Introduction and Site Description

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THE TUNDRA BIOME PROJECT

Biome Studies

The International Biological Program (IBP) was organized with the overall goal of discovering more about the biotic resources of the world through studies of the ecology of natural communities and of man himself. These studies took many forms in many countries but were generally small-scale efforts. It was decided that a part of the U.S. effort should be a series of large-scale, tightly coordinated studies of the ecology of a unit of the earth’s surface which would represent a major ecological classification (e.g., desert, grasslands). These units, called biomes, should ideally encompass a watershed or similar area where terrestrial and freshwater ecosystems, and their interaction, could be investigated. The use of mathematical models of whole systems was to be a major tool for the investigations.

Five biome studies were eventually established; one was the Tundra Biome. The site for the study, the flat coastal tundra near Barrow, Alaska, was suitable for terrestrial studies but was ideal for an aquatic study as ponds and lakes were abundant. Also, the well-equipped Naval Arctic Research Laboratory would provide logistic support and work space. The numerous ecological studies of this area over the preceding 25 years provided background information as well as a core of experienced scientists.

The goal of the Tundra Biome study was to obtain a detailed understanding of the ecology of this site. The flows of carbon, nitrogen, and phosphorus were to be quantified and a mathematical model was to be constructed which would incorporate the data of these fluxes, their controls, and the interactions with the physical and chemical environment. It was hoped that the models could then be used in a predictive manner to investigate possible changes in the environment due to man or to natural alterations in the climate.
The Tundra Aquatic Project

In 1970, a modest, pre-IBP grant from NSF allowed the pond studies to begin. The goal of this grant was to follow the effects of oil and nutrient fertilization on ponds. Two projects, that of V. Alexander on phytoplankton responses and that of R. Barsdate on nutrient and water chemistry, were started and the ponds chosen for whole-pond experimentation and for controls. One whole pond and several small subponds (plastic enclosures) were fertilized with P and N and one whole pond was treated with crude oil.

In 1971, the IBP funding began and a complete range of aquatic projects was started. The emphasis during this year was on obtaining the most complete data possible for carbon, nitrogen, and phosphorus flow for both a pond and a lake (Ikroavik). The projects of Alexander and Barsdate were continued and additional projects added that dealt with zooplankton (R. Stross), bacteria, decomposition, and benthic algae (J. Hobbie), fish (J. Cameron), dissolved carbon, particulate carbon, and benthic respiration (M. Miller), macrobenthos (D. Bierle), protozoa (R. Dillon), and macrophytes (P. McRoy). Observations on the manipulated ponds were continued throughout the entire project.

In 1972, the first modeling efforts began and a preliminary plankton model was developed. The field work at Barrow was oriented towards subpond experiments; treatments of nutrients (two concentrations), of added light, of darkness, and of higher temperatures were used. Because the outdated tracked vehicle continually broke down, travel to Ikroavik Lake became impossible and no more samples were taken.

During 1973, emphasis was shifted to modeling, and simulation models of benthic, planktonic, and zooplankton systems were developed. The field work was devoted mostly to developing the constants and rates needed for the models. Several specialists were brought in for the summer to work on areas of research that were still poorly-understood: (T. Fenchel, protozoan ecology; D. Kangas, zooplankton respiration; S. Dodson, invertebrate predation.) The summer of 1974 was spent in preparing reports.

Modus Operandi

To reach the goals of the project we first used traditional limnological techniques to identify and measure the important pathways of carbon and energy flow in the tundra ponds. Next, the modeling was begun and used both to plan future experimental research on the processes and to evaluate the importance of proposed research. The philosophy we have followed in modeling is as follows:
1. We must first understand as completely as possible the system to be modeled.
2. Only the important parts of a system, and their controls, can be modeled.
3. Wherever possible, constants, rates, and relationships included in the model must be measured and not taken from the literature.
4. The modeling exercise and the resultant simulations are regarded as tools to be used to further our understanding of how the ecosystem operates.
5. The modeling must be done by ecologists with the aid, if necessary, of a professional modeler rather than vice versa.

LIMNOLOGY OF THE ARCTIC

Circumpolar

For this report, the Arctic is defined as the region north of the tree-limit which has a mean air temperature of less than 10°C during the warmest month. Until very recently, arctic limnology was entirely organism-oriented. This was in part due to the great difficulties of carrying out anything more than expedition-type collecting activities and in part due to the particular interests of the people involved. Modern studies of the physical, chemical, and limnological processes in lakes and ponds began after 1950 or so when research stations became established (e.g., at Disko Bay, Greenland, and Barrow, Alaska). As a result, the first review of arctic limnology (Rawson 1953) mentioned only seven papers that dealt with arctic lakes.

The availability of these research stations, plus the realization that long-term studies were needed, led to a number of detailed investigations. In Scandinavia, the biology of Lapland lakes has been investigated by Ekman (1957), Holmgren (1968), and Nauwerck (1968). In Spitzbergen, water chemistry and zooplankton biology have been studied (Amren 1964a) and there are a number of reports of investigations of Greenland lakes (e.g., Hansen 1967, Holmquist 1959). Several investigators, such as McLaren (1964), Kennedy (1953), and Oliver (1964), worked in northern Canada. By far the greatest number of studies were made in northern Alaska (e.g., Livingstone et al. 1958, Hobbie 1964, Kalff 1967a, Stross and Kangas 1969, Carson and Hussey 1960) of the chemistry, biology, and physics of a wide range of lakes and ponds.

The results from all these and other arctic studies are summarized in reviews by Livingstone (1963a), Kalff (1970), and Hobbie (1973). In brief, arctic lakes and ponds have the following characteristics:
1. Arctic lakes and ponds seldom warm above 10°C and almost never stratify.
2. Arctic lakes and ponds shallower than 1.7 to 2.0 m usually freeze completely.
3. Ponds and lakes less than 2 m in depth do not contain fish. One consequence of the lack of predation is that the zooplanktonic crustaceans are almost all large species in ponds and shallow lakes.
4. The ice cover is 1 to 2 m thick and lasts for 8 or 9 months.
5. Arctic lakes and ponds usually contain low amounts of available nutrients and low total dissolved salts. However, as in the temperate regions, the total inorganic ion concentration is different for drainage basins in different types of bedrock.
6. Oxygen is usually present in saturation concentrations in open waters but becomes depleted to some extent near the end of the under-ice period. In shallow lakes the exclusion of oxygen during the freezing of the ice may result in super-saturation (200%).
7. The biota of shallow freshwater lakes and of ponds are subjected to strong physiological stresses as the ions may be concentrated 30-fold during freeze-up, while the water immediately after the spring melt may resemble distilled water.
8. Only nannoplankton are found in arctic lakes and ponds. These usually bloom beneath the springtime ice of lakes but total primary production is low and lakes and ponds are oligotrophic.
9. With a few exceptions, each species of zooplankton has a dormant phase in its life cycle.
10. Fish are very slow-growing, but large fish may live for 40 years.
11. There are no benthic animals that graze on aquatic plants or that shred large organic particles or leaves.
12. The number of animal species is small and some groups—for example, sponges, Notonectidae, Corixidae, Gyrinidae, Dytiscidae, and Amphibia—are rare or not present.
13. Decomposition rates are slow and large amounts of energy and nutrients are tied up in dead organic matter.

It is obvious that this list of characteristics was obtained from largely descriptive studies. Recently, two IBP projects were carried out that were designed to add experimental studies to the descriptive observations in order to gain an understanding of controlling factors and environmental interactions. These projects, one at Resolute Bay, Canada, and one at Barrow, Alaska, were located near airfields and studied only a single lake (Char Lake) or a small group of ponds in a single area (Barrow).

Some of the results of the Char Lake project have been published. A general description (Rigler 1972) indicates that the lake is ice-covered until early August, has a moss cover over 30% of its bottom, and has low
quantities of nutrients. Phytoplankton began to increase beneath the ice cover in February and reached a peak in May (Kalff et al. 1972). Morgan and Kalff (1972) found a maximum of $2 \times 10^5$ bacteria ml$^{-1}$ with peaks of glucose uptake in July and October. Zooplankton had low populations with *Limnocalanus macrurus* as the dominant form (Roff and Carter 1972). Most of the population hatched, grew, reproduced, and died between December and October, although a few adults were present during the entire winter. Finally, the long period of ice cover allowed the lake to be used as a sealed vessel respirometer to measure respiration of the ecosystem by changes in oxygen concentration (Welch 1974).

**Northern Alaska**

It was possible to carry out the IBP aquatic program only because of the experience and information provided by previous research in northern Alaska. Thus, even before the IBP aquatic project began, we knew such things as the primary productivity of the phytoplankton, the basic cycles of water chemistry, and the life cycles of many of the zooplankton species.

There are seven types of freshwater habitats in northern Alaska: deep lakes, shallow lakes, ponds, large rivers, small rivers, streams, and springs. The deep lakes, located in the mountains, were formed mostly behind end moraines that dam narrow valleys. These lakes are rather rare and may number only 20 or 30. Shallow lakes, very abundant (many thousands) on the flat coastal plain, were formed mainly by melting of the ice-rich permafrost. These are only a few meters deep and many will freeze to the bottom each winter. The area of these lakes can be large, with lengths reaching up to 10 km or so. Ponds are extremely abundant (tens or hundreds of thousands) in the coastal plain region, particularly in the old lake beds. Here, the growth of ice wedges has pushed up networks of small ridges that contain small (50 m on a side), shallow (10 to 50 cm) ponds. Most of the limnological investigations have been carried out on lakes and ponds; little is known about the flowing water systems. However, there are a number of large rivers in northern Alaska and parts of these rivers are deep enough to allow fish to survive. Small rivers and streams, in contrast, cease flowing completely each fall. Because of the flat landscape and small amount of total precipitation, the drainage is poorly developed in the Barrow area and sizable amounts of flow occur only during the melting period. The final habitat, springs, occurs only in the mountain and foothill area. Although some ten or twenty springs exist, they are a very minor part of the entire aquatic scene. The fact that they flow year-round, however, allows a rich fauna to develop and illustrates both the potential production of arctic water and, by contrast, the strong stresses on intermittent streams.
Deep mountain lakes were first investigated by Livingstone et al. (1958) who pointed out that most of the thermal, chemical, and biological events in these lakes were similar to those of oligotrophic temperate lakes. They thought that the major effect of the arctic environment was on the physiographic process affecting lake origins, sedimentation rates, and input from the drainage basins. An intensive study of two other deep lakes (Hobbie 1961, 1962, 1964) revealed that most of the yearly primary productivity of the plankton occurred beneath the ice cover in late spring and early summer. Later, both the light regime and the algal species and biomass responsible for this early season bloom were investigated in detail by Holmgren, Kalf, and Hobbie (reported in Hobbie 1973). It was found that when the snow depth was less than 10 cm, great amounts of light penetrated the ice. The light, plus the non-turbulent conditions beneath the ice, allowed large numbers of flagellates and diatoms to develop. After the ice left the lakes, conditions were poor for algal growth.

Most of the research on shallow lakes has centered on the question of the origin and development of the oriented lakes of the coastal plain. These lakes originate when permafrost melts and the soil subsides (Reynolds 1961) and receive their orientation from wind-driven currents which differentially erode the ends of the elongated lakes (Carson and Hussey 1960). Scattered bits of information that exist on Iqrovik Lake, near Barrow, show it to have low numbers of algae, nutrients (Prescott 1953), and benthic animals (Livingstone et al. 1958). The whitefish population has also been described (Wohlschlag 1953).

Another well-studied shallow lake is Imikpuk, which is not an oriented lake and which lies close to the Arctic Ocean. Chemistry of the lake has been reported by Howard and Prescott (1973) and Boyd (1959); the primary productivity by Howard and Prescott (1973) and Kalf (1967b); the zooplankton by Comita (1956) and Edmondson (1955); and the microbiology by Boyd and Boyd (1963).

All of the pond limnology in northern Alaska has been done near Barrow. The most extensive investigations were of the chemistry and plankton productivity (Kalf 1965, 1967a, 1971). In these ponds, phosphate, nitrate, ammonia, trace elements, and growth factors all stimulated photosynthesis at various times. Kalf concluded that nutrient deficiency did exist and that plankton productivity was extremely low (around 1 g C m$^{-2}$ yr$^{-1}$). Another series of studies dealt with reproductive cycles and controls of zooplankton (Stross and Kangas 1969).

The only large rivers studied in northern Alaska have been the Colville (Kinney et al. 1972) and the Sagavanirktok (Carlson et al. 1974). These studies were mostly concerned with water chemistry but zooplankton (Reed 1962), fish (McCart and Craig 1971), and discharge (Arnborg et al. 1966) have also been looked at. The rivers contain little plankton and a scanty bottom fauna.
Smaller streams are also little known and the research has been restricted to observational limnology. The best-studied area is at Cape Thompson (68°N, 165°W) where the discharge (Likes 1966) and biology (Watson et al. 1966a) on Ogoturuk Creek were investigated. Near Barrow, Brown et al. (1968) measured the hydrology of a small watershed (1.6 km²) over four summers and Lewellen (1972) reported on flow and chemical data from three other Barrow area watersheds.

Springs are present only in the foothills and mountains of arctic Alaska. One spring, Shublik Spring on the Canning River, has been sampled by Kalff and Hobbie (unpublished, quoted in Hobbie 1973). It flows year-round at 4.0 to 5.5°C, and contains a fantastic abundance of insects as well as a dwarf char (McCart and Craig 1973).

There are other reports that cover several aquatic habitats. Hydrology was reviewed by Dingman (1973), Kalff (1968), and Barsdate and Matson (1966).

GEOGRAPHY AND GEOMORPHOLOGY

Geographical Setting

Northern Alaska, all of which lies north of the tree limit, is cut off from the rest of the state by the east-west running Brooks Range, an extension of the Rocky Mountain System. North of the mountains, which have an area of 136,200 km², lie the Arctic Foothills (100,800 km²) and between the foothills and the Arctic Ocean lies the Arctic Coastal Plain which contains 70,900 km² (Walker 1973). Barrow lies on the northern tip of the coastal plain, some 175 km from the foothills (Figure 2-1).

Near Barrow, the flat coastal plain is covered either by large lakes, shallow ponds, or old drained lake basins (Figure 2-2). In places, freshwater lakes and ponds cover up to 40% of the surface. Despite the abundance of water, streams are small and most flow only during the spring melt. The remainder of the area is covered by grasses, sedges, mosses, and lichens. Usually, the standing dead stems and leaves of the grasses and sedges dominate the scene and color the tundra brown.

The Naval Arctic Research Laboratory is on the coast of the Chukchi Sea, 10 km from Point Barrow, and the town of Barrow lies 5 km further southwest (Figure 2-1). Research on tundra ecology has been carried out at this laboratory since 1947, while the National Weather Service has operated a first-class station at Barrow since 1920. The pond research site (71°18′N and 156°42′W) is halfway between the laboratory and the town and 2 km inland. A shallow lake, Imikpuk, lies adjacent to the laboratory and to the ocean, and a large lake, Ikroavik, lies 7 km south.
FIGURE 2-1. Aerial view looking north across the U.S. Tundra Biome research area. The ice-covered Arctic Ocean is in the background. The Naval Arctic Research Laboratory camp complex is in the upper right corner. The ice-covered water body is Middle Salt Lagoon. Polygonal terrain is visible in the foreground and the study ponds in the lower left corner. (Photograph by CRREL.)

Geomorphology

The Arctic Coastal Plain consists of unconsolidated silty sand and gravel of Quaternary age (Gubik Formation) deposited in a shallow sea (Black 1964). The uppermost section at Barrow was deposited and reworked over the past 35,000 years (summarized in Brown and Sellmann 1973). Radiocarbon dates and composition analyses of peat suggest that tundra existed in the Barrow area for as long as 14,000 years (Brown 1965). Based on a number of radiocarbon dates, it is believed that most of the soils and surficial features of the present land surface are not older than 8,000 to 10,000 years and perhaps are considerably younger.

Mean annual air temperatures on the North Slope of Alaska are below freezing; thus, there is continuous permafrost (perennially frozen ground) beneath the entire area. At Barrow, the frozen layer is 400 m thick (Brown and Sellmann 1973) but there is a layer of soil 25 to 100 cm thick that does thaw each summer. The depth of thaw is influenced by the type
of vegetation, amount of insulating plant litter, and type of soil. For example, beneath a thick vegetation mat the depth of thaw may be only a few centimeters while coarse-textured, south-facing materials may thaw to
a depth of 100 cm (Walker 1973). At the Barrow site, the maximum depth of thaw is around 25 cm below the grassy tundra while in the sediments of the ponds it may vary from 20 to 50 cm. Large rivers and lakes of this region may be underlain by extensive thawed areas. Brewer (1958) found 60 m of thawed material beneath Imikpuk Lake.

The presence of permafrost has important biological effects. Because the permafrost is impervious, the water cannot drain away, and the low-lying soils are saturated. Roots are restricted to the upper, thawed layer of soil which limits the total quantity of nutrients available. Finally, nutrients and energy are removed from circulation either when the permafrost level rises or when soil and sediments accumulate and become part of the permafrost.

The upper layers of permafrost on the coastal plain contain large quantities of ice. One form of this occurs as interstitially segregated ice (up to 80% of the top 3 or 4 m of permafrost) (Sellmann and Brown 1965). When this melts, due to disturbance of the plant cover or to heat transfer by flowing water, a depression is formed that may result in a pond. Another form of ice occurs when water runs into cracks formed by the winter contraction of the frozen tundra. The resulting buried ice takes the form of ice wedges that can range from a few centimeters to 8 m in width. Over many years, the wedges grow and eventually a network of ice wedges is formed. Sometimes these wedges are expressed on the surface as polygonal ground (Figure 2-3) caused by heaving or other surface processes that form troughs and ridges. Typically, these polygons may be 20 to 50 m across; polygonal ground covers almost the entire coastal plain.

In the early stages of growth of polygonal ground, the polygons are low-centered and often contain small ponds. The water changes the insulating properties of the surface and also traps heat so that the upper layers of the permafrost thaw, subsidence occurs as the ice melts, and a basin up to 0.5 m in depth is formed. These ponds frequently coalesce and may form a lake. Eventually, the lake may grow enough that a drainage divide is breached. Then the lake may drain and the polygonal ground start to form again; the whole process has been called the thaw-lake cycle (Britton 1957).

Many of the larger thaw lakes of the coastal plain display a striking elliptical shape with an elongated north-south axis. The exact reason for the orientation has been the subject of a number of studies and theories (Black and Barksdale 1949, Livingstone 1963a, Carson and Hussey 1960), but it is evident that differential erosion is still occurring today. For example, Lewellen (1972) measured a rate of elongation of 1.3 m per year in Twin Lakes. In similar lakes, Hussey and his co-workers measured currents at the ends of the lakes of up to 61 cm per second, which Livingstone (1963a) believed to be adequate to account for the elongation of the lake basins. However, Walker (1973) believes that the precise mechanism of elongation is still unexplained.
Another type of pond, called a trough pond, is formed when an ice wedge melts. Around Barrow, melting is often caused by destruction of the insulating vegetation by tracked vehicles.
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<td>38</td>
<td>175</td>
<td>385</td>
<td>526</td>
<td>557</td>
<td>447</td>
<td>262</td>
<td>120</td>
<td>42</td>
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<td>213</td>
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<td>-28.3</td>
<td>-26.3</td>
<td>-18.1</td>
<td>-7.3</td>
<td>-0.9</td>
<td>4.1</td>
<td>3.3</td>
<td>-0.9</td>
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<td>0.28</td>
<td>0.28</td>
<td>0.30</td>
<td>0.91</td>
<td>1.96</td>
<td>2.28</td>
<td>1.63</td>
<td>1.27</td>
<td>0.58</td>
<td>0.43</td>
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<td>5.1</td>
<td>5.6</td>
<td>5.1</td>
<td>1.0</td>
<td>1.8</td>
<td>1.8</td>
<td>7.4</td>
<td>17.5</td>
<td>9.4</td>
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<td>64</td>
<td>67</td>
<td>74</td>
<td>85</td>
<td>89</td>
<td>88</td>
<td>89</td>
<td>89</td>
<td>85</td>
<td>76</td>
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<td>78%</td>
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<td>Hrs fog day(^{-1})</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>8</td>
<td>12</td>
<td>13</td>
<td>11</td>
<td>5</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>65 days</td>
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<td>5.8</td>
<td>5.9</td>
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<td>Direction Mean sky cover (% of daylight hrs cloudy)</td>
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*Source: National Weather Service.*
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<td>50.0</td>
<td>45.2</td>
<td>47.0</td>
<td>87.4</td>
<td>96.5</td>
<td>84.3</td>
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<td>30.5</td>
<td>20.3</td>
<td>27.9</td>
<td>17.8</td>
<td>43.2</td>
<td>45.7</td>
<td>35.6</td>
<td>48.3</td>
<td>40.6</td>
<td>33.0</td>
<td>41.3</td>
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<td>-11.4</td>
<td>-12.0</td>
<td>-13.5</td>
<td>-13.8</td>
<td>-12.8</td>
<td>-12.2</td>
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<td>-12.1</td>
<td>-12.7</td>
<td>-15.2</td>
<td>-12.5</td>
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<td>Annual precipitation (cm), Jan. to Jan.</td>
<td>18.2</td>
<td>12.4</td>
<td>7.8</td>
<td>4.7</td>
<td>8.4</td>
<td>8.4</td>
<td>11.9</td>
<td>13.9</td>
<td>14.9</td>
<td>7.8</td>
<td>12.6</td>
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<tr>
<td>Rainfall (cm), Jun. to Sept.</td>
<td>13.2</td>
<td>6.6</td>
<td>4.1</td>
<td>1.7</td>
<td>3.8</td>
<td>3.4</td>
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<td>5.5</td>
<td>2.3</td>
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*Source: Lewellen 1972 and National Weather Service.*
Climate

The Barrow area has short, cool summers and long, cold winters (Table 2-1). At this latitude the sun is below the horizon from 18 November to 24 January but never sets between 10 May and 2 August. Usually, snow is on the ground for 9 months of the year.

The solar radiation is high during April and May but the albedo (reflection) of the snow cover is also high (80 to 90%) so little of the energy is available for warming or melting of the snow (Figure 2-4). After late May, the albedo gradually drops to 70% and then, during a 4- or 5-day period in mid-June, drops to 10% during the thaw (Kelley 1973). Albedos average 18% during summer but by mid-October they return to the winter levels. Solar radiation in the summer (Table 2-1) is strongly affected by the very cloudy weather and frequent fogs so that most of the annual solar radiation at Barrow occurs before the tundra ponds have melted.

Temperatures at Barrow average -12.4°C but there are only 109 days when the average temperature is higher than 0°C. Daily minimum temperatures are above 0°C for only 41 days each year so that low water temperatures and even snow can occur at any time during the summer. In winter, the low temperatures and the thin snowpack (Table 2-2) cause the ponds to freeze completely. February is generally the coldest month and July the warmest. Because of the nearness of the Arctic Ocean to Barrow and to the IBP site, the summer climate is strongly affected by the highly variable ice conditions in the ocean as well as by coastal fogs. As a result, temperatures are warmer in summers with little ice. While temperatures at the research site may be a little higher than those at the Barrow Weather Station, the main effect of the distance between the two stations seems to be lower insolation at Barrow than at the research site. Often the sun shines at the IBP site while fog covered Barrow only 2 km away.

The mean annual precipitation is 10.8 cm (as water). About 50% of this falls as snow; October and November have the highest amounts. During the summer, most of the precipitation falls as rain. Despite the low total precipitation, the relatively low evaporation and the impervious soils mean that the tundra has a great deal of water available, particularly in the early summer when the soils are saturated. The average snowpack is 40 cm in depth but there is tremendous variability due to drifting caused by the constant easterly winds. Drifts fill all depressions while ridge tops may be blown free of snow.

Winds at Barrow are almost continual and almost always from the east. The monthly averages of wind speed are remarkably uniform (Table 2-1) but some strong storms do occur in September and October. These data, however, are taken at 9 m and may not reflect the wind effect on the small ponds. Frequently we have observed a microinversion over a pond such that the pond surface was completely calm when there was wind at a 1.5 m height. Additional information on the decrease of wind close to the ground surface comes from 1971 micrometeorological data from the
IBP site 2 (Weller and Holmgren 1973). For example, on 7 July 1971 the average wind speed (m sec\(^{-1}\)) at 0.25, 1, 2, 4, 8 and 16 m above the ground was 2.5, 4.4, 4.5, 4.9, 5.2 and 5.5, respectively.

Hydrology

The vertical relief near Barrow is small; consequently the drainage is poorly developed and small ponds and lakes are common. There are no large rivers in this part of the coastal plain and the small streams are found only where polygonal ground is absent. There is some overland drainage from polygonal areas but only during the snowmelt or during rare periods of heavy precipitation when the ponds become completely filled. As a result, the two detailed studies that have been made concentrated on small streams with well-developed channels. One of these streams is located on a drained lake basin about 8 km northeast of Barrow (Brown et al. 1968). In this basin the total elevation change is 0.3 m, the area 1.57 km\(^2\), and open water covers about 5% of the area. The other study was carried out by the U.S. Geological Survey on two creeks near Barrow Village (Dingman et al. in press).

The snowpack reaches its maximum depth in February, March, and April (Table 2-1). The actual depth of the snowpack in any one place depends upon the microrelief, the wind during the snowstorms, and the amount of time available for the snow to age and harden before the next period of high winds. Not only is snow removed by the winds, but also there is almost continual drifting so that huge drifts accumulate behind every house and small drifts behind each ridge or hummock. Thus, even the ponds, which usually have a complete snow cover, will have a variable depth of snow cover depending upon their immediate surroundings.

The snowfall and snowpack are highly variable from year to year (Table 2-2) and averaged 91.7 and 41.3 cm, respectively, over the past decade.

In April and May there is an increase in insolation (Table 2-1) but the continuous snow cover still has an albedo of 85% so little melting occurs (Figure 2-4). Finally, in late May, the rising air temperatures and the increasing solar radiation cause the first snowmelt. As the snowpack begins to decrease and becomes saturated with water, the albedo falls and more solar radiation is absorbed. Dingman et al. (in press) have summarized the heat balance for the Barrow site for six periods in 1971 (Figure 2-5). The sudden change in the amount of energy going to melt the snow is mostly caused by the sudden decrease in albedo from 85 to 48%.

The snow has a mean extinction coefficient of 0.10 cm\(^{-1}\) (Weller and Holmgren 1974). Thus, little insolation penetrates the snow, and the pond ice does not begin to melt until all the snow is gone. Most of the melting occurs at the surface but some radiation also penetrates to the bottom
FIGURE 2-4. The evaporation rate and factors that affect it for six characteristic periods. Evaporation rates reported are from pans. (After Weller and Holmgren 1974.)

sediments and melts a little ice there. In general, it takes only 4 days for the pond ice to melt completely.

In lakes, the same events take place but the 2-m-thick ice sheets take much longer to melt. Consequently, the ice does not melt completely in the deeper coastal lakes until early- or mid-July, depending upon the thickness of the ice at the beginning of melt. Other complicating factors affecting the
ice melt in large lakes, such as ice albedo, crystal orientation, moat formation, and wind action, have been reviewed by Hobbie (1973).

Runoff begins on the day the snowpack becomes completely saturated with water and the maximum discharge occurs within 24 hours. In the next 4 days, 40 to 60% of the total spring runoff takes place—this is still before there is any thawing of the frozen ground. Around Barrow, the runoff from polygonal ground begins in the first half of June (it was 9-11 June from 1970 to 1973) and lasts until the first week in July. Runoff in the sloughs and larger creeks is delayed and prolonged. In the Colville River, for example, the maximum runoff does not occur until three weeks after

FIGURE 2-5. Heat balance for Barrow tundra for six characteristic periods. The width and direction of the arrows and the numbers at the base of each arrow indicate energy flux directions and rates. (After Weller and Holmgren 1974).
the onset of runoff. Following spring runoff at Barrow, the tundra is left saturated and covered with numerous flooded areas.

Precipitation during the summer season (Table 2-2) averaged 6.4 cm over the past decade (range 1.7 to 13.2 cm). Most of this fell as rain but snow can fall during any month. August and September are the wettest and cloudiest months. After the snowmelt period ended, less than 5% of the summer rainfall (3 cm) ran off from a 1.6-km² watershed during 4 years (Brown et al. 1968). There is virtually no water lost by runoff from ponds in polygonal ground during the summer, except in rare summers when the rainfall fills the ponds during late August. Permafrost blocks any downward water movement but some small quantities may move laterally.

One additional source of moisture during the summer is condensation of fog and dew on the vegetation. As seen in Table 2-1, the average relative humidity is high during this period and the condensation may be equal to 23 to 50% of the summer precipitation (L. Dingman, personal communication). Unfortunately, there are no good data on this, but condensation has little effect on the water balance of the ponds.

As the summer runoff is so small, the most important water loss occurs by evaporation. Brown et al. (1968) measured a pan evaporation of 16.0 cm in a “typical” precipitation year. However, it is well known that this method overestimates the true loss from land and vegetation and these authors estimated (from runoff and precipitation) that the actual losses were 6.0 cm. Mather and Thornthwaite (1958) measured about the same amount in large evapotranspirometers at Barrow. Thus, Brown et al. (1968) concluded that the summer precipitation was balanced by evapotranspiration in the watershed they studied. Rates of evaporation from the open water of ponds and lakes are close to the pan-measured rates and likely average 2 to 3 mm day⁻¹. During rainless periods of a month or so, many tundra ponds dry up.

The evaporation rate for the tundra, as well as the factors that affect it, was described by Weller and Holmgren (1974) (Figures 2-4 and 2-5). It is seen that neither wind speed nor air temperature changed appreciably from pre- to post-melting period; thus, the strong decrease in albedo when the snow melts and the resultant rise in absorbed solar radiation are the main factors in the increased evaporation.

**BIOLOGY**

The following information on the terrestrial biology at the IBP site is covered in greater detail in Bunnell et al. (1975) and Brown et al. (in press).
Soil

The Barrow soils (Brown and Veum 1974) have mostly formed on flat to gently sloping landscapes during conditions of low temperature and high moisture. These soils are relatively high in organic matter, of which some has accumulated in place and some has been mixed to various depths by frost churning. Additional organic matter results from the burial of pond or lake sediments in the thaw-lake cycle.

The Barrow soils have a strong thermal gradient during summer when the surface may reach 25°C while at the same time the horizons at 20 or 30 cm are below 2°C. This surface warming dries out the surface layers but the lack of drainage keeps the soil moisture contents at depths below 4 cm at greater than 85% of water-holding capacity. Consequently, vascular plants rarely lack moisture. On the other hand, the abundant moisture combined with low pore volume in mineral layers causes the deeper horizons to become anaerobic early in the summer.

Chemically, most of the soils are highly organic, strongly acid, and not very fertile (Bunnell et al. 1975). Apparently, the base nutrients are usually sufficient for plant needs; N and P, although stored in large quantities, are released only slowly from the organic matter.

Primary Producers

Plant production in the Barrow tundra has been extensively studied for many years; the data and results are reviewed in Bunnell et al. (1975), Tieszen (1978a), and Brown et. al. (in press).

In summer, the coastal tundra vegetation resembles a yellow-brown grassland, relieved only by strips of greener vegetation in troughs between polygons or at the edges of ponds. The yellow-brown color results from the large accumulation of dead plant parts of grasses and sedges. All plants are short (10 to 15 cm high) and many have broad, flat stems.

Compared with most ecosystems, the Barrow tundra is indeed uniform. Although there are 100 species of vascular plants (plus 96 bryophyte and 57 lichen species), the low relief of the coastal region produces only small environmental differences between lowlands and uplands. The result is that all species of the extensive marshes also occur on the uplands and most of the species of the driest upland sites are also found whenever hummocks appear in the wetter areas (Bunnell et al. 1975). Webber (1978) has divided this continuum of vegetation at the IBP site into eight plant assemblages. Five of these cover 91% of the area. They are: mesic Salix rotundifolia heath in dry, low-center polygons (7%); mesic Carex aquatilis/Poa arctica meadow on dry, flat, polygonized areas
(41%); moist *C. aquatilis/Oncophorus wahlenbergii* meadow in moist, flat sites (21%); wet *Dupontia fisheri//Eriophorum angustifolium* meadow in wet, flat sites and polygon troughs (7%); and wet *C. aquatilis/E. russeolum* meadow in low polygon centers and at pond margins (15%). The soil conditions controlling this distribution appear to be moisture, redox potential, and soluble phosphorus levels.

Only a small amount of green tissue is present at the base of the plant stems when the snow melts. Leaves are rapidly formed, however, partly by the translocation of carbohydrates stored below ground, and very rapid growth (0.2 g g\(^{-1}\) day\(^{-1}\)) begins around 15 June. This lasts for about 10 days and then declines to 0.03 g g\(^{-1}\) day\(^{-1}\); this rate continues until about 1 August when the peak aboveground biomass of 60 to 100 g m\(^{-2}\) is reached. Since the dead remains of several years’ previous growth may be still standing, the total plant material is between 150 and 300 g m\(^{-2}\). This production is drastically reduced when there are high numbers of overwintering lemmings. Not only do they cut down the stems and leaves during the summer, but also under the snow they feed almost exclusively on the green stem-bases.

Photosynthesis continues during August but the photosynthetic is mostly incorporated into belowground reserves. In addition, organic materials, minerals, and nutrients are transferred below ground. Roots appear to live 2 to 10 years; their production is around 65 g m\(^{-2}\) year\(^{-1}\) (Shaver and Billings 1975). Live biomass below ground is frequently 10 times that above ground.

Vegetative reproduction is more reliable than sexual in the short growing season and unfavorable climate, so flowering and seed set are greatly reduced. In four monocotyledons only 2.5 to 10% of the shoots were flowering shoots.

Bryophytes are abundant at Barrow but are mostly hidden by the vascular plant canopy. Yet, moss and liverwort primary production ranges up to 160 g m\(^{-2}\) yr\(^{-1}\) in wet meadows. These plants contain lower concentrations of macronutrients than do vascular plants but have higher amounts of micronutrients and calcium. This may explain the change in lemming diet to increasing amounts of bryophytes during the winter.

Lichen abundance is inversely correlated with soil moisture; they are absent in areas where there is any standing water for a week or so in the spring. On better drained meadow sites, the lichen biomass can exceed 50 g m\(^{-2}\). In spite of their low biomass, they are important nitrogen fixers. Unlike the situation in many tundra areas, at Barrow the vertebrates consume few lichens. Lemming stomachs, for example, seldom contain more than 2% lichens.

The plants in this arctic environment show a number of specialized adaptations. In the spring, at 0°C, they are able to mobilize carbohydrates and inorganic nutrients from belowground reservoirs; this allows very rapid growth early in the growing season. Compensation levels are very low in these plants so that net photosynthesis can proceed for 24 hours a
day. The leaves of the dominant graminoids are inclined at 65° from the horizontal; at the low solar altitude at Barrow (averaging 25° on 21 June), the erect leaves intercept almost all the solar radiation.

Herbivores

The brown lemming (*Lemmus sibericus*) is by far the dominant consumer at Barrow (Pitelka 1973). One leafhopper (Homoptera) and one leaf beetle do occur and root-piercing nematodes are present, but their impact on the vegetation is slight. In years when lemmings are abundant (Figure 2-6), every 2 to 5 years, their impact is great. Because they do not hibernate, they are active during winter and even reproduce as soon as there is a protective layer of snow (MacLean et al. 1974). By the end of the winter and before a summer high, the lemmings are at peak abundance and will have completely cut all standing plants. This accounts for 40% of the previous season’s production; even more important, the lemmings eat the stem bases and parts of the rhizomes, which slows down the initial growth of plants in the spring. Usually, the population declines throughout the summer following a spring high and about 25% of the primary production is consumed. At low population levels, lemmings consume about 0.1% of the total aboveground production.

Lemming grazing may sustain the monocotyledon dominance at Barrow. Some adaptations of these plants, such as vegetative reproduction

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**FIGURE 2-6. Abundance of lemmings at Barrow (based on trapline data from Pitelka 1973). Bars indicate summer. (After Bunnell et al. 1975.)**
and the large belowground storage of energy and nutrients, will help resist the effects of grazing. In fact, when lemmings are excluded from experimental plots, there is a buildup of standing dead vegetation, a reduction in the depth of seasonal thaw, an increase in the thickness of the moss layer, a decrease in vascular plant productivity, and a change in species composition.

No single factor has been found to control the lemming population cycles. One contributing factor may well be the high year-to-year variation in the nutrient content of plants; at the low levels found in Barrow plants, nutrients have been found to affect lemming reproduction. Another factor is the thickness and condition of the snow cover. Temperatures as low as \(-25^\circ C\), frequently found at the ground surface during winter, severely stress the animals and may prevent winter reproduction. Vertebrate carnivores may kill a significant percentage of the lemming population during the winter beneath the snow (weasels) or during the summer (jaegers, owls).

Carnivores

The lemming cycles also produce a cycle in abundance of their predators (Pitelka et al. 1955). In a high year, pomarine jaegers (*Stercorarius pomarinus*), snowy owls (*Nyctea scandiaca*), short-eared owls (*Asio flammius*), least weasels (*Mustela nivalis*), ermine (*M. erminea*), and arctic fox (*Alopex lagopus*) may all be abundant. The avian predators are migratory and arrive between late April and early June. Because these large birds eat four to seven lemmings a day, they breed only when lemmings are abundant. Weasels immigrate into the area when lemmings begin to be abundant; they reproduce during the winter and their number may be high \((150 \text{ km}^{-2})\) at snowmelt. Foxes breed inland from Barrow but appear at Barrow in late fall and will prey actively on lemmings when they are abundant.

The common smaller birds (seven species of shorebirds and two buntings) arrive in the first days of the spring melt and begin to breed at once \((80-100 \text{ pairs km}^{-2})\). They rely at first on Diptera larvae (especially craneflies) and on fat reserves. Later, when adult insects become available, the birds take these. At the end of the summer, the birds turn again to insect larvae, this time to the chironomids (Diptera). By the time emergence is complete, the smaller birds have cropped about 30% of the adult insects from the tundra surface; they have little effect on the larval insects (taking less than 1%).

Feeding by insectivorous birds serves to bring energy and material from belowground pools into aboveground circulation. These birds are also an alternate food source for the larger avian predators. The owls and jaegers usually nest and roost on elevated sites, such as mounds and
polygon ridges, which are consequently fertilized. This may be the only mechanism for nutrient movement onto the higher parts of the tundra.

Decomposition

Within 3 years of death, plant materials at Barrow lose 60% of their weight (see Brown et al. in press for details). Half of this loss occurs in the first year from Carex aquatilis (26.6%) and Eriophorum angustifolium (27.7%). Most of the first-year loss is by leaching of organic matter, but inorganic nutrients may also be rapidly lost. For instance, 70 to 80% of the phosphorus and potassium are lost during the first year. In contrast, calcium is immobilized in the cell walls and is lost very slowly. The pattern of total weight loss after the first year is the sum of two exponential decay rates; one rate is 49% per yr for rapidly metabolized compounds (ethanol soluble), the other rate is 11% per yr for recalcitrant compounds.

The factors controlling the rates of decomposition at the Barrow site include the duration of freezing, the low pH, the low oxygen concentrations in the soil, the low amounts of available nitrogen and phosphorus, and the effect of the low temperatures on microbial processes. Even though water is abundant, the standing dead plant parts are too dry for rapid decomposition. Thus, the loss of weight in standing plants is 4 to 5% per yr but this increases to 7 to 10% per yr once the material enters the litter layer.

The amount of carbon dioxide evolved from the soil was twice as high on polygon rims and in troughs as in polygon basins; evolution from meadow soils was even higher. Over a period of 85 days (26 June to 10 September) the evolution from meadow soils matched the net primary production (159 g C m⁻²). Despite the anaerobic soils, little methane leaves the soil. Respiration, and therefore decomposition, is increased when lemmings are abundant or where vehicles have pressed down the dead vegetation.

Both bacteria and fungi are abundant in the litter and soils; in fact, it is not their biomass but their activity that limits decomposition. Bacterial numbers, 10⁸ or 10¹⁰ cells (g dry weight)⁻¹ estimated as a direct count, are similar to those in temperate soils. Aerobic plate counts fall in the range 0.5 to 10 × 10⁶ cells g⁻¹. Mycelia length (per g dry wt) is from 200 to 2700 m, but despite this amazing length the fungal biomass is only a third to a quarter that of the bacteria.

Invertebrate Biomass and Production

The major invertebrates in Barrow soils are Nematoda, annelid worms (Enchytraeidae), mites (Acarina), springtails (Collembola), and
Diptera larvae (MacLean 1974). Their total biomass lies between 1.3 and 5.1 g dry wt m\(^{-2}\), which approximates the microbial biomass. Enchytraeidae dominate and make up 50 to 75% of the invertebrate biomass in all habitats. Most of these animals are aerobic; thus they are found mainly in the top 2.5 cm.

The relatively high densities and high biomass of invertebrates are, in part, a result of long life cycles. For example, two species of craneflies (Diptera) require at least 4 years to complete larval development. The annelid worms also have long life cycles. Despite the large biomass, the long lives of the soil invertebrates give rise to low productivity rates.

The biomass of soil macroinvertebrates (Nematoda, Enchytraeidae, Acarina, and Collembola) is positively correlated with net primary production rates but negatively correlated with accumulated organic matter. This implies that the greatest macroinvertebrate biomass occurs in habitats with the highest rates of energy and nutrient turnover. There is still an abundance of accumulated organic matter in all habitats, so the correlation of biomass with energy and nutrient turnover may reflect the better quality or greater abundance of microbes. Alternatively, the feeding of the invertebrates on the microbes may stimulate microbial activity and thus cause a greater removal of organic matter.

**ENERGY AND NUTRIENT CYCLING**

The information that supports the conclusions in the following sections is given in Bunnell et al. (1975) and Brown et al. (in press).

**Energy**

The entire aboveground biomass of the dominant tundra plants, the grasses and sedges, grows and dies each year. The belowground biomass lives longer but still turns over in 2 to 12 years depending upon the species. In addition, rootlets and root hairs last but a single season. Thus, there is a large annual input of fixed chemical energy to the system.

In view of the virtual absence of lemmings during the “lows” of the population cycle, it is amazing to discover that, on the average, the percentage of the primary production consumed by animals is higher at Barrow than in most other ecosystems. Vertebrate carnivores are, on the average, also very active relative to other ecosystems. In spite of this activity of the vertebrates, more of the energy of the system passes through the populations of soil saprovores, and especially microbivores, than through-the lemmings.
Organic matter is abundant in the soil at Barrow, but it is not known whether there is a long-term accumulation or loss. In part, the difficulty is caused by the great quantity of organic matter—from 22 to 45 kg m\(^{-2}\) (to 20-cm depth). This is 50 to 400 times the net annual primary productivity. Given this large quantity, small changes are difficult to measure. In part, the difficulty in calculating a long-term energy budget is caused by the spatial variation and by the tremendous changes in such things as climate and lemming effects from year to year.

Two hypotheses have been proposed:

1. The entire system is in steady state but the terrestrial system is accumulating organic matter, while aquatic systems (lakes and ponds) are degrading organic matter. Habitats at Barrow can change from meadows to polygons to ponds to lakes and back to meadows. Thus, the long-term effect is no net gain of organic matter as a given area of land moves through the thaw-lake cycle.

2. The system is not in steady state; accumulation continues until conditions change. This accumulation is deep in the soil where the decomposition decreases sharply with depth. Since the amount accumulated at Barrow is nowhere near as great as is found in peat bogs, this hypothesis requires that either 1) the Barrow tundra system is young; thus large peat deposits have not accumulated, or 2) recurrent disturbances reverse the pattern of accumulation in any habitat.

**Nutrients**

Like energy, nutrients are almost all contained in the pool of soil organic matter; less than 1% of both nitrogen and phosphorus is contained in living biomass (Figure 2-7). This contrasts with the rain forest, for example, where living organisms are a significant reservoir of nutrients.

There is only a small pool of soluble soil nitrogen and phosphorus available to plants; this is taken up or turned over many times during a season. This pool is replenished from a much larger pool of exchangeable nutrients, but the non-exchangeable pools are even larger. To replenish the nutrients absorbed by plants, the pool of soluble plus exchangeable nitrogen must turn over 11 times during a growing season; in this same period the pool of phosphorus must turn over 200 times (3 times per day). It is likely that there is a close connection between the rate of supply of nutrients and plant production. Therefore, primary productivity in tundra (as in tropic ecosystems) depends on the rate of decomposition.

The Barrow ecosystem is very conservative with nutrients. For example, most vascular plants have mechanisms for retaining nutrients, particularly phosphorus, in belowground parts rather than allowing them to be lost to decomposers. In the drier habitats, plants have mycorrhizae to facilitate phosphorus uptake. Overall, nitrogen, calcium, and potassium
FIGURE 2-7. Nitrogen and phosphorus budgets for the Barrow ecosystem (g m\(^{-2}\) yr\(^{-1}\)). (After Bunnell et al. 1975.)
concentrations are similar in plants from site to site in spite of great variations in soil concentration. In contrast, phosphorus concentrations in plants are highest in the most productive sites. These data suggest that phosphorus more strongly limits production than do other nutrients. Fertilization experiments tend to confirm this hypothesis, as they result in an increase both in production and in the phosphorus concentrations in plants; other nutrients cause no change in concentration.

Despite this limitation of phosphorus on plant productivity, it does not act through altered photosynthetic capacity of each leaf. Instead, all leaves produced have the same optimal photosynthetic capacity. The limitation of nutrients appears to act by controlling the rate of production of new leaves and may also influence the rate at which nutrients are removed from older leaves.

Vascular plants may lose a significant amount of potassium and perhaps phosphorus by leakage onto the leaf surface. These nutrients, plus those leached from standing dead, are subsequently washed off the leaves and form the major nutrient input to the bryophytes. Once nutrients are incorporated into bryophyte tissue, they are released slowly as decomposition of these forms is very slow. Recycling may be speeded up by the feeding of lemmings on bryophytes in winter.

The spatial distribution of nutrients is in part controlled by lemming activities. This control occurs in winter when lemmings build nests in polygon troughs but forage in other areas as well. Most of the lemming

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**Figure 2-8.** Nitrogen budget for coastal tundra at Barrow. All units are mg N m⁻² yr⁻¹. (After Barsdate and Alexander 1975.)
feces are deposited in the troughs and in this way the nutrients from many habitats are actually concentrated in the troughs. This concentration may contribute to the higher soil nutrients (especially phosphorus) found in the troughs which in turn may contribute to the higher rates of production and decomposition found in these areas.

Some of the same hypotheses came out of a study of the entire nitrogen budget (Barsdate and Alexander 1975). Nitrogen fixation was the most important input; precipitation was only one-third as great (Figure 2-8). The outputs were very small, with denitrification and runoff of organics and ammonia the major losses. Most of the input (65%) was stored. Thus, the system conserves its nitrogen (nitrogen appears to accumulate), and microorganisms (here, nitrogen-fixing algae) are important in controlling flux rates of nutrients and may well control the entire production rate.

In conclusion, the terrestrial ecosystem of the tundra is rich in total nutrients and energy but poor in amounts actually available and circulating. The activity of decomposers regulates the system.

SUMMARY

The Tundra Biome was one of five ecosystems studied in the U.S. under the International Biological Program. Both a terrestrial and an aquatic study were carried out at Barrow, Alaska, with the goals of developing an understanding of the ecology through measurements of the flux of carbon, nitrogen, and phosphorus through the ecosystem. Mathematical modeling was one of the tools to be used; the needs of this effort meant that much experimental work had to be carried out to define the interrelationships of the processes with an environment and to define the controls that were operating. In the aquatic project, whole ponds were fertilized with phosphate and nitrogen and one pond was treated with crude oil.

Past studies of arctic lakes and ponds have been largely descriptive. Only the present study, several previous studies at Barrow, and a Canadian IBP study have dealt with the dynamics of the ecosystems. Arctic lakes and ponds seldom warm above 10°C, are usually unstratified during the summer, and are covered with a 1- to 2-m-thick ice sheet for 9 to 10 months of the year. Ponds and shallow lakes usually freeze solid. Because much of the total water in lakes and ponds is meltwater from snow, the concentration of ions is low. There is some interaction with the soil so that areas that have calcareous bedrock will contain streams and lakes with relatively high ionic content, but the permafrost prevents much movement of water in and out of the soils. As a result of the low quantities of ions, and of the relative purity of the precipitation, the nutrient concentrations are low and the lakes and ponds are oligotrophic.
The algae of the plankton are all nanoplankton, mostly cryptophytes, chrysophytes, and greens. Productivity is low, usually 1 to 30 g C m\(^{-2}\) yr\(^{-1}\). Zooplankton are never abundant and only one calanoid copepod, one cyclopoid copepod, and one cladoceran are present while the most oligotrophic lakes have either only one species of copepod or no zooplankton at all. Fish are always present except where the body of water freezes solid. In shallow ponds, the absence of fish permits the fairy shrimp and large *Daphnia* to thrive. Chironomid larvae dominate the bottom fauna and may live for several years. Oxygen is usually close to saturation during the open water season but decreases during the winter and may disappear in the deepest part of a lake. Other primary producers (rooted plants, benthic algae) have not been studied, although mosses are abundant in deep, clear lakes.

In northern Alaska there are a few deep lakes (50 m) in mountain valleys, a few more moderately deep lakes (25 m) in the foothills, and tens of thousands of shallow lakes (2-3 m) on the coastal plains. Hundreds of thousands of shallow ponds have formed on the coastal plain in former lake beds. There are a number of rivers as well but these are virtually unstudied. The deep lakes are dominated by planktonic processes. Several receive glacial rock flour so they are quite turbid. The lack of stratification during open water causes poor conditions for algal growth; as a result, the maximum productivity occurs in the spring beneath the ice cover (light penetrates the ice sheet when the snow cover is less than 10 cm thick).

The shallow lakes research in northern Alaska has concentrated on the origin and development of the oriented lake basins (north-south). This orientation or elongation is caused by differential erosion by wind-driven currents. A non-oriented lake near Barrow (Imikpuk Lake) has been sampled extensively for microbes, algae, chemistry, and zooplankton. The few species of cladocera and copepoda enabled several life cycles to be worked out in detail. The chemistry and biology (taxonomy) of small lakes have been investigated at Cape Thompson.

Ponds near Barrow have been investigated by two projects which concentrated on nutrients, phytoplankton, and zooplankton. Primary productivity was extremely low, around 1 g C m\(^{-2}\) yr\(^{-1}\); different nutrients stimulated primary productivity at different times of the year. The dominant *Daphnia* species, *D. middendorffiana* and *D. pulex*, have only females in the population. The resting eggs, which overwinter, need to be frozen before they will hatch in the spring.

In a small watershed near Barrow, most of the runoff occurred in the spring melt period; summer precipitation was balanced by evapotranspiration. Large rivers, which have been little studied, contain virtually no plankton, but do harbor fish which breed in smaller streams and overwinter in deep pools or in streams near springs.

Air temperatures average below freezing so that permafrost underlies the area to a depth of 400 m. Some 20 to 50 cm of soil thaws each summer but the permafrost is impervious and water cannot drain. Low-lying soils
are saturated and ponds easily form. They are particularly abundant in old lake beds where ice wedges form in the soil and eventually push up the overlying soil into a ridge a few centimeters high. The ice wedges and ridges form connected polygons with “diameters” of 20 to 50 m. Each polygon is a separated basin; many contain ponds that form when the soil subsides due to destruction of the insulating vegetation.

The average temperature at Barrow is \(-12.4^\circ \text{C}\) while the summer temperature averages are \(-7.3^\circ, 0.9^\circ, 4.1^\circ, 3.3^\circ,\) and \(-0.9^\circ\) for May, June, July, August, and September. Approximately 50% of the 10.8 cm of annual precipitation falls in June, July, and August. Solar radiation in the summer is reduced by the cloudy and foggy weather so that most of the annual radiation occurs before the ponds melt. Winds are almost continual during the summer at 6 m sec\(^{-1}\) from the east. Microinversions frequently occur over a pond, however, so the wind speed at the water surface may be only one-third the recorded speed.

Snow normally reflects more than 85% of the solar radiation; in early June when the snow begins to melt and becomes saturated with water, the albedo drops to around 50% and the snow rapidly melts. Within a few days the snow is gone and the pond ice begins to melt. This melting is complete in 4 days. Lake ice is 2 m thick so does not disappear until mid- or late July.

The soils of the IBP site are highly organic, acid, and not very fertile. Nitrogen and phosphorus are abundant but are tied up in organic matter. Soil temperatures may reach 25\(^\circ\)C at the surface while the horizons 20 to 30 cm below are at 2\(^\circ\)C. There is some surface drying but soils are saturated below 4 cm.

The tundra vegetation at the site is a yellow-brown grassland. All plants are short (10-15 cm) and the large amount of standing dead vegetation hides the green plants. Although there are over 100 species of vascular plants, a few grasses and sedges dominate: Carex aquatilis, Eriophorum angustifolium, Poa arctica, and Dupontia fisheri. New leaves sprout from green tissue at the base of the plant stems as soon as the snow melts. Rapid growth occurs until about 1 August when the peak aboveground standing crop (new growth) of 60 to 100 g m\(^{-2}\) is reached. Production is reduced during lemming highs by summer grazing on stems and leaves and by winter feeding on the green stem bases. Roots live 2 to 10 years; their biomass is 10 times the aboveground weight and production is about 65 g m\(^{-2}\). All reproduction is vegetative.

Mosses and lichens are also abundant. Moss and liverwort production may be as high as 160 g m\(^{-2}\) yr\(^{-1}\) in wet meadows; lichen productivity is low but biomass may exceed 50 g m\(^{-2}\).

Plant adaptations to the arctic environment include the ability to translocate carbohydrates and nutrients at 0\(^\circ\)C, a low compensation level so that net photosynthesis proceeds for 24 hours a day, and an average leaf inclination (65\(^\circ\) from the horizontal) that allows almost complete interception of the low-angle solar radiation.
The brown lemming is the dominant consumer; their numbers increase from less than 1 ha\(^{-1}\) to nearly 200 ha\(^{-1}\) every 2 to 5 years. In "lemming high" years their impact on the vegetation is startling; they reproduce beneath the snow cover and completely cut all standing plants during the winter. Their consumption of the annual primary production varies from 40% to 0.1% but on the average they consume a higher percentage than any other grazer community on earth. No single factor has been found to control the lemming population cycles. Instead, control may occur by a combination of year-to-year variation in the nutrient content of plants, of the amount of protection by the snow, and of predation.

The lemming cycles also produce a cycle in abundance of their predators, the pomarine jaegers, snowy owls, short-eared owls, least weasels, ermines, and arctic foxes. The large birds eat four to seven lemmings per day and breed only when lemmings are abundant.

The common smaller birds (seven species of shorebirds and two buntings) arrive in the first days of the spring melt and begin to breed at once (80-100 pairs km\(^{-2}\)). They eat mostly insects such as larvae and adults of craneflies and midges. About 30% of adult insects and 1% of larvae are harvested.

On the tundra, about 60% of the weight of plant material disappears within 3 years of death. Half of this loss occurs in the first year. After the first year, the loss is the sum of two exponential decay rates, one of 49% yr\(^{-1}\) for rapidly metabolized compounds and one of 11% yr\(^{-1}\) for recalcitrant compounds. Factors controlling the decomposition rate include the duration of freezing, the low pH, the low O\(_2\) concentrations in the soil, the low amounts of available N and P, and the low temperatures.

Soil respiration is another way to measure decomposition. Over an 85-day summer period, the evolution of CO\(_2\)-C from meadow soils (159 g C m\(^{-2}\)) matched the net primary production. Most of the respiration is by microbes. Bacterial numbers, 10\(^8\) or 10\(^10\) (g dry weight\(^{-1}\)) are similar to temperate soils. The amount of fungal mycelia (g dry weight\(^{-1}\)) is 200 to 270 m but this is only a third to a quarter the biomass of the bacteria.

The major soil invertebrates are nematodes, annelid worms, mites, springtails, and dipteran larvae. Their total biomass is 1.3-5.1 g dry wt m\(^{-2}\) or about the same amount as the microbes. Enchytraeid worms dominate (50-75% of biomass). Most of the animals are found in the top 2.5 cm (aerobic layer). The craneflies and worms have long life cycles (up to 4 years). Thus, although the biomass is high, the productivity is low.

Despite the high average rate of lemming grazing, most of the energy passes through the soil saprovores and microbivores. There is so much organic matter in the soil (22 to 45 kg m\(^{-2}\) to a depth of 20 cm), that the total primary production for 1 year is only 0.25 to 2% of the total. Because of this large quantity of soil organic matter, the small changes each year can not be measured and it is impossible to discover whether the soil systems are gaining or losing organic matter. Two hypotheses have been
proposed: the entire system is in balance but there is accumulation on land and net decomposition in ponds; the system is accumulating organic matter and this will continue until conditions change.

Nutrients are tied up in the soil organic matter; less than 1% is in the biota. To replenish the nutrients absorbed by plants, the pool of soluble plus exchangeable nutrients must turn over 11 and 200 times a year for nitrogen and phosphorus. It is likely that this supply ratio, and also the primary productivity, depend upon the rate of decomposition. Despite differences in nutrient concentrations in the soil, almost all the nutrients are present in similar amounts from site to site. The exception is phosphorus where plants from the most productive sites have the highest concentrations. This evidence, plus evidence from fertilization studies, suggests that phosphorus more strongly limits primary production than do other nutrients such as nitrogen, calcium, or potassium. Nutrients may become concentrated into troughs between polygons during the winter. Lemmings build nests in the troughs and deposit most of their feces there but forage over a larger area.

A study of the nitrogen budget revealed that the most important input was nitrogen fixation which was 3 times the precipitation input. Outputs due to denitrification and runoff were small; 65% of the input was stored in organic matter.

It was concluded that the terrestrial ecosystem of the tundra is rich in total nutrients and energy but poor in amounts of nutrients and energy actually available and circulating. Decomposition rates regulate the system.