7

The Soils and Their Nutrients

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INTRODUCTION

Soils of the coastal tundra are formed under conditions of low temperature and high moisture. Mean annual precipitation is low, but relative humidity is high and drainage is impeded by permafrost; consequently, soil moisture content is high. Low temperatures and high moisture contents lead to the accumulation of organic matter. Because of the cold, impervious permafrost there are strong gradients of temperature and oxygen saturation within the thawed soil, but soil profile differentiation is retarded by the restriction of downward leaching and associated chemical transformations. Visibly distinct horizons are largely associated with organic matter, a product of organic input from primary production and physical redistribution via frost churning processes.

Overall, the soils of the coastal tundra at Barrow are similar to those of other tundra areas. In the data gathered by French (1974) on 27 soils from nine tundra sites studied during the International Tundra Biome effort, soil from a wet meadow of the Biome research area at Barrow falls near the middle of the range of values observed for most soil parameters, although this soil is somewhat wetter than those of most other circumpolar sites. In an analysis based on climate and soil factors (Rosswall and Heal 1975), five microtopographic units from the coastal tundra at Barrow (meadows, polygon troughs, rims and basins of low-centered polygons, and centers of high-centered polygons) were found to be similar to each other, but were also very similar to the meadow site on Devon Island and the moss turf and moss carpet on Signy Island, Antarctica. The soils near Barrow are different from those at Prudhoe Bay, 320 km to the east, which are calcareous and lower in organic matter (Douglas and Bilgin 1975, Everett and Parkinson 1977). The properties of the soils of the coastal tundra at Barrow are therefore the products of both the climatic factors common to arctic tundra regions and the specific geologic history of this area.

SOIL PHYSICAL PROPERTIES AND NUTRIENTS

Biological processes in the soils of the coastal tundra at Barrow occur in an organic-rich layer less than 50 cm thick that is thawed for less than four months of the year. This layer contains over 70% of the living biomass of the tundra ecosystem. In it, roots grow and take up nutrients and water, organic matter decomposes, invertebrates graze and prey upon one another, and lemmings burrow for summer protection from predators.

This shallow layer of thawed soil is the reservoir from which inorganic nutrients are initially supplied to the living organisms. Calcium, magnesium, potassium and sodium are all retained by the cation exchange complex, which is made up largely of humified soil organic matter. The organic matter itself contains the major pools of nitrogen and phosphorus. However, most of the available nitrogen is in the form of ammonium and is retained on the soil exchange complex, while most of the available phosphorus is bound to iron or aluminum ions. The pools of available nutrients are highly variable, both spatially, because of the different kinds of soils associated with the different microtopographic landforms, and temporally, in response to fluctuations in environmental conditions. The underlying permafrost affects the nutrient supply through its effects on temperature gradients in the thawed soil and by isolating large quantities of nutrients contained in the frozen soil.

Organic Matter

The predominant characteristic of the soils is their high proportion of organic matter. More than 95% of the total organic matter in the terrestrial tundra ecosystem is below the ground surface, and one-third is in the upper 10 cm of soil, where biological activity is concentrated. The large amounts of organic matter impose a particular structure on the soil, influence the flux of moisture, oxygen and heat, and modify the chemical properties, particularly in the cation exchange complex. The large proportion of organic matter in these soils has a strong effect on the nutrient supply, as is typical for arctic tundra soils (Babb and Whitfield 1977, Chapin and Van Cleve 1978).

Carbon and nitrogen, in an average ratio of 20:1, make up from 10 to 40% of the total soil weight (Figure 7-1). Total carbon contents in the upper 15 cm of soil typically range from about 12,000 to 16,000 g m^{-2} but may be less than 10,000 g m^{-2} in comparatively warm, nutrient-rich, wet Pergelic Cryaquepts of polygon troughs, where decomposition rates are high.
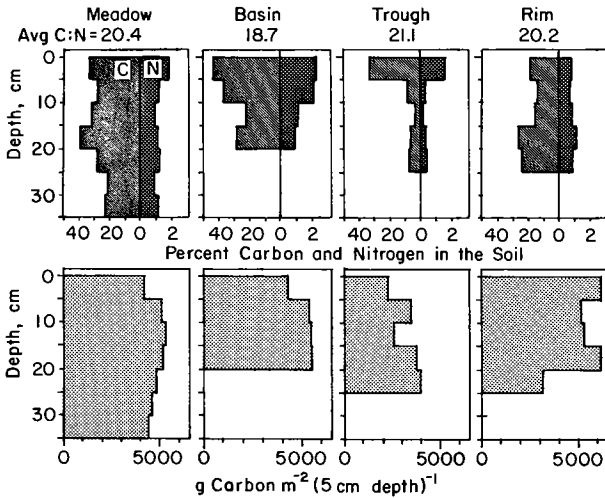
FIGURE 7-1. *The percentage of carbon and nitrogen in soils from different tundra microtopographic units, including meadows, basins of low-centered polygons, polygon troughs, and rims of low-centered polygons.*

In nearly all the soils, organic matter in the surface horizons is mostly fibric; the degree of decomposition increases with depth. Fibric organic matter includes slightly decomposed, reddish- to yellowish-brown fibrous materials whose generic characteristics can be recognized and which are usually interlaced by an abundance of living roots and rhizomes. Live belowground plant parts averaged 660 g m^{-2} in 1972, most of it in the upper 10 cm (Dennis et al. 1978). Fibric materials are commonly associated with wet meadow and polygon trough soils, but such materials rarely dominate the entire soil profile.

Sapric inclusions of black to dark reddish-brown, generically unidentifiable, fibrous to granular organic materials which disintegrate completely under the mildest mechanical manipulation are commonly found below the surface horizon. In the better drained, more highly oxidized soils such as are found on the tops of high-centered polygons and the rims of low-centered polygons, highly decomposed sapric organic matter may predominate throughout the entire active layer and continue down into the permafrost.

Hemic materials, those of intermediate decomposition, represent the most common form of organic matter in the soils. These generally range in color from dark grayish-brown to dark brown, and in nearly all cases

identifiable plant components can be recognized which disintegrate only after considerable mechanical manipulation. Such materials commonly dominate the entire soil profile in basins of low-centered polygons and in some of the large, very low relief orthogonal polygons of mesic and wet meadows.

Differences in the amount of organic matter over lateral distances of only 1 m can be more marked than differences with depth. In an apparently uniform area of wet non-polygonal terrain, the organic carbon in two soil profiles sampled only a meter apart differed by a factor of 2. However, differences between microtopographic units are generally 1.5 to 2 times greater than variations within these units.

Bulk Density, Porosity, and Texture

The bulk density of a soil has a strong effect on heat conduction and temperature, depth of thaw, soil water content and movement, soil porosity and air content, and the penetration of roots. Bulk densities in the soils of the coastal tundra at Barrow range from about 0.05 to about 1.50 g cm^{-3}. Differences in bulk density (D_b) along a microtopographic gradient are strongly associated with the percentage of organic carbon (C_{org}) present:

$$C_{org}(\% \text{ by weight}) = 1.1 - 57.15 \log(D_b) \qquad r = 0.93, n > 200$$

The lowest bulk densities are found in surface horizons, which have high contents of fibric organic matter, live and dead roots and moss (Figure 7-2). Within the thawed layer, soils of wet and mesic meadows have bulk densities that range from moderately high to low, with a tendency toward increasing bulk density with increasing wetness. Rims of low-centered polygons and centers of high-centered polygons have soils that range in bulk density from low to intermediate, depending on the nature
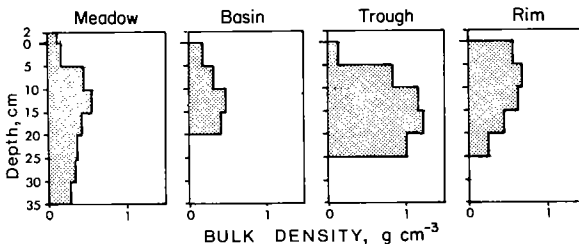

FIGURE 7-2. *Bulk density of soils from four different microtopographic units.*

of the soil formed before elevation of the rims and centers. Soils of the basins of low-centered polygons have low bulk densities. The general increase in bulk density between soils of basins and rims of these microtopographic units is partly due to the more highly decomposed organic matter in the rims and partly because the rims generally contain a higher content of fine-textured mineral matter. The relatively low content of organic matter in the Cryaquept soils found in most polygon troughs results in high bulk densities, although some soils in the troughs are highly organic, with correspondingly low bulk densities. The highest bulk densities of the coastal tundra at Barrow are generally encountered in the sandy soils along stream margins.

The bulk density of a tundra soil, as it reflects mineral content and water-holding capacity, is an important determinant of the depth of thaw (Gersper and Challinor 1975). Under similar moisture regimes, mineral soils generally thaw more deeply than organic soils because of their higher bulk density and consequent increased heat conduction. However, soils with low bulk density also tend to have high moisture content, which is also associated with deeper thawing. Although the variables are strongly covariant, multiple regression analysis suggests that bulk density alone accounts for 35% of the variation in thaw depth, while moisture content accounts for an additional 31%.

The soils are highly porous, with a range of porosity from 50 to 65% for mineral layers, increasing to more than 90% for organic layers (Figure 7-3). Thus, these soils are more porous than mineral soils of temperate regions, which range from 30 to 60% porosity (Hausenbuiller 1974).
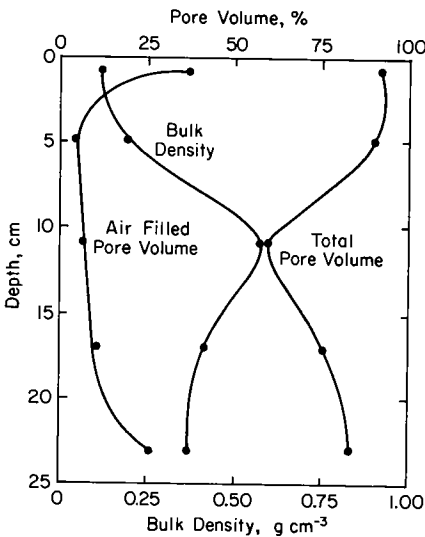
FIGURE 7-3. *Bulk density, percentage total pore volume, and percentage air-filled pore volume in soil of a moist meadow.*
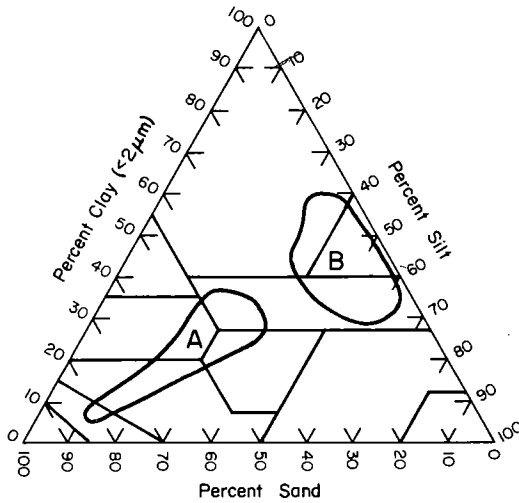
FIGURE 7-4. *Particle size distribution and texture of mineral horizons in soils from A) Aeric Pergelic Cryaquepts on sloping areas marginal to Footprint Creek (10 samples), and B) Histic Pergelic Cryaquepts and Pergelic Cryohemists in a moist meadow (86 samples). Textural diagram after Soil Survey Staff (1975).*

The very small particles and particle aggregates of sapric soils form a rather dense and relatively impermeable mass that is slow to transmit moisture or oxygen (Figure 7-3). Because of their highly aggregated condition, sapric soils have many small pores and retain large quantities of moisture, even in topographic positions that would normally be considered xeric. Further, the porosity of sapric soils may be high, especially in surface horizons, because of repeated ice segregation, which produces lenticular openings. However, vertical permeability is usually very low. In comparison, fibric materials are of low density and have a very large proportion of interconnected, free-draining macropores that permit rapid movement of air and water in all directions. Soils on low topographic positions have fibric surface horizons that remain filled with circulating water throughout much of the summer. Horizons containing hemic material have intermediate soil moisture properties.

Soils with high contents of clay- and silt-sized mineral materials generally tend to have very fine pores and consequently very low permeability to air and water. Mineral layers in soils of the coastal tundra at Barrow are generally of this type, although they are often admixed with porous organic matter and thus are more permeable. The dominant textures of the mineral horizons (Figure 7-4) are silty clay and silty clay loam, with some clays and a few soils of coarser texture. Mineral fractions of Histosols tend to be finer textured (silty clays) than the Inceptisols, which are silty clay loams, although Cryaquepts of polygon troughs and frost boils commonly have the finest textures. Sandy-textured and loam-textured soils are not common at the Biome research area, and appear to be restricted to alluvial positions and the stream banks along Footprint Creek.

TABLE 7-1 *Seasonal Averages of the Percentage of Moisture, Water Potential, and Redox Potential in the Upper 15 cm of Soil, and Soil Temperature During Summer 1972.*

| Micro-topographic unit	Dominant vegetation type	Percent moisture (g water gdw⁻¹)	Water potential (bars)	Redox potential (mV)	Temperature, 10 cm (°C)
Slough	VII	292	ND	306	8.1
Meadow	IV	331	−0.009	405	6.3
Rim	II or III	118	−0.044	511	7.3
Basin	VI	208	−0.033	423	7.7
Trough	V	265	−0.008	430	8.0
Top	I or II	158	−0.041	487	6.5

Soil Moisture and Aeration

Because of their very high content of organic matter and related high porosity, soils of the Biome research area have a high capacity to hold water. Field moisture contents range to over 1000% dry weight. However, the extreme variability in bulk density and porosity makes expression of soil moisture content on the basis of volume, rather than weight, more useful. In terms of soil volume, *maximum* moisture content in the upper 15 cm of meadow soils averaged 47% during the summers of 1970 and 1971. The underlying mineral layers ranged between 55 and 60% by volume. In these soils the *minimum* moisture content in the upper 15 cm averaged 67% in 1970 and 65% by volume in 1971. During the summers of 1970–73 the soils in much of the nonpolygonal terrain and in the lower-lying areas of polygonized terrain remained almost completely water-saturated within approximately the 5-to 15-cm depth interval. On polygonized terrain, in the relatively warm and dry summer of 1972, only the centers of high-centered polygons had moisture contents of less than 65% by volume in the upper 10 cm of soil on 31 July.

In 1972, moisture tension was measured using tensiometers in soils along a moisture gradient in the polygonal terrain (Table 7-1). In the driest soils, on the top of a high-centered polygon and on a polygon rim, water potentials averaged over the 0- to 5-cm depth interval were never lower than −0.070 bar during the summer (Figure 7-5). Potentials at 0- to 5-, 5- to 10- and 10- to 15-cm depth intervals at a given location were similar, but with a tendency toward progressively higher potentials with depth. The low water potentials in the soil indicate that most of the water present is available for plant uptake. Variations with time were similar at all three depth intervals and within each microtopographic unit across the entire moisture gradient (Figure 7-5). Despite the general wetness,
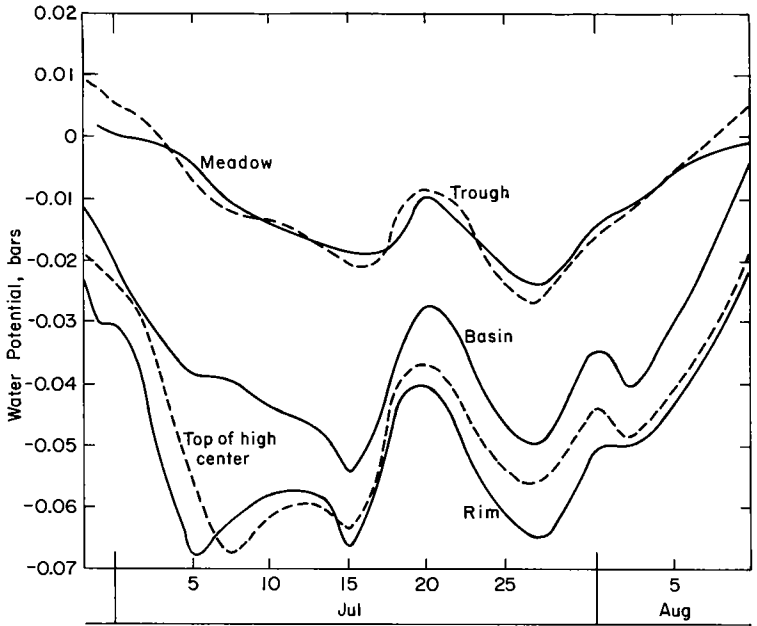
FIGURE 7-5. *Seasonal courses of soil water potential in the upper 5 cm of soils of different microtopographic units in 1972.*
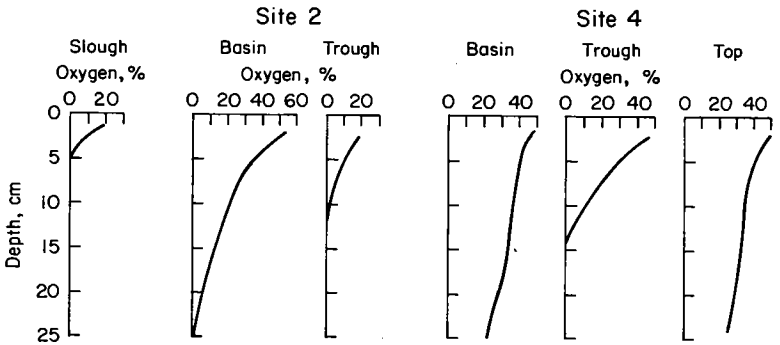
FIGURE 7-6. *Average oxygen saturation in soils of different microtopographic units in 1972. (Benoit, unpubl.)*

moisture regimes are sufficiently influenced by microtopography to result in differences in species composition and physiognomy of the aboveground plant community, and in the soil microflora and fauna.

Oxygen concentrations at 10 cm ranged from 40% saturation to 0%, with the highest values found in the tops of high-centered polygons and the lowest in the wet sloughs (Figure 7-6). As the soil thaws, the depth to fully anaerobic conditions follows the thaw front downward, and by mid-season oxygen saturation is zero at about 25 cm depth. Although the soil continues to thaw, the aerated layer in the wet meadow soil seldom exceeds 25 cm because oxygen flux is impeded by high bulk density and water saturation in the mineral horizons (Benoit, unpubl.).

Alternating organic and mineral layers in the soil can produce a very complicated pattern of air and water movement through the active layer (Figure 7-3). Histosols generally lack a continuous mineral layer and continue to drain freely as thaw progresses. These soils are unsaturated in the upper part, permitting air movement within the soil, except in wet summers. In contrast, the mineral layers of Inceptisols restrict drainage, and these soils often remain at or near saturation throughout the summer. Air movement is restricted, and reducing conditions prevail in and below the mineral layers.
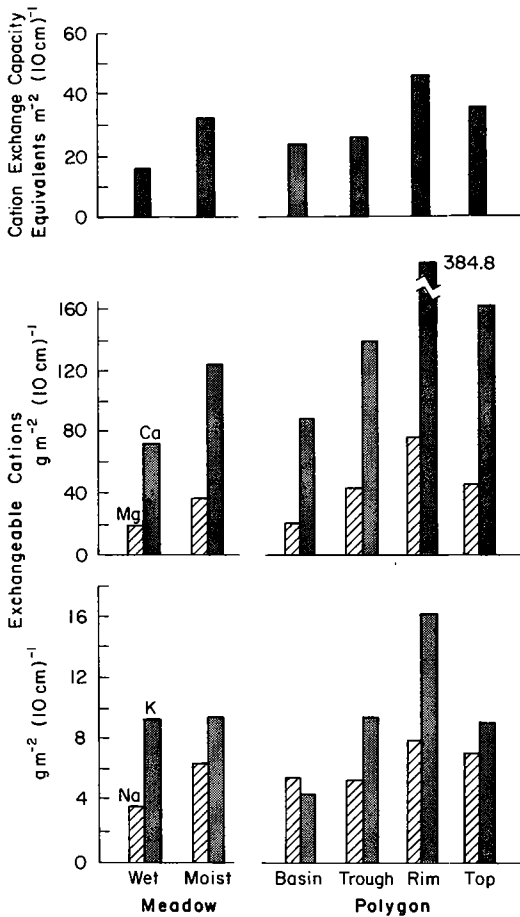
Cation Exchange Capacity and Acidity

The cation exchange capacity (CEC) of the soils is dominated by the organic fraction. Thus there is a strong correlation between CEC and organic carbon content. For example, within the upper 30 cm of meadow soils this relationship was:

$$CEC[meq(100 \text{ g})^{-1}] = 2.15 \, C_{org}(\%) + 15.54 \qquad r = 0.97, \, n = 86.$$

This equation indicates that the mineral clay fraction, which makes up an average of 27% by weight within the upper 30 cm of these soils, contributes 15 milliequivalents (meq) per 100 grams of soil to the CEC, while the organic fraction, which averages approximately 20% carbon, contributes 40 meq $(100 \text{ g})^{-1}$. These combine to give the average soil in the meadows a total CEC of 55 meq $(100 \text{ g})^{-1}$, which is well above that of most mineral soils.

In general, poorly decomposed fibric organic matter contains relatively few phenolic hydroxyl and carboxyl groups, and thus contributes comparatively little CEC to soil horizons in which it occurs. On the other hand, well-humified sapric organic matter generally contains many such groups, and in many of the soils may be the main source of the CEC.

Cation exchange capacities ranged widely among soils of the differ-

FIGURE 7-7. *Average quantities of exchangeable cations and cation exchange capacity in the upper 10 cm of the soils in 1972.*

ent microtopographic units. For example, average CEC within the upper 10 cm of soil in summer 1972 was approximately 50 meq $(100 \text{ g})^{-1}$ in wet meadows and 69 meq $(100 \text{ g})^{-1}$ in mesic meadows. In polygonized terrain the averages were 44, 70, 89 and 91 meq $(100 \text{ g})^{-1}$ in the troughs, rims, basins and tops of high-centered polygons, respectively.

Variations in CEC among the microtopographic units were different when measured on the basis of volume rather than weight of soil, because of variations in bulk density. For example, soils of polygon troughs had a CEC of approximately 27 meq $(100 \text{ cm})^{-3}$ in the upper 10 cm compared to 25 meq $(100 \text{ cm})^{-3}$ in the upper 10 cm of polygon basins (Figure 7-7), even though the CEC on a weight basis in the soil of the basins was more than double that of the troughs [89 versus 44 meq $(100 \text{ g})^{-1}$]. Thus, actual concentrations of nutrients in the soils of troughs were

higher than those of basins (Figure 7-7) because of the much higher bulk density of the trough soils.

Soil pH values from the different microtopographic units generally range from 5.1 to 5.7; thus these soils are moderately to strongly acid by agricultural standards. They are, however, less acid than those of peat bogs, which have pH values between 3.0 and 4.0 (Moore and Bellamy 1974). The high concentrations of H^+ ions in the soil tend to favor their adsorption by the cation exchange complex, and decrease the adsorption of metallic cations.

Soil acidity varies both spatially and temporally, is generally constant with depth, and shows some association between the more basic values and high plant production. Polygon troughs and the rims of low-centered polygons have relatively high soil pH values of 5.6 to 5.7, while the basins of low-centered polygons and the centers of high-centered polygons with peaty soils are the most acid sites, with soil pH values of 5.1 to 5.3. In studies of vehicle track disturbance the soil pH in the depressions where vegetative growth was abundant was 5.8, while in the control area it was 5.5 (Challinor and Gersper 1975). A drop in the mean soil pH in the mesic meadow from 5.4 to 5.1 between 1970 and 1971 was associated with a 20% drop in primary production (Dennis et al. 1978).


Major Cations

Over the range of microtopographic units from wet meadows to tops of high-centered polygons, the quantity of exchangeable cations per square meter in the upper 10 cm of the soil ranges from 3.7 to 7.9 g Na, 4.4 to 16.2 g K, 19.6 to 76.9 g Mg and 71.3 to 384.5 g Ca. The rims of low-centered polygons have the largest pools of all cations; however, potassium is equally abundant in the centers of high-centered polygons. Wet meadows are lowest in all cations except potassium, which is lowest in the basins of low-centered polygons. Mesic meadows are generally richer than wet meadows, and troughs are richer than basins in exchangeable cations.

Patterns of cation concentration in soil solution (Figure 7-8) differ sharply from those of exchangeable pools. Soil solutions used for the analysis of metallic cations were obtained using porous ceramic cups in situ and a mild suction of –0.75 bar. High cation concentrations in the soil solution of polygon basins and the tops of high-centered polygons occur with low plant production while low concentrations in the troughs occur with high plant production (Webber 1978). The properties of the soil solution fluctuate during the summer and range widely between years in response to thaw, precipitation, evapotranspiration, surface and subsurface flow, nutrient uptake by roots, and microbial activity.

TABLE 7-2 *Mean ($\bar{x}$) and Coefficient of Variation (C_v) for Cations (meq m^{-2}) in Soil Solution Extracted from the Upper 15 cm of Soil in Moist Meadow, 1970 (n = 60) and 1971 (n = 90)*

	1970		1971	
Cation	$\bar{x}$	C_v (%)	$\bar{x}$	C_v (%)
Calcium	48.2	17.0	59.4	13.6
Magnesium	40.9	12.2	58.4	16.7
Potassium	2.7	66.1	3.7	30.6
Sodium	62.8	11.1	79.7	6.3

The concentrations of soluble cations change markedly between years as well as throughout the season. Sampling in a mesic meadow site in 1970 and 1971 revealed changes in yearly averages up to 40% (Table 7-2). Averages of every nutrient were higher in 1971 than in 1970. The summer of 1971 was warmer and wetter than 1970. This may have produced an increase of mineral nutrients in solution due to increased mineralization of organic materials, or increased leaching of canopy and litter
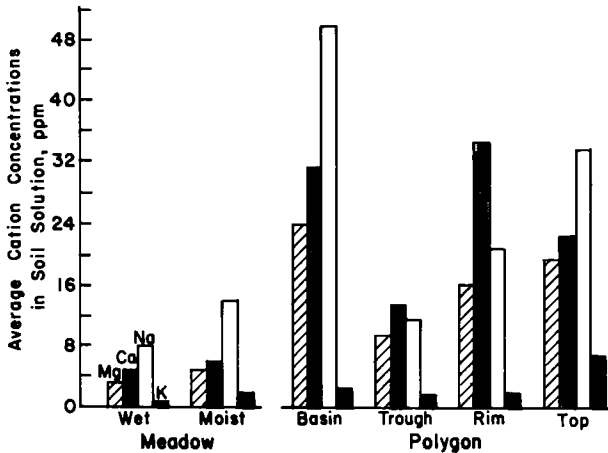
FIGURE 7-8. *Average concentrations of cations in solution extracted from the upper 10 cm of soils in 1972.*

as a result of more precipitation. Whenever soil solution was sampled immediately following precipitation, large increases in nutrient concentrations were observed, suggesting that leaching of aboveground plant materials may be a major factor in nutrient transport.

Of the major cations, only potassium occurs to a significant extent in a mineral form in soils. The clay mineral illite, which contains fixed potassium, is the dominant mineral in the clay fraction of the soils of the Barrow tundra (Douglas and Tedrow 1960). However, the bulk of the available potassium and almost all of the other metallic cations are bound on the exchange complex and are supplied from it to the soil solution.

Nitrogen and Phosphorus

The distribution of nitrogen and phosphorus is similar in that these elements are found mainly in the organic form in soil. The pools of nitrogen and phosphorus of the moist meadows were calculated for the upper 10 cm of the soil (Table 7-3), since this portion is relatively homogeneous and includes more than 75% of the live root biomass (Dennis et al. 1978) and microbial biomass (Chapter 8). A total of 432 g N m^{-2} was found in

TABLE 7-3 *Pools of Nitrogen and Phosphorus (g m^{-2} 10 cm^{-1}) in the Upper 10 cm of Soil in Moist Meadow*

	Nitrogen	Phosphorus
Living	**9**	**1.3**
Belowground plant parts	7	0.6
Microbial organisms		0.70
Bacteria (20 gdw)	2.3	0.64
Fungi (5.5 gdw)	0.1[1]	0.1[1]
Organic matter	**420**	**15.5**
Hydrolyzable N (6N HCl 15 hr)	336	
Readily hydrolyzable N (0.5N HCl 0.5 hr)	1.4	
Dissolved organic	0.2	0.0126
Inorganic matter	**3.0**	**7.8**
Resin-extractable P		0.0161
Dissolved inorganic	0.014	0.0006
NH_4^+	0.013	
NO_3^-	0.0006	
Total	**432**	**24.6**

[1]Nitrogen and phosphorus in fungi (Laursen 1975).

TABLE 7-4   *Exchangeable Ammonium*
Nitrogen of a Typical Per-
gelic Cryohemist in Moist .
Meadow, 1973

Depth (cm)	Bulk density (g cm^{-3})	Exchangeable ammonium	
		(meq 100 g^{-1})	(g m^{-2} cm^{-1})
0–5	0.191	1.006	0.269
5–10	0.656	0.350	0.321
10–15	1.043	0.424	0.620
15–20	0.479	0.480	0.322
20–25	0.600	0.753	0.634

Source: Flint and Gersper (1974).

the upper 10-cm section, with more than 95% bound in organic matter (Flint and Gersper 1974). The organic nitrogen can be divided into hydrolyzable and nonhydrolyzable fractions. The hydrolyzable fraction makes up 80% of the nitrogen in the soil organic matter, while the nonhydrolyzable fraction, which probably represents the most resistant core of the humus, makes up approximately 19.5%. Most of the remaining 0.5% is in the form of readily hydrolyzable nitrogen. This latter fraction is seasonally variable, indicating that it may be an integral part of the labile nitrogen in the system.

The nitrogen content of the living soil microorganisms is uncertain since separation of the organisms from the soil material is difficult. Fungal biomass and nitrogen content of the fungi were both determined (Laursen 1975), but bacterial biomass may exceed fungal biomass by an order of magnitude (Chapter 8), and no measurements exist of the nitrogen concentrations in the natural bacterial population.

The inorganic nitrogen in the soil is almost entirely in the form of ammonium ions bound on the cation exchange complex, and in equilibrium with the ammonium and other cations in the soil solution. The vertical distribution of exchangeable nitrogen affects its availability to plants and soil organisms. Although the concentration of ammonium on a weight basis is highest in the surface 5 cm (Table 7-4), the amount in the 10-cm rooting zone is only a little more than 25% of the total exchangeable pool in the active layer (Flint and Gersper 1974). Thus, a large fraction of the nitrogen present in exchangeable form is not physically accessible to most of the plants or microorganisms.

Soil solutions for nitrogen and phosphorus determinations were obtained from sample cores using pressure up to 9.4 bars (Barèl and Barsdate 1978). The soil solution contains dissolved and colloidal organic

nitrogen, ammonium, and nitrate, in approximately 10:1.0:0.1 ratios. Most of the organic nitrogen in solution is readily decomposed, but plant uptake is from the inorganic nitrogen in the soil solution, and diffusion processes act primarily within this pool. The average concentrations of ammonium and nitrate in the soil solution in 1973 were 145 and 6 ppb, respectively (Barèl and Barsdate, unpubl.).

The total amount of nitrogen in the soils of the drier microtopographic units is commonly greater than 500 g m^{-2} (10 cm)$^{-1}$, slightly more than in the moist meadow soils, but the amounts of exchangeable nitrogen are similar. The average nitrate concentration in the soil solution of the polygon rim was 5.9 ppm NO_3-N in 1973, almost three orders of magnitude higher than the nitrate concentration in the wet meadow. The ammonium concentration on the rim was 750 ppb, also higher than in the meadow. The ratios of ammonium to nitrate in the soil solution change from 10:1 in the moist meadow to 0.1:1 on the rims of low-centered polygons. Nitrate is also found in greater concentrations than ammonium in the centers of high-centered polygons with mineral soil, but ratios drop below 1 in the other, slightly moister high-centered polygons with peaty soil and in mesic meadows.

The total soil phosphorus in the upper 10 cm of the moist meadows is approximately 25 g m^{-2}, of which two-thirds is in organic form (Table 7-3). Dissolved organic phosphorus is not believed to be available to plant roots but it is apparently susceptible, like dissolved organic nitrogen, to rapid hydrolysis. The ratio of dissolved to total organic phosphorus is very low, 0.0008:1 (Barèl and Barsdate 1978), even when compared to that for organic nitrogen (0.002:1). The organic phosphorus contributed by soil microorganisms has not been determined, but calculations based on decomposer biomass and species composition indicate that the standing crop of decomposers ties up a far larger fraction of soil phosphorus than nitrogen, 3% vs 0.4%. Thus, fluctuations in microorganism populations may have a significant effect on the overall distribution of phosphorus.

The fraction of the inorganic phosphorus that is in equilibrium with the soil solution appears very small when measured by extraction onto an anion-exchange resin (Barèl and Barsdate 1978), and the concentration of inorganic phosphorus in the soil solution is correspondingly low, averaging 10 ppb in 1973. However, chemical fractionation of the inorganic phosphorus from the moist meadow soils indicated that a large fraction is extractable under reducing conditions (Chang and Jackson 1957). This fraction may contribute considerably more to the exchangeable and dissolved pools of phosphorus under anaerobic, reducing conditions such as exist in the soils of wet meadows and polygon troughs than is apparent in laboratory analyses performed under aerobic conditions (Khalid et al. 1977). Most of the available phosphorus is bound to iron or aluminum ions (Prentki 1976).

On the rims of low-centered polygons and the tops of high-centered polygons with mineral soil, total phosphorus in the surface horizon is somewhat more abundant than in the wet meadow soils, but a greater fraction of the total phosphorus is in an organic form, and inorganic phosphorus is less abundant. The inorganic phosphorus of the drier site is mainly NH_4-F soluble, and considered to be readily available to plants (Barèl and Barsdate 1978). Increased availability of phosphorus is also indicated by a higher average value of resin-extractable phosphorus (22.6 mg m^{-2}) in the drier soils. However, the amount of inorganic phosphorus in solution is lower than in the wet meadow. On the tops of high-centered polygons the phosphate in the soil solution drops from 8 to 4 ppb at the boundary between organic and mineral soil, 4 cm below the soil surface (Barèl and Barsdate 1978).

INPUTS AND OUTFLOWS
OF NITROGEN AND PHOSPHORUS

The major input of nitrogen to the soils of the coastal tundra at Barrow is through the fixation of atmospheric nitrogen by blue–green algae, either alone or in symbiotic relationships. The inorganic ions in precipitation are the major sources of phosphorus and also add to the pool of inorganic nitrogen. Inorganic forms of nitrogen move in the soil by diffusion, but phosphorus ions are relatively immobile. Losses of nitrogen and phosphorus, in both inorganic and dissolved or suspended organic forms, occur through surface and subsurface flow. Nitrogen can also be lost through reduction to gaseous forms, nitrogen oxides and nitrogen gas. Even though a large portion of the tundra surface is covered with lakes and small ponds, movement of nutrients between the terrestrial and aquatic subsystems seems to be restricted to the period of snowmelt, when there is a small net loss of nitrogen and phosphorus to the ponds (Prentki et al. 1980).

Nitrogen Fixation

Fixation supplies the bulk of the nitrogen input to the terrestrial system, although amounts entering by this pathway vary markedly between microtopographic units. Measured rates increase from 8 to 180 mg N m^{-2} yr^{-1} along a moisture gradient from dry polygon rims to wet meadows.
Blue–green algae are the most important agents of nitrogen fixation. These algae, primarily *Nostoc commune*, occur as free-living or moss-associated filaments, or symbiotically in lichens of several genera. Although *Peltigera aphthosa* is the most abundant nitrogen-fixing lichen,

Peltigera canina, Lobaria linita, Nephroma spp., *Solorina* spp., *Stereocaulon* spp. and other *Peltigera* spp. also occur in significant amounts. With ambient temperatures of about 15°C nitrogenase activity ranges from 4.5 μg N gdw^{-1} hr^{-1} in *Stereocaulon tomentosum* to 41.5 μg N gdw^{-1} hr^{-1} in *Nostoc commune.* Nitrogen fixation per unit of biomass in the *Peltigera* species is high (8.8 to 25.8 μg N gdw^{-1} hr^{-1} at 15°C), considering the large proportion of its biomass contributed by fungus and thus not directly involved in nitrogen fixation.

Heterotrophic bacteria also may contribute to nitrogen fixation (Chapter 8). *Azotobacter* was isolated from a mesic meadow, but the numbers were low, 10^2 to 10^3 cells (gdw soil)$^{-1}$, and nitrogen fixation within the soil was consistently less than 1 μg N m^{-2} hr^{-1}. If heterotrophic bacteria are indeed active fixers of nitrogen in the soils, their activity is very low compared with the free-living and symbiotic blue-green algae of lichens.

No significant nitrogen fixation was found to be associated with any higher plants (Alexander and Schell 1973). Alpine tundra soils in central Alaska, however, have a substantial input of nitrogen from vascular species, including *Dryas* spp., *Lupinus, Astragalus* and *Oxytropis* spp., which are abundant in the alpine sites and in the Prudhoe Bay region but absent or rare in the coastal tundra at Barrow.

Similar constellations of organisms have been found dominant in the nitrogen-fixation regimes of other tundra sites (Alexander 1974, 1975, Jordan et al. 1978). *Nostoc commune* is a cosmopolitan species that is important in nitrogen fixation in a variety of natural ecosystems (Fogg et al. 1973). In particular, the *Nostoc*-moss association, which has drawn much attention in circumpolar studies, also appears to be an important feature of the grassland ecosystem (Vlassak et al. 1973).

Biomass of Nitrogen-Fixing Organisms

Nitrogen fixation rates for any location on the tundra depend primarily on the distribution and biomass of the nitrogen-fixing organisms and secondarily on the various abiotic variables that influence nitrogenase activity within organisms. The distribution of nitrogen-fixing organisms is correlated with moisture regime and vegetation. *Nostoc commune* occurs in wet environments, and is especially abundant in wet, low-lying meadows, where it may occur as extensive mats floating over the moss layer. One low-lying area contained 19.5 g *Nostoc* m^{-2}, 10% of the standing crop (Williams et al. 1978). Additionally, *Nostoc* forms an epiphytic or intercellular association with various genera of mosses.

The nitrogen-fixing lichens, primarily *Peltigera aphthosa*, tend to occur at intermediate moisture levels such as the slopes between troughs

and rims, although *P. aphthosa, P. canina* and *Lobaria linita* are common in wet meadows, as well as in depressions between clumps of *Eriophorum vaginatum* in better-drained meadows (Williams et al. 1978). In the microtopographic units that are more favorable for lichens, such as the rims of low-centered polygons, a total lichen biomass as high as 180 g m^{-2} has been observed; however, only about 2 g m^{-2} of this is capable of nitrogen fixation. Thus the biomass of nitrogen-fixing organisms increases from dry to wet areas, with the major fraction made up of free-living or moss-associated *Nostoc*, which is confined to wet areas, and the remainder composed of nitrogen-fixing lichens, which are relatively more abundant in the mesic areas.

Environmental Controls on Nitrogen Fixation

In laboratory studies the principal environmental factors modifying rates of nitrogenase activity in nitrogen-fixing organisms are temperature, moisture, light and oxygen tension. Response of *Nostoc* and *Peltigera* to climatic factors, and to some inorganic nutrients, is described by Alexander et al. (1978). Diurnal temperature fluctuations of 10 °C for the rim of a low-centered polygon and 15 °C for a polygon trough were recorded in July 1972. Thus rather high temperatures can be attained in the immediate vicinity of the maximum algal biomass. Fluctuations in both light and temperature appeared to exert a strong influence on field rates of nitrogen fixation (Alexander et al. 1974).

The most critical environmental factor in determining the rate of nitrogen fixation is moisture. The response of *Peltigera* to moisture (Figure 7-9) shows that saturation of nitrogenase activity does not occur until the moisture content exceeds 250% of dry weight (Alexander et al. 1978), a response similar to that shown by other nitrogen-fixing lichens (Kallio 1973). Although no similar data exist for *Nostoc*, it shows no activity at all when dry, but rapidly resumes activity when moistened above 100% dry weight. The nitrogen-fixing organisms appear to be well adapted to handle periodic desiccation, and are able to make effective use of moisture whenever it is available.

On a season-long basis, highest inputs from nitrogen fixation occur on wet, mossy areas. In drier areas, seasonal nitrogenase activity is limited by available moisture (Alexander et al. 1974), and overall rates are somewhat lower during summers with low rainfall. Extremely wet areas devoid of moss cover also have very low rates of nitrogen fixation. In dry summers, such as 1972, there was a decline in fixation in moderately moist areas as the season progressed and soil moisture declined. The total seasonal input from nitrogen fixation, integrated over an area comprising a variety of microtopographic units, was lower in 1972 (85 mg N m^{-2})
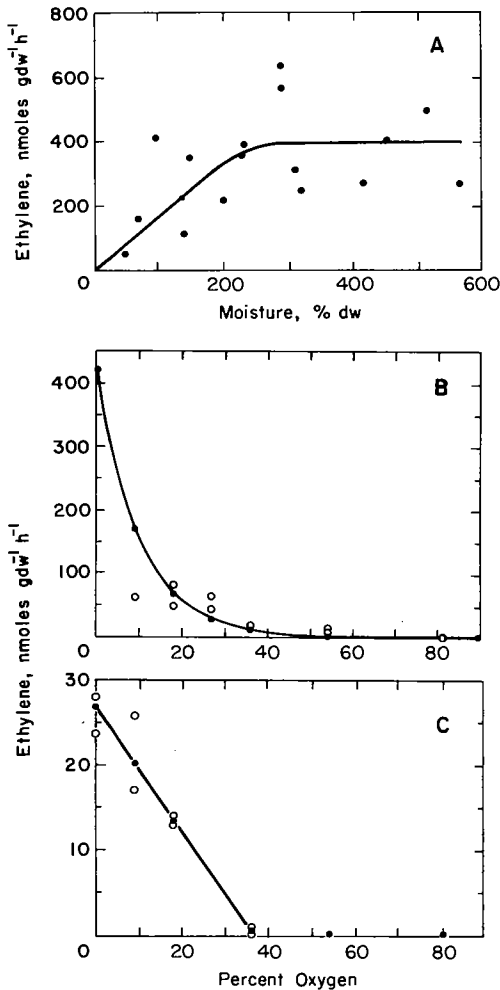
FIGURE 7-9. *Response of nitrogen fixation rates of* Peltigera aphthosa *to moisture (A) and oxygen concentration (B), and of* Nostoc commune *to oxygen concentration (C). (After Alexander et al. 1974 and Alexander 1978.)*

than in the wet summer of 1973 (119 mg N m^{-2}), the difference being due primarily to a higher rate of fixation in the relatively dry areas during the wetter year. These differences between years are considerably less than the differences between specific microtopographic units. For example, in the wetter summer seasonal input on the dry rim of a low-centered polygon was only 6.7 mg N m^{-2}, whereas in a nearby low, mossy area it was 150.4 mg N m^{-2}.

The response of *Nostoc commune* to oxygen tension is of special ecological interest, since the greatest nitrogenase activity of this organism occurs in wet, mossy areas, where these algae exist in extremely close association with mosses. In the water associated with the mosses, oxygen saturation may range from 5 to 24% over 24 hours (Alexander et al. 1974).

The strong inverse relationship between oxygen tension and nitrogenase activity (Figure 7-9) indicates the variation could be a very significant factor influencing rates of nitrogen fixation by algae associated with moss. Similar relationships have been described for a mire site in Sweden (Granhall and Selander 1973). The relationship between nitrogen fixation in lichens and oxygen is complex, particularly because there appears to be a strong interaction between light and oxygen requirements and a conflicting influence between the inhibitory effects of oxygen on the nitrogenase enzyme and the need for photosynthetically produced sources of energy.

A simple model, NFIXR, was developed that integrates the available laboratory measures and permits evaluation of their general applicability against field observations (Bunnell and Alexander, unpubl.). The model assumes that the influences of temperature, moisture and oxygen interact in a multiplicative fashion. Thus fixation is reduced as any single environmental control departs from the optimal range, even though other conditions may not be limiting. Seasonal courses of nitrogen fixation for specific genera can be predicted from measured environmental variables and compared with observed fixation rates (Figure 7-10).

Although actual magnitudes differ, the observed seasonal courses of nitrogen fixation in polygonal terrain at both the Biome research area and in a birch site at Kevo, Finland, are similar to those predicted by the model. Apparently, the measured relationships are broadly applicable to lichens and algae inhabiting a variety of sites. The inaccurate prediction of the magnitude of rates of fixation apparently is largely due to the difficulties in estimating biomass of the fixing organisms, particularly algae. Blue–green algae are relatively more important at Barrow than at Kevo, and the predictions for Barrow are therefore less accurate.

In light of the recent observation that non-heterocystous blue–green algae also contain the enzyme nitrogenase and are capable of nitrogen fixation under conditions of low oxygen (Kenyon et al. 1972, Stewart 1973), special interest centers on the ecology of these moss-associated algae. Present findings suggest that the majority of blue–green algal forms found in the moss layer may contribute to nitrogen fixation, and that estimates of nitrogen-fixing biomass based only on heterocystous algae may be greatly in error both in the wet, mossy layer and in soils.

There is no marked adaptation by the major nitrogen fixer, blue–green algae, to the arctic environment. The predominant nitrogen-fixing form, *Nostoc commune*, is found in the Antarctic and in all circumpolar tundra regions. Its temperature optimum is not greatly different from temperature optima for blue–green algae from temperate and tropical regions. Arctic lichens, however, appear to be rather well adapted. Nitrogenase activity of lichens recovers after freezing, with the rate of recovery depending on the length of time the lichens were kept frozen and the tem-
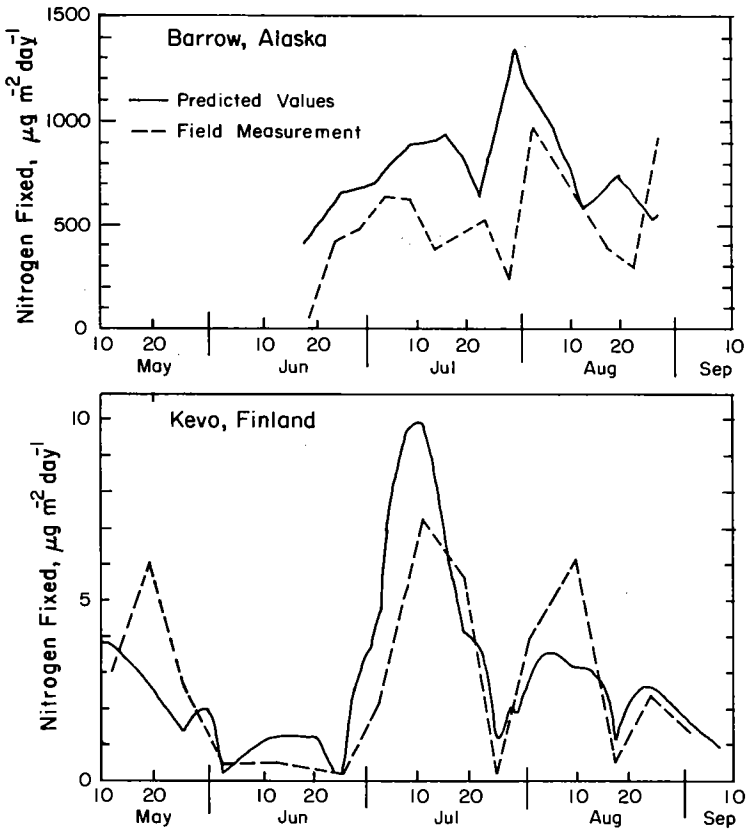
FIGURE 7-10. *Comparison of simulated and measured rates of nitrogen fixation at Barrow and at Kevo, Finland. (Bunnell and Alexander, unpubl.)*

perature at which recovery is taking place (Kallio and Alexander, unpubl., Kallio 1973). Rates of nitrogen fixation per unit of ground surface measured for arctic lichens are somewhat higher than those measured in other Biomes (Stewart 1969).

Inputs of Nitrogen and Phosphorus by Precipitation

Snowfall includes approximately 30% of the total nitrogen supplied by precipitation. Ammonium is the predominant form of nitrogen found in snowfall (Dugdale and Toetz 1961), although organic nitrogen has not been measured. The fraction of the inorganic nitrogen present as nitrate

in snowfall declined from almost 30% to less than 10% between early September and late October of 1960 (Dugdale and Toetz 1961). Nitrite concentrations in fresh snow are extremely low, with an upper limit of about 1 μg N liter^{-1}. Comparisons of these values with nitrogen distribution in snow columns in May indicate that ammonium may be converted to nitrate in the snowpack. The concentration of inorganic nitrogen in both samples was similar, approximately 80 μg liter^{-1}, but the concentration of nitrate in the spring sample was higher by 15 μg N liter^{-1}. Concentrations of all three inorganic forms of nitrogen are higher in rain than in snow. The total concentration of nitrogen in summer precipitation is 340 μg liter^{-1}, of which ammonium contributes 75% and organic nitrogen less than 20% (Prentki et al. 1980).

The yearly input of nitrogen by precipitation was calculated by Barsdate and Alexander (1975) as 23.4 mg m^{-2}. However, revised values of total snowfall (Chapter 2) and the inclusion of organic nitrogen indicate that this value should be raised to 30.5 mg m^{-2} yr^{-1}. The majority of this input occurs during the summer. Although the amount of nitrogen in precipitation is very small in comparison with the total nitrogen pool, most of this nitrogen enters the system in inorganic forms and supplies an amount equal to 1% of the inorganic pool in the upper 10 cm of the soil. The nitrate content of precipitation seems particularly large from this viewpoint, more than seven times greater than the nitrate pool in the soil.

Precipitation is the major external source of phosphorus for the soil of the coastal tundra at Barrow (Table 7-5). As with nitrogen, phosphorus concentrations are lower in snow than in summer precipitation, 4.0 vs 7.9 μg liter^{-1} (Prentki et al. 1980); slightly more than half of the total input occurs during the summer. The inorganic phosphorus added by precipitation is equal to 6% of the labile phosphorus pool and is actually larger than the amount of dissolved inorganic phosphorus. The input of phosphorus in precipitation thus may be important in supplementing the small amounts of available phosphorus in the soil as well as in counteracting long-term losses to runoff.

Loss of Nitrogen and Phosphorus in Runoff

The major pathway for nitrogen outflow from the coastal tundra at Barrow is in surface runoff during the brief period of snowmelt (Table 7-5). The portion of winter precipitation that runs off during this time varies from as low as 51% at the Biome pond site to 95% at Esatkuat Creek (Miller et al. 1980). To produce a generalized nitrogen and phosphorus budget for the Barrow area, an intermediate runoff value of 83% was selected which corresponds to the spring runoff at the Biome pond

TABLE 7-5. *Nitrogen, Phosphorus, and Water Budgets for the Coastal Tundra Land Surface*

|	Inputs			Exports			
	Summer	Winter	Annual	Spring	Summer	Annual	Net
Nitrogen (mg m^{-2})							
Precipitation or runoff							
Ammonium	16.3	6.8	23.1	1.0	0.8	1.8	21.3
Nitrate	1.6	1.9	3.5	0.3	0.1	0.4	3.1
Nitrite	0.1	0.0	0.1	t	0.0	t	0.1
Organic*	3.8	ND	3.8	31.4	3.2	34.6	−30.8
Denitrification	—	—	—	ND	3.4	3.4	−3.4
Total without fixation	21.8	8.7	30.5	32.7	7.5	40.2	−9.7
N-fixation	69.5	ND	69.5	—	—	—	69.5
Total	91.3	8.7	100.0	32.7	7.5	40.2	59.8
Phosphorus (mg m^{-2})							
Precipitation or runoff							
Inorganic	0.46	0.16	0.62	0.21	0.01	0.22	0.40
Organic*	0.04	0.27	0.31	2.01	0.05	2.06	−1.75
Total	0.50	0.43	0.93	2.22	0.06	2.28	−1.35
Water (liters m^{-2})							
Precipitation or runoff	64	106	170	88	3	91	79
Dead storage and evapotranspiration	—	—	—	18	61	79	−79

t indicates trace.
ND indicates no data.
*Includes suspended particulates which are predominantly organic in origin.
Note: Concentrations of the various forms of nitrogen and phosphorus in precipitation and runoff were taken from Dugdale and Toetz (1961), Kalff (1965), Barsdate and Alexander (1975), Prentki (1976) and Prentki et al. (1980). Each input or export was calculated as the product of the appropriate nitrogen or phosphorus concentration and the water volume indicated in the table.

site in 1972. For the average winter precipitation of 106 mm (Chapter 2), this yields 88 mm of spring runoff, which is similar to the 85-mm June average discharge for Nunavak Creek for the period 1972-76 (U.S. Geological Survey 1971-76). During snowmelt 32.7 mg N m^{-2} is lost, more than the amount gained annually from precipitation. However, most of the nitrogen in the runoff is in organic form, and only a small fraction of the inorganic nitrogen present in the snowpack is lost. The retention of inorganic nitrogen from the snowpack is remarkable, since meltwater concentrations early in the snowmelt period range as high as 214 μg N liter^{-1}, almost twice as high as found in the snowpack (Barsdate and Alexander 1975). However, ammonium and nitrate concentrations decline rapidly, and were below those in the snowpack by 18 June in 1973 (Figure 7-11).
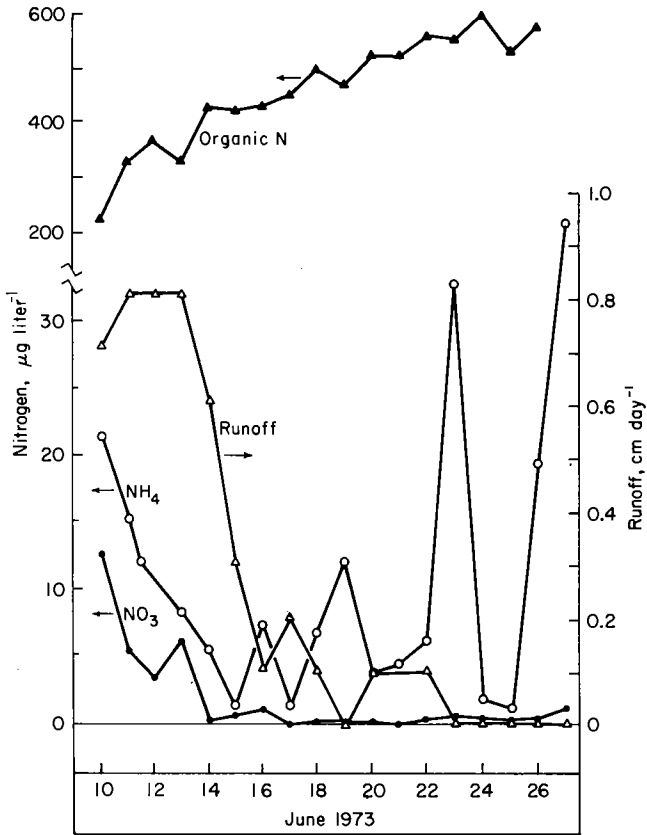
FIGURE 7-11. *Daily runoff and its concentration of NO₃-N, NH₄-N, and organic nitrogen during June 1973. (Data from Miller and Alexander, unpubl. and Barsdate and Alexander 1975.)*

The relatively low concentrations of nitrate at the start of snowmelt suggest that the high ammonium levels observed at this time are produced by leaching of animal excreta and plant material, rather than being the result of the concentration in the early meltwater of the ions already present in the snowpack. Leaching of biological material is also suggested by the high levels of organic nitrogen, since little or no organic matter is contributed by snowfall. During the summer, only an estimated 3 mm of the 64 mm of precipitation is lost in runoff. The loss to summer runoff is 7.5 mg N m^{-2}—approximately 20% of the loss during snowmelt, or one-third of the input from precipitation during the summer.

The dynamics of phosphorus loss by runoff are somewhat different from those described above for nitrogen (Table 7-5). A phosphorus loss

of 0.06 mg m^{-2} in summer runoff was calculated by the techniques used for nitrogen. Total phosphorus losses in runoff are 2.28 mg m^{-2} yr^{-1}, less than 0.01% of the total phosphorus in the upper 10 cm of soil. The phosphorus lost is mainly in the organic form, with particulate matter constituting almost 36% of the runoff loss (Prentki 1976). The high loss of phosphorus in particulate form is in contrast to nitrogen losses, where particulate organics make up less than 10% of the organic nitrogen fraction (Barsdate and Alexander 1975). The dissolved organic phosphorus lost in runoff constitutes approximately 10% of the pool of organic phosphorus in the soil solution. The major loss of phosphorus occurs during snowmelt, and the inorganic phosphorus lost during this period is greater than the input of inorganic phosphorus from snow.

The effects of precipitation and runoff on the nitrogen and phosphorus pools described above are integrated over a variety of microtopographic units. The effects of precipitation and, in particular, runoff differ among these units but quantitative assessment of this variation is difficult. In the absence of overland flow out of basins of low-centered polygons, these basins accumulate any nutrients that were present in the snowpack above them or on the inner sides of the polygon rims. Polygon troughs, on the other hand, are pathways for water flow, and may therefore be enriched in inorganic nitrogen and depleted of organic nitrogen and phosphorus by the meltwater. Drier areas retain a greater fraction of the water, and thus lose less of the inorganic nutrients associated with the rainfall or the dissolved or particulate organic matter that is assumed to be lost with the summer runoff.

Loss of Nitrogen in Gaseous Form

The soil nitrogen of the coastal tundra at Barrow is depleted by denitrification as well as by runoff losses. In anaerobic conditions such as are common in the soils, many bacteria can utilize nitrate rather than oxygen. This process can lead to denitrification, to the production of nitrogen oxide or nitrogen gas, to assimilation of nitrogen by the bacteria, or to the production of ammonia (Verstraete 1978). The population of facultative anaerobes in soils is large. Lindholm and Norrell (pers. comm.) measured the production of nitrite from nitrate in incubations at high nitrate levels. At 5 °C the microflora from a polygon trough showed average rates of nitrite production equivalent to the reduction of 430 μg N (g soil)$^{-1}$ day^{-1}. Samples from the tops of high-centered polygons showed a lower average rate, reducing 270 μg N (g soil)$^{-1}$ day^{-1}. The denitrifying bacteria isolated from the same soils were predominantly aerobic *Pseudomonas* spp. In a test of aerobically isolated bacteria from the upper 2 cm of a wet meadow soil, only 5 to 10% were capable of denitrification, although 68% were facultative anaerobes.

Direct measurements of denitrification in the field were made in midsummer. The rates of denitrification per gram of soil were six orders of magnitude lower than the rates of nitrate reduction measured *in vitro*. Although concentrations of nitrate were considerably lower in the field than in the laboratory incubations, 0.17 mg liter^{-1} vs 69 mg liter^{-1}, the extreme difference in rates suggests that most of the nitrate reduction that occurred in the laboratory tests did not result in denitrification. Focht (1978) discusses evidence that nitrate losses are significantly greater than denitrification when organic carbon is readily available and ammonium concentrations are low. The mean denitrification rate in the field results in a loss of 52 μg N m^{-2} day^{-1} from the surface of the wet meadow. The time course of denitrification in situ has not been established. However, the potential for nitrate reduction in soils from the wet meadow remained high for 65 days in 1972. If denitrification rates follow the same pattern, a net loss of 3.4 mg N m^{-2} yr^{-1} would occur, more than five times the amount of nitrate present in the upper 10 cm of the soil.

The rates of denitrification in other microtopographic units are generally lower than those in the wet meadow. No detectable denitrification occurred in field experiments on the top of a high-centered polygon. This is consistent with the low potential nitrate reduction rate in samples from similar microtopographic units. Nitrate concentrations in soils of tops of high-centered polygons are relatively high (2.5 ppm), indicating that the lack of denitrification activity here is not due to substrate limitation. In the mesic meadow, where nitrate concentrations were intermediate (0.33 ppm), denitrification rates in the field were 19 μg N$_2$ m^{-2} day^{-1}, only a third as high as those from the wetter area. Simultaneous addition of glucose and phosphate to these samples produced a more than four-fold increase, to 89 μg N$_2$ m^{-2} day^{-1}, over a 16-day incubation period. Munn (1973) also found a five-fold increase in apparent denitrification when a wet meadow was fertilized with urea.

Lack of denitrification in the soils from relatively dry polygon tops may be caused by the high aeration. Even though moisture contents remain high, the high pore volume and permeability of these soils may deter the development of anaerobic microenvironments. The strong response of denitrifying activity to glucose plus phosphate indicates that either energy or phosphorus is limiting under natural conditions in the mesic meadow. The stimulatory effect of easily decomposable organic matter on denitrification has been shown for temperate soils (Bremner and Shaw 1958). Lack of phosphorus can also inhibit the breakdown of organic matter (Chang 1940, Munevar and Wollum 1977), and this may occur in soils of the coastal tundra at Barrow. No analysis of the effect of pH on denitrification was made, but soil conditions are more acid than is optimal for denitrification in temperate soils (Bremner and Shaw 1958).

Overall, there is a net gain in the inorganic forms of both nitrogen

and phosphorus because of the high level of conservation of incoming nutrients. Losses to denitrification do not eliminate the positive balance for inorganic nitrogen. When organic and inorganic forms are considered jointly, there is a net loss of both nitrogen and phosphorus from the combined activity of the abiotic processes of precipitation and leaching. However, the transformation of atmospheric nitrogen by nitrogen-fixing organisms into a form available to the rest of the system leads to a gain in total system nitrogen. Apparently, a net phosphorus loss has occurred, as has been documented in bog tundras of Glenamoy and Moor House (Heal et al. 1975, Moore et al. 1975).

TRANSFORMATION AND TRANSPORT OF NITROGEN AND PHOSPHORUS WITHIN THE SOIL

The preceding discussion presented the major pathways by which the total amounts of nitrogen and phosphorus in soils are increased or decreased. Changes in the locations and forms of these nutrients within the soil are also important in determining the supply available for biotic processes. The following section describes the major transformations of nitrogen and phosphorus that occur in the soils of the coastal tundra at Barrow and their transport within the soils.

Mineralization and Immobilization

Since plants take up nitrogen and phosphorus in inorganic forms and return these nutrients to the soil bound in organic matter, the process of remineralization must be a major source of inorganic nitrogen and phosphorus in any soil close to a steady state. Mineralization, the release of inorganic nutrients from dead organic material by microbial action, occurs whenever the concentrations of these nutrients in the organic material are greater than those necessary to support the production of new microbial biomass. As summarized by Frissel and Van Veen (1978), the net mineralization rate is controlled by the microbial decomposition rate, the concentrations of organic nitrogen and phosphorus in the material being decomposed and in the microbial biomass being produced, and the efficiency of the microbial population, i.e. the ratio of microbial biomass produced to organic matter decomposed. For any given ratio of mineralization to decomposition, the rate of release or uptake by the microflora will be affected by all the factors that control decomposition rate (Chapter 9).

The nutrient levels in the organic matter in soils, expressed by the ratios of carbon to nitrogen (C:N) and carbon to organic phosphorus

TABLE 7-6   *Ratios of Total Carbon to Organic Phosphorus in Soils of Different Microtopographic Units and Associated Vegetation Types and States of Organic Matter Decomposition*

Micro-topographic unit	Vegetation type	Decomposition state, top horizon	C:P_o ratio				
			Depth in centimeters				Avg
			0–5	5–10	10–15	15–20	0–15
Meadow							
Wet	VI	Fibric	439	480	597	ND	517
Moist	IV	Fibric–hemic	448	531	681	1046	565
Basin	VI	Hemic–sapric	590	893	1072	1072	826
Trough	V	Fibric	505	346	352	322	385
Rim	III	Sapric	356	334	457	825	376
Top							
Low relief	I or II	Fibric	424	429	594	ND	472
High relief	I	Hemic	474	469	635	ND	507

ND indicates no data.

(C:P_o), appear unfavorable for mineralization. The C:N ratio is close to 20:1 throughout the range of undisturbed soils in the tundra at Barrow. In general, C:N ratios below 20:1 produce net mineralization of nitrogen and ratios greater than 20:1 lead to the microbial transformation of inorganic nitrogen into organic forms, or immobilization (Frissel and Van Veen 1978). The ratios of carbon to phosphorus are calculated from organic rather than total phosphorus since a significant fraction of the total phosphorus is present in inorganic form rather than in the microbial substrate. The lowest C:P_o ratios, which indicate the most favorable conditions for mineralization, are between 300 and 400:1 (Table 7-6). These values occur in the surface soils of all microtopographic units except rims and basins of low-centered polygons, and to depths of 10 to 15 cm in the polygon troughs. Ratios generally increase with depth, reaching values above 1000:1 in the 15- to 20-cm depth of rim soils and the 10- to 20-cm section of the basin soils. Cosgrove (1967) considered 0.2% (290:1) as the critical level of phosphorus in organic matter. Kaila (1949) found no net mineralization or immobilization of phosphorus from the decomposition of organic material with 0.3% P (194:1). It would appear that weak net immobilization of nitrogen and strong net immobilization of phosphorus should occur in the soils of the coastal tundra at Barrow.

However, mineralization must exceed immobilization in the soils since the net inputs are far too low to maintain the observed rates of plant production (Flint and Gersper 1974). Net mineralization could result from decreases in microbial efficiency as compared with values found in temperate soils. However, the tundra microflora appear rela-

tively efficient when evaluated *in vitro*. Net mineralization might also be due to the microbial utilization of specific fractions of the organic matter containing above-average nutrient concentrations. The additional possibility is that tundra microorganisms produce biomass with concentrations of organic nitrogen and phosphorus below those found in temperate organisms. Some indication of this is given by the nitrogen levels of fungal hyphae, which were around 2% (Laursen 1975), considerably lower than the average levels of 5 to 6% reported from temperate regions (Cochrane 1958).

The efficiency of fungi (grams of fungal biomass produced per gram substrate degraded) is generally higher than that of bacteria (Alexander 1961), and the efficiency of bacteria decreases markedly under anaerobic conditions (Hattori 1973). Therefore, the anaerobic conditions that exist in the soils (Figure 7-6) may enhance mineralization by excluding fungi and decreasing bacterial efficiency. Low temperatures may also decrease microbial efficiency, since the microflora includes species which continue respiration, and therefore substrate degradation, at temperatures below the minimum for growth. Thus the environmental conditions of the soils lead to decomposer populations with average efficiencies lower than those of the same species in better drained and warmer soils.

Field and laboratory studies of nitrogen transformations support these conclusions. Maximum rates of immobilization are expected to occur during the early growing season, since overwintering, standing dead vegetation and fresh litter with C:N ratios from 30:1 to 60:1 (Flanagan and Veum 1974) have been incorporated into the soil surface, moisture from melting snow is plentiful, and temperatures are rising. Early season rates of nitrogen immobilization have been calculated from changes in the pools of available nitrogen and microbial biomass (Table 7-7). All these methods are indirect but agreement between them is reasonably good. The maximum rate observed was consistently around 0.025 g N m^{-2} cm^{-1} day^{-1} for the three organic horizons studied: moss, hemic and buried sapric.

Net rates of nitrogen mineralization in the field have been estimated by observing changes in size of nitrogen pools (Flint and Gersper 1974), in particular the buried sapric horizon of a wet meadow soil at 14 to 20 cm depth. Just after thaw there was a sudden increase in exchangeable ammonium in the horizon, which was interpreted as net mineralization. The computed rate, corrected for diffusion, is 0.077 g N m^{-2} cm^{-1} day^{-1}. Conditions were probably somewhat anoxic during the measurement period. Moreover, the horizon was cold, about 1 °C after thaw, indicating that nitrogen mineralization can occur at significant rates at very low temperatures. Phytotron experiments under anaerobic conditions showed a maximum mineralization rate of 0.075 g N m^{-2} cm^{-1} day^{-1} for a hemic horizon at 6°C, while the buried sapric horizon at 2°C gives an

TABLE 7-7 *Rates of Nitrogen Immobilization (g N m^{-2} cm^{-1} day^{-1}) in Soils During 1973, Estimated by Different Methods*

		Method			
Horizon	Depth (cm)	Change in pool size of NH_3-N*	Change in bacterial biomass†	Change in readily hydrolyzable N*	Change in fungal biomass**
Moss	0–2	0.0034 (15-29 June)	0.026 (10-29 June)	0.0019 (4-16 Aug)	0.006 (18-28 June)
Surface hemic	2–8	0.027 (15-19 June)	0.012 (29 June-27 July)	0.0093 (22-26 July)	
Subsurface sapric	14–20	ND	ND	0.026 (21-26 July)	ND

*From Flint (unpubl.).
†From Benoit (unpubl.).
**From Laursen and Miller (unpubl.).

estimated rate of 0.049 g m^{-2} cm^{-1} day^{-1}. The mineralization rates obtained in the phytotron experiments are close to those obtained in the field, and both indicate that mineralization exceeds immobilization in the soil during periods of rising temperature.

The mineralization of phosphorus was not studied in the field. However, simulations of decomposition and of nitrogen and phosphorus release in the soils (Barkley et al. 1978) indicate that anaerobic conditions stimulate the net mineralization of phosphorus. Although anoxic conditions reduce the decomposition rate, the decrease in substrate breakdown and gross phosphorus release is outweighed by the decrease in microbial growth and phosphorus uptake per gram of organic matter decomposed. Decreased microbial efficiency due to low temperatures will also increase the release of phosphorus, as well as nitrogen, resulting from a given rate of organic matter decomposition. However, Chapin et al. (1978) have hypothesized that slow decomposition is the major limitation in the Barrow phosphorus cycle and that the mineralization rate is limited by the microbial recovery rate following periodic population crashes.

The ratio of mineralization to decomposition may be enhanced by selective degradation of high-nutrient substrates. The constancy of C:N ratios exhibited by the soils over a wide range of decomposition states and depths indicates that high-nitrogen material is not being selectively degraded. However, for phosphorus, $C:P_o$ ratios increase with depth, and high $C:P_o$ ratios are generally found in microtopographic units where organic material shows the most advanced states of decomposition (Table

7-6). Decomposition may operate first on the material highest in phosphorus, leading to the release of mineralized phosphorus. If the phosphorus associated with the more resistant organic matter is insufficient to support microbial growth, decomposition of the accumulated organic matter might lead to lowering of phosphorus availability. Thus, the factors that have allowed the gradual accumulation of organic material, such as the occurrence of permafrost and the burial of the sapric organic layer beneath a relatively impermeable mineral horizon, may in fact be acting to increase the availability of phosphorus in the system. Further work would be necessary to evaluate this hypothesis.

Nitrification

Although nitrification neither produces nor removes available nitrogen from the soil, it affects nitrogen transport and utilization. The products of nitrification, nitrate and some small amounts of nitrite, are not involved in exchange processes with cation exchange sites. These anions are therefore much more mobile than ammonium in a system with high cation exchange capacity and move vertically and horizontally in the soil by diffusion and are lost by leaching or surface runoff. Nitrate, the major product of nitrification, is also available to denitrifying bacteria as an oxygen substitute, and may be reduced to dinitrogen gas or nitrous oxide and lost. In agricultural systems, nitrate is the form of nitrogen most readily taken up by plants, but in the tundra, as in natural grasslands (Porter 1975), ammonium may be equally preferred.

Nitrifying bacteria are scarce in the soils of the coastal tundra at Barrow. Munn (1973) attempted to measure the nitrification potential in soil samples taken from the moist meadows throughout the 1972 summer season. He detected no conversion of ammonium to nitrate in soil samples under aerobic conditions perfused with an ammonium sulfate solution at 23 °C and pH 5.6 to 6.3. No nitrifying bacteria were found among 200 aerobic isolates from the 0- to 2-cm horizon of the wet meadow soils, tested at 15 °C (Benoit, unpubl.). However, Viani (unpubl.), using the most probable number technique, was able to detect low numbers of nitrifying organisms in several soils from polygonal terrain. Norrell and Anderson (unpubl.) measured nitrification in the laboratory and reported average rates of 1.5 and 0.75 μg N (g soil)$^{-1}$ day^{-1} at 10 °C for dry and wet sites, respectively. These may represent the maximum potential rates for these soils, although alternate incubation conditions were not tested. Norrell and Anderson further indicated that temperature was a major limiting factor, nitrification being only occasionally detectable at temperatures below 5 °C. Efforts to isolate psychrophilic nitrifiers from the soils were unsuccessful, with no activity detected after 6 months of incubation at 2 °C.

While it is impossible to obtain absolute rates of nitrification from fluctuations in the amount of nitrate in the soil, it is possible to estimate rates that are equal to or usually less than the true rate. However, differences in concentration due to field variability or sample treatment may lead to overestimation. Since nitrification is the principal source of nitrate, an increase in the nitrate pool gives a minimum value for nitrification, disregarding small spatial transfers. The net rate observed is usually lower than the actual production of nitrate because some nitrate is denitrified or taken up by plants. Therefore, the most rapid rate of increase is used for the estimate. With this approach, data for the wet meadows from different investigators indicated nitrification rates in the surface 10-cm soil layer of 0.024 and 0.0045 mg N m^{-2} cm^{-1} day^{-1} in 1971 and 1973, respectively (Barèl and Barsdate, unpubl.). Rates in the deeper soil are consistently higher, 0.045 and 0.012 mg N m^{-2} cm^{-1} day^{-1} in 1971 and 1973. Denitrification in the 7- to 15-cm soil layer accounted for a total of 0.05 mg N m^{-2} day^{-1} at a similar site in 1972. The uptake of nitrate by the plants can also be added into the rates of change in the nitrate pool to produce another estimate of nitrification rate. In 1971, an experiment using ^{15}N indicated plant uptake rates in the wet meadow of 1.7 mg NO$_3$-N m^{-2} cm^{-1} day^{-1} (Munn, unpubl.). The apparent nitrification rates in the drier areas are much higher than those in the meadows. In 1973, the estimated rates of nitrification on the rims of low-centered polygons were 1.5 and 2.0 mg N m^{-2} cm^{-1} day^{-1} in the surface 10 cm and the buried organic layer (Barèl and Barsdate, unpubl.). The 1973 data indicate turnover times for the nitrate pools ranging from 5 to 25 days, with rates on the rims of low-centered polygons lower than those in the meadow soil.

Transport of Nitrogen and Phosphorus

Vertical transport of ammonium and nitrate ions in the soil solution should occur by diffusion if a concentration gradient exists with depth. The extremely wet conditions and low bulk densities in most soils of the coastal tundra at Barrow are favorable for diffusion, although it is slowed by low temperatures. The patterns of ammonium and nitrate concentrations with depth (Figure 7-12) suggest that the diffusive movement of ammonium during the summer of 1973 was into the silt loam mineral layer (8 to 16 cm), from both above and below. The diffusion gradient for nitrate, on the other hand, led to its movement into the surface organic layer (0 to 8 cm) from the mineral and buried peat material. In late September, concentrations of both ammonium and nitrate were highest in the mineral layer, leading to diffusion outward from this layer.

Preliminary results using ^{15}N document that ammonium is trans-
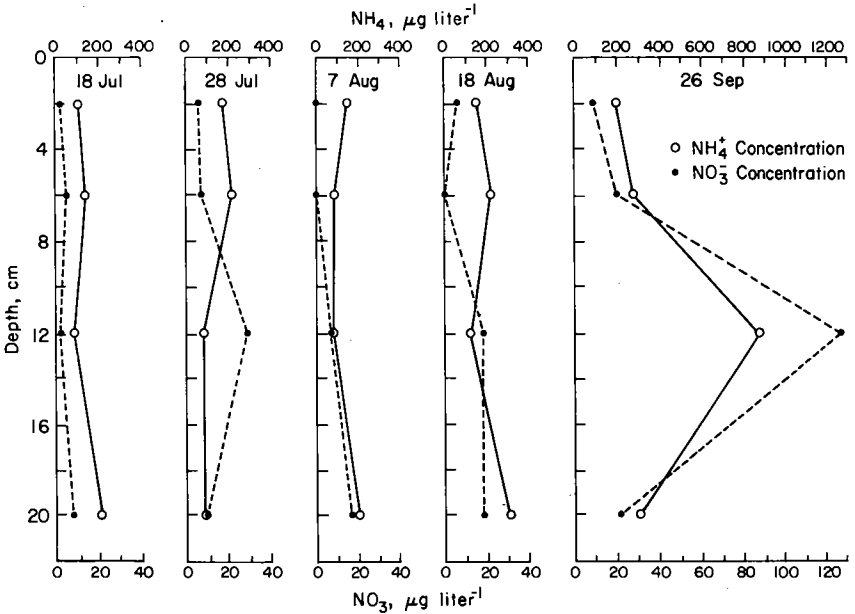
FIGURE 7-12. *Profiles of NH₄⁺ and NO₃⁻ concentrations in the soil solution from the moist meadow.*

ported from depths of 20 cm or more to the surface of a wet meadow soil during the growing season. In 1973 detectable transport began on about 20 July and continued into September. During this period the maximum net rate of flux from the well-decomposed organic layer into the mineral layer above it was about 0.049 g m⁻² day⁻¹. At this rate at least 2 g N m⁻² could be transferred from the subsoil to the rooting zone in a period of about 60 days. The mechanism of transport has not yet been verified. However, concentration profiles of exchangeable ammonium in the soil through the summer period indicate that a diffusion mechanism is operating along the soil exchange complex. This may be the primary mechanism of nitrogen transport, far exceeding the amounts that diffuse through the soil solution. Results also indicate that the amount of nitrogen transported by diffusion is strongly affected by soil temperature, thaw depth, and length of the thaw season.

No experimental studies have been conducted on phosphate diffusion in the soils of the coastal tundra at Barrow, but diffusion rates can be assumed to be generally low (Olsen et al. 1962) and added phosphorus fertilizer is strikingly immobile. Ten years after the last treatment, plots fertilized with phosphorus by Schultz (1964) still showed levels of labile and dissolved organic phosphorus that were 50 times as high as those of

adjacent control plots, suggesting lack of movement of phosphorus (Barèl and Barsdate 1978).

Other Effects

Considerable quantities of both nitrogen and phosphorus can be transferred directly to available pools in the soil during a lemming high. During these population peaks lemmings consume up to 40 g m^{-2} yr^{-1} of graminoid plant material, nearly 50% of the annual aboveground production, and most of the minerals in this are excreted. However, this effect on available pools of nitrogen and phosphorus may be relatively insignificant during population lows, when consumption may fall below 1 g m^{-2} yr^{-1} (Chapter 10). Nitrogen is mainly excreted in the urine and is immediately available to plants and microorganisms. Phosphorus is distributed between urine and feces (Barkley 1976). Leaching experiments using an analogue of the surface runoff showed over 90% removal of phosphorus from feces in 24 hours (Chapin et al. 1978). During a high year, lemming feces would release about 90 mg P m^{-2}.

The freeze–thaw effect, described by Saebø (1968) for *Sphagnum* peat, is another way nutrients may be transferred from unavailable to available pools. After freezing and thawing, peat samples showed concentrations of dissolved and dilute acid-soluble phosphorus several times higher than did the control samples. The solution concentration returned to control values after remaining thawed for 48 hours, but values for acid-soluble phosphorus remained somewhat above controls for the same time period (Saebø 1968). Patterns of dissolved and resin-exchangeable inorganic phosphorus in the soils of the coastal tundra at Barrow indicate that the same effect is occurring (Barèl and Barsdate 1978). A similar effect was observed in solution concentrations of ammonium and nitrate (Barèl and Barsdate, unpubl.) and in soluble carbohydrates in soils of other areas (Gupta 1967). These similarities, and the lack of any effect on calcium levels, indicate that the freeze–thaw mechanism may involve a physical disruption of the organic matrix. The mechanics of the effect, and its magnitude, are still unclear.

The mineral fraction of the soil contains a significant fraction of the total phosphorus pool in non-exchangeable form (Chapin et al. 1978). Chemical transformation of the mineral matrix in which the phosphorus is bound would allow the transfer of some phosphorus to the exchangeable pool. Although weathering rates are low in arctic conditions (Douglas and Tedrow 1960), this source of inorganic phosphorus may not be negligible under the low-phosphorus regime of the wet meadow soils.

SUMMARY

Organic matter, generally in a partially decomposed (hemic) state, dominates the soil profiles of the coastal tundra at Barrow, and constitutes the major pool of fixed carbon in the ecosystem. The bulk density of the highly organic soil is low, but increases with advancing decomposition. The soils remain very moist throughout most summers, have high cation exchange capacities, and are moderately acid, with the lower pH levels correlated with lower primary productivity.

Almost all the nitrogen in the soil is present in organic form, and a large fraction of this is associated with poorly decomposed material. A small and variable amount of labile organic N is also present. In wet meadows inorganic nitrogen is mainly in the form of ammonium, and more than half is found below the primary rooting zone. In the wet areas, nitrate concentrations in the soil solution are very low, but in the driest units, nitrate concentrations exceed those of ammonium. Most of the soil phosphorus is also in organic forms, and the concentrations of inorganic phosphorus in the soil solution are extremely low.

Nitrogen fixation by blue–green algae is the major input mechanism for nitrogen. These algae may be free-living forms, but in many cases are associated with mosses or occur symbiotically in lichens. The predominant algal and lichen forms involved in nitrogen fixation are *Nostoc commune* and *Peltigera aphthosa*, respectively, although several other lichen species are also active. The biomass of nitrogen-fixing organisms is highest in wet, mossy areas, and is extremely low in dry areas. In mesic sites, moisture is usually the major factor controlling the input of nitrogen, but oxygen concentration and temperature are also important. The low oxygen concentrations that occur in wet, mossy areas may enhance the rates of nitrogen fixation. A simulation model indicates that a simple multiplicative interaction between these factors may be involved, and that the control mechanisms for nitrogen fixation may be similar at other tundra sites.

Inorganic nitrogen and phosphorus enter the system through precipitation. The amounts added are small in comparison to the total pools of these elements, but substantial with respect to available inorganic pools. The major losses of nitrogen and phosphorus occur in runoff during snowmelt and are mainly of organic forms. The combination of precipitation and runoff yields a net loss of nitrogen and phosphorus. Some nitrogen is also lost by denitrification, but the rate is low compared to the potential for nitrate reduction that exists in the wetter microtopographic units. Nitrogen fixation is sufficient to lead to a net accumulation of soil nitrogen.

The ratios of carbon to nitrogen and organic phosphorus are suffi-

ciently high to suggest that weak nitrogen immobilization and strong phosphorus immobilization should be associated with decomposition. However, nitrogen mineralization has been shown to occur under cold, anaerobic conditions, perhaps because of low tissue nitrogen concentrations and low efficiency in the decomposer population. Phosphorus mineralization may respond to these same factors and be further facilitated by selective degradation of phosphorus-rich substrates.

Nitrifying bacteria are not common in the soil, and their activities are inhibited by low temperatures. Changes in the amount of nitrate present indicate low rates of nitrification in the wet meadows, and higher rates in drier microtopographic units.

Several internal pathways may aid in replenishing inorganic nutrients in the rooting zone. Studies with ^{15}N indicate a substantial flux of N from the subsoil to the surface. Freezing and rethawing of the soil liberate some available nitrogen and phosphorus. Weathering of minerals containing non-exchangeable phosphorus may also occur. In a high lemming year, lemming excreta contribute substantial amounts of available nitrogen and phosphorus.