnia longiremis, Bosmina longirostris, Diaptomus pribilofensis,* and *Cyclops scutifer* (Fig. 5). These last two species commonly occur in other type of lakes but *B. longirostris* and especially *D. longiremis* are indicative of grayling-only lakes.

With the presence of lake trout come many changes in the invertebrate communities. The zooplankton community tends to be a blend of the small species mentioned above and some intermediate sized species *Daphnia middendorffiana* and a predaceous copepod *Heterocope septentrionalis* (Fig. 5). In the absence of lake trout, snail densities are much greater and individual snails much larger than when lake trout are present (Merrick et al. 1991) (Fig. 6). Our diet studies of lake trout confirm that snails make up most of their diet. Only rarely are small fish found in the stomachs of lake trout in the Toolik region. Furthermore in the presence of lake trout the spatial distribution of sculpin, a benthic dwelling fish, is shifted from the soft sediments, where their chironomid prey dwell, to the rocky cobble along the shoreline of the lakes where the sculpin can find refuge from the lake trout (Merrick et al. 1991). This has a secondary effect on the density of chironomids, which are the favored food of sculpin. Chironomids are more abundant in lakes with lake trout (Fig. 7) due to the habitat shift of the sculpin in the presence of lake trout.

Experiments

We have gained a great deal of understanding of the functioning of arctic lakes through a series of whole lake manipulations (Fig. 8). One of the most successful experiments was dividing a lake with a polyethylene curtain and adding inorganic nitrogen and phosphorus for six summers to the down-stream sector of the lake (Hershey 1992). The nutrient loading levels were 2.91 mmols N m^{-2} day^{-1} and 0.23 mmols P m^{-2} day^{-1} which is five times the estimated nutrient loading of Toolik Lake. The phytoplankton, as measured by chlorophyll *a*, responded positively to the nutrient addition, which began in 1985; each year the treated sector had significantly more phytoplankton than the reference sector (Fig. 9). However, for the first four years of the experiment there was no carryover from one year to the next. That is, in the early summer both sectors looked the same and indeed had virtually identical chlorophyll levels even though the chlorophyll levels may have differed by as much as eight times at the end of the previous summer. The reason for this was that during the first four summers none of the added phosphorus was recycled from the sediments. This was verified through the use of benthic chambers, which can measure nutrient fluxes from the sediment. Some nitrogen did recycle early in the experiment but it was not until the fifth year of the experiment that any phosphorus was released from the sediment of the treated sector of lake N-2 (Fig. 10)

The lack of phosphorus flux from the sediments of Lake N-2 and some other lakes of the area is due to the unique nature of these sediments (Johnson and Kipphut 1988.) The rate of sedimentation in lakes of this region is so low that Mn and Fe can diffuse upward at a rate that can keep up with the sedimentation. They are then available to form insoluble compounds with phosphate. In most other lakes these important phosphorus-scavenging compounds are simply buried by the inorganic sediment. This and the oxic nature of the hypolimnion of area lakes make these sediments very nutrient scavenging. However, as the experiment continued, the hypolimnetic oxygen concentration in the treated sector of Lake N-2 declined and a layer of organic sediment formed from settling seston. As a result, the mineral sediments were covered and some phosphorus flux occurred (Sugai and Kipphut 1992) (Fig. 10).

The response of the zooplankton densities in Lake N-2 to the nutrient addition was mixed. The zooplankton assemblage in Lake N-2 is typical of lakes that have only grayling. *D. longiremis* was the species with the most positive response where its density significantly increased with increased phytoplankton density in five out of the six years of nutrient addition (Fig. 11). The other three zooplankton species were less responsive to increased phytoplankton abundance, caused by nutrient addition. The density of the calanoid copepod, *D. pribilofensis* was only significantly different from the reference sector three years out of the six years of treatment, while *B. longirostris* was only significantly different one out of the six years of treatment. Strangest of all was *C. scutife*r that never responded during nutrient treatment but did respond positively after the nutrient addition had ceased.

The response of fish was not estimated in this study partly because only a few grayling were tagged in Lake N-2 but more importantly those that were tagged often ended up in the other sector of the lake. To get some estimate of the response to fish, especially lake trout, to nutrient addition we undertook another nutrient addition experiment (Fig. 8). In this case we added nutrients to a whole lake, Lake N-1. Nitrogen and phosphorus were added at about 75% the level of the N-2 addition but the results were more dramatic. The phytoplankton increased markedly; the chlorophyll *a* densities in three of five years of treatment were greater than chlorophyll levels at comparable years of treatment in Lake N-2 (Fig. 12). Part of the explanation for this is that the sediments in Lake N-1 are less able to scavenge nutrients than those of Lake N-2 and nutrients recycled more in this study. Furthermore the zooplankton did not respond at all to increased phytoplankton production with the exception of *D. middendorffiana* in the last year of nutrient addition.

Not only did we have some unexpected positive effects in Lake N-1 we had some negative effects as well. The level of productivity and the settling of seston into the hypolimnion severely reduced the amount of suitable summer habitat for lake trout. The warm summer epilimnion is always unsuitable habitat for these coldwater fishes however; the increased production caused severe hypolimnetic oxygen depletion. This combined with the warm upper waters left only a 2-meter thick layer in which optimal conditions for lake trout growth existed during the summer. The net result for lake trout was no increase of the adult population density and absolutely no recruitment into the population. However, while the density of lake trout did not increase and the fish did not successfully spawn those fish in the population grew at remarkable rates (Fig. 13).

We have also added and removed predators from certain lakes (Fig. 8). The addition of *H. septentrionalis* to a pond containing the small-bodied species *B. longirostris* and *D. pulex* proved quite revealing. For a number of years it was thought that competition from large zooplankton kept small zooplankton from colonizing lakes and ponds without fish. (O'Brien in press)Thus it was doubted that invertebrate predators such as *H. septentrionalis* could structure the zooplankton community much the way planktivorous fish may do. However, the small-bodied zooplankton, that were present prior to the introduction of *H. septentrionalis*, decreased in population density by three to four orders of magnitude after the introduction of the predaceous copepod (O'Brien 2001) (Fig. 14).

Synthesis

We are in the early stages of whole lake modeling although we have previously developed a planktivorous feeding model of arctic grayling and applied existing lake trout bioenergetics models to arctic lake trout (McDonald et al. 1996). However, the most extensive model is the Pelagic Arctic Lake Model (PALM). Shown here are the basic components of the model (Fig. 15). We have taken great care to try and verify that the model accurately simulates arctic lakes. With weather data as input the model can simulate the water temperature at 2.5 m throughout the year for Toolik Lake (Fig. 16). Notice the lake freezes at temperatures below 2° C and the model does as well. We can also successfully simulate summer water temperature as well as vertical temperature profiles. The model also successfully predicts summer oxygen vertical profiles as well (Fig. 17). One prediction of the model that we had not fully appreciated is that most arctic lakes thermally stratify very soon after ice out, sometimes within three to four days of ice out. Hence there is essentially no spring mixing and any winter oxygen deficit is carried over in the hypolimnion during the subsequent summer.

We have also used the model to predict the percentage of bottom that would remain suitable habitat for lake trout under different phosphorus loading levels and with lakes of increasing depth (Fig. 18). The model comes quite close to simulating what occurred in Lake N-2. For the first three summers of the N-2 experiment the model over-predicts the amount habitable at 30% whereas between 40-50 % was actually habitable. These were the years with no recycling of phosphorus. In the year 1988 the model was right on but when phosphorus recycling really took off the lake was worse than the prediction. Further the model predicts that very shallow lakes could be very vulnerable to phosphorus loading with winter kills occurring in all lakes with even modest nutrient loading. Clearly, the greater the phosphorus loading the less percent habitable bottom, although lake depth ameliorates this effect to a great extent.

Still shallow arctic lakes seem to be very vulnerable to eutrophication and great care should be taken in using nutrient addition as a management tool. We also ran the model with a 5° C increase in air temperature; the curves then shifted to the right although there was no effect on lakes deeper than 20 m.

Conclusions

Thus, measurable changes have occurred in Toolik Lake during our period of study. Lake trout populations are declining because of recreational fishing. Both temperature and alkalinity are increasing, presumably because of climate change. Although nutrients in stream water may increase because of increased depth of thaw in the soils, the lakes have a degree of protection from eutrophication because of the ability of the lake sediments to scavenge phosphorus from the water. On the other hand, the rapid thermal stratification in the early summer will magnify oxygen by carryover of low oxygen conditions from one year to the next.

We have found that many of the predators in arctic lakes exert considerable force on their prey where the landscape can act as a filter in allowing selected fish species to colonize lakes. Lake trout control the size and density of snails and the habitat selection of slimy sculpin. Sculpin in turn regulate their chironomid prey. Grayling, when the only pelagic fish in lakes, limit the zooplankton community to very small-bodied species. *Heterocope,* the very predaceous copepod, can in turn eliminate small-bodied zooplankton species in lakes where it is the sole predator. Most of these major findings have broad ecological application to lakes in other biomes.

Future Plans

We will monitor many of the continuing whole lake experiments (See Fig. 1) as well as develop new experiments. To accomplish this, we will have to scale back the frequency of monitoring of continuing experiments. The major new experiment is the enrichment of Lakes E-5 and E-6 with low level nutrient additions (twice the estimated nutrient loading of Toolik Lake). As discussed above, our two previous whole lake nutrient addition experiments led to very different results; thus with these experiments we expect to fine-tune our understanding of the impacts of eutrophication on arctic lakes. We also plan the introduction of the Young of the Year (YOY) arctic grayling into two lakes, one with a grayling population and the other without any fish at all. This experiment is designed to test the hypothesis that YOY and juvenile grayling are the agents that actually exclude large zooplankton from grayling lakes. Our modeling has show that adult grayling populations can prevent the invasion of large-bodied zooplankton but cannot exclude these populations once established. Further we plan to study in greater detail arctic grayling foodwebs. Our recent stable isotope studies of grayling food chains reveal that the base lies in the benthos rather than in the plankton. Hence we plan to focus more effort on measuring benthic primary productivity and the emergence of benthic invertebrates. Lastly, we plan a major emphasis on modeling. Currently PALM is an excellent model of the physical and chemical limnology of arctic lakes and does a good job of simulating the pelagic foodweb of these lakes. However, two major gaps exist. First the benthic foodweb is not included and the lakes are not linked to hydrologic processes in the watershed. The addition of these components will greatly enhance the utility of PALM.

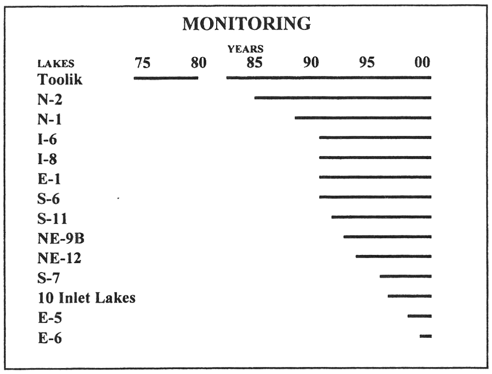


Fig. 1. Bar graph of the lakes that have been monitored and the duration of the monitoring.

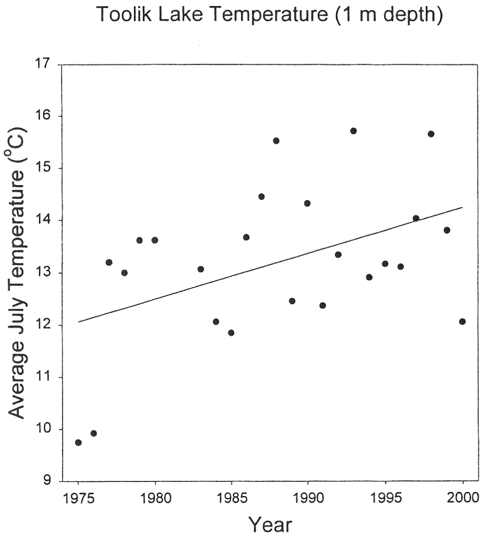


Fig. 2. Regression of average water temperature in Toolik Lake at 1 m for the month of July versus year. $p = 0.025$

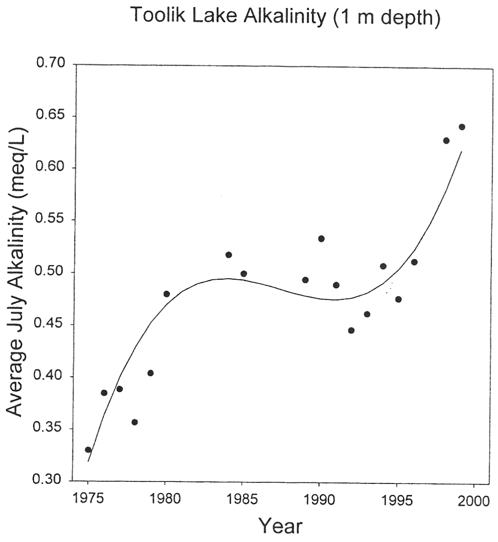


Fig. 3. Cubic regression of average alkalinity in Toolik Lake at 1 m for the month of July versus year. $p > 0$.

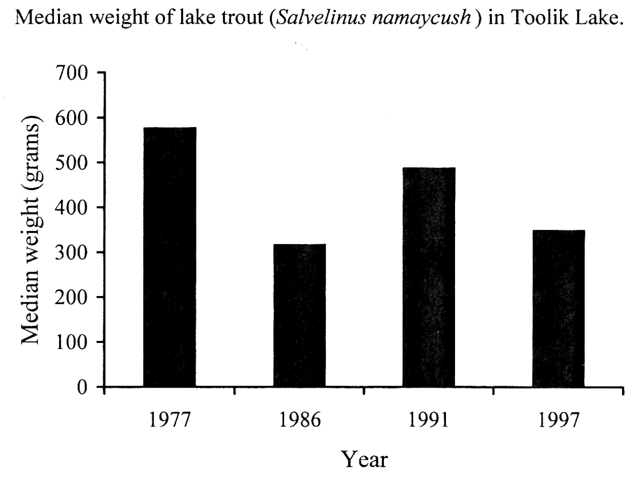


Fig. 4. Median weight of lake trout (*Salvelinus namaycush*) in Toolik Lake for the years 1977, 1986, 1991, 1997. The weights for 1977 versus 1986 are significantly different (McDonald and Hershey 1989).

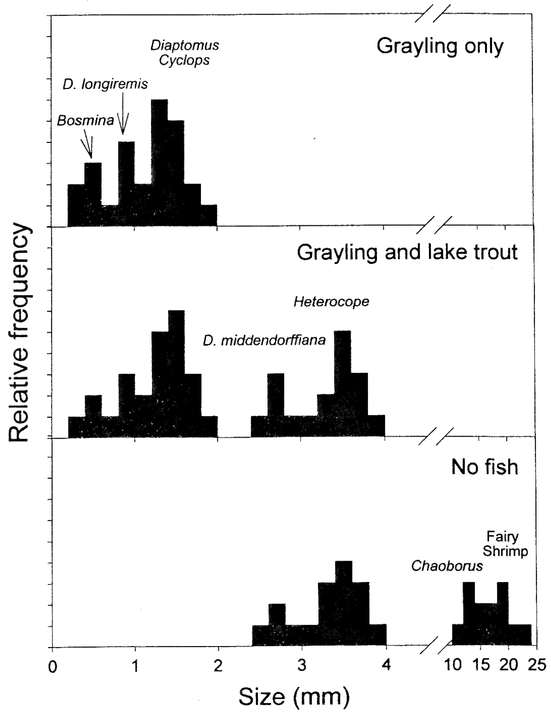


Fig. 5. Size frequency of zooplankton body lengths in three types of lakes: lakes with only grayling, lakes with grayling and lake trout, and lakes with no fish.

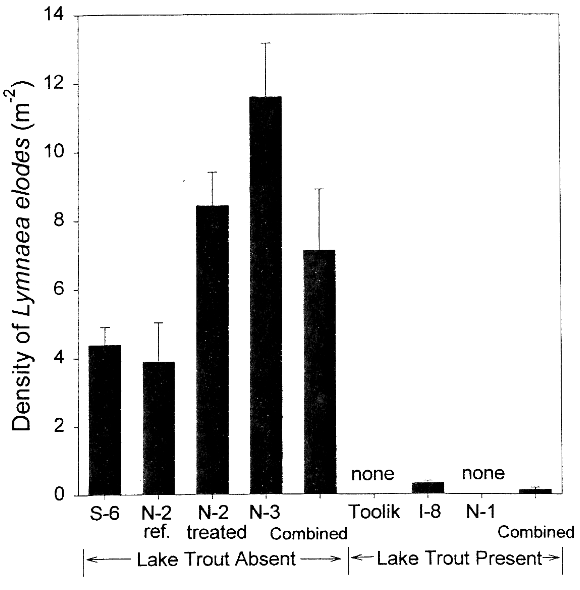


Fig. 6. Densities of the snail *Lymnaea elodes* in lakes with and without lake trout.

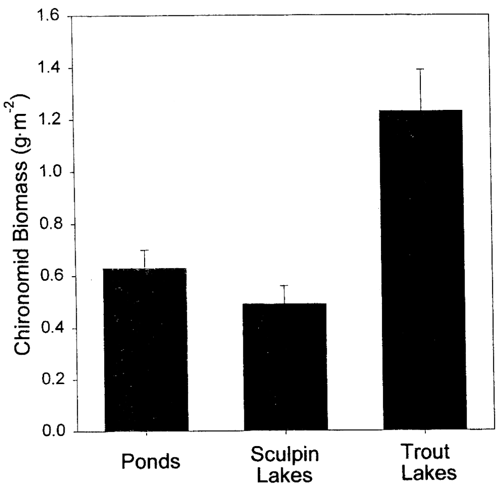


Fig. 7. Biomass of chironomids in ponds with no fish, in lakes with sculpin but no lake trout, and in lakes with both sculpin and lakes trout.

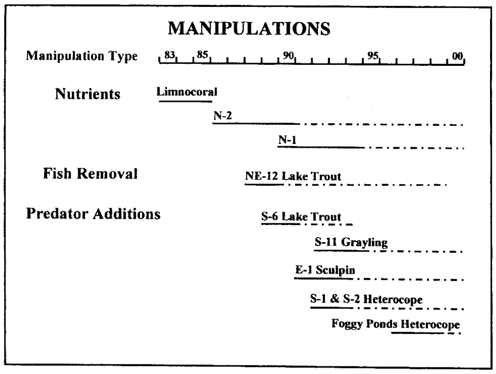


Fig. 8. (Right) Matrix showing the various whole lake manipulations and the duration of each study. The solid lines indicate that the treatment was still being applied while the dashed line indicates that the system was still being monitored.

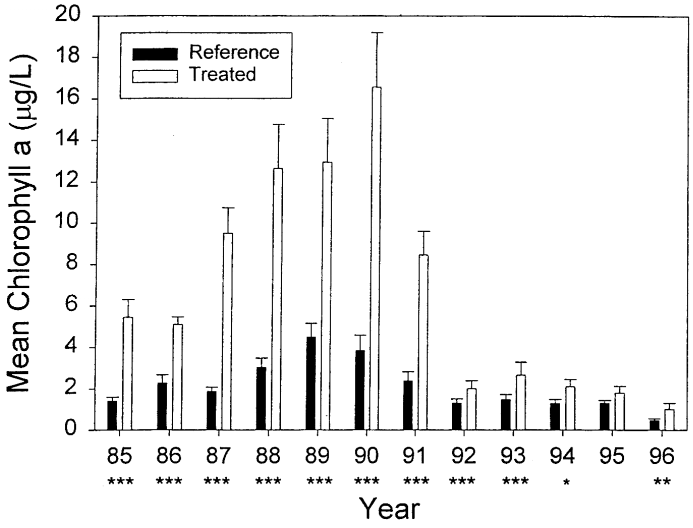
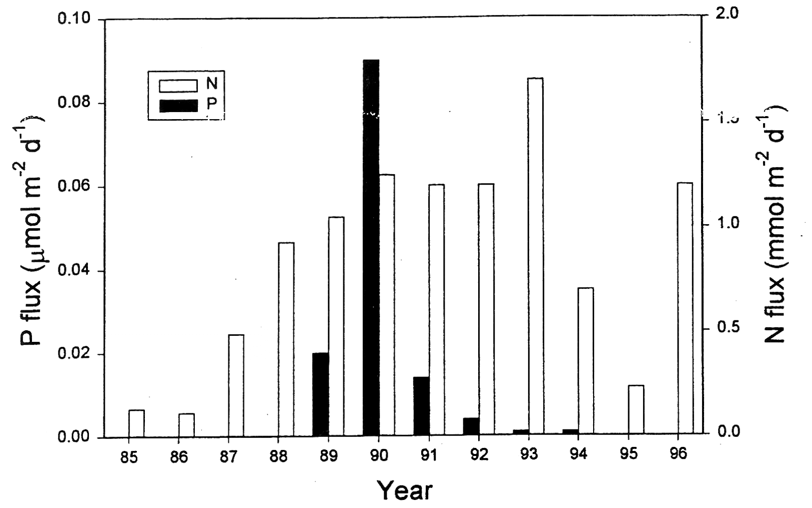
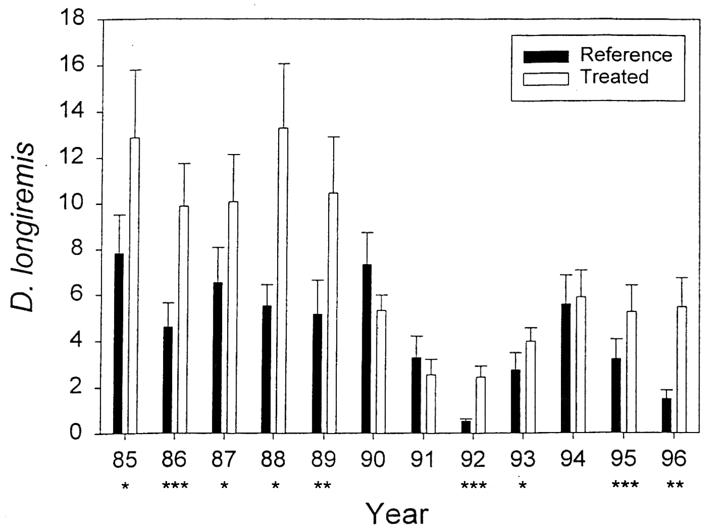


Fig. 9. The mean annual chlorophyll *a* density for the upper three meters of the sectored Lake N-2. The open bars represent the treated sector of the lake while the solid bars represent the reference sector of the lake. The asterisks under each year gives an indication of the level of significant difference between the treated and reference sector for that year.





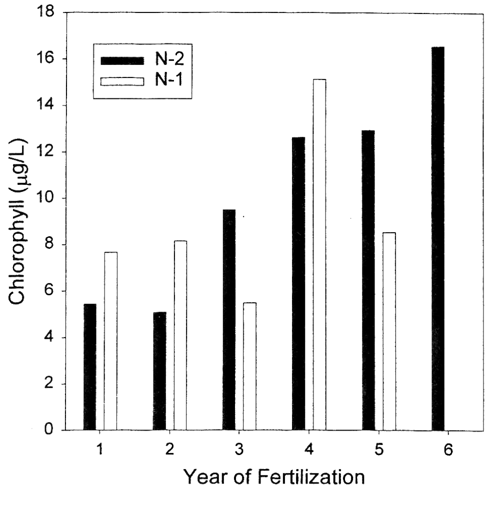


Fig. 10. (Top) Sediment flux of inorganic nitrogen and phosphorus from the treated sector of Lake N-2. The open bars represent the flux of nitrogen while the solid bars represent the flux of phosphorus.

Fig. 11. (Middle) The mean annual density of *D. longiremis* in the upper 5 m of the treated and reference sectors of Lake N-2. The open bars represent the treated sector while the solid bars represent the reference sector of the lake.

Fig. 12. (Bottom) Comparison of the mean annual chlorophyll in the upper three meters of Lake N-2 and Lake N-1. Year 1 is calendar year 1985 for Lake N-2 but calendar year 1990 for Lake N-1. The open bars represent Lake N-1 and the solid bars represent Lake N-2.

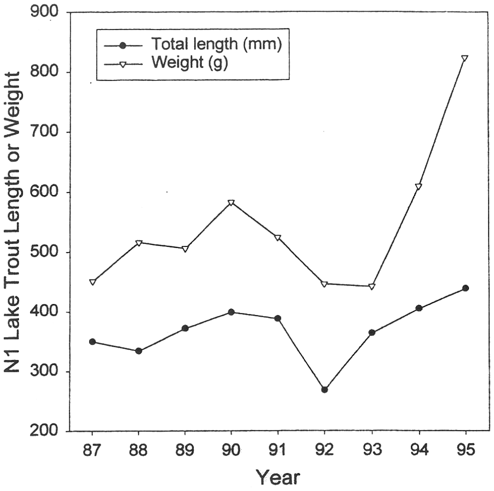


Fig. 13. The average total length or weight of lake trout in Lake N-1. The years of nutrient addition ran from 1990 through 1994.

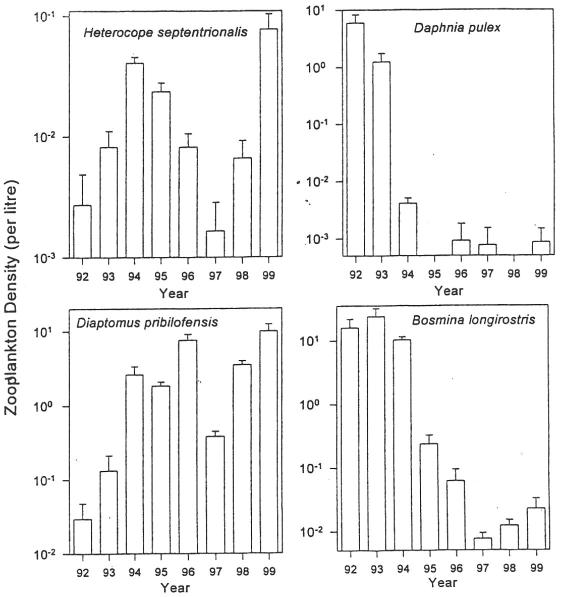
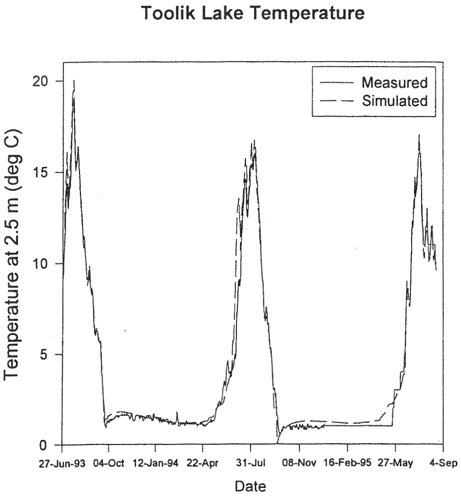


Fig. 14. (Top) The mean annual density of the four zooplankton species in Pond S-2. The upper left panel shows the density of the predaceous copepod *Heterocope sententrionalis* that was introduced to the pond in 1992. The upper right panel shows the mean annual density of *Daphnia pulex*. The lower right panel shows the mean annual density of *Bosmina longirostris*. The lower left panel shows the mean annual density of *Diaptomus pribilofensis*.

Components of the model	Processes		Status of Processes		
	Static	Dynamic	Current	Exper-iment	Litera-ture
Solar heat input		**	**	**	
Longwave radiation, sensible heat and evaporation		**	**		
Time to stratification after ice out		**	**		
Hypolimnetic temperature		**	**		
Epilimnetic temperature		**	**		
Heat loss of lake and date of freeze up		**	**		
Sediment heat storage		**	**		**
Growth and decay of ice cover		**	**		**
Nutrient loading	**		**	**	
Phytoplankton from nutrients		**	**		**
Epilimnetic nutrient loss to sediments	**		**	**	
Hypolimnetic loss of oxygen due to decomposition		**	**	**	**
Oxygen depletion during the winter		**	**	**	**
Fish exclusion by temperature and oxygen		**	**		**
Chain of lakes		**	**		
Benthic invertebrate growth					
Fish feeding on benthic invertebrates					

STATIC refers to processes that have an equation driving them which has no dynamic input.
DYNAMIC refers to processes that have an equation driving them which has variable input.
CURRENT refers to what processes are presently in the model.
EXPERIMENT refers to whether a given process is measured or experimentally studied.
LITERATURE indicates that parameters are obtained from the literature.

Fig. 15. (Left) A matrix showing some of the key components of the Pelagic Arctic Lake Model (PALM) with some indication how the components operate.



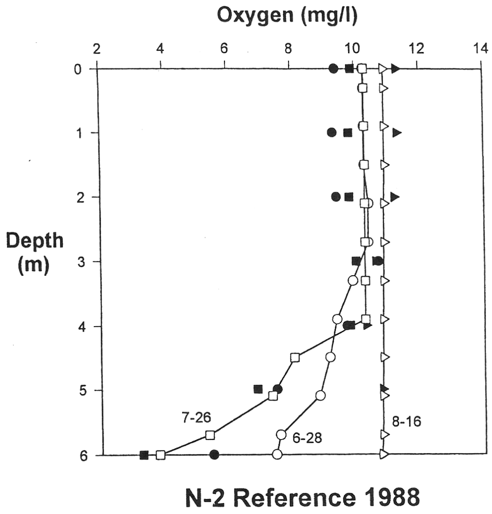


Fig. 16. Measured and simulated Toolik Lake temperature at 2.5 m depth. The solid line is the measured temperature while the dashed line is the simulated temperature. In both cases the lines represent 3 day running averages. Note the squared off measured temperatures in spring 1995 are due to a very long averaging in the data logger.

Fig. 17. Measured and simulated oxygen concentrations in the reference sector of Lake N-2. The open symbols represent the simulations while the solid symbols represent the measured concentrations.

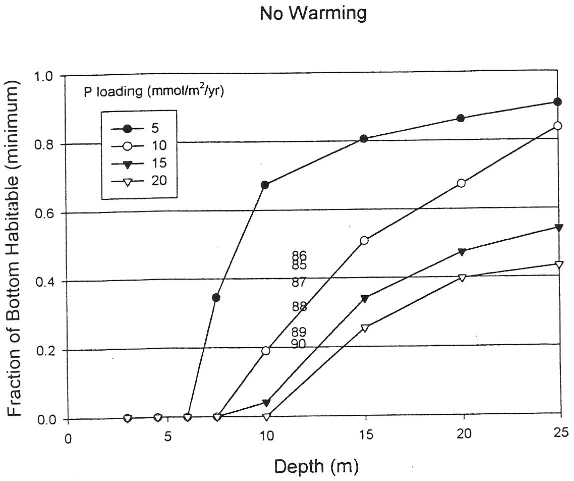


Fig. 18. Output from the PALM model showing the percentage of the volume of a lake that had oxygen concentrations above 3 mg O_2 L^{-1}. The phosphorus loading was increased from 5 through 20 mmol m^{-2} yr^{-1} and lake depths from 1 to 25 m were simulated. The numbers within the graph represent the years of the nutrient addition to Lake N-2 and the placement of the numbers indicates the percentage of the lake that would have been unsuitable habitat for lake trout.

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