Chapter 19

ARCTIC ECOSYSTEMS OF NORTH AMERICA

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INTRODUCTION

The North American Arctic constitutes about 20% of the land mass of the continent, extending from 55°N along the coast of Hudson Bay at Cape Henrietta Maria and Churchill (58°30′N) to Alert, Ellesmere Island, Canada (82°30′N) and Peary Land, Greenland (83°N). Tundras extend from about 61°W longitude in Newfoundland to 168°W in Alaska. The greatest area of arctic tundra and polar desert is in Canada, with smaller amounts in Greenland and Alaska (Table 1). Over this vast area there is considerable variation in climate, topography, ice cover, soils, size and diversity of floras and faunas, and complexity of plant and animal communities and ecosystems. The objectives of this chapter are to discuss this physical and biological diversity and the adaptations of animals and plants that occupy these landscapes.

As used here, the "Arctic" refers to those lands beyond the climatic limit of the boreal forest and tree line. Small pockets of trees extend beyond the tree line in protected habitats (river terraces, south-facing slopes) while uplands are dominated by tundra vegetation. Throughout these lands, the soils are permanently frozen (permafrost) with only the upper portion (typically 20–60 cm, but 100–200+ cm along rivers and elsewhere on well-drained soils), the active layer, thawing each summer. These cold soils greatly influence the distribution of animals, from soil invertebrates to small mammals, and plants.

The North American Arctic has been divided into various units or zones. Polunin (1951) divided the Arctic into High, Mid, and Low; Porsild (1951) divided the Arctic into ice desert, rock desert, and tundra; and Young (1971) into four zones, all based upon floristics. Tedrow (1977) divided the Arctic into tundra, subpolar–desert, and polar–desert zones based upon soils.

In this presentation the Arctic is divided into the Low Arctic and High Arctic (Fig. 19.1) based upon both physical and biological characteristics (Table 19.2). These broad zones each have a mosaic of

TABLE 19.1

Land areas ($\times 10^6$ km^2) within the North American and Greenland Arctic and their subdivision into Low Arctic, High Arctic and ice

Geographic Region	Alaska	Canada	Greenland
Low Arctic	0.356	0.880	0.116
High Arctic	0.004	1.456	0.156
Ice Caps	–	0.144	1.794
Total area	0.360	2.480	2.066

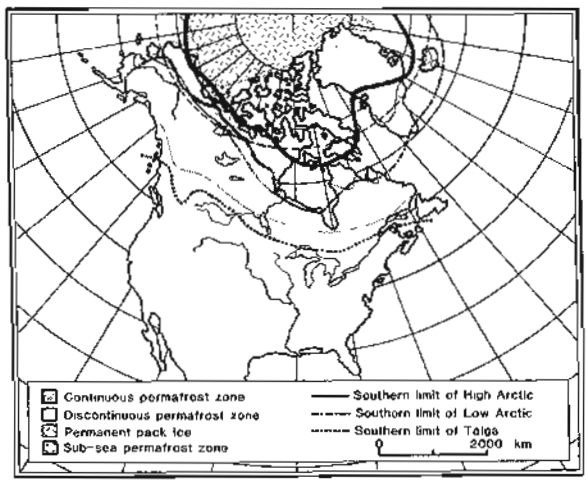

Fig. 19.1. Patterns of discontinuous and continuous permafrost zones, sub-sea permafrost, and the southern limits of Taiga, Low Arctic, and High Arctic in North America.

TABLE 19.2

Physical and biological characteristics of the Low and High Arctic within North America

Characteristics	Low Arctic	High Arctic
Environmental		
Length of growing season (mo)	3–4	1.5–2.5
Mean July temperature (°C)	4 to 12	3 to 8
Mean January temperature (°C)	−20 to −28	−25 to −35
Mean annual temperature (°C)	−1 to −13	−7 to −19
Accumulated degree-days above °C	600–1400	150–600
Mean precipitation June–August (mm)	35–150	25–100
Mean annual precipitation (mm)	120–800	60–425
Active layer depth (cm)		
fine-textured soils	20–60	20–60
coarse-textured soils	100–200+	70–150
soil temperature at −10 cm (°C)	5–12	2–8
Soil pH	mostly 5–6.5	mostly 6–8
Organic layer (cm)		
lowlands	50–300+	5–50
uplands	2–20	0–1
Biological		
Total plant cover (%)		
tundra	80–100	80–100
polar semidesert	20–80	20–80
polar desert	1–5	1–5
Plant height (cm)		
shrubs	10–500	5–200
forbs	5–30	2–10
graminoids	10–50	5–20
Shoot:root ratios (alive)		
shrubs	1:1	1:1
forbs	1:1–2	1:0.5–1
graminoids	1:3–5	1:2–3
Vascular plant flora (species number)	700	380
Bryophytes	Abundant including *Sphagnum* species	Abundant, but few *Sphagnum* species
Lichens	fruticose and foliose growth forms common	foliose and crustose growth forms common
Plant growth forms	woody and graminoid are common	cushion, rosette and graminoid common
Large land mammals (species number)	4–8	2–4
Large ungulates	*Rangifer tarandus* *Ovibos moschatus*, *Alces alces*	*Rangifer t. pearyi* *Ovibos moschatus*
Small land mammals (species number)	15–30	5–12
Nesting birds (species number)	30–60	2–20
Fishes, freshwater (species number)	10–22	1–9

subtypes, as will be shown in the various sections to follow. Tundras predominate in the Low Arctic, whereas the High Arctic is characterized by polar semideserts and polar deserts with tundras accounting for only 5–8%, and only 1–2% in the Queen Elizabeth Islands of Canada (northern islands only). "Tundra" is a generic term that includes vegetation types that range from tall shrubs (2–5 m high) to dwarf-shrub heath (5–20 cm high), and graminoids and mosses (10–50 cm high). Tundra landscapes are the best known and typically have a total plant cover of 80–100%, including lichens and mosses (cryptogams), in most habitats.

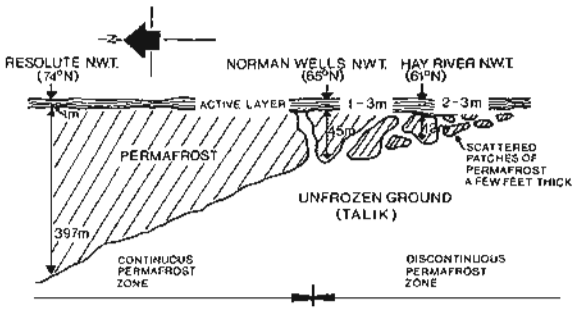

Fig. 19.2. Idealized cross-section of discontinuous to continuous permafrost. The active layer decreases northward as the permafrost thickens. Adapted from Brown (1970).

PERMAFROST AND PATTERNED GROUND

Of the various surface features in arctic environments, some of the most conspicuous involve patterned ground. In the Arctic these features are related to permafrost, ground that remains frozen two or more years. The most massive ones result from large masses of ground ice, the palsas and pingos, and influence plant distribution, animal activity, and soil development. These different features will be described, their origins briefly discussed, and their general pattern on the landscape illustrated.

Permafrost

The term "permafrost" was coined by Muller (1947) to refer to permanently frozen ground. It is used to describe soil, rock, and sea-floor conditions where the temperature remains below 0°C for two or more years. Ice is generally an important component, although water under pressure or containing salts may be unfrozen especially in permafrost warmer than −5°C. Dry permafrost also occurs in coarse gravels and frozen rock where there is little ice. Ice content by volume of permafrost thus ranges from only 1–5% to about 100% in massive ice wedges and ice lenses. The amount of ice decreases with depth, so that most massive ice is within 50–60 cm of the surface (Williams and Smith, 1989).

Permafrost underlies about 26% of the world's land (Washburn, 1980) and it extends into the sea as well (Fig. 19.1). In both Canada and Russia, permafrost (continuous and discontinuous) underlies about one-half of the total lands. It also occurs at high elevation in mountains, especially the Tibetan Plateau and at more northern latitudes. Permafrost regions can be divided into two components, the discontinuous zone to the south within the northern boreal forest (taiga) and the continuous zone throughout the Arctic. The boundary between continuous and discontinuous permafrost generally occurs where the mean annual air temperature is −8.3°C and the mean annual ground temperature is −5°C just below the surface, with no annual variation in temperature (Brown, 1970; Crawford and Johnston, 1971). General characteristics of these permafrost zones are illustrated in Fig. 19.2.

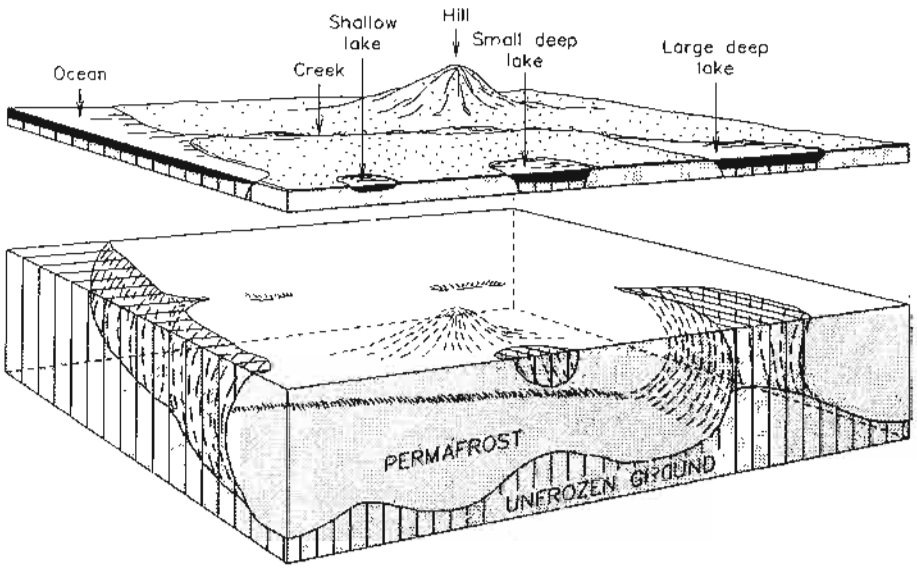

Fig. 19.3. Schematic diagram of the effect of water bodies of different size on permafrost. Adapted from Gold and Lachenbruch (1973).

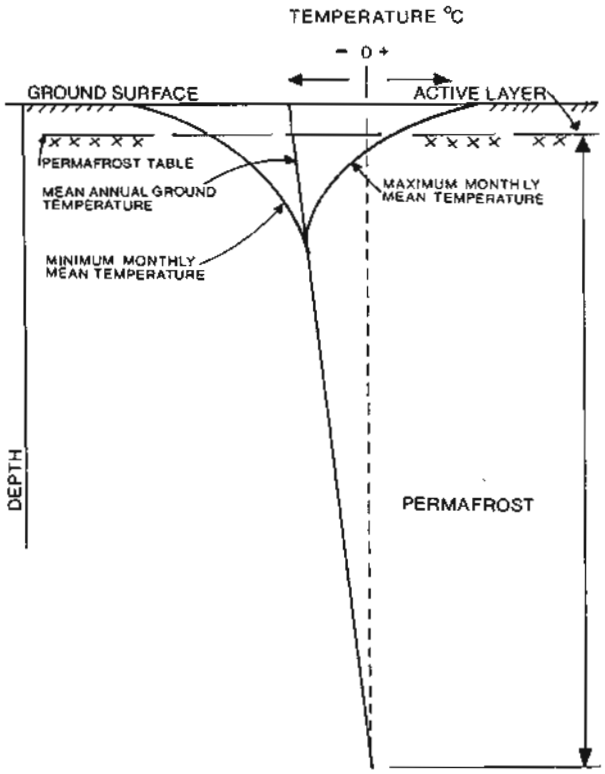

Fig. 19.4. A generalized diagram of ground temperature regime in permafrost terrain. Adapted from Brown (1970)

Bodies of water have an interesting effect on the pattern of permafrost (Fig. 19.3). Under large deep lakes, large rivers, and in deeper ocean waters there is no permafrost. Smaller, deep lakes have a thawed basin underneath with permafrost below, but the bottom of the permafrost is somewhat elevated. Shallow lakes (<1.5 m) freeze to the bottom in winter and have no unfrozen layer below the lake, but the permafrost may also be a bit thinner. In general the bottom of the permafrost rises under hills and is somewhat depressed under valleys (Fig. 19.3).

The depth of permafrost depends upon mean annual temperature, thermal conductivity of soil and rock, proximity to the sea, and topographic position. Permafrost thickness is about 320 m at Barrow, Alaska (Brewer, 1958), 500–600 m in the Mackenzie Delta region of Canada (Mackay, 1979), 395 m at Resolute and 450 m at Winter Harbour, Melville Island, Canada (Brown, 1970). On the Truelove Lowland, Devon Island, Canada permafrost thickness varies from 210–250 m near the coast to 385–590 m within the lowland, and 515–660 m on the plateau at 306 m elevation (Judge, 1977).

Analyses of geothermal gradients at Barrow indicate that, near the top of the permafrost (0.2–2.0 m), mean annual temperature has risen 2°C or more in the last several decades to a century (Lachenbruch and Marshall, 1986). At Resolute, N.W.T., it is estimated to have taken about 10,000 yr for the ground to have frozen to a depth of 395 m (Brown and Johnston, 1964).

In summer, arctic soils thaw to a depth of 20–60

Fig. 19.5. Typical soil boils in the High Arctic of Cornwallis Island, N.W.T.

Fig. 19.6. Pingo near Tuktoyaktuk, N.W.T. Note the raised-center polygons with *Carex aquatilis* in troughs in the foreground and prostrate heath species on the polygons.

cm where peats and fine-textured soils occur, but 50–300 cm in sands and gravels. This is called the active layer and it occurs above the permafrost table (Figs. 19.2, 19.4). Depth of thaw depends upon plant cover, soil texture and the amount of ice that forms each year as the active layer refreezes. In many locations, 60–80% of the annual thaw occurs within 3–4 wk of snowmelt (Bliss and Wein, 1971; Haag and Bliss, 1974; Addison, 1977; Muc, 1977), slowing later in the season as net radiation is reduced and more heat is required to melt the colder soils at increased depth. Soil temperature oscillates on an annual basis to a depth of 6–15 m (Fig. 19.4), depending upon the mean annual temperature and thermal conductivity of the soil and rock. Soils refreeze from the permafrost table upward and from the surface downward as air temperature and net radiation drop in August and September. This often results in unfrozen material, under pressure at depth, being squeezed to the surface forming "soil boils" (Fig. 19.5).

Permafrost is often ice-rich and takes the form of ice wedges and ice lenses. Where massive ice occurs, elevated landforms often break the monotony of a subdued landscape. Surface features associated with permafrost in the discontinuous zone are less massive and numerous. Permafrost "islands" in peatlands and peat bogs often result in low mounds called *palsas*. These mounds often grow in size as water moves to these ice cores and freezes, resulting in low ridges and peat plateaus (Brown, 1970; Zoltai and Tarnocai, 1971).

The most spectacular features within the continuous permafrost zone are pingos (Fig. 19.6). *Pingo* is the Inuit word for conical hill, and as is now known these are ice-cored hills covered with soil and vegetation. There are about 1450 pingos in the Mackenzie Delta region. They also occur on Banks Island, Canada, northern Greenland and Alaska, Russia and the Qinghai-Tibet Plateau in China (Mackay, 1979). The tops of many pingos have relatively warm and dry soils compared with the surrounding landscape, and they may serve as homes for arctic ground squirrels and arctic foxes. Pingos as ice-cored hills can grow in one of two ways. If water moves downslope from a distant source it is a hydraulic-system pingo or the 'Greenland Type' (Mackay, 1979); the older term was an 'open-system pingo' (Müller, 1959). This process is typical for Alaskan pingos (Holmes et al., 1968). The second type is the hydrostatic-system pingo or 'Mackenzie Delta Type' (Mackay, 1979); the older term was a 'closed-system pingo'. These typically develop in partially drained lakes when water moves under hydrostatic pressure as local perma-

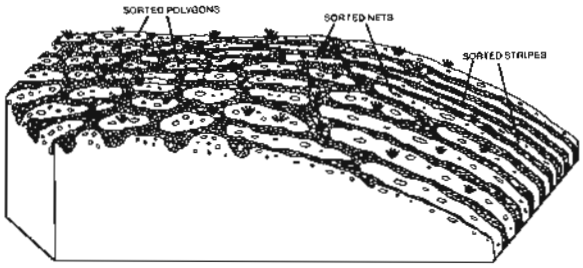

Fig. 19.7. The pattern of sorted polygons on level land with sorted stripes on slopes. After Sharpe (1938).

frost develops in a previously unfrozen large lake bed, a "window" in the regional permafrost. As permafrost aggrades, water under pressure moves to the developing ice mass where it may freeze as segregated ice and also form a sub-pingo water lens. This second method of pingo building is believed to be most important (Mackay, 1979), based upon the artesian flow of water following drilling into the top of a pingo (Mackay, 1978). In 1977 the top of the pingo subsided 60 cm to a height below its position in 1971. Based upon surveying 14 pingos on the Tuktoyaktuk Peninsula, N.W.T., Mackay (1981) found that the fastest pingo growth averaged 35 cm yr^{-1} for a four-year period. There are also collapsed or fossil pingos in this region (French, 1976) I shall return to pingos when I discuss the pattern of plant communities in the Mackenzie Delta region.

Ice-rich permafrost presents a difficult challenge for northern community and industrial development. Unless the ground is kept frozen, ice melts, the ground slumps, and thermokarst topography forms, with resultant shifts in roads, railroads, and buildings (Brown, 1970; Klein, 1970; Bliss and Peterson, 1975: Bliss and Klein, 1981).

Patterned ground

Patterned ground is a collective term for circles, polygons, nets including earth hummocks, steps and stone stripes. The classification of patterned ground and reviews of suggested origins and their occurence are presented by Washburn (1956, 1973, 1980). While not restricted to permafrost regions, they reach their best development and largest size there. In the Arctic, circles, polygons, and stripes may be 10–25 cm across each mesh or unit, ranging more commonly to meshes 5–10 m and a few 50–100 m in diameter. Features of smaller size are more often found in alpine environments with circles, stripes and polygons 1–3 m in size. In both arctic and alpine environments circles, nets, and polygons occur on level areas to slopes of only 1–2°. Elongated polygons and circles may occur on slopes 2–7° with steps and stripes on slopes >7° (Fig. 19.7). Patterned-ground features may be nonsorted (lacking a border of stones) or sorted (having a stone border). While many of these features are active today, others are inactive and can be recognized by the presence of plants, including lichens and mosses, across the old soil surfaces and lichens on the exposed surfaces of rocks. The following describes and illustrates the various forms of patterned ground and shows how these features influence plant distribution.

Circles

Sorted (Fig. 19.8a) and nonsorted (Fig. 19.8b) circles have a mesh that is circular, often with plants on their margin: they may occur singly, but more commonly in groups. The mineral soils are generally silts and clays and they may have a thin

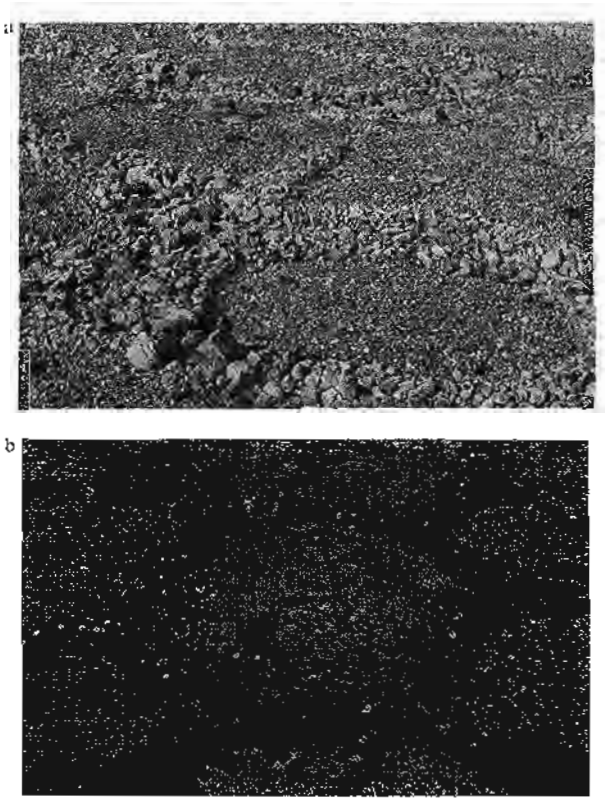

Fig. 19.8. Sorted circles (a) and nonsorted circles (b) from Cornwallis and Melville Islands respectively. Note the abundance of plants surrounding the nonsorted circles.

Fig. 19.9. Polygons resulting from desiccating cracks on King Christian Island, N.W.T.

layer of small stones across the surface. Organic soils develop on the borders where plants help stabilize them, compared with raw soils in the center that have churned upward and from the center outward (Washburn, 1989). These active soils inhibit plant establishment. Small sorted circles (20–50 cm) have small stones and large sorted circles (0.5–3 m) have larger stones on their borders. Surface soils frequently contain desiccation–cracked nonsorted polygons (Washburn. 1980). With time and soil stability, cyanobacteria, lichens, mosses, and vascular plants may completely cover the soil surface, resulting in less distinguishable patterns. In sharp contrast are newly formed nonsorted circles ("soil boils") that are totally devoid of plants.

Polygons

Of the various forms of patterned ground, these are some of the most interesting because of their varying size and influence on plants and animals. On many landscapes in the High Arctic, polygons 10–30 cm in diameter predominate, often well covered with plants. These polygons result from desiccation-cracking in these relatively dry summer environments (Fig. 19.9). Larger nonsorted polygons are common in the barren landscapes of the polar deserts.

Nonsorted large polygons (>1 m) are common in arctic lowlands (Fig. 19.10). These polygons have an ice wedge coincident with their border, and the border is raised or depressed with respect to the polygon center, depending upon whether the ice wedge is growing or progressively melting each year (Washburn, 1973). Within wetlands, ice-wedged polygons have either raised or depressed centers; the latter melt each summer forming small ponds that contain algae, zooplankton, and often fairy shrimp. Some raised-center polygons contain an ice core (French, 1976; Jankovska and Bliss, 1977) in addition to ice wedges on their border. In the High Arctic nonsorted polygons often occur as very large features in coarse sands and gravels.

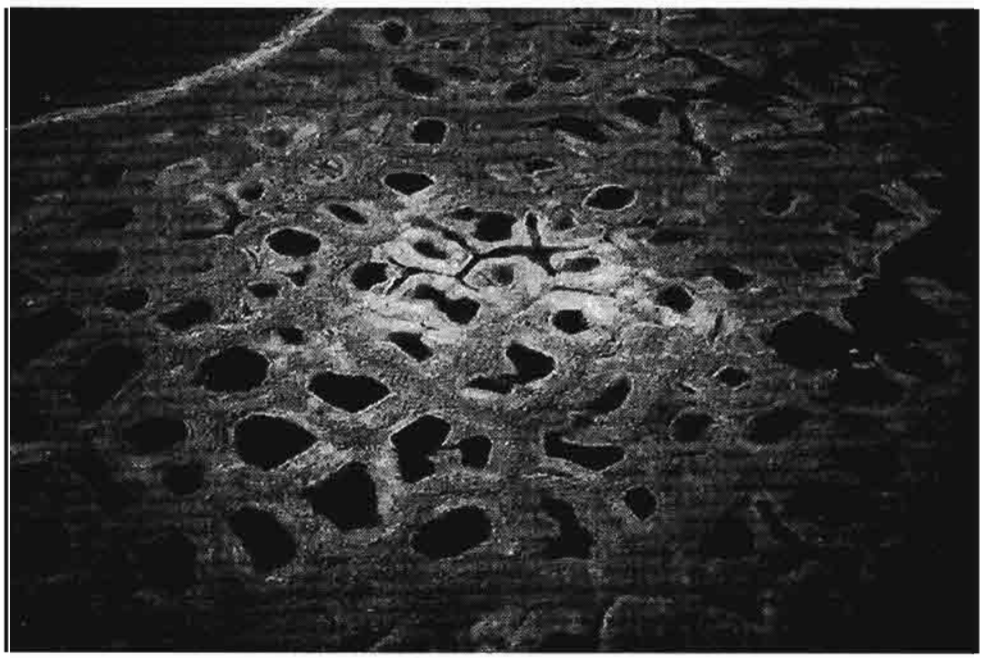

Fig. 19.10. Depressed-center polygons on the coastal plain, northern Alaska. *Salix* spp. and graminoids dominate the raised rims.

Fig. 19.11. Soil hummocks on a gentle slope, northern Banks Island, N.W.T.

Troughs that are 10–20 cm deep accumulate more snow and may contain snow-loving plants such as arctic heather (*Cassiope tetragona*), and these troughs also provide more shelter for lemmings. In numerous areas, winter activity of lemmings is much greater in the troughs of high-center polygons where there is deeper snow and more insulation from the low temperatures near the snow surface.

Earth hummocks

Earth hummocks 20–50 cm and less frequently 1–3 m in diameter occur throughout the Arctic (Tarnocai and Zoltai, 1978). They occur from level areas to gentle slopes (3–10°). In all sites observed by the writer, earth hummocks are plant-covered with considerable amounts of organic matter incorporated in the soils (Fig. 19.11). Carbon dating of 25 earth hummocks gave a preponderance of dates from 5000 to 3000 yr BP. Climate change around 4500 yr BP that resulted in intense soil churning (cryoturbation) is believed to have been causal in their development (Zoltai et al., 1978). Stones are a minor component of the fine-textured soils of earth hummocks.

Steps and stripes

These are features restricted to slopes, usually 5–20°. They occur in arctic environments where soils move downslope along the water-lubricated permafrost table. The steps with their vegetated risers and less vegetated, more wind-exposed treads, provide contrasts in both microenvironments and in plant species (Fig. 19.12). There may be downslope movement of the riser, burying organic matter beneath the tread. Large steps occur in alpine sites in Alaska and Canada, and in the Canadian High Arctic. These risers may have shrubs 20–50 cm in height growing at their base where snow covers them in winter.

Stone stripes both active and inactive are common in the Arctic (Fig. 19.13). These may be sorted or nonsorted, vegetated or essentially without plant cover. As with polygons, finer textured soils occupy the stripe centers.

Origins of patterned ground

Patterned ground is of polygenic origin, for similar kinds of features can result from different processes, and they occur in different environments (Washburn, 1956, 1973). Although numerous hypotheses have been proposed to explain the origin of the different patterns there is no general consensus. A few general processes have been accepted, and these are discussed below. The pressures generated by freezing water are exerted in all directions, but they are expressed in upward move-

Fig. 19.12. Solifluction steps on slopes with *Betula* and *Salix* at the base of each riser, central Alaska.

ment of soils and stones as "frost heaving" and as the horizontal movement of soil and stones termed "frost thrusting" (Washburn, 1973, 1980). The lateral movement of stones within fine-textured soils occur by often-repeated freezing and thawing (multigelation). Silts and clays hold more water than the coarse material. Upon freezing the fines expand more and contract more with thawing than the coarse material. With repeated freezing cycles the coarse materials are pushed outward leaving the fines in the center. Frost heaving and frost thrusting occur in both alpine and arctic environments, where they are important processes in the development of sorted circles, sorted polygons, and stone stripes (Washburn, 1956, 1980).

Fig. 19.13. Stripe patterns on gentle slopes, northern Cornwallis Island, N.W.T. Note the abundant mosses, herbs, and dwarf-shrubs in mesotopographic sites of stable soils.

Desiccation-cracking is probably the major factor in the formation of nonsorted polygons <1 m in diameter in both arctic and alpine environments (Washburn, 1980). Small nonsorted polygons in northern Greenland (Tedrow, 1970) and Ellesmere Island, Canada (Smith, 1961) have been ascribed to desiccation-cracking. Air-drying may dominate in the formation of the smaller (< 50 cm) ones and freeze-drying with water moving to the colder surfaces at depth (permafrost table) in the larger ones. The formation of polygons with the drying of muds in small ponds and pools is also a common phenomenon in temperate regions.

Needle-ice formation in moist surface soils is common when there are cold nights and moderately warm soils, resulting in steep temperature gradients. This affects the upper 1–3 cm of soil, often lifting soil and small stones on top of the ice–soil platforms. Small-scale soil churning effectively prevents most flowering plants from becoming established where needle-ice frequency is high.

Ice-wedge polygons (nonsorted) are initiated as ice veins which crack with the thermal contraction of permafrost in autumn and early winter. Melting snow and surface water in spring enter the cracks,

Fig. 19.14. Ice rings at the base of soil hummocks, Ellef Ringnes Island, N.W.T. *Alopecurus alpinus* and mosses dominate the hummocks.

and the ice vein develops into an ice wedge with an annual growth rate of only a few millimeters (Washburn, 1973). Ice wedges currently form in landscapes where the mean annual temperature is −6 to −8°C or lower (Péwé, 1966). As ice wedges grow in width and depth, soils are pushed higher on the flanks forming a raised rim on the polygons.

In uplands in the High Arctic, many areas have nonsorted polygons without massive ice wedges at their periphery. Instead there are often ice-rich lenses of permafrost at the margins and intersections of the polygons. Frost cracks within the vegetated margins fill with water during snowmelt and the limited summer rains. This water enriches the ice veins and the ice-rich permafrost table below (Price et al., 1974). In early summer, pure ice rings frequently occur at the base of small earth hummocks, the result of melting snow (Fig. 19.14). As this ice melts with the development of the active layer, water is drawn to the cold surface of the permafrost table, enriching its ice content.

Cryostatic pressures produced in fall, with the downward freezing from the surface and upward freezing from the permafrost table, entrap fluid soils which may rise to the surface forming soil hummocks and nonsorted circles (Zoltai et al., 1978). More recent field and laboratory studies (Mackay, 1980) have shown that soils within earth hummocks move with a cell type of circulation, resulting from radially inward and upward movement of saturated soil and not cryostatic pressure freeze-back.

Earth hummocks are an important phenomenon where silt and clay soils predominate in the High Arctic. Earth hummocks are also a common feature where shallow soils are underlain by rocks. These hummocks are typical in the transition zone from beach ridge slopes to sedge-moss meadows. Their origin appears to relate to desiccation cracks and inter-hummock erosion rather than to cryostatic pressures, for they contain little mineral soil. As stated by Williams and Smith (1989), the diversity of hummocks indicates different processes in their formation.

The downslope movement of saturated soil and stones has been termed solifluction. In the Arctic where slow movement is over the permafrost table the preferred term is gelifluction. These rates of movement average 1–5 cm yr^{-1} (Washburn, 1973, p. 179), and result in gelifluction lobes and benches. Terraces or steps are believed to develop from circles, polygons, and earth hummocks on slopes (Washburn, 1973). For a more detailed account of patterned ground, rates of soil move-

ment, and the relation of vegetation in Greenland, see Raup (1969, 1971).

The International Conferences on Permafrost (1966, 1973, 1978, 1983) have resulted in publication of many papers on the origin of permafrost and its extent, chemistry and physics, ecology of natural and disturbed terrain, and engineering and mining problems in permafrost terrain. Various aspects related to patterned ground will appear elsewhere as general landscapes, plant and animal communities are discussed.

SOILS

Soils in arctic environments, as elsewhere in the world, are a product of climate, parent material, topography, soil organisms and plants, that act through time (Jenny, 1941, 1980). Arctic soils are generally less well developed than in temperate regions because of the cold climate, limited growing season, surface instability, often reduced plant cover, and their young age (<12,000 yr) in much of the region. The presence of ice-cemented permafrost and the nearness of the frost table to the surface physically limit the thickness of the soil profile. In spite of these limitations, many of the same soil-forming processes occur in these cold environments as occur in forested lands to the south. Soil, as a distinct body in nature consisting of a dynamic system of interacting components, was first recognized by the Russian scientist, Dokuchaev, toward the end of the 19th century. He provided the first genetic classification of world soils that recognized tundra as a zonal soil for the arctic regions (Afanasiev, 1927). The Russian naturalist Gorodkov (1939) was the first to develop pedogenic concepts for the Arctic, and recognized the processes of podzolization and gleization and the presence of an additional zone, the polar desert. Major summaries of arctic soils have been presented by Rieger (1974, 1983) and Tedrow (1977).

General soil characteristics

Soils are composed of four components: mineral matter, organic matter, water, and air. The combination of soil texture (percent sand, silts, and clay) and percent organic matter are important in determining the water holding capacity and the general nutrient status of most soils. The topographic position of a soil (upland, well-drained site or lowland, poorly-drained site) plays a key role in the degree of weathering and leaching within a soil profile and the kinds of plants that the soil will support (see landscape profiles pp. 564–567). Soil water content is a product of climate, soil texture, percent, organic matter, and topographic position. Soils composed of silt and clay may contain 10–20% water (by weight) at field capacity (maximum amount of water held against gravity), whereas a sandy soil may hold only 2–5% water, and peats 200–400% water, expressed on the dry weight of the material soil. The amount of water that plants can extract from a soil depends upon the rooting pattern of the species (depth and volume of soil occupied), upon the solute concentration of the cell sap of the plant, and upon the degree of stomatal control that the species can exercise over water loss. More details of this will be given below (pp. 621–639).

Two important features of arctic soils are the presence of permafrost and the churning of soils in certain sites (cryoturbation) with their resultant patterned-ground features. Ice-cemented permafrost prevents the vertical drainage of water unless the active layer is thick (80–150 cm) and there is a dry permafrost of low ice content. A shallow active layer or thaw layer (20–50 cm), resting on permafrost with fine-textured or organic soils in areas of low relief, results in saturated or waterlogged conditions. This characterizes the coastal plain in Alaska and the Yukon, but is less common in eastern Canada (mainland) and in the arctic islands, where soils that are well-drained, 2–3 wk after snowmelt, occupy large areas.

The churning of soils and the development of patterned ground greatly influence soil development. Needle-ice formation, especially in spring and fall, keeps surface soils loose and friable and often kills small plants by lifting them out of the soil. Mechanical weathering by frost action is a major factor in soil development.

The short growing season and low air and soil temperatures result in soil conditions sub-optimal for chemical and biological processes. Consequently, chemical decomposition of minerals and organic matter, the release of nutrients, and the synthesis of new minerals from weathering progress very slowly. The limited amount of plant growth and slow decomposition rates add to the general condition of low nutrient availability within these soils of cold environments (Everett et al., 1981). As with other aspects of soils, the

development of horizons is generally less pronounced in arctic environments for the reasons given above.

In wetlands, deep peats may develop, especially in the Low Arctic. These soils have an organic matter content >20%. In many well-drained arctic soils, however, the organic horizon is <1 cm thick and is often lacking. The mineral soils of uplands generally contain an A or E horizon with B and C horizons below.

Soil-forming processes

Early in the development of arctic soil science, it was believed that processes of soil formation were quite different from those in temperate regions. This has given way to the realization that the same soil-forming processes occur in the Arctic as in temperate regions, but often at greatly reduced rates (Tedrow, 1977; Ugolini, 1986).

Podzolization, the process so common in soils of coniferous and deciduous forests, is weakly developed in the Low Arctic. This process is favored by an acid lichen-heath plant community, and where acid parent material predominates. Organic acids, including fulvic acid, act as proton donors and as chelating agents with the mobilization and transport of iron (Fe) and aluminum (Al) into the B horizon. This results in the development of a weakly leached E horizon, a dark humus-iron-rich horizon (Bhs), and a sesquioxide-enriched horizon (Bs) (Ugolini, 1986). Arctic Podzol soils are limited in extent in northern Alaska, but Ugolini et al. (1982) have demonstrated by soil-solution studies (lysimetry) that they are presently developing.

Brunification is based upon the concept of bonding the iron, clay, and humus within the upper mineral soil. The formation of stable clay-iron-humus complexes near the surface prevents the migration of organo-metal complexes that occurs in podzolization (Ugolini, 1986). Plants that produce a mull type of humus, organic material incorporated with mineral matter, and parent material rich in iron and clay are necessary for brunification. This process typically occurs where parent material is derived from igneous rocks but can occur on carbonate materials, provided decarbonation occurs (Duchaufour, 1982). The Arctic Brown soils of northern Alaska (Tedrow and Hill, 1955; Tedrow, 1977) and of the Canadian High Arctic (Walker and Peters, 1977) are more commonly found where lichen-*Dryas* rather than lichen-heath communities predominate. Brown and Tedrow (1964) and Bockheim (1979) have shown that the Arctic Brown soils of northern Alaska and on Baffin and Cornwallis Islands in Canada did not have illuviated iron in their A-B-C profiles as would be expected under the process of podzolization.

Melanization is a soil-forming process associated with soils developed from carbonates or volcanic ash where substrates are high in silicates, and where the vegetation is usually herbaceous including *Dryas*. If production of soluble organic acids and carbon dioxide is maintained by the plants, calcite is dissolved from the surface and insoluble silicate residue accumulates (Duchaufour, 1982). Plant communities, dominated by *Dryas*, dry-site grasses and sedges, legume species, and dwarf willow shrubs, often develop a dark A horizon, but not as thick or dark as in temperate grasslands (Ugolini, 1986). Rendzina soils with a mollic horizon have been reported from the Brooks Range (Ugolini and Tedrow, 1963), from the coastal plain in Alaska on pingos and high-center polygons developed from sediments of the thaw-lake cycle (Everett and Parkinson, 1977), and from the Hudson Bay area (Payette and Morisset, 1974).

Gleization is a very important soil-forming process in poorly-drained soils of slopes and level uplands. These soils, with little free drainage, lack an illuviated horizon leached of iron, aluminum and organic matter (spodic horizon), but are characterized by a dull-colored or mottled B horizon (cambric horizon), often dull gray in color (Rieger, 1983). Organic acids released in decomposition and secreted by organisms bring iron into solution as ferrous iron. Most organic matter is in the O horizon, which can result in development of an umbric, mollic, or histic epipedon in the A horizon (Rieger, 1983). Vegetation is often dominated by cotton-grass (*Eriophorum*) tussock tundra with abundant heath shrubs, or by wetland sedges and grasses. These soils have been called Tundra or Meadow soils (Tedrow, 1977). Soils with a cambric horizon have been described from northern Alaska by Tedrow and Cantlon (1958) and Tedrow (1977) and from the High Arctic by Everett (1968) and Walker and Peters (1977).

The process of **paludification** occurs commonly along the shores of lakes, ponds, depressed-center polygons and in uplands that are constantly wet. Peat accumulation results from the abundant growth of sedges and mosses. Mineral matter is

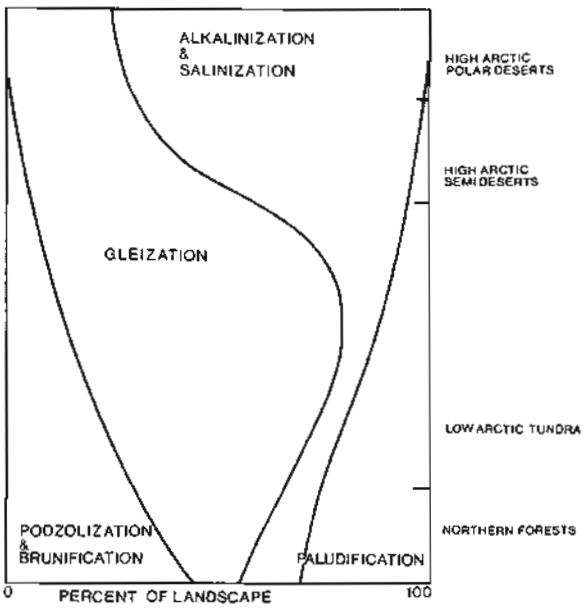

Fig. 19.15. Distribution of soil-forming processes over the landscape from the taiga to the polar deserts of North America.

generally a minor component, and the soils are usually acid (pH 4.5 to 6.0). Depending upon the degree of decomposition, the organic horizon may be fibric (little decomposition) or sopric (highly decomposed). These Histosols (Bog or Half-bog soils) are typical of the coastal plain of northern Alaska and the Yukon Territory and throughout mainland Northwest Territories, but are less common in the Canadian Arctic Archipelago, especially in the northern islands. This results from reduced plant growth and the relatively short time since deglaciation for peats to accumulate.

The process of **calcification** is common in the polar deserts of the High Arctic where limestones and dolomites predominate but also where eolian carbonaceous material is deposited. Calcium carbonate often precipitates on the underside of stones and under soil clasts. In the Polar Desert soils there is essentially no plant cover, and consequently there is little if any incorporated organic matter and only limited horizon development. These alkaline, Polar Desert soils are widely distributed in the High Arctic (Tedrow, 1968; Everett, 1968; Walker and Peters, 1977; Bliss et al., 1984). Figure 19.15 depicts these general changes in the magnitude of soil-forming processes resulting in genetic soils, in going from boreal forests to polar deserts.

Soil classification

One of the most confusing aspects of soil science is the lack of a uniform classification system. Several systems have been used in Russia, others in Western Europe, two major ones in the United States, another one in Canada (Rieger, 1983), and one developed by FAO-UNESCO (1974). In this section I shall discuss the USDA Soil Taxonomy (Soil Survey Staff, 1975) and the Canadian System of Soil Classification (1978) (Tables 19.3, 19.4). The Canadian system is similar to that of the USDA, except that it recognizes a soil order for soils underlain by permafrost, the Cryosolic Order. Rieger (1983) has discussed the classification of arctic soils in relation to the USDA and Tedrow (1977) systems.

John Tedrow and his associates have worked throughout arctic Alaska, Canada, and Greenland as well as in Antarctica. They devised a classification system, expanded by Tedrow (1977, pp. 272–274), that is based upon a genetic scheme in which the transfer of matter and energy is central. Although Tedrow (1977, p. 141) recognized three geographic soil zones (tundra, subpolar desert, and polar desert), I have chosen to present the system in a pattern similar to that of arctic vegetation (Low Arctic, High Arctic–polar semidesert, polar desert). Each region contains Great Soil Orders (Table 19.3) divided into genetic groups (subgroups) (Table 19.4).

Low arctic soils. Windy, exposed ridge tops often have limited plant cover with Arctic Regosol soils (Pergelic Cryothents). Well-drained sites including ridge tops, edges of escarpments, stabilized

TABLE 19.3

Comparison of Great Soil Orders for three classification systems of arctic soils

Arctic System (Tedrow, 1977)	USDA System (Soil Survey Staff, 1975)	Canadian System (Can. Soil Survey Comm., 1978)
Polar Desert soil	Entisol	Cryosol
Regosol	Entisol	Regosol
Rendzina	Mollisol	Chernozemic, Cryosol
Podzol	Spodosol, Inceptisol	Podzol, Brunisol
Arctic Brown	Inceptisol, Entisol, Mollisol	Cryosol, Brunisol
Tundra soil	Inceptisol	Gleysol
Bog soil	Histosol	Fibrisol

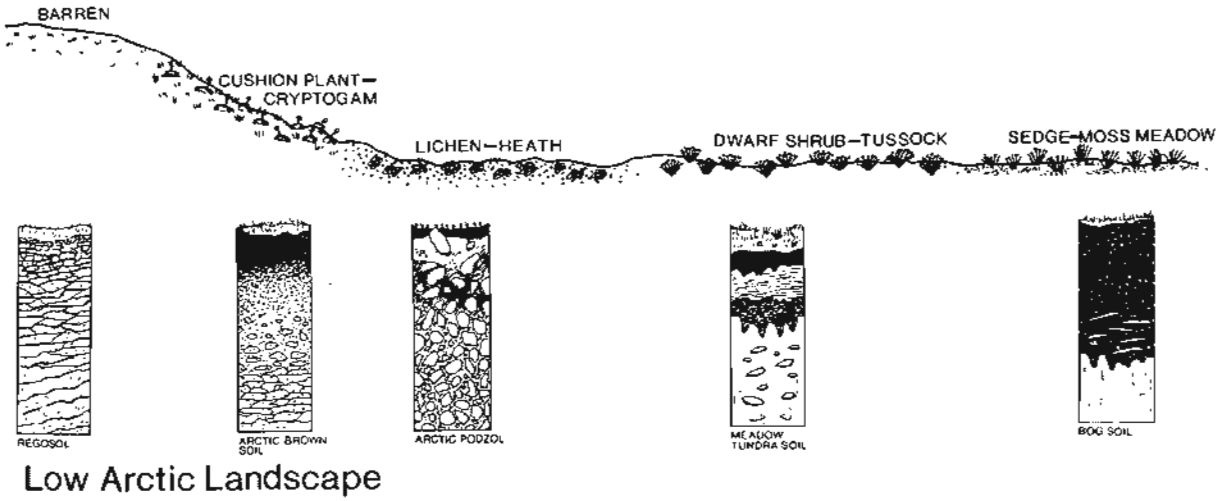

Fig. 19.16. Idealized diagram of the location of genetic soils on a landscape of the Low Arctic along with idealized soil profiles. Based upon Tedrow (1977) and Ugolini (1986).

old sand dunes, river terraces, and old beach ridges typically contain Arctic Brown soils (Pergelic Cryochrepts, Pergelic Cryumbrepts-Inceptisol Order, or Pergelic Cryoborolls–Mollisol Order). However, in limited areas where a lichen heath rather than a *Dryas* heath develops on acid parent material, Arctic Podzol soils (Pergelic Cryorthod, Pergelic Cryochrept–Spodosol Order) or Rendzina soils (Pergelic Cryoborolls–Mollisol Order) are expected (Ugolini et al., 1982, 1987; Ugolini, 1986). The Arctic Podzol and Arctic Brown soils are differentiated on the basis of vegetation and morphology. In the podzol the A2 or E horizon present is accompanied by migration of iron (Fe) and aluminum (Al) into the B horizon. Organic matter may be 10–20% in the Arctic Brown but 20–30% in the Rendzina soils (Tedrow and Hill, 1955; Ugolini and Tedrow, 1963); organic matter decomposes slowly (Douglas and Tedrow, 1959). In most Alaskan arctic landscapes these soils comprise only 1–2% of the landscape (Tedrow et al., 1958), yet their presence demonstrates the diversity of soil-forming processes. Arctic Brown and Arctic Podzol soils are also found in Greenland (Hansen, 1969; Ugolini, 1966a,b; Ugolini et al., 1981) and the mountains of the Yukon Territory. Figure 19.16 depicts these landscapes and their associated soils.

TABLE 19.4

Taxonomic correlation of soil subgroups (genetic groups) for three classification systems of arctic soils

Arctic System (Tedrow, 1977)	USDA System (Soil Survey Staff, 1975)	Canadian System (Can. Soil Survey Comm., 1978)
Polar Desert	Pergelic Cryorthent	Regosolic Static or Turbic Cryosol
Arctic Regosol	Pergelic Cryorthent	Regosolic Static Cryosol
Arctic Rendzina	Pergelic Cryoboroll Cryic Rendoll	Rego Black
Arctic Podzols	Pergelic Cryorthod, Cryochrepts or Cryopsamments	Podzolic Static Cryosol
Arctic Brown	Pergelic Cryochrept Cryumbrept, Cryoboroll	Brunisolic Static Cryosol Orthic Static Cryosol
Upland tundra	Pergelic Cryaquept	Gleysolic Static Cryosol
Meadow tundra	Pergelic Cryaquept	Gleysolic Static or Turbic Cryosol
Half bog	Histic Pergelic Cryaquept	Gleysolic Static Cryosol
Bog	Pergelic Cryofibrist	Fibric Organo Cryosol

Large areas of arctic Alaska, northern Yukon, and western Northwest Territories contain imperfectly to poorly drained soils where the process of gleization predominates (Tedrow and Cantlon, 1958; Tedrow, 1977; Everett and Brown, 1982). These Meadow and Tundra soils (Pergelic Cryaquepts–Inceptisol Order) develop subangular to angular structure depending upon organic matter and soil texture. The B horizon is typically blue-gray to gray in color with iron-oxide mottles, the result of alternating reduction and oxidation processes (Tedrow, 1977). Downward translocation of clays and minerals is minor; the soils are nutrient-poor and generally acid (pH 6.5 to 4.5) (Table 19.5). A detailed summary of soil properties of wetland soils from 14 locations in Alaska was presented by Everett and Brown (1982).

Soils of wetlands are poorly drained; consequently organic matter accumulates to varying depths. Where peats are thin (15–40 cm) and overlie mineral soils, these are frequently termed Half-bog soils (Histic Pergelic Cryaquepts). Where peats are thicker (>40 cm) Bog soils (Pergelic Cryofibrists) occur. The peats are generally a sedge–moss mixture, but on the Alaskan coastal plain a sedge–grass peat predominates. These soils are generally acid (pH 6.5–5.0) and there appears to be little translocation of ions within the profile. In some parts of the coastal plain in Alaska and the Yukon, and in the Mackenzie River Delta region, peats may be 3 to 10 m in depth. Figure 19.16 illustrates these lowland landscapes and their soils.

In the Prudhoe Bay area, landforms and soils have been classified into seven soils within four soil orders. Tops of pingos and well-drained high-center polygons contain Pergelic Cryoborolls (Arctic Browns) of the Mollisol Order. Arctic Browns (Pergelic Cryochrepts–Mollisols) also occur on slopes, interfluves and other high-center polygons that are well-drained. Drained lake basins and low-center polygons contain Half-bog soils (Histic Pergelic Cryaquepts–Inceptisols) and peats (Pergelic Cryofibrists–Histosols). Sand dunes and river terraces have Pergelic Cryopsamments and Pergelic Cryorthents respectively; both belong to the Entisol Order and were earlier termed Regosols (Everett and Parkinson, 1977).

High arctic soils. As stated earlier, soil patterns mirror plant- community patterns in may ways. This is especially true in the High Arctic, where there are lowlands with sedge–moss or grass–moss communities with shallow peats (2–20 cm) on gleyed soils (Pergelic Cryaquepts), cushion plant–cryptogam communities on weakly-developed Arctic Brown soils (Pergelic Cryochrepts) and cryptogam–herb communities on weakly developed Tundra soils (Pergelic Cryaquepts). In exposed uplands where there is little plant cover, Polar Desert soils (Pergelic Cryorthents) and plant

TABLE 19.5

Chemical characteristics of major genetic soils within the Low Arctic of northern Alaska

Horizon	Depth (cm)	pH	Exchangeable Cations (meq kg^{-1} soil)				N (%)	Cation Exchange Capacity (meq kg^{-1} soil)	Saturation (%)	Organic Matter (%)	Authors
			Na	K	Ca	Mg					
Rendzina (Lithic Cryoboroll)											
A1	0–10	7.5					1.3			41.2	
BW1	10–20	7.7					0.4			15.0	Ugolini and Tedrow,
BW2	20–30	7.9					0.2			11.2	1963
Arctic Brown (Pergelic Cryochrept)											
A1	0–20	4.3	2.6	2.0	11	7.0	0.4	200	11.1	11.5	
BW1	20–46	6.1	1.5	2.0	19	9.2	0.0	30	93.2	0.7	Drew and Tedrow,
BW2	46–69	7.2	1.5	2.0	–	–	0.0	20	–	0.4	1957
C	69+	8.2	0.3	1.0	–	–	0.0	20	–	0.6	
Tundra (Pergelic Cryaquept)											
A1	0–10	4.6	9.0	1.0	31			210		7.1	
E	10–30	4.6	9.0	1.0	47			250		10.0	Douglas and Tedrow,
Bg	30–76	5.2	7.0	2.0	272			640		32.0	1960
C	76–114	6.4	6.0	2.0	156			210		5.7	

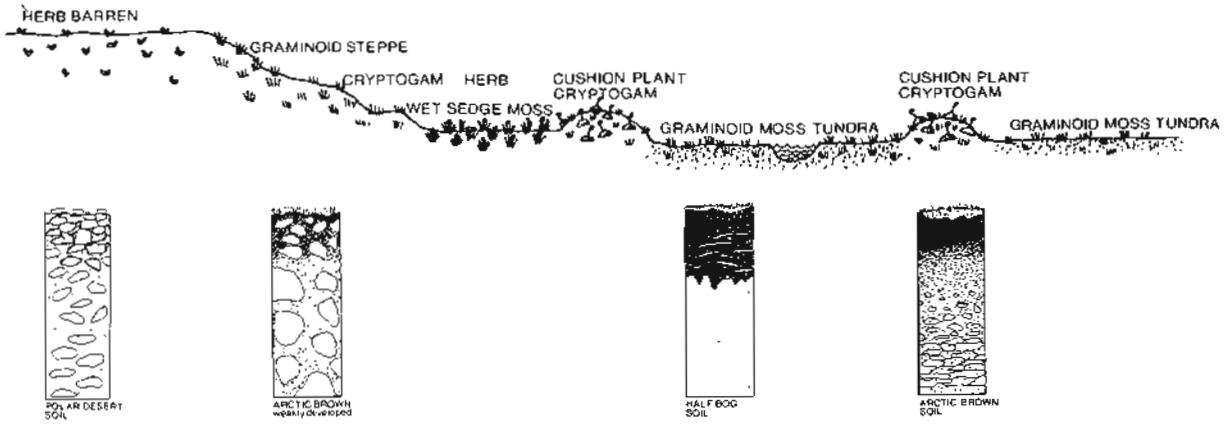

Fig. 19.17. Idealized diagram of the location of genetic soils in the High Arctic. Based upon Tedrow (1977), Walker and Peters (1977) and Ugolini (1986).

communities of the herb barrens are found (Fig. 19.17). River-bank terraces, slopes up from the sea and many other sites are often nearly devoid of plants. Soils in these locations are Regosols (Pergelic Cryopsamments or Pergelic Cryothents) in which there is very little, if any, modification of the parent material because of limited water percolation, youthfulness of the landscape, lack of organic matter, limited plant cover and limited soil micro- and macro-organisms. The soils of all of these habitats are more weakly-developed versions of those found in the Low Arctic (Fig. 19.16). The sequence of soils on the Truelove Lowland, Devon Island, Canada, and the chemical analyses of these soils are quite typical for these northern lands (Table 19.6).

In the Mesters Vig District (Scoresby Land) in northeast Greenland (72°4′ N) soils occur (Ugolini, 1966a,b) that are similar to those at comparable latitudes (72–74° N) in the Canadian High Arctic. These include weakly-developed Podzols (Spodosols) under a relatively luxuriant plant cover of *Betula nana, Dryas integrifolia, Salix arctica*, grasses, and mosses; Arctic Brown soils (Inceptisols) under a "heath" with *Cassiope tetragona, Lycopodium selago* and *Salix arctica*;

TABLE 19.6

Chemical characteristics of major genetic soils within the Truelove Lowland landscape of Devon Island (from Walker and Peters, 1977)

Horizon	Depth (cm)	pH	Exchangeable Cations (meq kg^{-1} soil)				N (%)	Cation Exchange capacity (meq kg^{-1} soil)	Organic matter (%)
			Na	K	Ca	Mg			
Regosol (Pergelic Cryorthent, Gleisolic Turbic Cryosol)									
CgK1	0–21	7.8	–	–	–	–	0.03	–	0.2
CgK2	21–36	7.7	–	–		–	0.03	–	0.0
Arctic Brown (Pergelic Cryochrept, Brunisolic Static Cryosol)									
Ak	0–8	7.1	1.0	1.0	590	190	0.81	670	8.4
Bwk	8–23	7.7	–	–	–	–	0.10	–	1.4
Ck	23–61	7.8	–	·	–	–	0.20	·	0.0
Tundra (Pergelic Cryaquept, Gleysolic Static Cryosol)									
Oi	0–23	6.2	1.0	2.0	490	150	2.24	760	26.1
Cgk	23–28	7.6	–	–	–	-	0.04	–	0.0
Bog (Pergelic Cryofibrist, Fibric Organic Cryosol)									
Oi1	0–8	6.5	2.0	4.0	1110	350	3.06	1330	38.1
Oi2	8–31	6.2	2.0	4.0	940	230	2.68	1280	42.2

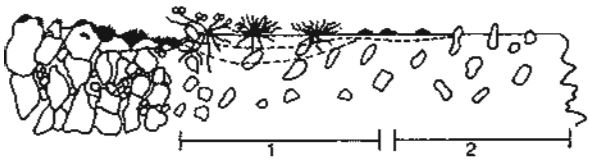

Fig. 19.18. Soil development in relation to sorted circles, Mesters Vig District, NE Greenland; 1 represents an Arctic Brown (Inceptisol) and 2 represents a Polar Desert soil (Entisol). From Ugolini (1966b).

and Tundra soils (upland and meadow tundra soils–Inceptisols) on poorly-drained to very poorly-drained sites, with sedges, *Salix arctica*, mosses, and the typical black crust of Cyanobacteria (blue-green algae) and crustose lichens, often called a cryptogamic crust or patina. These Pergelic Cryaquepts USDA System (Gleysolic Static Cryosols Canadian System) are characterized by grayish-brown subsoils with mottling by yellowish-brown streaks. The annual freeze – thaw cycles can result in angular to blocky structure in the subsoils as elsewhere in the Arctic.

Where sorted circles or nets (polygons) occur, the soils across a sorted feature have an interesting soil gradient (Fig. 19.18). Loose organic material occurs on the rock ring, through weakly-developed Arctic Brown soils to an upland Tundra or Regosol soil in the "soil boil" center (Ugolini, 1966a). Relationships between patterned ground and soils have also been described from Alaska (Drew and Tedrow, 1962).

Within the polar deserts, >95% of the landscape is a polar barren with only 1–3% total plant cover. The soils are equally poorly developed. Large areas are covered with a veneer of stones, the desert pavement (Fig. 19.19). In some areas there are salt-encrusted surfaces of chlorides and sulfates of magnesium and calcium. Much of this results from salts deposited at the surface by strong evaporation during those short periods (3–10 d) in summer with bright sunshine and moderate winds. Salt lakes, saline soils, and salt-tolerating species are found in the more continental climate near the head of fjords in western Greenland (Böcher, 1949; 1959) and on some of the western Queen Elizabeth Islands, Canada (Bliss et al., 1984; Bliss and Svoboda, 1984).

Other minor soils include weakly-developed Tundra and Arctic Brown soils in relation to the small areas of greater plant cover. Polar Desert soils (developed under the process of calcification) contain no or little surface organic matter, have no distinct soil horizons, and have little if any development of soil structure. The surface soils (1–10 cm) are generally basic (pH 7.9–8.5), have very limited organic matter (0.5 0 1.2%), are high in calcium (300–400 meq kg^{-1} soil), low in magnesium (10–30 meq kg^{-1} soil), and have essentially no phosphorus and nitrogen (Table 19.7). While most Polar Desert soils are base-saturated and have free carbonates, some soils, derived from the Beaufort Formation on Banks Island, Canada (Tedrow, 1966), the Kanguk Formation on Lougheed Island

Fig. 19.19. Typical polar desert landscape with a veneer of stones on nonsorted polygons, plateau on Devon Island, N.W.T.

(Edlund, 1980), and sheet-eroded surfaces of recent marine sediments on King Christian Island, Canada (Bliss and Svoboda, 1984) have surface soils with a pH of 4.8 to 3.5, essentially no nitrogen, and low levels of cations and phosphorus. These soils have little plant cover (0–1%).

Where snow-flush plant communities of cushion plants and mosses, or mosses and graminoids, occur, and where the water table is close to the surface, very weakly gleyed soils develop. They have little if any horizon development, and have a pH and nutrient content similar to those of the polar deserts (Bliss et al., 1984). Plant cover and its limited input (1–3%) of organic matter (surface and roots) have little influence on these youthful soils.

Based upon the literature and personal observations in more than 20 locations in the Canadian Arctic Archipelago, there are few if any sites with organic soils because of limited plant growth and the relatively short time since deglaciation. Most of the soils in lowlands are termed Half-bog (Histic Pergelic Cryaquept) soils.

ARCTIC CLIMATOLOGY

To many people the Arctic is a region of perpetual snow and ice, characterized by continuous light in summer and continuous darkness in winter. The summers are short with only 1.5 to 4 months free of snow and the winters are long, cold, and have a continuous cover of snow and ice. Yet a region as large as the Arctic is diverse in topography, land–sea relationships, and in latitude, all contributing to a diversity in local climates. The combination of local climate and soil–topographic conditions result in some areas having a diversity of animals and plants (local oases), while other lands at the same latitude are nearly devoid of life (polar deserts).

Understanding arctic climates and the major factors that control their dynamics has been delayed due to the paucity of observational and synoptic weather data. The meager network of arctic stations is located at great distances from population centers. The dynamics of the arctic atmosphere have been well established since the 1950's by radiosonde data, more recently supplemented with satellite imagery. The establishment of weather stations on ice islands, large and thick (30–40 m) ice masses from northern Ellesmere Island, Canada, has greatly increased this network. The first Russian "North Pole" station was established in 1937 and through 1968 Russian scientists occupied eighteen floating stations and the Americans six stations (Vowinckel and Orvig, 1970). These ice islands drift in the pack ice at an average rate of 6.2 km d^{-1}, although the drift varies from month to month and from year to year.

In summer, arctic air masses seldom extend south of 50–60° N, and commonly lie along the arctic tundra–forest transition zone. In winter, with a continuous snow cover across southern Canada and into central United States, cold and dry arctic air often penetrates to northern Florida and central Texas. The unusually cold winters of 1983-1984 and 1990-1991 attest to the climatic and economic severity of these outbreaks. One does not have to be at 70 or 75° N to experience arctic climatic conditions in winter. Temperatures of −30 to −40°C are common across the north-central part of the continent (Alberta to Ontario; Montana to Minnesota). These storms often result in

TABLE 19.7

Chemical characteristics of major genetic soils within polar desert landscapes of the High Arctic (from Bliss et al., 1984)

Horizon	Depth (cm)	pH	Exchangeable Cations (meq kg^{-1} soil)			N (%)	Cation Exchange Capacity (meq kg^{-1} soil)	Organic Matter (%)
			K	Ca	Mg			
Polar Desert (Pergelic Cryorthent, Gleysolic Turbic Cryosol)								
C	0–10	8.4	2.0	410	29	0	50	0.5
C	0–10	8.5	1.0	390	9.0	0	33	1.2
Arctic Brown (Pergelic Cryorthent, Brunisolic Static Cryosol)								
C	0–10	8.4	3.0	390	28	0	130	3.0

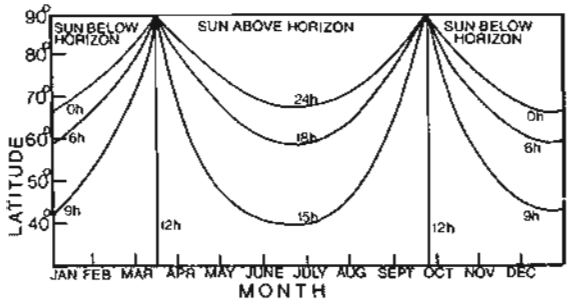

Fig. 19.20. Duration of daylight hours from 40° to 90° latitude.

heavy snowfalls as the cold and dry air pushes moist, mild Pacific or Gulf air aloft.

Macroclimate

Solar energy budget

Solar radiation is the fundamental climatic driving variable on a global basis. In the Arctic, more than at lower latitudes, this has a strong seasonal and latitudinal pattern. An energy-balance equation for a horizontal area at the earth's surface is:

$$Rs - Rr + R\ell\downarrow - R\ell\uparrow + H + LE + G = 0, \quad (1)$$

where Rs = incoming short-wave (global) radiation, Rr = reflected radiation from surfaces (albedo), $R\ell\downarrow$ and $R\ell\uparrow$ = atmospheric downward and terrestrial upward long-wave radiation, H = sensible heat flux, LE = latent heat flux (evaporation and transpiration), and G = subsurface heat flux in soil and water.

In the Arctic, as elsewhere, solar radiation has a strong seasonal and latitudinal pattern. Annual total solar radiation, incident at the ground surface, is about 4200 MJ m^{-2} at 50° N near the southern boundary of the boreal forest, 1600–2000 MJ m^{-2} at the tree line and 500 MJ m^{-2} at 75° N (Hare and Hay, 1974).

Although the Arctic is a region of greatly reduced solar radiation, due to high albedo from snow cover until mid to late June and to high cloud cover in summer, annual net radiation is generally positive. Net radiation (Rn) represents the energy available at the ground and on plant and animal surfaces for heat-transfer processes:

$$Rn = H + LE + G + P, \quad (2)$$

where P = photosynthesis, and the other terms are explained in (1). Photosynthesis is always minor and for practical purposes can be ignored. In general, net radiation is 45–50% of global (short-wave) incoming radiation. As will be seen later, in some high-arctic environments with nearly constant cloud cover, long-wave radiation ($R\ell\downarrow$) may constitute a significant percentage of the energy-balance equation.

Net radiation, like total radiation, decreases poleward. It averages 1000–1200 MJ m^{-2} yr^{-1} in the northern boreal forest, 750–800 MJ m^{-2} yr^{-1} across Canada, but only 670 MJ m^{-2} yr^{-1} across Alaska at the tree line. In the Arctic net radiation averages 200–400 MJ m^{-2} yr^{-1} for much of the Canadian Archipelago, dropping to near zero in northern Ellesmere Island and Greenland. Over the permanent pack ice, negative net radiation values occur, down to −100 to −200 MJ m^{-2} yr^{-1} (Hare and Hay, 1974; Barry and Hare, 1974). As discussed later in this section, net radiation data, higher than predicted, have been recorded at some northern stations.

A positive energy balance on an annual basis results from energy transfer from lower latitudes via cyclonic air masses and the continuous daylight in summer. This offsets the strong radiative cooling ($R\ell\uparrow$) over the long winter months.

The sun is continuously above the horizon for about 2.5 months at 70° N, about 4 months at 75° N, and 6 months at 90° N with an equally long period of total darkness in winter (Fig. 19.20). However, the total period of darkness is much less at each latitude due to the hours of twilight when the sun is only a few degrees below the horizon. This is in sharp contrast with equatorial regions where days and nights are of nearly equal length throughout the year and where twilight is measured in minutes rather than hours.

Land surfaces are generally snow-free for about 3–4 months in the Low Arctic and for about 1.5–2.5 months in the High Arctic. At elevations above 100–200 m snow remains longer, 1–2 weeks longer on the level, and often throughout the summer in snowbanks 3–5 m deep in June.

Large-scale circulation

Early in the century meteorologists depicted pressure distribution in the Arctic as a shallow high-pressure system resulting from radiative cooling, with a deep low-pressure system above in the stratosphere. It is now known that the surface high-pressure system is not centered over the Polar or Arctic Ocean but occurs over the continental land masses where radiative cooling is intense. The

North American high-pressure system typically occurs over the Yukon Territory and western Northwest Territories. In winter when the outward flow of cold, dry air (anticyclone) is strong, cyclonic (low-pressure) systems with their warmer and moister air are maintained in temperate latitudes and seldom penetrate the Arctic except over the relatively warm waters of the Norwegian Sea and Barents Sea. This well-defined pattern in winter is weakened in spring and summer with the reduced latitudinal thermal gradient as land surfaces warm and snow melts (Hare, 1968; Barry and Hare, 1974). In summer the entire Arctic has uniform sea-level pressures north of the sub-Arctic lows. With weaker zonal flow in summer, cyclonic systems are able to penetrate the Arctic, often with increased precipitation. The frequency of these storm systems is low (5–10%) except between Alaska and Siberia, in the Gulf of Alaska, and off the east coast of Baffin Island (>15–>25% frequency). In winter the centers of cyclonic activity are the Gulf of Alaska and over northern Baffin Island of Canada near the open sea, within Baffin Bay, west of Greenland (McKay et al., 1970). The complexity of these sea-level pressure charts long obscured the surprising simplicity and uniformity of the Arctic Core above these shallow layers of air that respond to thermal contrasts at the air–sea, air–ice, and land–sea surfaces (Hare, 1968).

In temperate regions with mountain and valley systems, cold-air drainage at night with warmer air aloft (temperature inversion) frequently occurs. This same phenomenon often occurs in northern bogs in summer, with rapid reradiation at night, resulting in cold surface air masses in the small to large topographic depressions. Inversions on a much larger scale occur over the Polar Ocean, especially in winter. With intense reradiation during the long polar night, surface temperatures are often −30 to −50°C over the pack ice, yet, 1–2 km higher at the top of the inversion layer, temperatures are −20 to −25°C. These surface inversions have an 80–90% frequency in winter and 15–20% frequency in summer (Vowinckel, 1965; Vowinckel and Orvig, 1970).

These complex surface and near-surface temperature and pressure systems of the arctic troposphere (from surface up to about 10 km) are generally characterized by rapid cooling from the surface to the top of this layer (tropopause). The lower part of the stratosphere (about 20–24 km) has a near-constant, low temperature (−55°C) and is clear air, the zone where jet airliners prefer to fly. Near the top of the stratosphere (45–48 km) the temperature is much higher (−2°C). There is considerable heat transfer from the troposphere to the stratosphere (Hare and Boville, 1965). Above the stratosphere the thin air heats gradually out into space as the sun's energy heats the ozone.

Role of uplands and mountains

Mountain systems play a major role in controlling weather systems on a global and a continental basis. The Aleutian low-pressure systems are cut off from the Polar Ocean by highlands in Alaska and northeastern Siberia. Cyclonic storms that reach Greenland are diverted northward along the west coast. The low-pressure systems that approach Cape Farewell, Greenland, often split, with one system moving into Baffin Bay and the other moving east towards Iceland (Putnins, 1970). Icelandic lows often extend their influence to the Polar Basin, for there are no barriers (Barry and Hare, 1974). The intense arctic high-pressure systems swing south and east along the east side of the Rocky Mountains, which partially block the penetration of cold and dry polar air into British Columbia, Washington, and Oregon.

An added climatic feature in the eastern Arctic, including Greenland, is the downslope movement of air from adjacent uplands (föhn or katabatic winds). This provides both heating as the air settles and contracts, and strong winds that may average 15–25 m sec^{-1} for several hours (Courtin and Labine, 1977; Barry and Jackson, 1969). The biological implications of these warm, strong winds will be discussed later.

Forest–tundra bioclimatic boundary

Historically the Arctic has been defined as the region north of the climatic limit of forest. This poses the question: what sets the northern limits for tree growth? Temperature was the first environmental parameter considered. Köppen (1918) proposed that arctic climate occurs where the temperature of the warmest month (July) is less than 10°C. In general, in North America and Europe, this places the line north of actual tree line. The Nordenskjöld line incorporates a component of winter temperature into the equation:

$$Tw = 9 - 0.1\ Tk, \qquad (3)$$

where Tw is the mean temperature of the warmest

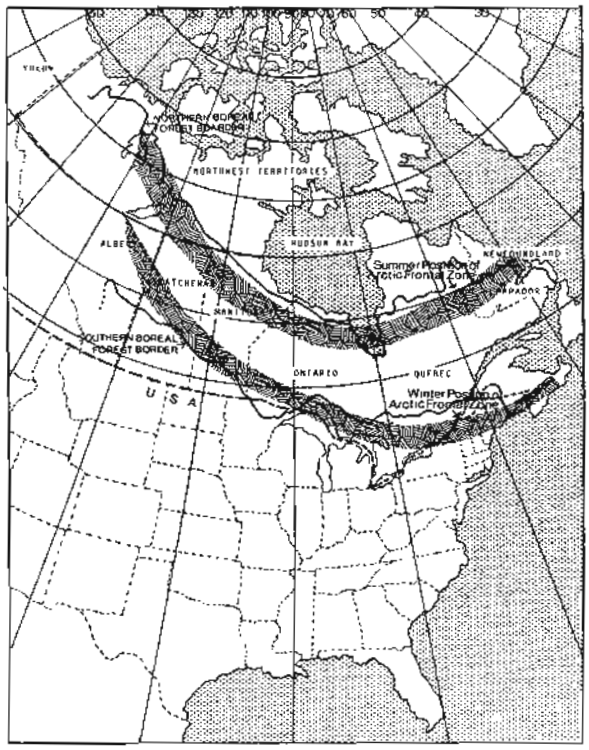

Fig 19.21. Mean positions of the Arctic Front in summer (upper position) and in winter (lower position) in central and eastern North America. Based on Bryson (1966)

month and Tk is the mean of the coldest month (°C) (Nordenskjöld and Mecking, 1928). This line more closely parallels the tree line. Hare (1950, 1954) utilized mean annual temperature, length of the growing season and potential evapotranspiration (P − E in cm) in demonstrating a relationship with the broad vegetation zones of tundra (30.5–31.7 cm), forest–tundra ecotone (35.5–36.8 cm), lichen woodland (41.8–43.1 cm), and closed boreal forest (47.0–48.2 cm).

A more recent and accepted understanding of the relationship between vegetation and climatic boundaries is the relative position (>50% frequency) of the Arctic Front (leading edge of arctic or polar air masses) in summer (Bryson, 1966; Larsen, 1971) and the magnitude of annual net radiation (Hare and Ritchie, 1972).

Bryson (1966), using the July mean air-mass boundary (derived from air-mass movement, from maximum temperatures, and from storm tracks), found a strong agreement with the tree line. Throughout the year the Arctic Front moves back and forth over the boreal forest (taiga), effectively covering the Arctic with arctic air throughout the year. The boreal forest is dominated by arctic air masses in winter (high-pressure systems) and by Pacific air masses (low-pressure systems) in summer (Fig. 19.21). The ecotone or transition between forest and tundra, about 50–100 km in width, has probably existed for the past 3500 to 4000 yr based upon radiocarbon dating and plant macro- and microfossils (Bryson et al., 1965; Larsen, 1965, 1973; Nichols, 1967, 1975, 1976). The width of the ecotone results from past climatic change, the role of fire, and the ability of tree, shrub, and herbaceous species to become established following fire.

Hare (1968) and Hare and Ritchie (1972) hypothesized that the location of the Arctic Front over the northern tree line in summer results from: 1) differences in albedo; 2) differences in aerodynamic roughness between the green coniferous and the yellow-brown shrubs and herbs of the tundra; and 3) differences in evaporation potential between forest and tundra. There is a significant relationship between net radiation and northern vegetation zones including the tree line, across Canada and Alaska. Hare and Ritchie (1972) pointed out that the pattern in Alaska is complicated by the presence of the Brooks Range in the general region where the ecotone should occur, and also by the cloudy, windy and cool maritime climate of western Alaska and the Aleutians.

Whether arctic and forest vegetation in this tension or transition zone is responding to an assemblage of climatic variables, especially to air masses as suggested by Bryson (1966), or whether the Arctic Front takes its position because of changes in albedo, evapotranspiration, and surface roughness as suggested by Hare (1968), both biotic limits and air-mass systems are responding to radiation controls. This approach stresses that broad vegetation units are responding to and are being controlled by a complex of factors and interactions rather than a response to a single environmental factor. More data are necessary before one will know whether the Bryson or the Hare–Ritchie model, or some combination, provides the climatic control for the limits of these major vegetation types.

Regional climatic characteristics

Greenland (see also Chapter 20)

This great island, (2,186,000 km^2 including is-

lands) extends from 66° to 83° N. About 80% of Greenland is covered by the ice cap and isolated peripheral glaciers. The ice cap reaches a height of 3230 m and nearly 33% of its area extends below sea level. Greenland is literally a group of islands buried in ice! Because of its great length which lies across the path of the westerlies, the splitting of the Gulf Stream along the southern coasts, and the massive ice cap, the climates of Greenland are variable.

Earlier studies indicated that the ice cap was dominated by a semi-permanent "glacial anticyclonic system", the result of intense radiative cooling. While this pattern generally holds for the northern part of the ice cap, central and southern Greenland are strongly influenced by cyclonic storms. These frequently move up the west coast and pass over the ice cap, providing snow from these low-pressure systems which maintains the ice cap.

In summer the adiabatic cooling of rising, mild, and moist air results in snow over the ice cap. On a few days rain may even fall. Katabatic winds, reaching gale force, may flow off the plateau and down the fjords. This often results in warm inner fjord valleys, while the coast may be cool and fog-bound (Putnins, 1970). At the edge of the ice cap strong radiation melts the surface, converting snow to névé and producing "ice lakes". Summer daily low temperatures are −5 to −10°with daily maxima of −5 to −3°C. During summer storms the mixing of moist maritime air with the cold air of the ice cap (a shallow inversion layer) results in "heating" the local climate. After the storm passes, and the sky clears, the air temperature drops 15 to 20°C within two days (Miller, 1956).

In autumn cyclonic activity increases, resulting in increased snowfall on the ice cap. Temperatures drop rapidly with reduced solar radiation, but along the coast open water delays cooling. Strong katabatic winds blow off the plateau and move down the fjords. There is a considerable shift from cyclonic to anticyclonic air masses; winter is on its way! In winter, temperatures drop rapidly and an intense inversion develops with warmer air aloft, as over the Polar Ocean. Mean minimum temperatures are −40 to −45°, with extreme lows <−60°C. Over southern Greenland, cyclonic storms may penetrate, bringing warmer air, clouds and snow. Precipitation is low on the ice cap, averaging only 500 to 250 mm through central Greenland west to east, but to the north only 260 to 130 mm (Putnins, 1970).

The coastal region of Greenland is subjected to the interactions of the polar air masses and the mild, maritime air masses of the ocean. This results in sharp changes in meteorological conditions, especially along the fjords. The inner fjords become warmer in summer and there are often strong contrasts in coastal vs. inland vegetation, with more and larger woody species inland. The winds frequently have a diurnal and annual pattern. In summer with warm, rising air inland, air flows into the fjord. During the "night" and in winter, with warmer air offshore, air flows out of the fjord (Putnins, 1970).

Northern Greenland, even near sea level, is a polar desert characterized by very low mean annual temperature, strong winds and low precipitation, but high rates of evaporation. This results in salt crustation on soils and even salt lakes. In summer the temperatures are quite mild, and thus vegetation and wildlife are more abundant than one would expect by looking only at mean annual temperature (−16.4°C at Nord, 81°36′N). Freezing starts rapidly in autumn, and warm weather comes quickly in spring (Putnins, 1970).

The climate diagrams in Fig. 19.22 depict very well the diversity of climate from north to south and also from east to west. One may note the low annual precipitation at Nord (204 mm) compared with Godthaab (481 mm) and Ivigtut (1137 mm) along the southwestern coast. Strong gradients in temperature also occur. The east coast north of 67–68°N receives much less influence from the warm Gulf Stream current, and therefore the summer and mean annual temperatures at Scoresbysund (70°25′N) are considerably lower than at Jakobshavn (69°13′N) on the west coast. In contrast, Angmagssalik (65°37′N) on the east coast and Godthaab (64°10′N) on the west coast have maritime climates that are more similar (Fig. 19.22).

At Station 2 east of Thule on the ice cap (76°59′N, 56°30′W, 2,128 m), precipitation averaged 435 mm over a 62-yr period and mean annual temperature for four years averaged −24.2°C. The warmest month (July) averaged only −7.1°C with an extreme maximum of 2.2°C in August, 1955 (Putnins, 1970).

At the coastal stations of Greenland the mean annual temperatures are not low by arctic standards. Nord is the coldest (mean annual −16.4°C) with a mean annual temperature range of 34°, indicating a continental climate although the sta-

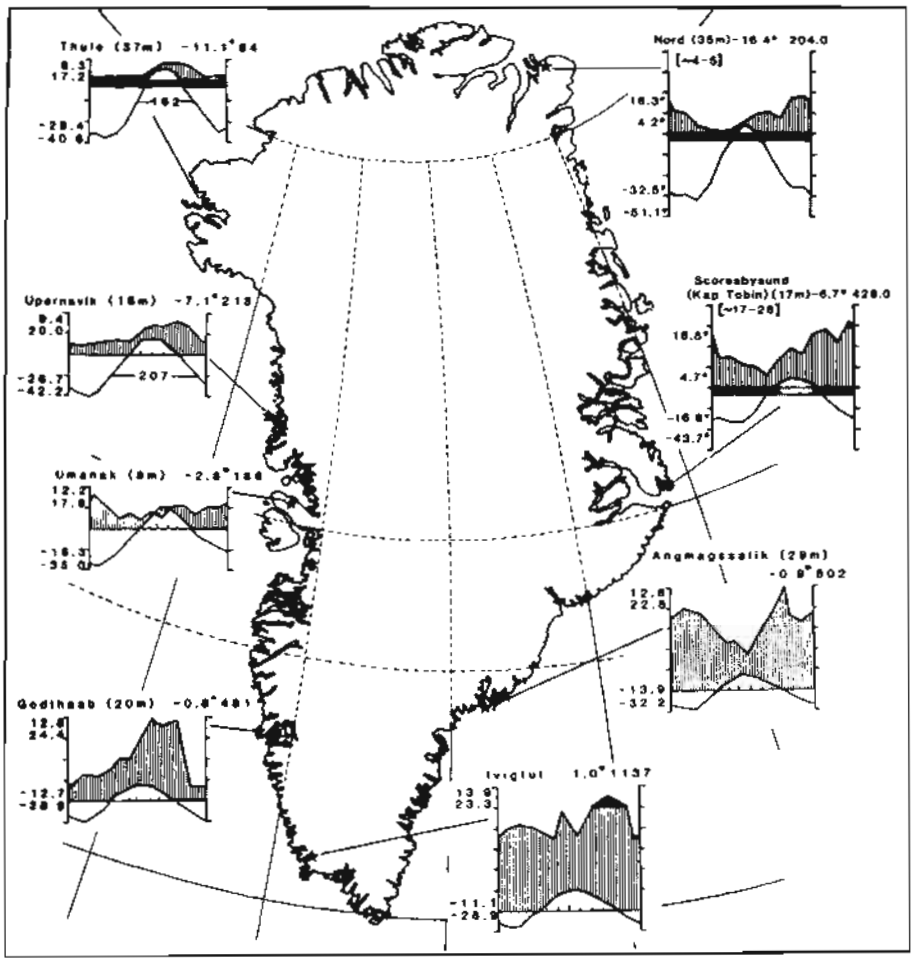

Fig. 19.22. Climate diagrams for selected stations in Greenland.

tion is coastal. Ivigtut (1.0°C) and Angmagssalik (−0.9°C) in southern Greenland have quite high mean annual temperatures and a much smaller range of annual temperature (15° and 22°C respectively) due to cyclonic storms and the Gulf Stream current. This results in an arctic maritime climate.

Canada

The Canadian Arctic is also a huge land area, approximately 2,500,000 km^2, with the Canadian Arctic Archipelago contributing 1,442,000 km^2 of the total. The latitudinal extent is from 55°N near Cape Henrietta Maria, Hudson Bay to Cape Columbia, Ellesmere Island at 83°39′N. Longitudinally the Arctic extends from Cape Dyer, Baffin Island (61°37′W) to the Yukon-Alaskan border (141°W). The eastern Arctic is characterized by mountains and glaciers (Ellesmere, Devon, Baffin islands), the mainland is of low relief, heavily glaciated with many lakes, the "Barrens"; and the northwestern arctic islands are of low relief and surrounded by ice nearly every summer.

The basic meteorological information has been presented earlier (pp. 568–571). In winter intense high-pressure systems develop over the Yukon–Northwest Territories, with deep low-pressure systems near the Aleutian Islands and between Greenland and Iceland. Cyclonic storms from the resulting westerlies penetrate the Arctic between Baffin Island and Greenland and northeast of Greenland. In summer a shallow low-pressure system is frequently located in northern Quebec and southern Baffin Island. This results in a maritime arctic climate with a high degree of cyclonic activity in

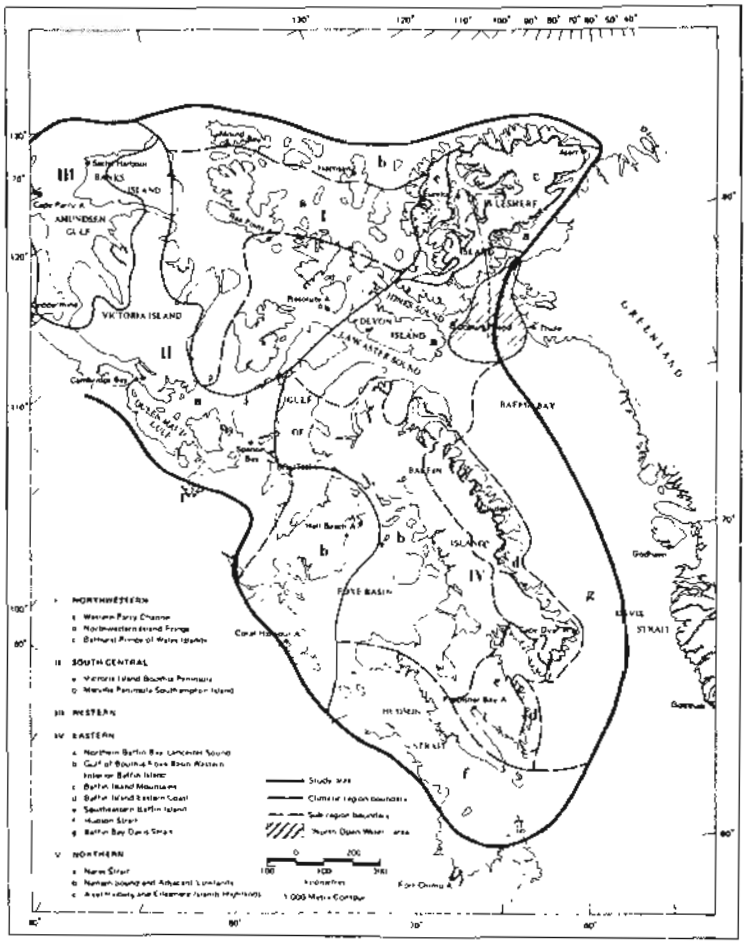

Fig. 19.23. Major climatic regions within the Canadian Arctic. Based upon Maxwell (1981).

the southeastern Canadian Arctic, while the northwestern arctic islands are dominated by cold, dry arctic air masses (anticyclonic systems) most of the year.

Arctic archipelago

Maxwell (1981) has divided the Canadian arctic islands into five climatic regions (Fig. 19.23, Table 19.8). Region I, the northwestern islands, is characterized by a dominance of anticyclonic activity

TABLE 19.8

Summary of climatic data for the climatic regions of the Canadian Arctic islands (based upon Maxwell, 1981)

Region	Temperature (°C)			Precipitation (mm) Annual	Net radiation (MJ m^{-2} y^{-1})
	Mean Daily		Mean Annual Range		
	January	July			
I (Northwest)	−33 to −35	3 to 8	37 to 40	<100 to 150	200–400
II (South-Central)	−30 to −35	5 to 8	36 to 45	100 to 300	300–600
III (Western)	−28 to −30	5 to 8	36	125 to 175	400–600
IV (Eastern)	−20 to −33	3 to 8	22 to 37	150 to 600	300–1200
V (North)	−28 to −35	0 to 5	35 to 43	<100 to 200	200–400

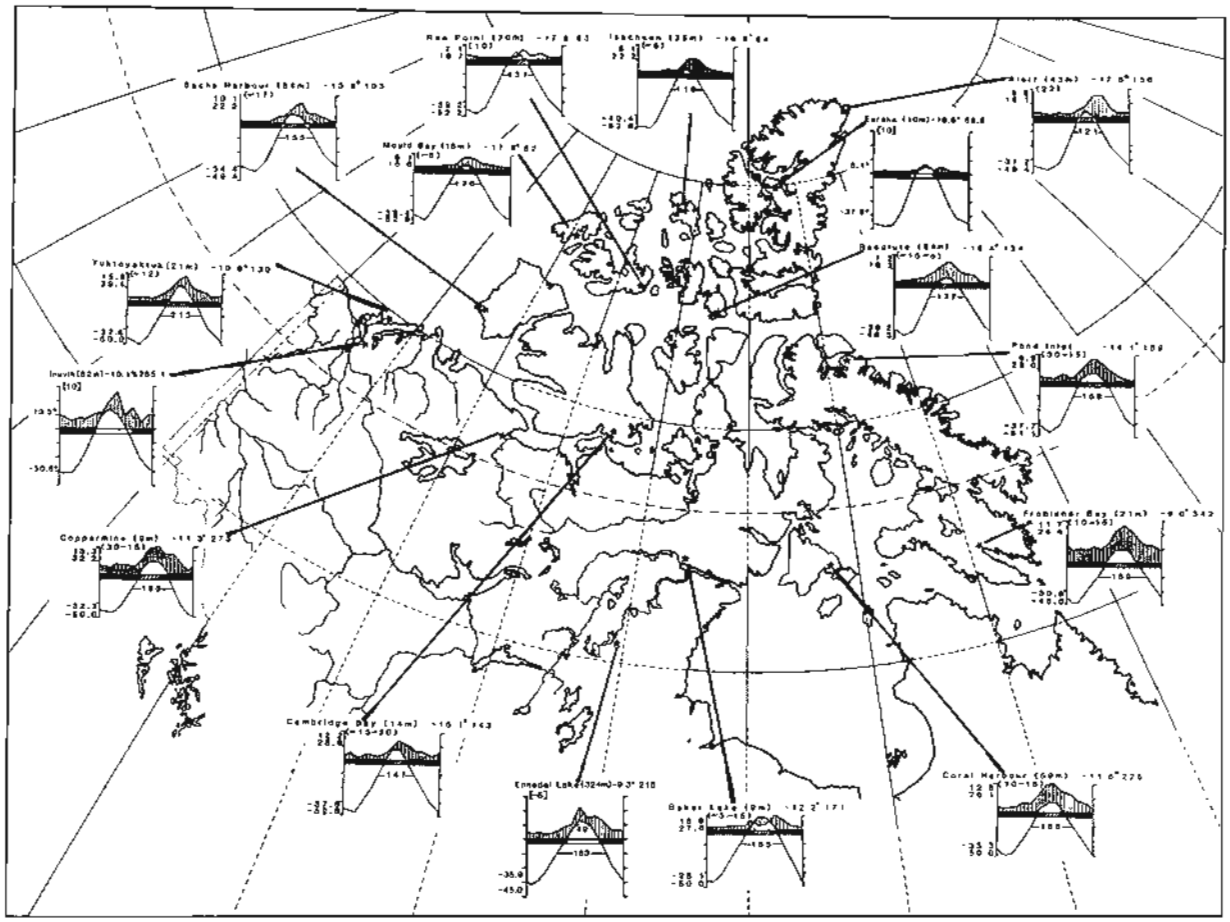

Fig. 19.24. Climate diagrams for selected stations in the Canadian Arctic.

throughout the year, low precipitation (80–140 mm), very low mean annual temperatures (−16 to −18°C), and a mean annual temperature range of 38 to 40°C. All four climatic stations in the region have a similar pattern to their climatic diagram (Fig. 19.24). Annual net radiation is high for two stations within this region [590 MJ m^{-2} yr^{-1} at Mould Bay, Prince Patrick Island and 875 MJ m^{-2} yr^{-1} at Isachsen, Ellef Ringnes Island (Maxwell, 1981)] compared with the earlier estimated data (Hare and Hay, 1974). These high radiation values seem unusual considering the dominance of low stratus cloud and fog in summer for much of the region. The sea ice has open leads and there are many pools of water on the ice, all contributing to the water source. Snow cover generally lasts from late August through mid-June with an average depth of 10–30 cm. Strong winds rework the snow, filling many depressions to a depth of 3–5 m. As a result there is even less relief to the landscape, often making it difficult to differentiate land from sea ice in winter with only twilight conditions a few hours per day for weeks.

Region II includes much of Victoria and King William Islands, and the Boothia and Melville peninsulas. With its more southerly location, mean annual temperatures are higher (−11 to −15°C), mean annual temperature range is greater (36 to 45°C), and mean annual precipitation increases (100–300 mm). Where anticyclonic conditions predominate (Victoria and King William Islands), precipitation is low (100–300 mm), but increases eastward where cyclonic activity increases (Maxwell, 1981).

Region III, including southern Banks Island, western Victoria Island and the coast from Tuktoyaktuk to near Coppermine, is again a region of low precipitation (125–175 mm) and less severe annual temperature (−11 to −14°C) compared with Region I. Alternating cyclonic and anticy-

clonic activity characterizes this region in contrast with the others where either anticyclonic (Regions I, II) or cyclonic activity (Regions IV, V) predominates. Degree-days and the number of days with temperature above 0°C are significantly greater in Region III than in Regions I and II. This results from generally higher levels of net radiation (Table 19.8). Sea ice is generally first-year ice, which melts completely by fall, in contrast with the three northern regions (I, III, V) with their multi-year ice. This is important for shipping as well as for offshore petroleum exploration by drill ships. In contrast, multi-year sea ice in Region I was flooded in winter to produce ice platforms 6–8 m thick from which gas wells were drilled and on which commercial jet aircraft landed with heavy loads of supplies in the late 1970s and early 1980s).

Region IV is the largest geographically, including Baffin Island, most of Devon Island, southern Ellesmere Island, and the North Open Water area (Dunbar, 1970) (Fig. 19.24). The region is characterized by a dominance of cyclonic systems, first-year ice, much open water in summer, and mountainous terrain including massive ice fields (Devon ice cap). All of these factors result in an arctic maritime climate with cold winters, cool summers, high levels of coastal fog, and, for the Arctic, high precipitation (mostly 300–600 mm). Mean annual temperature range is 25 to 30°C along southern Baffin Island, increasing to 33 to 36° in northern Baffin Island (Maxwell, 1981). Snow generally occurs from early September through mid to late June. Average depths are 30–50 cm, though much deeper where snowdrifts develop. Föhn winds are a common phenomenon in some areas, where they help to account for the more equable summer climate.

Region V is the smallest, and includes the most northerly islands (Axel Heiberg and Ellesmere). The region is characterized by high mountains, large ice caps and glaciers, relatively low precipitation (100–150 mm, 200 mm at higher elevations), and local areas of föhn winds. Eureka (80°N) has a more continental climate (−19.1° mean annual temperature, 43° mean annual temperature range) than at Alert (82°30′N) on the north coast of Ellesmere Island (−17.8°C mean annual, 38° mean annual range). Fog and low stratus clouds are less frequent in this region than the others, except at higher elevations (Maxwell, 1981). Although net radiation is generally low in this region (Table 19.8), net radiation is high in some valleys and lowlands (420 and 675 MJ m^{-2} yr^{-1}). This provides the very basis for "arctic oases", as discussed elsewhere. The considerable reduction in cyclonic storms entering Davis Strait and Baffin Bay accounts for the reduced precipitation. Over much of the Arctic Archipelago 30–40% of precipitation is liquid, falling in a period of only 1.5 to 3.0 months. Rain is a higher percentage in Region IV, the region of highest cyclonic activity and the most open water averaging 40–55% of the total (Maxwell, 1981).

Mainland. The arctic climate of mainland Canada is continental. Mean annual temperatures are not as low (−9 to −12°C) as locations further north with their longer periods of darkness and temperature inversions, but the mean annual temperature range is greater (44°C). This results from much warmer summers. Precipitation ranges from 150 to 300 mm. It is greatest during July through September, when the Arctic Front moves back and forth over the region and cyclonic storms penetrate the predominant high-pressure systems further north. Snow cover is present from September through early June, with an average depth of 40–65 cm. Settlements and thus weather stations are uncommon in this huge landscape because of its general reduced biological productivity except in and near the Thelon Sanctuary.

Alaska

Arctic climatology across Alaska is less complex than in the previously described areas due to simpler patterns of air-mass movement, the general low relief except in the Brooks Range, and the much smaller region. The Brooks Range effectively straddles the climatic and vegetation boundary between the arctic and boreal-forest biomes, thus further providing a sharp delineation between north and south. As described earlier, low-pressure (cyclonic) systems dominate over the Gulf of Alaska and the Bering Sea, but storms that move east seldom reach the Arctic coast, although they dominate the weather systems along the Aleutian Islands and in the southwestern mainland. Precipitation is much higher along the coast facing the Bering Sea than the Arctic coast (Barry and Hare, 1974). Along the Arctic coast and south towards the Brooks Range anticyclonic systems predominate, with surface temperatures −30°C or lower in the temperature inversion that is often 750–1000 m thick; winds are moderate.

Ice fog from industrial and domestic combus-

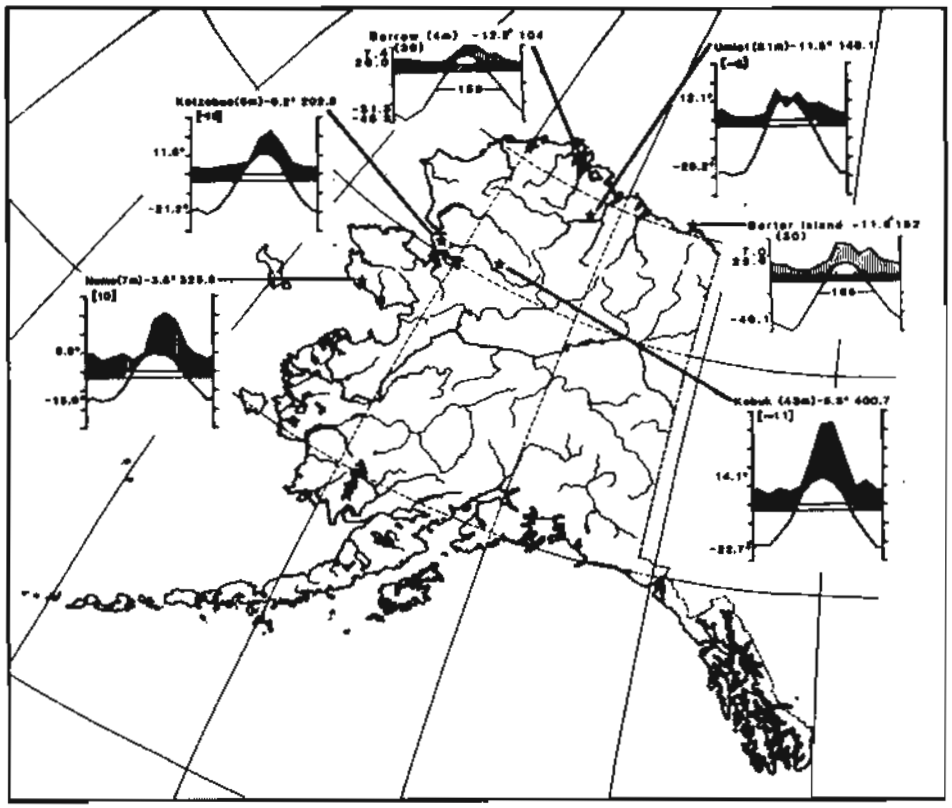

Fig. 19.25. Climate diagrams for selected stations in the Alaskan Arctic

tion of natural gas and gasoline has become a growing problem with temperatures below −15° to −20°C, especially in valleys where temperature inversions develop with little wind. The cold air becomes saturated with water vapor (frozen) and various pollutants. This is especially a problem at Fairbanks, Whitehorse, and Yellowknife within the boreal forest, but also for the coastal settlements of Barrow, Prudhoe Bay, Tuktoyaktuk and others.

Spring comes more rapidly to the western and northern Arctic in Alaska because of the easy penetration of mild Pacific air masses. Consequently, at a given latitude in April and May, temperatures are often 15°C higher than in the Canadian Arctic (Barry and Hare, 1974). The winter snow cover, averaging 30–60 cm on the level, typically melts in early to mid-June, a period of high sun angle and high levels of sunshine. Summer and autumn (late June–September) are characterized by mild temperatures in the Piedmont and Foothill provinces (8° to 12°C), but with lower temperatures along the coasts (5° to 8°C). The greater cloud frequency and higher precipitation result from the common occurence of cyclones traveling near the Arctic Front. The Arctic Front is generally at a height of 300–600 m over the coast, and reaches ground level halfway between the coast and foothills (Conover, 1960). Inland thunderstorms occur in July and August as they do in the Canadian Arctic mainland. Such storms are very rare in the Canadian Arctic Archipelago.

Along the northern coast, at Barrow and Barter Island, mean annual temperature averages −12°C, mean annual temperature range is 33 to 34°C and mean annual precipitation averages 100–180 mm. Inland at Umiat the climate is more continental, with a 44°C annual temperature range and 150 mm annual precipitation. On the west coast facing the Bering Sea the climate is less severe (mean annual temperature −3 to −8°C, mean annual temperature range 25–28°C) and precipitation is generally greater (250–280 mm) (Fig. 19.25).

Recent climate trends

An old saying goes "if you do not like the

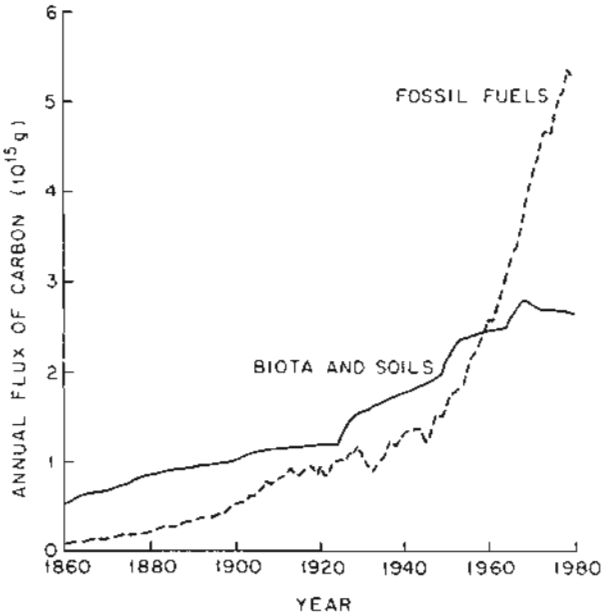

Fig. 19.26 Net flux of carbon to the atmosphere from fossil fuels, biota and soils. Based on Houghton et al. (1983).

weather, wait a bit (hours to a few days)". The same can be said for climate, though the cycles and changes occur over a longer time period. The greater interest in climate and climate change stems from the justified concerns that climate warming will result from increased atmospheric concentrations of carbon dioxide (CO_2), resulting in the "greenhouse effect" as CO_2 absorbs long-wave terrestrial reradiation. The CO_2 concentration has increased from an estimated 265 p.p.m. in 1850 to about 350 p.p.m. in 1990. The burning of fossil fuels is assumed by many people to be the only important source of the increase, yet studies by Woodwell and Houghton (1977), Woodwell et al. (1978) and Houghton et al. (1983) have shown the importance of land-use practices (harvest of forests, conversion of forest to agriculture, afforestation, regrowth of harvested forests and build-up of soil organic matter) in the CO_2 global budget. Until about 1960 the release of carbon from terrestrial systems exceeded release from fossil fuels (Fig. 19.26). The annual increase in atmospheric CO_2 is now 1–1.5 p.p.m., and the rate of increase is accelerating, so that by 2030 A.D. concentrations could reach 600 p.p.m. (Keeling and Bacastow, 1977).

Through modeling, a doubling of CO_2 in the atmosphere is expected to result in a global warming of 2–4°C (Manabe and Stouffer, 1979). However, in the Arctic a 3 to 10°C temperature rise is predicted as the product of the greenhouse gases, resulting from a 0.5–1.0°C rise in summer but an 8–10°C rise in winter. Precipitation may increase 20–30% (Environ. Can., 1989). Kelly and Jones (1981) summarized data from 1881–1981 for 65 Arctic stations. They reported that 1881–1920 was a cold period, followed by warming until the early 1950s. Arctic warming has prevailed in the western Canadian Arctic in the 1980s and 1990s, but is less pronounced in the eastern Arctic. However, on a global and a circumpolar basis, several years in the 1980s and 1990s have been the warmest in recorded history, giving support to the belief that global warming is already in progress. Other indications of warming in the Arctic are the earlier melt of snow in the North American arctic tundra (Foster, 1989) and the rise in permafrost temperature of 2°C or more in the last few decades (Lachenbruck and Marshall, 1986).

Assuming climate warming, Williams (1980) modelled climatic data from the 10 warmest arctic summers and winters for the past 70 years. She found that circulation changes resulted in large coherent anomalies elsewhere, with some areas warmer, other areas cooler. The warmer winters were characterized by larger amplitude anomalies in the Arctic and elsewhere. As pointed out by Hare (1977) and Williams (1980), climate models to date are not complex enough to provide the level of accuracy needed. Yet they point to a time when they will become a major tool for determining the potential response of climatic systems to natural and human-induced perturbations.

Past climatic patterns

To set the climatic background for the later discussion of arctic vegetation, one needs to consider the late glacial and post-glacial times – the last 14,000 years. Based upon pollen analysis, the maps of *Picea* (mostly *P. glauca*) show that its northern limit was near the United States–Canadian border about 12,000 yr B.P. Between 12,000 and 10,000 yr B.P., *Picea* reached the lower Mackenzie Valley region with the development of a forest–tundra ecotone (Ritchie and MacDonald, 1986). The forest ecotone was near Hudson Bay about 6,500 yr B.P. (Bryson et al., 1965) and reached its present position in Labrador–Ungava about 5,000 yr B.P. (Short and Nichols, 1977). Based upon pollen analyses, data from climatic

stations, and tree-ring chronologies, Diaz et al. (1989) concluded that inferred climate variation in the past 5,000 years has resulted from planetary-scale waves and north–south shifts in the mean boundary of the Arctic Front.

Spruce occurred 100 km north of the modern tree line east of Inuvik, N.W.T., as recently as 5,500–4,000 years B.P. (Ritchie and Hare, 1971) and 160 km north of the modern tree line in southern Keewatin, 3,000–2,000 years B.P. (Nichols, 1975, 1976). According to the 1772 map of Samuel Hearne (at the end of the Little Ice Age) the "woods edge" was 125–200 km further south from Churchill to Great Slave Lake but only 10–75 km further south, north of Great Bear Lake (Ball, 1986). Forests near the tree line were reported to be sexually inactive, and thus vegetative reproduction predominated (Elliott-Fisk, 1983), yet this was not true east of the Mackenzie Delta area (Black and Bliss, 1980), nor could this have been the case with the rate of forest advance after the Little Ice Age across central Canada. Assuming that the forest–tundra ecotone was in climatic balance, then the past oscillations of these ecotones indicate significant shifts in climatic boundaries in the past and potentially in the next 50–100 years, should climatewarming continue.

There is evidence of climatic warming in the High Arctic from 9,000 to 3,500 years B.P., followed by climatic deterioration based upon pollen and macrofossil plant remains in peat on Axel Heiberg Island at 79°25′N (Hegg, 1963) and northern Greenland at 82°19′N (Fredskild, 1969), and a lake core from Baird Inlet, east-central Ellesmere Island, at 78°29′N (Hyvarinen, 1985). The meager pollen record and the lack of driftwood younger than 2,700 ± 100 years B.P. indicate that a cold, dry climate has prevailed in northern Greenland since about 2,100 years B.P. (Fredskild, 1969) and since 3,500 years B.P. in east Ellesmere Island (Hyvarinen, 1985). Climatic changes to polar desert occurred about 3,900 years B.P. at Nord, Greenland (87°36′N). Funder and Abrahamsen (1988) believed that the change to colder summers initiated the polar deserts. Based upon pollen and leaf remains in peat deposits on Devon Island (75°33′N), little climatic or vegetation change has occurred for the last 2,450 years (Jankovska and Bliss, 1977).

Putnins (1970) reported on the climatic trends in Greenland. The Norsemen settled Herjolfsnes, southwestern Greenland, in 985 A.D. They brought sheep and cattle and developed a farming society that lasted about 400 years. The combination of hard living conditions, genetic isolation, pathological conditions and climate change led to their extinction. Climate amelioration has taken place in recent times, especially since 1920, exemplified by both temperature increase and the further retreat of most glaciers. At four settlements in west Greenland (Ivigtut 61°N to Upernavik 73°N), mean annual temperature has risen 1.3°C in the south to 1.9°C in the north, comparing the 1881–1910 period with the 1914–1943 period. As in the Canadian Arctic, temperature changes were more pronounced in winter than in summer (Kelly and Jones, 1981).

Arctic microenvironments

The environmental conditions 1–2 m above and below the soil surface constitute the microenvironment for a local area or habitat. Microenvironments are characterized by the radiation, temperature, wind, and moisture regimes of this near-surface, soil–atmosphere layer. These regimes are controlled by regional climate as modified by local topography, plant structure, and cover. It is the environmental conditions of these local habitats to which most arctic plants and animals must be adapted.

Snow cover

Generally speaking, snow covers arctic vegetation in winter except for tall shrubs (3–5 m) along rivers, streams, and steep slopes in the Low Arctic. Plants on wind-exposed ridges of uplands are sometimes blown free of snow for days or weeks. However these are the exception, for in most locations snow comes in late August through September when frontal storms can penetrate the dominant high-pressure systems. Snow rapidly smooths out the landscape, filling the depressions and greatly reducing surface roughness. Snow depth gradually increases over winter, reaching a maximum prior to snowmelt from late May through early July. With a snow cover and diminishing daily solar radiation, net radiation becomes negative and remains so until snowmelt (see radiation and energy balance, below). Strong radiative cooling results in surface inversions, setting up quite steep temperature gradients from the relatively warm, yet frozen, soils to the snow surface. These conditions result in a flow of heat and

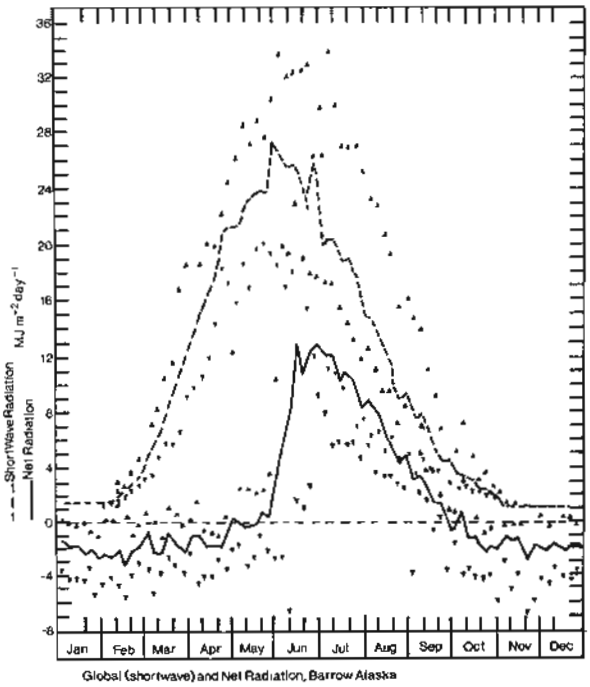

Fig. 19.27. Global shortwave and net radiation at five-day intervals over sedgelands at Barrow, Alaska. Based upon Dingman et al. (1980).

moisture from the soil surface to the upper snow surface. Over time this produces a layer of hoar crystals in the snow (Dingman et al., 1980). A loose depth-hoar layer (ice crystals) provides little resistance to lemming feeding on sedges and mosses, and the hard snow crust above provides some protection from predators. In general, lemming activity is much greater under deep snow where there is more insulation. At Barrow, Alaska, there was a greater density of winter lemming nests in polygonal troughs than on the top of polygons with their thin snow cover (Batzli et al., 1981). At the Truelove Lowland, Devon Island, Canada, there were also more nests under the deep snowdrifts (1–3 m) in the lee of beach ridges than in adjacent sedge meadows (30–40 cm snow depth).

Snow is a good insulator, and consequently soil temperatures change little while surface snow temperatures fluctuate greatly. During a six-day period in early March at Barrow, temperatures ranged from −47° to −35°C at the snow surface, but only from −27° to −26°C at the soil surface; snow depth was 30 cm (Dingman et al., 1980). At the Truelove Lowland, five-day temperature means were −33°C just above the snow (25 cm in depth) and −24°C at the −1 cm level. Minimum surface temperatures were not reached until mid-April under an average 25–35 cm snow cover. This demonstrates the long period of heat loss from soils each winter.

Radiation and energy balance

As presented on page 569, the radiation balance describes the partitioning of radiant energy into incoming and absorbed, long-wave incoming and outgoing, and reflected radiation. Insulation is greatly influenced by cloud cover, which averages 65–70% annually at Barrow. Similar values are reported at other arctic weather stations. This results in an increase in long-wave radiation scattered downward in summer. Albedo or reflected energy is another important component. At Barrow, Alaska, albedo averages 80–90% of total solar radiation over snow-covered surfaces and drops to 10–20% in summer (Dingman et al., 1980). At the Truelove Lowland, Canada, albedo averaged 70–85% from March through May, and dropped to about 15% over a wet sedge–moss surface and to 18% over a dry gravelly beach-ridge surface with cushion plants (Courtin and Labine, 1977). Lower albedo (65–75%) occurs with old snow, and a component of fine soil and organic debris (Teeri and Barrett, 1975).

Long-wave incoming radiation (RR$\ell\downarrow$) is a significant percentage of total solar radiation in many arctic sites because of their high cloud cover. Net radiation in these sites is a relatively small percentage of total solar (extraterrestrial) radiation (Table 19.9). This is in contrast with temperate regions with more direct sunshine.

Annual patterns of incoming short-wave radiations, net radiation and albedo are presented in Figs. 19.27 and 19.28 for Barrow and Truelove Lowland respectively. One may note that Barrow

TABLE 19.9

Longwave incoming and net radiation in relation to total solar (extraterrestrial) radiation at select arctic sites in summer (July)

Location	Total solar radiation ($MJ\ m^{-2}d^{-1}$)	Long-wave %	Net radiation %
Axel Heiberg, I., N.W.T.	41.1	63	23
Barrow, Alaska	43.4	59	26
Truelove Lowland, N.W.T.	39.9	65	20
King Christian I., N.W.T.	27.2	68	23

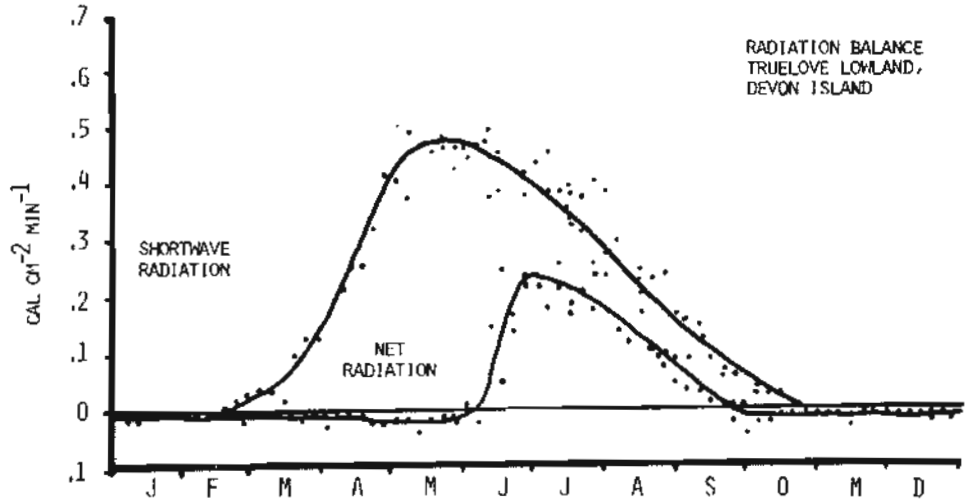

Fig. 19.28. Global shortwave and net radiation at five day intervals over cushion-plant cryptogams at Truelove Lowland, Devon Island, N.W.T. Based on Courtin and Labine (1977).

at 71°N has a positive radiation balance throughout the year, but at 75°N short-wave radiation becomes negative in October and positive in February. At each site net radiation does not become positive until snow melts in June. For most arctic sites about 50% of the annual solar radiation is received and dissipated before snowmelt. It is no wonder that the growing season is so telescoped and that the capture of energy by plants occurs in an environment with decreasing available energy.

TABLE 19.10

Net radiation and its components[1] in different Canadian arctic habitats and in Barrow, Alaska

Location	Plant Community	Month and # of days	Rn (MJ $m^{-2}d^{-1}$)	Fluxes (%)			Bowen Ratio (%)	Reference
				LE	H	G		
Low Artic								
Tuktoyaktuk 69°N	low shrub–heath	July 31	9.09	56	25	19	45	Haag and Bliss, 1974
Barrow 70°N	wet sedge moss	July 14	9.96	66	32	2	48	Weller and Holmgren, 1974
High Arctic								
Sachs Harbor 72°N		July 31	10.17	38	45	18	119	Vowinckel and Orvig, 1971
Truelove Lowland 74°N	cushion plant	July 4	10.17	21	70	9	333	Addison, 1977
Truelove Lowland 74°N	wet sedge–moss	July 4	8.96	53	37	10	70	Addison, 1977
Cape Abernethy 77°N	cryptogam–herb	July-Aug 30	6.30	26	61	13	235	Addison and Bliss, 1980
Axel Heiberg 79°N	cryptogam–herb	July 31	9.60	48	38	14	79	Ohmura, 1982

[1]See text for symbols

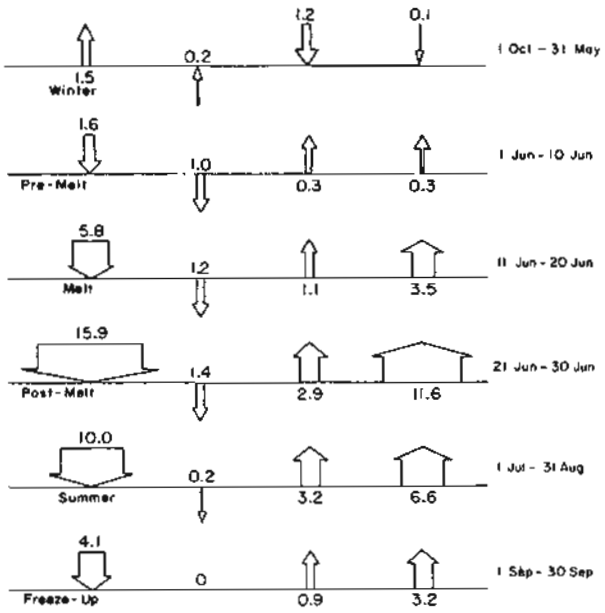

Fig. 19.29. Six environmental seasons based on partitioning net radiation at Barrow, Alaska. Based on Dingman et al. (1980).

Knowing the partition of net radiation at plant–soil surfaces is of great importance to understanding the kinds of stresses to which plants are subjected. In general, microenvironments that have abundant water dissipate much of the energy as latent heat of evaporation and transpiration (LE). These habitats usually support plants of a larger size, plants that grow more rapidly, and that provide more forage for herbivores. In contrast, plants that grow in relatively dry habitats generally are of smaller size, grow slowly, and provide less plant cover and forage.

The data in Table 19.10 show how net radiation is partitioned in different arctic microenvironments. One striking feature is the great similarity in net radiation during July extending from 69° to 79°N. The only low value is at Cape Sparbo, King Christian Island, Canada, a very cloudy environment (Addison and Bliss, 1980). In microenvironments that have wet to moist surface soils in summer, evapotranspiration dominates, while in sites with drier surface soils much more energy is dissipated as sensible heat (H). Soil heat flux (G) is generally 10–20% except at Barrow, a site with wet soils and very high humidity all summer and thus a low vapor-pressure gradient.

Establishing seasons based upon partitioning of net radiation is illustrated in Fig. 19.29. These data clearly show the dramatic shifts in the three components of net radiation over the course of a year.

Temperature

Of the environmental factors temperature is the most commonly measured, and also the easiest to measure. Consequently there are abundant data on the temperature regime of arctic microenvironments. Air temperature within arctic vegetation differs from air temperature above because of the heat exchange between air, plant surfaces, and soil surfaces. The vertical profile of air temperature through the canopy depends on solar angle and density of the plant canopy. In wet sedge–moss plant communities, which are common at Barrow, Alaska, and the Truelove Lowland, Canada, the steepest temperature gradient is within 10–15 cm of the ground (Fig. 19.30a,c), but only 5–8 cm within cushion plants (Fig. 19.30b). In a shrub plant community the temperature gradient is steepest within 50 cm of the soil surface (Fig. 19.31a,b). In both sedge–moss and shrub communities, temperatures were highest at the soil surface, the main surface receiving solar radiation. Temperature drops rapidly above and below as the convected energy upward and the conducted energy downward heat the air and soil respectively. However, within frozen soils below 20–50 cm, the soil temperature gradient is very steep. Surface and near-surface air temperatures remain higher than air above the plant canopy (50–100 cm) because net radiation remains positive throughout the arctic "summer day". In late July when the sun is nearer the horizon for several hours each "night", net radiation becomes negative and surfaces cool (Fig. 19.31b). Under conditions of bright sun and little wind, soil surfaces can be 20 to 30°C higher than the air 50 cm above. These relatively warm microenvironments permit much higher rates of metabolic activity for animals and plants than would occur otherwise. Temperature drops rapidly within the soil, for soils typically remain frozen below 35–50 cm even in late summer.

Leaves and flowers, as well as invertebrates on the soil surface, often maintain higher temperatures than the adjacent ambient air. Krogg (1955) reported that willow catkins with transparent hairs reflected solar radiation to the inner surfaces, trapping the longwave (infra-red) radiation. This raised catkin temperatures 2–4°C above that of the ambient air. Leaves of *Dryas integrifolia*, a cushion plant, had leaf temperatures above 45°C for 3 hr

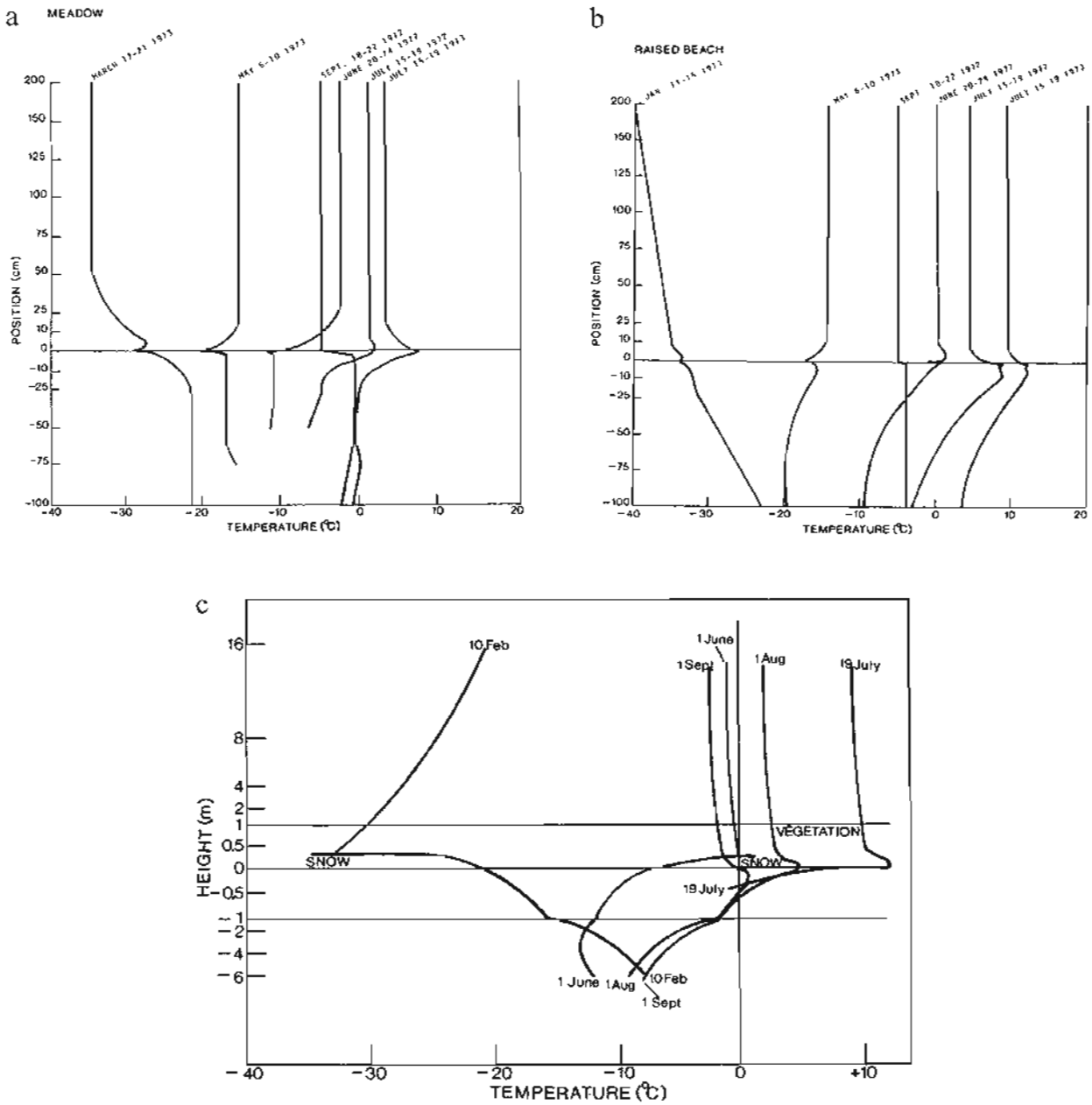

Fig. 19.30. Temperature gradients throughout the year within sedge–moss (a) and cushion-plant (b) communities at Truelove Lowland, N.W.T. and sedge–moss communities (c) at Barrow, Alaska. Based upon Courtin and Labine (1977) and Bunnell et al. (1975) respectively.

on a sunny day, 15–20°C higher than adjacent air (Addison, 1977). In contrast, sedges growing in wet and cold soils had leaf temperatures elevated 5–10°C on sunny and 0–2°C on cloudy days. Flowers, especially those with a parabolic shape and that turn with the sun (heliotropic), heat considerably on sunny, calm days, and consequently flower temperatures may be elevated by 5–10°C (Mosquin and Martin, 1967; Kevan, 1973). Kevan (1975) found that various insects use *Dryas* and *Papaver* flowers as basking sites, which results in elevating their body temperatures by 7 to 17°C. Yellow flowers that appear red to insects are more commonly visited by insects.

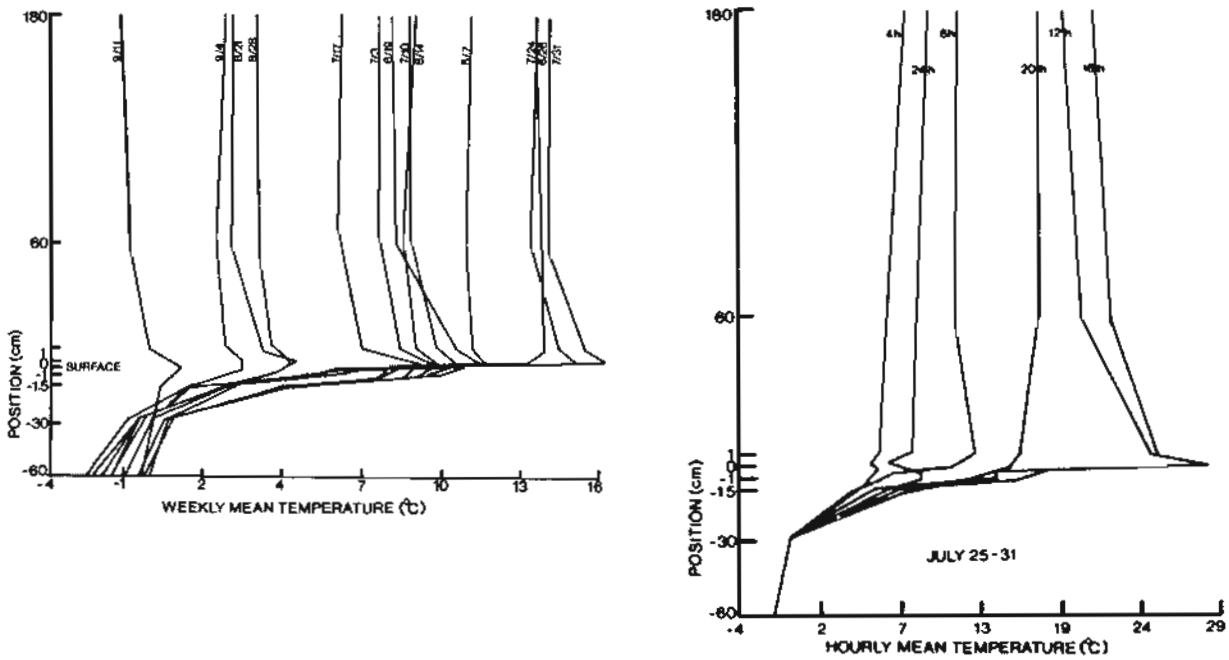

Fig. 19.31. Seasonal (a) and diurnal (b) progression of a temperature gradient at Umiat, Alaska. Based on Bliss (1956).

Plant and animal microenvironments are also influenced by topographic location of the sites. At Umiat, Alaska, the solar angle of incidence at noon on 22 June ranged from 80° on a south-facing slope to 36° on a north-facing slope. These values decreased to 56° and 12° respectively at the 22 September equinox. While air temperatures at 10 cm were higher on the two south-facing slopes compared with the level and north exposure, differences in soil temperature (−10 cm) were more pronounced. Soil temperatures were 50–70% lower on the north than on the steeper south exposure throughout the summer and 35–50% lower on the 8° than on the 36° south exposures for the same period (Table 19.11). As will be discussed later, differences in soil temperature are often more important than differences in air temperature in influencing plant growth.

On a somewhat larger scale (mesoscale) one can consider the microenvironments of an area, the Truelove Lowland, and how temperature changes during the summer throughout this 43 km^2 area

TABLE 19.11

Mean maximum, minimum and mean monthly temperatures (°C) at 10 cm air and −10 cm soil levels for four sites, Umiat, Alaska 69° 22′ N[1]

Site	Plant Community	Height (cm)	June (15d)			July (31d)			Aug (28d)		
			Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
South-facing, 36°	Grass and medium shrubs	+10	17.6	5.6	13.6	18.6	4.2	11.4	13.1	2.0	6.9
		−10	11.1	7.2	9.2	13.0	8.1	10.4	10.9	7.0	8.7
Ridge top, 0°	Dwarf shrubs	+10	15.8	4.4	12.8	16.4	3.9	10.6	11.5	1.5	6.1
		−10	5.0	3.1	4.0	6.9	4.4	5.5	5.5	3.9	4.6
North-facing, 8°	Heath–tussock grass	+10	15.9	5.0	12.5	16.6	3.1	10.5	11.2	1.1	5.8
		−10	3.9	2.0	2.3	5.9	3.9	4.9	4.4	2.8	3.4
South-facing 10°	Heath–tussock grass	+10	15.8	4.2	10.2	18.5	3.3	11.2	13.1	1.3	6.7
		−10	5.5	3.0	4.4	8.6	5.0	6.7	6.1	3.5	4.6

[1] From Bliss (1956).

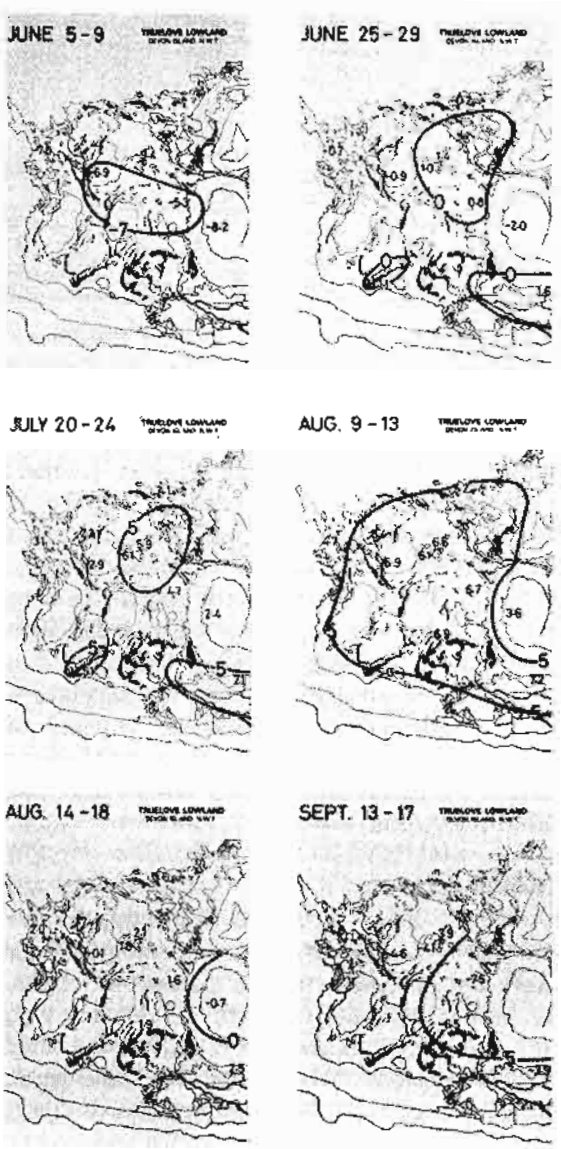

Fig. 19.32. Isotherm maps showing the seasonal progression of temperature throughout the Truelove Lowland, N.W.T. Based on Courtin and Labine (1977).

(Fig. 19.32). In early June, the entire lowland was covered with snow and was below freezing (Fig. 19.32a). Although still largely snow-covered in late June, three areas were above freezing, the Truelove Valley, a large beach ridge near the Truelove Inlet, and a central area with large granite outcrops of rock. This latter area probably is also warmed by the outflow of air moving down the Gully River Valley (Courtin and Labine, 1977) (Fig. 19.32b). In late July the entire lowland has warmed, but the three "heat islands" remain (Fig. 19.32c).

Maximum temperatures were reached in early to mid-August, just before the return to freezing conditions the following week (Fig. 19.32d,e). In some summers there is a 2–3 week lag between peak season and a return to freezing temperatures. This demonstrates the dramatic shift from summer to fall and then winter conditions as the sun reaches the horizon each "night". These high-arctic ecosystems are very dependent upon solar radiation. By mid-September early winter had arrived with a thin snow cover, and all sites had temperatures well below freezing (Fig. 19.32f). At most high arctic weather stations, once the mean daily temperature drops below freezing it seldom rises above freezing for more than 3–5 days until next spring.

Precipitation, air and soil moisture

Except for the arctic maritime climate of Baffin Island and southern Greenland, most arctic areas receive limited precipitation (see Figs. 19.22, 19.24, 19.25). Consequently various writers have referred to large portions of the Canadian Arctic Archipelago as a polar desert (Tedrow, 1966; Charlier, 1969; Bliss, 1979, 1981; Aleksandrova, 1980; Bliss et al., 1984). Bovis and Barry (1974) used various climatic data and analysis techniques to determine what areas are deserts and semi-deserts. They concluded that delimiting polar deserts on the basis of physical climatic data could not be done. This writer would agree, for other factors such as geologic formations, soil development and nutrients, and availability of water after snowmelt are important. In general, the high percentage of cloud cover, high relative humidity, and accompanying reduced evapotranspiration result in reduced rates of soil drying.

Precipitation from June through August (30–70 mm) is generally 30–50% of the annual total, with most of this falling as rain. In general, cold summers have less rain than warm summers, largely as a function of the amount of moisture that an air mass can hold in relation to its temperature. Since most summer precipitation occurs as light rain or mist every few days, rather than infrequent heavy rains, surface soils dry relatively little in most years, except in the High Arctic.

Based upon limited data from the High Arctic, relative humidity is generally 80–90% from June through August. For short periods (usually hours) with bright sunshine, relative humidity can drop to 40–50%, but seldom lower.

In most arctic sites, soil moisture remains high

all summer, seldom dropping much below field capacity (−0.3 bars or −0.03 MPa). Soil moisture is expressed in thermodynamic terms rather than as percentages of water, for the latter concept does not indicate direction of water movement or the response of a plant to the amount of water present. Water potential (ψ) is a measure of the free energy of water in relation to the free energy of pure water at a given pressure and temperature. The water potential of pure water is assigned 0 MPa. Since the free energy of plant and soil water is lower than pure water, all data are expressed in negative numbers. I shall return to this topic when I discuss soil–plant–air relations, but for now I shall deal only with soil water potential (ψs).

In most arctic environments, ψs ranges from −0.03 to −0.5 MPa within the rooting zone of plants (−5 to −20 cm). However, in exceptionally dry summers and in those microenvironments with well-drained soils (uplands, slopes, gravelly soils), ψs may drop to −2.0 to −4.0 MPa or lower. These conditions are more common in the High Arctic than in the Low Arctic of Alaska, northern Yukon, and across the mainland N.W.T. Arctic soils are also moister because of the capillary rise of water as the frozen soil within the "active layer" thaws each year. The permanently frozen soils below prevent downward movement of water.

Wind

Wind velocity is influenced by the frequency of cyclonic storms and the steepness of atmospheric pressure gradients and by topography. The limited plant cover and its short height results in winds being more noticeable and influential at ground level in the Arctic than in forest- or shrub-dominated environments. In general, wind velocities are no greater than in mid latitudes and considerably less than in alpine environments. Wind velocity decreases dramatically from 1–2 m down to the ground surface or to the canopy of plants. Courtin and Labine (1977) calculated that winds decreased 25% from 10 to 1 m and about 30% from 10 m to 0.5 m. Throughout the summer wind-speed averaged 1.1 to 3.7 m sec^{-1} at three locations in the Truelove Lowland at 0.5 m, and 2.4 to 5.2 m sec^{-1} at 10 m. Föhn winds were much higher, averaging 11 to 23 m sec^{-1} in five separate storms (Courtin and Labine, 1977). During these storms temperature increased 5 to 12°C and relative humidity decreased 5 to 44%. Föhn winds resulted in melting 10–20 cm of snow across the Lowland in a 36-hr period on 26 June, 1970. Another dramatic storm occurred on 21 October, 1971 when snow melted, then refroze, sealing many plants in ice and reducing the forage available to musk-oxen and lemmings that winter. Sudden thawing followed by refreezing can occur over large areas of the High Arctic in the fall. These conditions are believed to cause the death of large numbers of Peary's caribou and musk-oxen, as occurred in the winter of 1973–1974 (Parker et al., 1975). These are the most dramatic biological influences of temperature and wind in the Arctic.

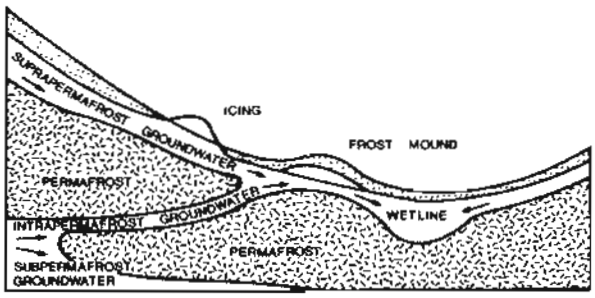

Fig. 19.33. Hydrologic processes on a slope underlain by permafrost. From Woo (1986). Note that ⁘ represents seasonal frost and ⁘ represents permafrost.

Hydrology

Until the 1970s, relatively little was known about the dynamics of arctic hydrology. Major reviews on hydrology within permafrost terrain have been prepared by Ryden (1981) and Woo (1986). The hydrologic year is generally divided into three seasons (Woo, 1986; Woo and Steer, 1986; Everett et al., 1989), although Ryden (1981) described four seasons. Winter is characterized by prolonged darkness, and intense heat loss from the ground into the snow and adjacent air. It is inferred that an upward vapor pressure gradient exists in the frozen active layer, enabling the soil to be rendered more porous and susceptible to meltwater penetration in spring (Smith, 1985; Woo and Steer, 1986). Exposed ridges are often swept bare, but snow is trapped in gulleys and concavities.

Spring snowmelt begins in mid-May to mid-June when radiation is high, which allows rapid snowmelt and the development of the active layer. The summer solstice occurs about the time that the land becomes snow-free. Sublimation accounts for about 10–20% of annual precipitation (30 mm at Resolute and 20+ mm at the Truelove Lowland (Ryden, 1977). In small catchment areas drained

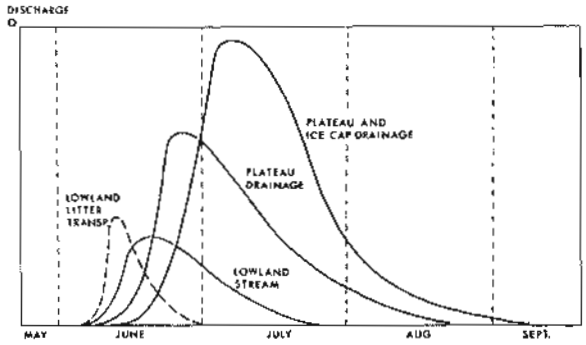

Fig. 19.34. Generalized runoff hydrograms for three types of water systems on the Truelove Lowland, N.W.T. based upon three years of record. From Ryden (1977).

by a stream system, 80–90% of the annual runoff occurs in a 2–3 week period (McCann et al., 1972; Dingman et al., 1980; Woo and Steer, 1986; Everett et al., 1989). Downward movement of meltwater is impeded because of a shallow active layer.

The summer hydrologic season is characterized by limited stream flow, the result of snowbank melt and further thawing of the active layer. On slopes in the Low Arctic (Shaver et al., 1990) and the High Arctic (Woo and Steer, 1983) there is limited downslope subsurface flow. These waters not only recharge ponds and small lakes, but also provide nutrients that often enhance plant development (Shaver et al., 1990). Light summer rains generally infiltrate, providing little, if any, runoff, as a result of intensive evaporation in July. Evaporation results in considerable surface-drying of soils, especially in the High Arctic. If heavy rains do occur, flooding often results in lowlands, because these drainage basins are near saturation throughout the summer.

During snowmelt and heavier summer rains, a shallow overland flow of water occurs in lowlands (Ryden, 1977) and on slopes (Lewkowicz and French, 1982; Woo and Steer, 1982). When the water table rises above the ground surface, both overland and rill flow occurs. These surface flows result in the redistribution of litter and nutrients (Muc, 1977; Ryden, 1977; Oberbauer et al., 1989). Considerable subsurface flow can also occur (Fig. 19.33).

The runoff pattern and its magnitude is very different if one compares drainage basins of different size (Fig. 19.34). These generalized runoff hydrograms, based upon limited field data (Holecek and Vosahlo, 1974; Ryden, 1977) from the Truelove Lowland, depict the time and magnitude of water release from catchments. The small catchment (0.12 km^2) was on the Lowland, the medium-sized catchment, the Gully River basin (22.4 km^2), on the plateau, and the large Truelove River basin (370 km^2) included part of the Devon ice cap. Meltwaters from the ice cap greatly increased the magnitude of streamflow and the length of time for discharge (3 mon). There was also a time lag (about 12 hr) of diurnal discharge, with minimum occurring in early afternoon and maximum flow near midnight throughout the summer.

Water budgets have been calculated for the Barrow and Truelove Lowland coastal tundra (Table 19.12). Although these stations are separated by four degrees of latitude, their water budgets are very similar. Evapotranspiration is considerably higher at the Truelove site, due to its higher solar radiation and probably lower relative humidity in summer.

PLANT COMMUNITIES AND FLORISTICS

With the diversity of topography and climate that exists in different mountain systems and in the Arctic, it is not surprising that the diversity of

TABLE 19.12

Annual water balance for two arctic sites (all data are in mm)

Site	Precipitation			Runoff	Evaporation		Total	Reference
	Snow	Rain	Total		Snow	Plant soil		
Barrow, Alaska 71°N	113	62	175	103	9	63	72	Bunnell et al., 1975
Truelove Lowland, Devon Island, N.W.T. 75°N	137	48	185	84	20	81	101	Ryden, 1977

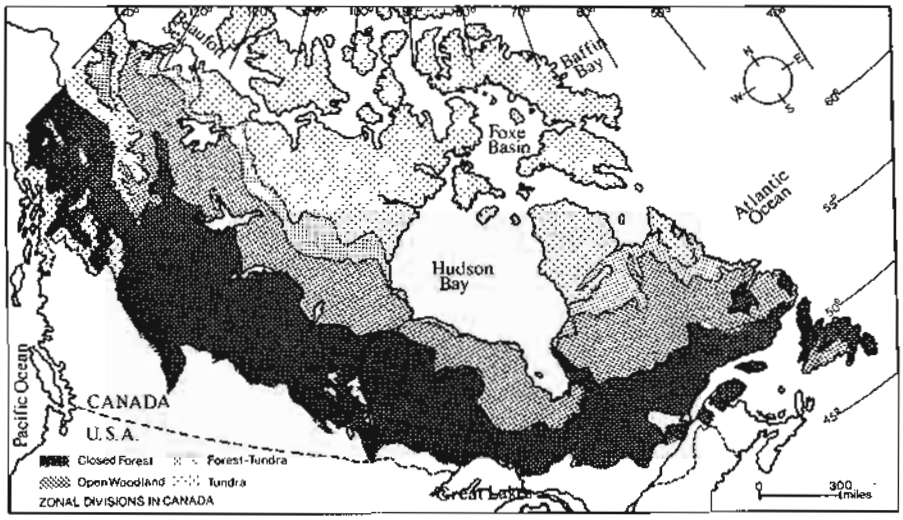

Fig. 19.35. Delimitation of the three subdivisions of the Taiga: closed forest, open woodland or lichen woodland, and forest tundra.

species and the plant communities they comprise is also great. The North American Arctic extends from 55°N along Hudson Bay to northern Greenland and Ellesmere Island at 83°N. Plants occur from sea level to the edge of glaciers and ice caps at 350 to >500 m in Greenland, Baffin, Devon, Ellesmere, and Axel Heiberg Islands of Canada.

Alpine environments extend into the Arctic via the Brooks Range in Alaska and the Richardson and British mountains of the Yukon Territory. In these northern mountains, the designation alpine or arctic is academic, for one system blends imperceptibly into the other.

As used here *vegetation* refers to the general structure and pattern of the dominant species within a region. The largest landscape unit of vegetation with a similar appearance or physiognomy is the *plant formation*, or *biome* when animals as well as plants are included. While there is a general appearance to the vegetation within a biome, not all vegetation has the same structure, therefore different *vegetation types* occur (shrub, herbaceous, graminoid, cryptogam). The dominant plants of a vegetation type have the same physiognomy and life form (position of the overwintering buds). Within a vegetation type, different habitats may have different groupings of species. Species seldom occur at random but occur along environmental gradients in response to their physiological and morphological adaptations. A group of plants with a similar floristic composition and plant structure of the dominant species (based upon cover or biomass) comprise a *plant community*.

Taiga, open woodland, and forest tundra

While this book is devoted to describing arctic and alpine ecosystems, some orientation to the adjacent forests is appropriate. The taiga or boreal coniferous forest (biome) is typically divided into three major south to north zones. These are the closed forest, open woodland or lichen woodland, and forest tundra (Rowe, 1972; Hare and Ritchie, 1972) (Fig. 19.35).

North of the closed forest in Canada lies a broad zone 150 to over 300 km in width of lichen woodland and forest tundra. Permafrost becomes more continuous, the rooting zone is shallower, and the climatic conditions for tree growth are less favorable than in the closed forests to the south. Stands with widely spaced *Picea glauca*, in places *Pinus banksiana*, are underlain by a carpet of fruticose lichens often 10–20 cm in thickness and with scattered herbs and low shrubs. Lowlands are dominated by *Picea mariana* and to a lesser extent *Larix laricina*. Open woodland with lichen ground cover is relatively minor in the Mackenzie Delta region due to frequent forest fires, the longer time required for lichen cover to develop (150–200 years), and the general abundance of shrubs in the understory (Black and Bliss, 1978). Open woodland is minor in the northern Yukon and Alaska due to the presence of mountains where, climati-

cally, this forest type should occur.

Fire is important in these open forests, for without it most would develop into closed forests in ~200 years. Lichens play a key role by reducing water flux, making more water available to the scattered trees and providing fuel for the frequent fires (Rowe and Scotter, 1973; Kershaw, 1978; Black and Bliss, 1978).

Throughout northern Alaska and Canada there is a relatively narrow zone (10–50 km) of forest tundra. This vegetation zone consists of scattered clumps of trees in more protected sites where snow accumulates, and shrub tundra in more wind-exposed habitats. In many areas the transition from forest tundra to shrub tundra is marked only by the loss of the stunted trees. Because of this patterning, Russian ecologists have considered shrub tundra a part of the subarctic rather than Arctic (Aleksandrova, 1970, 1980) for they believe that repeated fires have converted open woodland and forest tundra to shrub tundra. Across Canada *Picea mariana* generally is found on poorly-drained land or sites with a shallow active layer (Larsen, 1971, 1972; Black and Bliss, 1978). It is the predominant species in uplands at the tree line in northern Canada (Rowe, 1972; Payette et al., 1985) and Alaska (Viereck and Dyrness, 1980). In the Yukon Territory and Alaska, *Picea glauca* generally extends further north in better drained uplands and river terraces (Drew and Shanks, 1965). *Picea glauca* also forms the northern limit of trees on south-facing slopes and along river terraces in the Mackenzie River Delta region.

Repeated fires within these subarctic plant communities have little effect on the understory vascular plants, but a profound effect on lichens and mosses for many years. Shrub species resprout rapidly after fire (2–10 years) but it takes more than 200 years for an extensive lichen cover to develop in the Mackenzie Delta region on fine-textured soils (Black and Bliss, 1978), in contrast with areas to the southeast where shrubs are minor and lichen cover develops in 60 to 120 years on coarse, sandy soils (Maikawa and Kershaw, 1976). Fire also plays a key role in the life history of *Picea mariana* by altering the thermal regime of the soil (Rouse and Kershaw, 1971), preparing a seed bed (Ahlgren, 1959) and opening the semi-serotinous cones (Vincent, 1965). Fire in the forest tundra can eliminate tree establishment should the general climate be in a cooling regime (Nichols, 1975; Black and Bliss, 1980). Since relatively high surface temperatures (15°C) are necessary for seed germination, seedling establishment can be prevented during cooler climatic periods. A "window" of 5–8 years occurs for seedling establishment following fire near the tree line, the product of short seed viability, rapid seed release from surviving cones and seed destruction in the soil by rodents and insects. Even-aged stands, after a fire, result from this short time period for seedling establishment. Massive fires could force the tree line 50–100 km further south should they occur during a cool period (Black and Bliss, 1980). This helps to explain the past oscillation of the tree line in addition to climatic change during the Hypsithermal, when mean daily temperature is estimated to have been 4 to 5°C warmer in June–August at Ennadai Lake in the Keewatin (Nichols, 1976) and at Tuktoyaktuk (Ritchie and Hare, 1971). The warmer period, based upon pollen records and radiocarbon dating, lasted from 5550 to 4500 years B.P.

Picea glauca and *P. mariana* are limited in their northward migration in Labrador and Ungava by higher elevation and limited soil development (Elliott and Short, 1979). In the District of Keewatin, N.W.T., sexual reproduction seems to limit these species at their margin (Elliott, 1979), whereas in the Mackenzie Delta region and the Brooks Range, Alaska, these species reproduce sexually and *P. mariana* also by layering (Black and Bliss, 1980; Goldstein et al., 1984).

Summaries of the boreal forest include those by Larsen (1980, 1982), Ritchie (1984, 1987) and Elliott-Fisk (1988).

Arctic tundras and polar deserts

Classification of the Arctic into botanical units has been based largely on floristics. Studies over the last 20 years have shown that there are many physical and biological factors that demonstrate that this vast region can best be divided into the Low and High Arctic (Table 19.2). A brief summary of the biogeographic zones and major vegetation types within each zone is presented in Table 19.13. The Low Arctic (Fig. 19.1) includes all of Alaska but Barrow, most of mainland arctic Canada, southern Baffin Island, and southern Greenland. It should be noted that the Low Arctic extends to 73°N along the warmer west coast of Greenland, but to only 68°N along the colder east coast (see also Chapter 20).

Arctic tundras in the Low Arctic

This large area has a vascular flora of over 600 species and a vegetation that covers 80–100% of the soil surface; lichens and mosses are very important. Large areas of the rocky Precambrian Shield of Canada have a lower plant cover because of limited soil development. In most areas shrubs comprise a significant component of the vegetation except in the wetlands (mires) where sedges, bryophytes, and scattered grasses predominate. In areas with medium to well-drained soils, lichens and mosses cover most soil surfaces. Organic horizons are typically 10–30 cm thick in upland areas, but on the Arctic Coastal Plain of Alaska and in the Mackenzie Delta region, peats reach a thickness of 3–10 m (Fig. 19.36). Bird species are numerous, with many species of water fowl. Jaegers, ptarmigan, loons, and geese are characteristic species in many areas. Grazing by snow geese (*Chen caerulescens*) and ptarmigan (*Lagopus* spp.) have the greatest influence on vegetation. Barren-ground caribou (*Rangifer tarandus groenlandicus*) are the most characteristic large mammals, overwintering in the open woodland and forest tundra where they feed on lichens, low shrubs and herbs. They migrate to mountain and coastal tundras to calve and graze in summer. Lemmings, at least in a lemming "high", produce more net annual production and often have a greater biomass per unit area than the conspicuous caribou. This is also true for invertebrates in the vegetation and soils.

The major tundra vegetation types are (1) tall shrub tundra (*Alnus, Betula, Salix*; 2–5 m high) occurs along river terraces, stream banks, steep slopes, and lake shores; (2) low shrub tundra (*Betula, Salix*; 40–60 cm high) occurs on slopes and uplands beyond the forest tundra; (3) dwarf-shrub heath tundra (5–20 cm high) and dwarf-shrub heath–cottongrass tussock tundra occurs on soils of intermediate drainage; (4) graminoid–moss tundra (mires) (20–40 cm) occurs on poorly-drained soils; and (5) cushion-plant–herb–cryptogam (2–5 cm high) vegetation occurs on wind-exposed slopes and ridges where there is limited snow cover. This last vegetation type is commoner in the High Arctic and is a part of the polar semidesert complex (Bliss, 1980, 1988).

Tundra, as used throughout, refers to the vegetation of the Low Arctic where plant cover is nearly complete and where woody species, sedges, and grasses predominate. This excludes the cushion-plant vegetation (#5 above) which is considered part of the polar semideserts to be discussed later "Tundra" originates from the Finnish *tunturi*, the treeless uplands in northern Finland. The concept was used early in northern Eurasia for wet sedge-lands beyond the tree line. The word "tundra" was

TABLE 19.13

Biogeographical zones and major vegetation types within the Arctic

Andreyev and Alexandrova 1980	Tundra					Polar Desert	
	Sub-arctic Tundra			*Arctic Tundra*			
	Southern variant	Middle variant	Northern variant	Southern variant	Northern variant	Southern variant	Northern variant
Tedrow 1974	Low Arctic Tundra				Mid Arctic Subpolar Desert	High Arctic Polar Desert	
Bliss 1975, 1981	Low Arctic				High Arctic		
			Tundra		*Tundra*	*Polar Semidesert*	*Polar Desert*
	Tall shrub tundra	Low shrub tundra	Dwarf-shrub–heath tundra	Dwarf-shrub–heath–tussock-tundra	Graminoid–moss tundra Low shrub tundra Dwarf-shrub-heath tussock tundra	Cushion-plant–cryptogam Cryptogam–herb	Herb–cryptogam
	Graminoid–moss tundra		Cushion-plant–cryptogam tundra				

Fig. 19.36. Deep peats along the Colville River, northern Alaska

applied to similar climatic, floristic, and vegetational units in arctic North America and then to alpine areas.

Vegetation types

Tall shrub tundra. The larger rivers that flow from the taiga into the tundra have sand and gravel bars and islands that clog their meandering channels, and one or more old erosion surfaces, the terraces that mark their lateral banks. These habitats are commonly covered with various mixtures of *Alnus, Betula*, and *Salix*, to a height of 2–5 m, and usually with a dense understory of forbs and grasses. The same shrub species and often the same associated herbaceous species occur along steep slopes above rivers and lakes, and along small streams. These are habitats with well-drained soils that are often somewhat higher in nutrients, are warmer in summer, and have a deeper active layer (1–1.5 m) than the surrounding uplands. They also have deeper winter snow cover (2–3 m).

In arctic Alaska and the channels of the Mackenzie River in its delta, *Salix alaxensis* predominates on the coarser-textured alluvium. Associated shorter shrubs (1–2 m high) of lesser importance, and of varying floristic composition from site to site, include *Alnus crispa, Salix arbusculoides, S. glauca, S. lanata* ssp. *richardsonii*, and *S. pulchra* (Bliss and Cantlon, 1957; Drew and Shanks, 1965; Johnson et al., 1966; Gill, 1973; Komarkova and Webber, 1980).

Depauperate remnants of this vegetation type occur along rivers, on raised-center polygons and steep slopes on Banks and Victoria Islands (Kuc, 1974; Bliss and Svoboda unpublished). This community of *Salix alaxensis, S. lanata* ssp. *richardsonii, S. pulchra*, and rarely *Betula nana* ssp. *exilis* is typically associated with sedges rather than forbs, grasses, and the dwarf-heath species as on the mainland.

In southern Greenland, *Betula pubescens* 3–4 m high with an understory of *Anthoxanthum odoratum, Deschampsia flexuosa, Nardus stricta*, and *Poa nemoralis* occurs in warm, protected sites at Narssarssuaq (61°N) near the southern tip. At Ivigtut, just to the west along the coast, *Salix glauca* ssp. *callicarpaea* grows on slopes with grasses and a rich forb understory. *Alnus crispa* scrub, 2–3 m high, occurs along the river at Gronnedal and near Ivigtut (Böcher, 1954).

In Alaska and northwestern Canada, tall shrub vegetation is an important habitat for moose (*Alces alces*) whose range extends northward because of this vegetation. Arctic hares (*Lepus arcticus monstrabilis*) and ptarmigan feed on willow in both summer and winter.

Low shrub tundra. In Alaska and northwestern Canada, low shrub tundra is common beyond the forest tundra (Hanson, 1953; Hettinger et al, 1973; Corns, 1974). In the Mackenzie Delta region and in western Alaska, low-shrub tundra often dominates the landscape 50 to over 100 km beyond the forest tundra. As stated earlier, some ecologists believe that open woodland and forest tundra occupied these areas in the past, and that fire and changing climate have forced the tree line south (Ritchie and Hare, 1971). Within the Brooks Range, low-shrub tundra extends beyond the tree line on the southern slopes and into some of the passes, but on the northern slopes this vegetation type is uncommon.

The open canopy of shrubs is 40–60 cm high and is dominated by *Betula nana* ssp. *exilis, Salix glauca* ssp. *acutifolia, S. lanata* ssp. *richardsonii*, and *S. planifolia* ssp. *pulchra*. The ground cover includes scattered clumps of *Carex lugens* and tussocks of *Eriophorum vaginatum*, numerous forbs and grasses, and heath subshrubs (10–20 cm high). Various combinations of *Arctostaphylos alpina, A. rubra, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Rubus chamaemorus, Salix* spp., *Vaccinium uliginosum*, occur and, where snow lies late, *Cassiope tetragona* is seen, intermixed with the sedges and other heath species. Lichens and mosses provide a ground cover between the clumps and tussocks of *Carex* and *Eriophorum* respectively. Common species of lichen include *Cetraria cucullata, C. nivalis, Cladonia (Cladina) mitis, C. rangiferina, Cladonia gracilis, Thamnolia vermicularis*, and the mosses *Aulacomnium turgidum, Hylocomium splendens*, and *Polytrichum juniperinum*.

More limited areas of low-shrub tundra occur in the Chesterfield Inlet on the northwestern side of Hudson Bay, in northern Quebec and in southern Baffin Island (Polunin, 1948). The dominant species are *Betula glandulosa, Salix glauca* ssp. *callicarpaea*, and the heath species listed above. This vegetation occurs on well-drained slopes and rocky areas that are warmer in summer and that have a 50–100 cm cover of snow in winter. In much of the northeastern mainland Arctic of Canada, low-shrub tundra is minor, presumably because of limited winter snow and strong abrasive winter winds (Savile, 1972).

In western central and southwestern Greenland, willow scrub dominated by *Salix glauca* ssp. *callicarpaea* with *Betula glandulosa* and *B. nana* occurs on steep slopes and along streams and rivers from Disko Island (69°N) and Søndre Strømfjord (67°N) southward. These low-shrub tundras generally occur in the inner fjord regions that have a warmer and more continental climate. The willows may reach a height of 1–2 m, but in many areas are less than 1 m and often with few associated species other than *Cystopteris fragilis* ssp. *dickieana, Draba aurea,* and *Pyrola grandiflora* (Böcher, 1954, 1959). Heath communities rich in species are commonly associated with the willow scrub on south-facing slopes (Hansen, 1973).

Dwarf-shrub heath tundra. Dwarf-shrub heath forms an important understory within the previously discussed low-shrub tundra, in addition to occurring separately as a vegetation type on well-drained soils. Heath species are an integral part, along with *Eriophorum vaginatum* and *Carex bigelowii*, or *C. lugens* in the heath–cottongrass tussock tundra. "Heath" as used here refers to species within the Ericaceae, Empetraceae and Diapensiaceae. Some authors broaden the concept to include *Dryas* and dwarf species of *Salix* as part of heath-tundra vegetation. A diagnostic aspect of this vegetation type is the evergreen-leaved species, although several are deciduous (*Arctostaphylos alpina, A. rubra, Vaccinium uliginosum*).

In western Alaska (Hanson, 1953; Churchill, 1955; Johnson et al., 1966), northern Yukon (Hettinger et al., 1973) and the Mackenzie Delta region (Corns, 1974), communities in which heath species (10–20 cm high) predominate have been described. These include in varying combinations *Arctostaphylos alpina, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Loiseleuria procumbens, Rhododendron kamtschaticum, R. lapponicum, Vaccinium uliginosum* ssp. *alpinum, V. vitis-idaea* ssp. *minus*, and where snow remains into early July, *Cassiope tetragona. Rubus chamaemorus*, a member of the rose family, is a common associate along with *Betula nana* ssp. *exilis* and one or more species of dwarf *Salix*.

To the east of Peely Lake (101°03′W, 66°03′N) in the Keewatin District, Canada, dwarf-shrub heath predominates on north exposures, fellfields, and gravel summits. The dominant species are *Cassiope tetragona, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum* ssp. *alpinum*, and *V. vitis-idaea* ssp. *minus. Arctostaphylos alpina* and *Betula glandulosa* are rare here compared to the Ennadai

Lake area (101°W,61°N) further south (Larsen, 1965; 1972). At Ennadai, fine-textured soils in the fellfields (rock fields) are dominated by heath vegetation (*Arctostaphylos alpina, Ledum palustre* ssp. *decumbens, Loiseleuria procumbens, Vaccinium uliginosum* ssp. *alpinum,* and *V. vitis-idaea* ssp. *minus*). Where winter snow is deeper and where summer soil moisture is greater, *Betula glandulosa* and highly deformed *Picea mariana* (60–90 cm) occur. Important mosses include *Aulacomnium turgidum, Polytrichum juniperinum* and *Ptilidium ciliare* (Larsen, 1965). Low-shrub and dwarf-shrub tundra vegetation is not a dominant feature in the District of Keewatin. Fellfields, outwash plains, and gravel ridges, all coarse-textured material, dominate the landscapes.

At Chesterfield Inlet (90°42′W, 63°20′N) on the west coast of Hudson Bay, in northern Quebec, and Lake Harbour (60°53′W, 62°51′N), Baffin Island, heath vegetation is common with *Carex bigelowii, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Phyllodoce caerulea, Pyrola grandiflora,* and *Vaccinium uliginosum* ssp. *alpinum* occurring in varying combinations. Where snow lies into July, *Cassiope tetragona* dominates with *Carex misandra, Dryas integrifolia, Luzula nivalis, Salix herbacea, S. reticulata,* and many lichen and bryophyte species (Polunin, 1948; Payette and Filion, 1984; Payette et al., 1989).

In west Greenland, species-rich heath vegetation occurs on steep, moist slopes that are warmer in summer and where soil organic matter is quite high. Many of these habitats are in the inland valleys with their warmer and drier continental climate than the cooler and moister maritime climate along the coast (Böcher, 1954). Species dominating in various combinations include *Cassiope tetragona, Ledum palustre* ssp. *decumbens, Loiseleuria procumbens, Phyllodoce caerulea, Rhododendron lapponicum, Vaccinium uliginosum* ssp. *microphyllum,* and *V. vitis-idaea* ssp. *minus* (Sørensen, 1943; Böcher, 1954, 1959, 1963; Böcher and Laegaard, 1962; Hansen, 1969). *Ledum, Loiseleura,* and *Phyllodoce* drop out in the Melville Bugt region (72–75°N). In the Thule area only *Cassiope tetragona, Salix arctica,* and *V. uliginosum* ssp. *microphyllum,* are found and heath vegetation is minor (Sørensen, 1943).

In the Angmagssalik District (65°30′ to 66°30′N), southeastern Greenland, Daniels (1982) reported that dwarf-shrub heath vegetation dominated on acid to moderately acid soils. Various combinations of *Arctostaphylos alpina, Empetrum nigrum* ssp. *hermaphroditum, Loiseleuria procumbens, Phyllodoce caerulea, V. uliginosum* ssp. *microphyllum,* and in places *Betula nana* dominate. Shrub height is generally <20 cm. In southern Greenland *Cassiope tetragona* is restricted to the continental inland fjords. Lichens and mosses are abundant as ground cover. The herbs *Carex bigelowii, Festuca rubra, Hieracium alpinum, Juncus trifidus, Poa arctica,* and *Polygonum viviparum* are common.

Dwarf-shrub heath–tussock tundra. Communities dominated by dwarf-shrubs and tussocks of *Eriophorum vaginatum* occupy large areas of western and northern Alaska (Hanson, 1953; Churchill, 1955; Britton, 1957; Spetzman, 1959; Johnson et al., 1966; Komarkova and Webber, 1980), central and northern Yukon Territory (Hettinger et al., 1973; Wein and Bliss, 1974) and limited areas of the Northwest Territories (Larsen, 1965; Corns, 1974). This type of tundra is absent from most of the eastern Canadian Low Arctic with the exception of Baffin Island (Lake Harbour) and northern Quebec, where tussock tundra occurs in limited areas (Polunin, 1948). The Alaskan and western Canadian cottongrass is *Eriophorum vaginatum* ssp. *vaginatum* while *E. vaginatum* ssp. *spissum* occurs in the eastern Canadian Arctic.

Although cottongrass is the conspicuous species, the dwarf-heath species usually predominate. Various combinations of *Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum* ssp. *alpinum,* and *V. vitis-idaea* ssp. *minus* comprise the major heath species. Scattered *Betula nana* ssp. *exilis, Carex lugens, Salix pulchra* and several species of forbs are often present. The cryptogam layer is usually well developed and includes the mosses *Aulacomnium palustre, A. turgidum, Dicranum elongatum, Hylocomium splendens, Rhacomitrium lanuginosum, Sphagnum* ssp., *Tomenthypnum nitens,* and the lichens *Cetraria cucullata, C. nivalis, Cladonia (Cladina) mitis, C. rangiferina, Cladonia sylvatica, Dactylina arctica,* and *Thamnolia vermicularis* (Bliss, 1956; Johnson et al., 1966). Communities of this vegetation type occur on rolling topography and flats with soils of intermediate drainage.

These landscapes are important grazing lands for barren-ground caribou, especially in the early summer when cottongrass is in flower, providing nutrient-rich forage for lactating females. Rela-

tively large populations of passerine bird species and microtines are also common within these dwarf-shrub heath–tussock communities.

Graminoid–moss tundra (mire). The concept of arctic tundra, for many people, is associated with wetlands (mires) in which species of *Carex, Eriophorum,* and sometimes the grasses *Alopecurus, Arctophila* and *Dupontia* predominate, with an abundance of bryophytes but few lichens. Communities of sedge–moss and sedge–grass–moss tundra are minor in the Brooks Range (Britton, 1957) and the northern Yukon Mountains (Hettinger et al., 1973) because of well-drained soils and small valley floors. However, these wetland meadows increase in importance in the Foothill Province of Alaska and they dominate the Coastal Plain Province (Churchill, 1955; Britton, 1957; Spetzman, 1959; Webber, 1978; Komarkova and Webber, 1980) and extensive areas in the outer Mackenzie Delta region (Hettinger et al., 1973; Corns, 1974). The dominant sedges are *Carex aquatilis, C. membranacea, C. rariflora, C. rotundata, Eriophorum angustifolium, E. russeolum,* and *E. scheuchzeri.* The grasses *Arctagrostis latifolia, Arctophila fulva* and *Dupontia fisheri* occur along a gradient from drier sites to saturated soils and standing water. In shallow waters of lakes and ponds (50–60 cm deep), *Arctophila fulva, Equisetum variegatum* and *Menyanthes trifoliata* predominate with *Hippuris vulgaris* and *Potentilla palustris* in water 20–30 cm deep. The various species of *Carex* and *Eriophorum*, and *Dupontia fisheri*, occur with little (10–20 cm deep) or no standing water. *Carex aquatilis, Eriophorum angustifolium,* and *E. scheuchzeri* are common in depressed-center polygons and the troughs of raised-center polygons (Britton, 1957; Hettinger et al. 1973; Corns, 1974).

These northern wet meadows have a nearly continuous cover of mosses including species of *Aulacomnium, Calliergon, Ditrichum, Drepanocladus, Hylocomium splendens, Sphagnum,* and *Tomenthypnum nitens* (Britton, 1957; Johnson et al., 1966).

Study of plant succession, in the thaw-lake cycle of northern Alaska, has shown that high-center polygons form in drained lakes from the melting of ice-wedges. Pioneer plants include the moss *Psilopilum cavifolium* and the flowering species *Arctophila fulva* in the wet sites, *Duponitia fisheri* and *Eriophorum scheuchzeri* in the moist swales. *Carex aquatilis* and *Eriophorum angustifolium* enter somewhat later, but their vegetative growth in time permits them to dominate later stages (Britton, 1957; Billings and Peterson, 1980).

Carex and *Eriophorum* meadows are also found in the Ennadai Lake area (Larsen, 1965), Chesterfield Inlet, northern Quebec, and Lake Harbour (Polunin, 1948). Common species include *Carex stans* (more typical of the High Arctic), *C. membranaceae, C. rariflora, Eriophorum angustifolium, E. scheuchzeri,* and in some areas *Arctagrostis latifolia.* Common mosses include species of *Aulacomnium, Calliergon, Dicranum, Drepanocladus, Meesia,* and *Sphagnum* (Polunin, 1948).

Cushion plant–cryptogam semidesert. From the Rocky Mountains of Montana north to the Yukon Territory and Alaska, wind-swept slopes and ridges are often dominated by cushions or mats of *Dryas integrifolia* and *D. octopetala.* A similar vegetation type occurs throughout much of the central and western High Arctic of Canada and in Greenland. In the High Arctic, this will be considered part of the polar semidesert complex rather than tundra because of the much sparser nature of the vascular plant cover. Here I shall discuss only the Low Arctic component, a vegetation that is often called *Dryas* fellfield or *Dryas* tundra.

In the Brooks Range, Spetzman (1959) and Cooper (1986) have described *Dryas*–lichen vegetation as dominating rubble slopes, ridges, alluvial fans, and well-drained outwash at low and mid elevations (800–1500 m). *Dryas* often constitutes 80–90% of the vascular plant cover. Associated species included *Anemone parviflora, Carex capillaris, C. rupestris, Kobresia myosuroides, Polygonum viviparum* and *Silene acaulis. Both Dryas integrifolia* and *D. octopetala* and their hybrids predominate. Cushions of *Dryas* are often 0.5 to 1.0 m across, and they seldom reach a height greater than 2–5 cm. The ground cover of herbs, lichens, and mosses is generally sparse.

In the Cape Thompson, Alaska, area, *Dryas* cushion vegetation covers 30% of the catchment, dominating the exposed slopes and uplands on thin soils derived from limestone and dolomite rocks.

A ground cover of *Cladonia alpestris* and *Dryas integrifolia* dominates steep (35–45°) south-facing slopes on the dolomite and limestone in the Campbell-Dolomite Uplands near Inuvik, N.W.T. This is within the Boreal Forest Woodland zone where very open stands of *Picea glauca* predominate (Ritchie, 1977). Associated prostrate woody species include *Arctostaphylos uva-ursi* and *Junipe-*

rus communis, species characteristic of dry lichen-dominated open forests to the south.

Across the Mackenzie and Keewatin Districts of the Northwest Territory there are many barren rock and lag gravel surfaces. The cushion plants *Dryas integrifolia, Saxifraga oppositifolia, S. tricuspidata*, and *Silene acaulis* are common, although *Dryas* does not assume a predominant role on these acidic soils of granite origin as it does to the west on the calcareous soils derived from sedimentary rocks. The grass *Hierochloë alpina*, the lichens *Alectoria nitidula, A. ochroleuca, Cetraria cucullata*, and *C. nivalis*, and the moss *Rhacomitrium lanuginosum* are common in the Snow Bunting Lake, Peely Lake, and Repulse Bay areas (Larsen, 1972).

Vegetation and plant community patterns of selected areas

The previous section dealt with a summary of the major vegetation types and dominant species encountered across the Low Arctic, including some specific areas where these types occur. However, this gives no impression of the landscape in a given location. This section will cover that aspect.

Cape Thompson, Alaska. In the Ogotoruk Valley–Cape Thompson area, Johnson et al. (1966) recognized 13 plant community types. Eight of these were termed vegetation types. Dwarf-shrub heath–tussock tundra (*Eriophorum* tussock), sedge–moss tundra, and cushion plant–cryptogam tundra (*Dryas* fellfield) comprise 82% of the 99.3 km^2 area. The flora of this area is large: 300 species and varieties of vascular plants, 100 species of bryophytes and 81 species of lichens (Table 19.14)

Plant communities dominated by cushion plants and cryptogams dominate the exposed windswept uplands, dry ridges, and bedrock exposures within the valley (Fig. 19.37). Solifluction steps and stone stripes are also dominated by *Dryas*, but with a greater number of vascular plant species (floristic richness). Several species of *Minuartia* and *Saxifraga* are commonly found along with *Androsace ochotensis, Oxytropis nigrescens, Silene acaulis*, the dwarf willows *Salix arctica* and *S. phlebophylla* and the graminoids *Carex microchaeta, Kobresia myosuroides, Luzula confusa*, and *Hierochloë al-*

TABLE 19.14

Size of arctic floras for select areas

Location		Number of species			Author
		Vascular plants	Lichens	Bryophytes	
Northern Ellesmere Island	80–83°	143	*	209	Brassard, 1971; Brassard and Beschel 1968
Peary Land, Greenland	83°	105		133	Holmen, 1960; Fredskild, 1966
Expedition Fiord, Axel Heiberg	79°	130	–	131	Beschel, 1970; Kuc, 1973
Landing Lake Area, Prince Patrick Island	76°	40	123	72	Bird, 1975
Truelove Lowland, Devon Island	76°	96	182	162	Bliss, 1977a,c
Reindeer Reserve, near Inuvik, N.W.T.	69°	420	–	179	Cody, 1965; Holmen and Scotter, 1971
Cape Thompson, Alaska	68°	305	81	100	Johnson et al., 1966
Barrow, Alaska	71°	139	106	224	B.M. Murray and D.F.Murray, 1978
Arctic Alaska	68–71°	435	–	555	Wiggins, 1962; Steere, 1978
High Arctic (Alaska, Canada, Greenland)	>71°	209		–	Porsild and Cody, 1980
Low Arctic (Alaska, Canada)	69–71°	696	–	–	Porsild and Cody, 1980

* = no data available

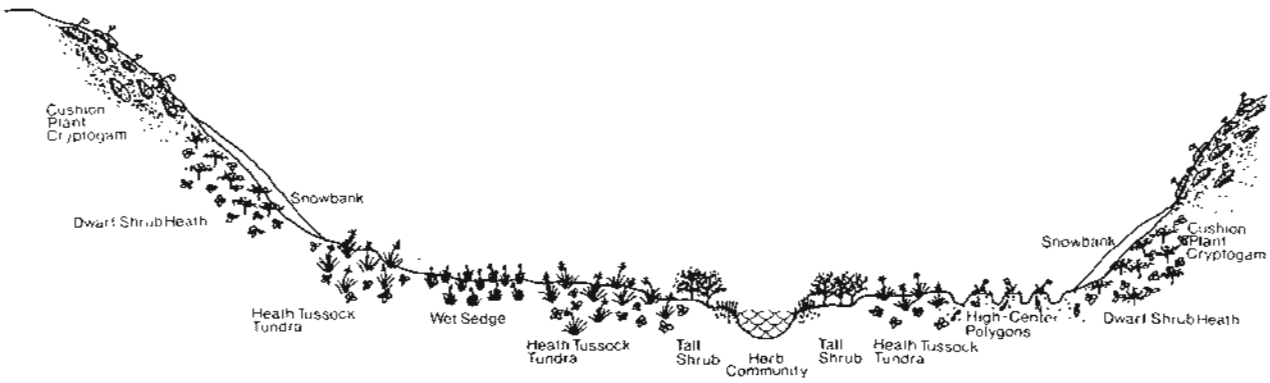

Fig. 19.37. Mesotopographic profile of vegetation types, Cape Thompson, Alaska.

pina. Common lichen species include *Alectoria ochroleuca, A. pubescens, Cetraria islandica, Cornicularia divergens*, and *Thamnolia vermicularis*. This vegetation type had the highest number of species of those studied.

On slopes with depressions where snow accumulates and melts in July, small patches of dwarf-shrub heath occur. These are dominated by the most characteristic (indicator) species *Cassiope tetragona* along with *Arctostaphylos alpina, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum,* and *V. vitis-idaea* ssp. *minus*.

Benches with gentle slopes may contain high-center polygons with ice-wedge troughs between. The raised centers are dominated by *Carex bigelowii, Ledum palustre* ssp. *decumbens, Salix phlebophylla, S. pulchra, Vaccinium vitis-idaea,* ssp. *minus*, and abundant lichens and mosses. The troughs, often moist all summer, contain *Eriophorum vaginatum*.

Gentle slopes with imperfect drainage contain dwarf-shrub heath–tussock tundra dominated by *E. vaginatum*, the common heath species, *Betula nana* ssp. *exilis*, *Salix pulchra*, and abundant mosses and lichens. Where ice-wedge polygons occur, the troughs contain *Carex aquatilis, Eriophorum angustifolium*, and *Sphagnum* spp. Extensive flats that are poorly drained contain wet sedge–moss tundra. The dominants are *C. aquatilis* and *E. angustifolium* with many bryophytes including *Sphagnum balticum*, and *S. imbricatum*. Scattered clumps of *Betula nana* ssp. *exilis* and *Salix fuscescens* along with the herb *Pedicularis parviflora* ssp. *pennellii* are also common.

Terraces and gravel bars within Ogotoruk Creek support herb communities on open areas and thickets of tall shrub tundra. The forbs include *Artemisia arctica, A. tilesii, Epilobium latifolium, Hedysarum alpinum, Lupinus arcticus*, and the graminoids *Elymus mollis, Festuca rubra, F. vivipara*, and *Luzula confusa*. Nearer the sea coast the willows *Salix alaxensis* and *S. pulchra* dominate; inland *S. pulchra* predominates.

Umiat, Alaska. The Colville River valley and the rolling topography beyond are typical of much of the Foothill Province on the North Slope. This description is based upon the papers by Churchill (1955), Bliss (1956) and Spetzman (1959).

The rolling uplands are dominated by dwarf-shrub heath–tussock tundra (Fig. 19.38). Churchill

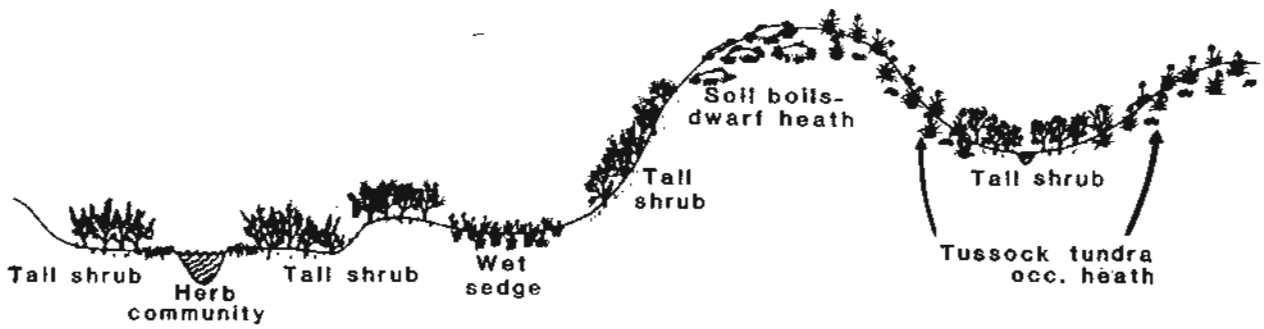

Fig. 19.38. Mesotopographic profile of vegetation types, Umiat, Alaska.

Fig. 19.39. Soil boils surrounded by dwarf-shrubs of *Empetrum, Ledum, Salix* and *Vaccinium*, Umiat, Alaska.

(1955) recognized four major communities, two dominated by *Carex lugens* and *Eriophorum vaginatum*, one by *Carex lugens* and the fourth by *Arctagrostis latifolia*. In all of these communities *Empetrum nigrum* ssp. *hermaphroditum*, *Ledum palustre* ssp. *decumbens*, *Vaccinium uliginosum* and *V. vitis-idaea* ssp. *minus* are important along with *Betula nana* ssp. *exilis*, and one or more species of *Salix*. Lichens and mosses are always important components.

On wind-swept ridge crests, where there is little winter snow cover, *Dryas integrifolia* with dwarf willows (*Salix phlebophylla, S. reticulata*), *Arctostaphylos alpina*, *Empetrum nigrum* ssp. *hermaphroditum*, *Rhododendron lapponicum* and a few herbs predominate. Frost scars (frost boils, soil boils) are a common feature of these relatively small-area, yet conspicuous, communities along ridges (Fig. 19.39).

Steep slopes along the river valley and some gentle slopes in the uplands are dominated by medium to tall shrub tundra. Spur slopes often contain a mixture of forbs and grasses, while the drainages contain dense thickets of willow and birch. The drier sites are dominated by *Arctagrostis latifolia, Arctostaphylos alpina, Hedysarum alpinum, Lupinus arcticus, Poa lanata*, and *Potentilla fruticosa*. Shrub communities include *Alnus crispa, Betula nana* ssp. *exilis, Salix glauca* ssp. *desertorum, S. glauca* ssp. *glabrescens*, and *S. pulchra*. In some areas *S. alaxensis* is also a part of the shrub complex on steep slopes. Various groupings of willow and birch commonly form thickets along streams where they are covered with snow in winter, and where there is more soil moisture and a deeper active layer (≃ 50 cm) in summer.

A complex of plant communities and vegetation types is found on the benches and terraces (2–5 km wide) along the Colville River. This includes lakes and ponds with shoreline communities of *Andromeda polifolia, Arctophila fulva, Caltha palustris, Carex aquatilis, Equisetum fluviatile, Eriophorum angustifolium, E. scheuchzeri, Hippuris vulgaris, Menyanthes trifoliata, Pedicularis labrador-*

Fig. 19.40. Raised site (5–10 cm) with dwarf heath shrubs and cottongrass tussock community in slightly wetter soils, Umiat, Alaska.

ica, and *Potentilla palustris*. Shrub communities of *Alnus*, *Betula*, one or more species of *Salix*, and the common heath shrubs generally predominate on the medium-drained soils above the shoreline. Other large areas with impeded drainage are dominated by wet sedge–moss communities with *Carex aquatilis*, *Eriophorum angustifolium*, and *E. scheuchzeri*. Imperfectly-drained soils contain dwarf-shrub heath where drainage is greater (Fig. 19.40), elsewhere communities of dwarf-shrub heath–tussock and heath–tussock–alder are found.

The lower terraces and river bars are a complex of herbaceous communities on exposed sands and gravels near the main channels. Further back, well-developed soils contain thickets of *Salix alaxensis* with an understory of forbs and grasses where the active layer is deep (>1 m, late July). Further away from the channels on higher ground, where spring flooding deposits fine sand and silt and where an organic mat begins to develop, other willow species share dominance with *Salix alaxensis*. These include *S. arbusculoides*, *S. glauca* ssp. *desertorum*, *S. hasta* var. *farrae*, *S. lanata* ssp. *richardsonii*, *S. niphoclada* var. *muriei* and *S. pulchra*. *Alnus crispa* is also present in these "decadent" felt-leaf willow communities. In late July the active layer was 0.5–0.7 m in depth. On the first terrace above the river sand and gravel bars, *Salix alaxensis*, *S. hasta* var. *farrae*, and *S. niphoclada* var. *muriei* drop out; the other willow species remain important and *Alnus crispa* becomes the dominant tall shrub. The active layer was only 25–40 cm in late August, again illustrating the influence of a developing organic mat and the finer-textured soils (Bliss and Cantlon, 1957). Heath shrubs, *Betula nana* ssp. *exilis*, *Carex lugens*, and many lichens and mosses form on important understory component.

Barrow, Alaska. Superficially, the Barrow area east to Prudhoe Bay and beyond is a monotonously flat landscape of lakes, ponds, and wetlands covered with sedges, grasses, and mosses. While this generally describes the landscape, the mesotopography, though minor in relief (1–3 m) compared with other areas, does permit species to sort out into plant communities depending upon their requirements along the moisture gradients (Fig. 19.41).

The tops of high-center polygons, old lake shorelines, raised beach ridges nearer the coast, and sloping land along creek banks where winter snow cover is less and where soils are warmer and drier in summer, are dominated by herbs and lichens. The most common species are *Luzula arctica*, *L. confusa*, *Pedicularis lanata*, *Poa arctica*, *Potentilla hyparctica*, *Salix rotundifolia*, and *Stellaria edwardsii*. Common mosses include *Dicranum elongatum*, *Pogonatum alpinum*, and *Polytrichum*

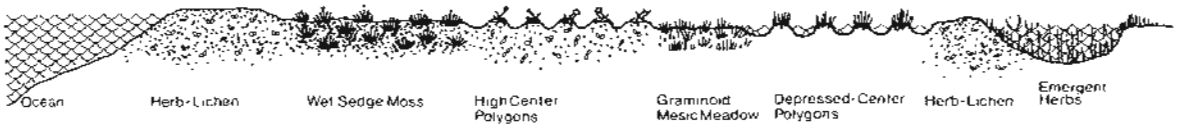

Fig. 19.41. Mesotopographic profile of vegetation types, Barrow, Alaska.

juniperinum; lichens include *Alectoria nigricans* and *Cetraria cucullata* (Webber, 1978).

Mesic to wet meadows are dominated by various combinations of graminoids in which *Carex aquatilis* predominates. On slightly better-drained lands with hummocky surfaces or slightly raised polygons, a community dominated by *Carex aquatilis* and *Poa arctica* and with lesser amounts of *Dupontia fisheri, Eriophorum angustifolium, E. russeolum,* and *Saxifraga cernua* occurs. Common mosses include *Dicranum elongatum, Oncophorus wahlenbergii,* and *Pogonatum alpinum*; many lichens are present but *Cetraria cucullata, C. islandica* and *Dactylina arctica* are most common.

Wet flats and polygon troughs are covered with *Dupontia fisheri, Eriophorum angustifolium, E. russeolum,* and *Saxifraga cernua*. Species of *Bryum, Calliergon sarmentosum* and *Pogonatum alpinum* dominate the bryophyte flora. Low-center polygons and pond margins contain *Carex aquatilis* and *Eriophorum russeolun*, while shallow pond waters contain *Arctophila fulva* and *Ranunculus pallasii* (Fig. 19.42). The mosses *Calliergon sarmentosum* and *Drepanocladus brevifolius* predominate in the former plant community while *Calliergon giganteum, Campylium stellatum,* and *Drepanocladus brevifolius* dominate in the shallow ponds. Lichens are very minor, if at all present, in these wet lands (Webber, 1978).

Of the low arctic sites described, this one is

Fig. 19.42. Low-center polygons and ponds at Barrow, Alaska with *Carex aquatilis* in the wet soils, *C. bigelowii* on higher ground, and *Arctophila fulva* in the ponds.

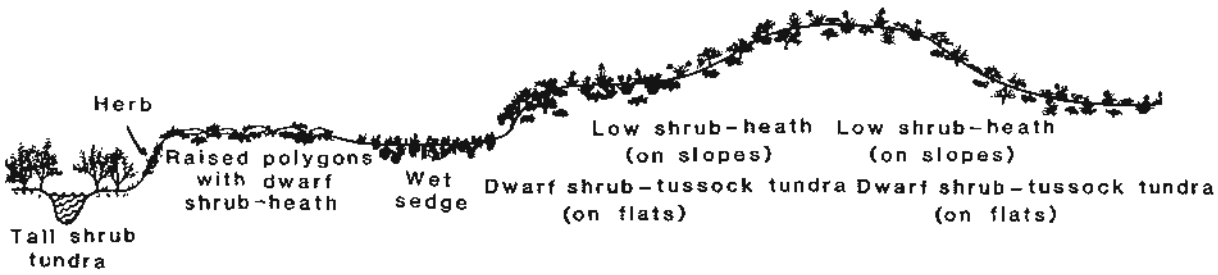

Fig. 19.43. Mesotopographic profile of vegetation types, near Tuktoyaktuk, N.W.T.

floristically the poorest, has only a few woody species, and has a predominance of graminoids. These features all indicate the close ecological relationship of this area to the High Arctic, as will be discussed later.

Mackenzie Delta, N.W.T. Lands on the east side of the Mackenzie River Delta have been studied intensively at five locations, ranging from the Caribou Hills north of Inuvik, N.W.T. (100–150 m above sea level) to Atkinson Point near sea level on the Tuktoyaktuk Peninsula (Corns, 1974). A total area of 314 km2 was mapped in detail out of an area of about 13,500 km2. With the exception of the wet sedge tundra at Atkinson Point, the area is characterized by tall to dwarf woody species to a greater degree than the areas described in Alaska. The total vascular plant flora sampled, however, was small (70 spp), although 420 species have been collected in this area, east to the Anderson River (Cody, 1965). The Tuktoyaktuk area south of the Imperial Oil Exploration Camp was selected for general description (Fig. 19.43).

Tall shrubs of *Alnus crispa, Salix alaxensis* and *S. lanata* ssp. *richardsonii* occur on gravelly beaches from receding shorelines of lakes on the silty–sandy banks of the river channels, and on steep slopes above the river. Along streams in the rolling upland topography *Alnus crispa, Salix lanata* ssp. *richardsonii*, and *S. pulchra* dominate. Where silts and sands accumulate from annual flooding, various combinations of *Arctagrostis latifolia, Arctostaphylos alpina, Calamagrostis canadensis, Equisetum arvense, Hedysarum alpinum, Pyrola grandiflora, P. secunda,* and *Vaccinium uliginosum* may be found. Lichens and mosses are not part of these communities, where the annual silt layer is often 2–4 cm in thickness.

Low-shrub heath tundra is the most common vegetation type in this area (35%), dominating in the rolling uplands with tall shrubs along the stream channels (Fig. 19.44). The shrubs *Betula nana* ssp. *exilis, Salix glauca* ssp. *acutifolia,* and *S. pulchra* are almost always present along with the heath species *Arctostaphylos rubra, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Vaccinium uliginosum,* and *V. vitis-idaea* ssp. *minus.* Common herbs include *Carex lugens, Lupinus arcticus, Pedicularis kanei, Petasites frigidus,* and *Saussurea angustifolia.* Lichens and mosses are abundant.

Dwarf-shrub heath–tussock tundra dominates lower benches where soils are imperfectly drained. The common heath species listed above predominate, along with *Eriophorum vaginatum* and in places the tussock-forming sedge *Carex lugens.* Small amounts of *Arctagrostis latifolia, Pyrola grandiflora, P. secunda,* and *Rubus chamaemorus* are generally present. This vegetation type covers about 10% of the landscape (Corns, 1974).

Sedge–moss tundra (mire) dominates lowlands that are poorly drained. Plant communities of *Carex aquatilis, C. rariflora,* and *Eriophorum angustifolium* occupy the wet polygon centers with *Andromeda polifolia, Rubus chamaemorus, Salix arctophila,* and *Tofieldia pusilla* communities on the raised polygon rims. Lichens and mosses are important components of these communities on the slightly better-drained soils.

More specialized habitats and plant communities include lake and pond margins with *Arctophila fulva, Caltha palustris* ssp. *arctica, Carex aquatilis, Eriophorum angustifolium, Hippuris vulgaris* and *Potentilla palustris.* This mixture of species often forms a floating mat as ponds and small lakes slowly fill in with organic matter. Herbaceous communities often occur on dry, steep slopes above river channels, mostly on west- and south-facing slopes. These are dominated by *Artemisia frigida, A. tilesii, Calamagrostis purpurascens, Hedysarum alpinum, H. mackenzii,* and *Pulsatilla ludoviciana.* Most of these species occur on river gravels in northern Alaska and to a lesser extent

Fig. 19.44. Low-shrub heath tundra on the interfluves (uplands) with tall shrubs of *Salix* and *Betula* in the drainages and along lakes; pingos in the background, near Tuktoyaktuk, N.W.T.

on the sandy and silty bars along the lower Mackenzie River. In general these river sites are too wet and the annual accretion rates of silt appear too great for these species to reach a greater importance.

A third group of plant communities is found in relation to the raised-center polygons that are generally 2–4 m across and have troughs (above ice wedges) 50 cm–>1 m in depth. The dry, wind-exposed polygon tops are dominated by a moss–heath–birch community in which *Betula, Ledum, Rubus chamaemorus,* and *Vaccinium vitis-idaea* ssp. *minus* dominate. Where the troughs are relatively dry in summer, yet hold much snow in winter, *Betula nana,* ssp. *exilis, Carex lugens, Chamaedaphne calyculata,* and *Vaccinium uliginosum* are common. Where the troughs contain water in summer, *Arctophila fulva, Carex aquatilis,* and *Eriophorum angustifolium* are abundant (Fig. 19.45).

Communities of dwarf-heath tundra with abundant lichens and mosses are limited in the Mackenzie Delta region to old beaches of gravel near lakes. *Empetrum nigrum* ssp. *hermaphroditum, Ledum,* and *Vaccinium vitis-idaea* ssp. *minus* predominate along with the lichens *Cetraria cucullata, C. nivalis, Cladonia* (*Cladina*) *alpestris, C. mitis, Dactylina arctica,* and others. Snowbanks typically melt in early July, and consequently heath communities dominated by *Cassiope tetragona,* herbs, lichens, and mosses are a very minor landscape feature. More commonly the late-lying snow protects medium to tall shrubs of *Alnus, Betula,* and *Salix* in this part of the Low Arctic (Corns, 1974).

Arctic tundras in the High Arctic

In contrast with the Low Arctic, the High Arctic is characterized by herbaceous rather than woody species and generally has much less plant cover, especially of flowering plants. Vast areas are dominated by lichens and mosses with only 5–25%

Fig. 19.45. Raised-center polygons with dwarf heath shrubs and *Betula nana* ssp. *exilis* on the polygonal tops and *Arctophila fulva*, *Carex aquatilis*, and *Eriophorum angustifolium* in the troughs; near Tuktoyaktuk, N.W.T. Tussock tundra on bench beyond with low-shrub heath tundra on slope above.

cover of flowering plants, the polar semideserts. Equally large areas have almost no cryptogams (0–3% cover) and only a 0.1–4% cover by vascular plants, the true polar deserts (Table 19.13).

Based upon vegetation types, the High Arctic can be divided into small areas of tundra (low shrub, dwarf-shrub heath–tussock, and graminoid–moss), vast areas of cushion-plant cryptogam and cryptogam–herb polar semidesert, and the herb barrens and limited snowflush sites of the polar deserts. Except for few locations, mostly on the Banks and Victoria Islands of Canada, woody species other than dwarf willows and the semiwoody *Dryas* are a very minor component of these northern lands.

Vegetation types

Graminoid–moss tundra (mire). Of the vegetation types common in the Low Arctic only the graminoid–moss tundra is ecologically important in the High Arctic. It occupies 20–40% of the lands in central and western Banks Island and 5–15% elsewhere on Banks, Victoria, and Prince of Wales Islands. Less than 2% of the Queen Elizabeth Islands contain graminoid–moss meadows, yet this vegetation type provides the major grazing habitat for musk-oxen and breeding grounds for waterfowl and shorebirds because of the associated ponds and lakes.

The most important species are *Carex stans* (*C. aquatilis* spp. *stans* in some publications) and *C. membranacea*, with lesser amounts of *Alopecurus alpinus*, *Arctagrostis latifolia*, *Dryas integrifolia*, *Dupontia fisheri*, *Eriophorum scheuchzeri*, *E. triste*, *Salix arctica*, and species of *Draba*, *Pedicularis* and *Saxifraga*. When present, the small clumps of *Dryas* and *Salix* are restricted to moss hummocks or rocky areas within the meadows, the best drained and aerated microsites.

Communities of this vegetation type occur where drainage is impeded along river terraces, small valleys, and coastal lowlands with series of raised beaches (Beschel, 1970; Bird, 1975; Muc, 1977; Thompson, 1980; Sheard and Geale, 1983; Bliss and Svoboda, 1984; Muc et al., 1989). *Carex stans* dominates wet meadows in the eastern Arctic and as far west as the Sabine Lowlands, Melville Island (Bliss and Svoboda, 1984) and at Mould Bay, Prince Patrick Island (Bird, 1975). Bryophytes are abundant in the various kinds of plant communities, including *Campylium arcticum*, *Cinclidium arcticum*, *Ditrichum flexicaule*, *Drepano-*

cladus revolvens, Orthothecium chryseum, and *Tomenthypnum nitens.* Cyanobacteria (bluegreen algae) are abundant, usually *Nostoc commune*; lichens are minor, but include *Cladonia pyxidata, Peltigera aphthosa, Solorina saccata,* and *Xanthoria elegans.*

While wetlands in the southern and eastern High Arctic are dominated by sedges, those in the northwestern Canadian islands, including northern Melville Island, are not. At Sherard Bay, Melville Island, Cameron Island, and Hoodoo River, Ellef Ringnes Island (Bliss and Svoboda, 1984) and Isachsen, Ellef Ringnes Island (Savile, 1961), the grass *Dupontia fisheri* dominates. Where there are shallow ponds, *Pleuropogon sabinei* occurs (ecological equivalent of *Arctophila fulva* to the south); *Juncus biglumis* and sometimes *Eriophorum scheuchzeri*, and *E. triste* occur on moist soils. The above-listed mosses, other bryophytes, and cyanobacteria are generally present.

Dwarf-shrub heath tundra. Compared with the Low Arctic, this vegetation type has very few heath species, and is almost always restricted to snowbed sites that melt by early July. These habitats often have abundant rock that provides more heat in summer. There are usually numerous herbaceous species and mosses in addition to the cushion plant *Dryas*. The most characteristic species is *Cassiope tetragona*, although *Vaccinium uliginosum* ssp. *microphyllum* is present in a few locations in the eastern Arctic. Other abundant species include *Carex misandra, Salix arctica*, and *Saxifraga oppositifolia*. Common bryophytes include *Dicranum elongatum, Ditrichum flexicaule, Hylocomium splendens, Hypnum revolutum, Polytrichum juniperinum, Rhacomitrium lanuginosum,* and *Tomenthypnum nitens.* Abundant fruticose lichens include *Cetraria cucullata, C. delisei, C. laevigata, C. nivalis, Dactylina arctica* and *Thamnolia subuliformis*. Heath-dominated plant communities have been described for the Thomsen River, Banks Island and Holman, Victoria Islands (Bliss et al., 1994a), Truelove Lowland, Devon Island (Bliss et al., 1977), Expedition Fiord, Axel Heiberg Island (Beschel, 1970), Van Hauen Pass (Brassard and Longton, 1970) and Alexandra Fiord, Ellesmere Island (Muc et al., 1989), and Coral Harbour, Southampton Island (Reznicek and Svoboda, 1982) of Canada.

The northern and central Baffin Island heaths are richer floristically. *Cassiope tetragona* dominates while *Carex bigelowii, Luzula confusa, L. nivalis, Salix arctica, S. herbacea,* and *Vaccinium uliginosum* ssp. *microphyllum* are common. Important mosses include *Aulacomnium turgidum, Drepanocladus uncinatus, Hylocomium splendens*, and *Rhacomitrium lanuginosum* and the lichens *Cladina mitis, Dactylina arctica, Stereocaulon alpinum,* and *Thamnolia vermicularis* (Polunin, 1948).

Heath vegetation in western Greenland is sparse in species and covers only small areas. *Cassiope tetragona* again dominates with lesser amounts of *Dryas integrifolia, Luzula confusa, L. nivalis, Salix arctica* and numerous lichens and mosses (Sørensen, 1943).

Eastern Greenland has fewer land masses free from ice, is generally colder, and winter snow depth is greater than in western Greenland. Continuous ice-free areas extend from 70° to 77°N. Only limited areas of heath-shrub tundra occur, and many are in the warmer inner fjords (Seidenfaden and Sørensen, 1937; Oosting, 1948; Raup, 1971). In the Mesters Vig District (73°N) heath tundra is dominated by *Cassiope tetragona, Salix arctica,* and *Vaccinium uliginosum* ssp. *microphyllum* (Raup, 1971). Less common species are *Arctostaphylos alpina, Betula nana, Dryas octopetala,* and *Rhododendron lapponicum*. The heath tundra occurs on well-drained sandy and sandy loam soils. In the outer fjord region at 72–74°, Oosting (1948) reported heath dominated by *Cassiope tetragona* and *Vaccinium uliginosum* ssp. *microphyllum*; within the inner fjords *Arctostaphylos alpina, Empetrum nigrum* ssp. *hermaphroditum,* and *Rhododendron lapponicum* form the heath vegetation. *Betula nana*, while uncommon, occurs on the south-facing slopes and sites that are drier than the areas of heath.

Tussock tundra. On Banks and Victoria islands, small areas, usually 1–2 ha in size, of tussock tundra occur. These are dominated by *Eriophorum vaginatum* with scattered plants of *Vaccinium vitis-idaea* ssp. *minus*, a few lichens and mosses. This vegetation type usually occurs in snow-flush sites where imperfect soil drainage occurs. They are related to the heath–tussock tundras of the Low Arctic, but are floristically impoverished and of very minor areal extent (Bliss et al., 1994a).

Tall shrub tundra. This vegetation type is also of minor extent, and the shrubs are of low stature (0.5–2.0 m) compared with the Low Arctic. In warm valley bottoms and southern slopes on Banks Island and western Victoria Island, small areas of willow scrub occur, dominated by *Salix*

alaxensis and *S. pulchra*. There are few associated species (Kuc, 1974; Edlund and Egginton, 1984; Bliss et al., 1994b).

Polar semideserts–High Arctic

Arctic vegetation and plant communities included within this landscape unit have generally been termed polar desert, especially by the Soviet scientists (Gorodkov et al., 1954; Aleksandrova, 1970, 1980; Andreyev and Aleksandrova, 1981). However, plant cover, plant and animal biomass, species richness, and soil development are very different from the barren polar deserts (Bliss, 1975, 1981). Areas designated as polar semidesert constitute about 25% of the landscape of the Queen Elizabeth Islands and about 50–55% of the southern islands and mainland high arctic of Canada. The two major vegetation types include cushion plant–cryptogam and cryptogam–herb. Bliss and Matveyeva (1992) have summarized circumpolar arctic vegetation, including previous systems of classification.

Vegetation types

Cushion plant–cryptogam semidesert. This vegetation type is closely related ecologically and floristically to that of the Low Arctic, although there it is a minor type, restricted to mountain slopes and uplands where snow cover is thin and the soils are well-drained. It is usually found as transitional to upper elevations where only scattered herbs occur, here termed alpine desert.

Cushion plant–cryptogam vegetation predominates in the southern islands and to some extent in the Boothia Peninsula. In these areas, the type covers hundreds of square kilometers of rolling upland terrain. Northward it remains an important type at low elevations in the eastern arctic (Devon, Ellesmere, Axel Heiberg Islands). To the northwest it becomes less important on Bathurst and Melville Islands and is of no ecological importance on the northwestern islands of Canada (northern Prince Patrick, Mackenzie King, Borden, Lougheed, King Christian, Amund Ringnes, Ellef Ringnes). The vegetation type is also very minor on northern Baffin, western Devon and on Cornwallis and Somerset Islands where uplands and even lowlands are dominated by rock-strewn surfaces, fine-textured soils, a cold climate, and a late snowmelt.

Where this type occurs it is dominated by *Dryas integrifolia*, generally but not always on calcareous-derived soils. Mats to rounded cushions are generally 20–100 cm across. Associated abundant species include *Salix arctica, Saxifraga oppositifolia* and 2–4 species each of the rosette-forming species of *Draba* and *Saxifraga*, 2–3 species each of *Minuartia* and *Stellaria*, and *Papaver radicatum*. The graminoids *Carex nardina, C. rupestris, Luzula confusa*, and in the western islands *Alopecurus alpinus* are common associates. Vascular plant cover is generally 5–25% with another 30–60% cover provided by lichens and mosses. Common lichens include *Cetraria cucullata, C. nivalis, Dermatocarpon hepaticum, Ditrichum flexicaule, Thamnolia subuliformis*, and *Tortella arctica*.

This vegetation type is common on gravelly raised beaches that are drier, warmer, and have a deeper active layer than sedge–moss mires. Plant communities have been described from Devon Island (Svoboda, 1977), Ellesmere Island (Brassard and Longton, 1970; Muc et al., 1989), Bathurst Island (Sheard and Geale, 1983; Bliss and Svoboda, 1984), and Southampton Island (Reznicek and Svoboda, 1982).

Although plant cover and biomass are less than in the graminoid–moss vegetation, the *Dryas*-dominated cushion vegetation is the principal habitat of Peary's caribou (*Rangifer tarandus pearyi*), the collared lemming (*Dicrostony groenlandicus*), ptarmigan, and several species of passerine birds.

Cryptogam–herb semidesert. This is a very general vegetation type that predominates on the central and western Queen Elizabeth Islands where the previous vegetation type is minor or totally absent.These landscapes are generally low-rolling uplands and beaches where the soils are sandy to silty loams and clay loams. Rock-strewn surfaces are minor. Vascular plants contribute 5–20% cover and cryptogams contribute 50–80% cover (Bliss and Svoboda, 1984).

In general this vegetation is characterized by the abundance of bryophytes and crustose and foliose lichens (rather than fruticose lichens as in the Low Arctic); the general appearance is that of graminoids. These include *Alopecurus alpinus, Luzula confusa*, and *L. nivalis* where soils are wetter. The total absence of upland sedges is a very obvious difference. Important forbs include rosette species of *Cerastium, Draba, Minuartia, Papaver radicatum, Ranunculus sulfureus*, and *Saxifraga*. Where fine-textured, black soils derived from shale occur,

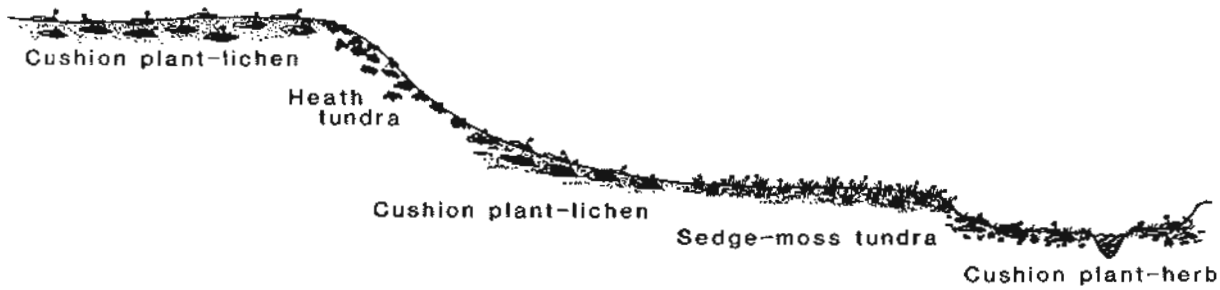

Fig. 19.46. Mesotopographic profile of vegetation types, Thomsen River, Banks Island, N.W.T.

Alopecurus alpinus is the only important species, although 2–4 vascular and 4–6 cryptogam species are also present, but in small amounts (≃ 1–2% cover) on the small soil mounds (frost boils or hummocks).

Abundant bryophytes include *Aulacomnium turgidum, Dicranoweisia crispula, Ditrichum flexicaule, Pogonatum alpinum, Polytrichum juniperinum, Rhacomitrium lanuginosum, R. sudeticum, Schistidium holmenianum, Tomenthypnum nitens,* and in wetter soils the hepatic *Gymnomitrion corallioides.* Important lichens include *Cetraria cucullata, C. delisei, Cladonia gracilis, Dermatocarpon hepaticum, Lecanora epibryon, Lepraria neglecta,* and *Parmelia omphalodes.* There is often a black cryptogamic crust on the surface which some authors have called patina. This is usually a mixture of black crustose lichens and cyanobacteria, a thin layer that is capable of fixing nitrogen in these nutrient- deficient soils.

Vegetation of this type has been described from Axel Heiberg Island by Beschel (1970), who called it a polar steppe (where *Luzula* predominated) and for Melville, Cameron, King Christian, Ellef Ringnes (Bliss and Svoboda, 1984) and for Lougheed (Edlund, 1980) and Prince Patrick islands (Bird, 1975).

In these cold, dry environments saline areas, often only tens of meters square, occur where there are rocks of high carbonate content. The dominant species include *Cochlearia officinalis, Puccinellia phryganodes,* and *P. vaginata.*

Vegetation and plant community patterns of selected areas

Five representative areas of High Arctic will be described in more detail, areas that have sufficiently diverse topography to provide a greater habitat diversity. One area is in the eastern and four are from the western High Arctic of Canada.

Thomsen River, Banks Island. In northern Banks Island the rolling uplands are dominated by cushion-plant polar vegetation and the flats, especially around ponds and lakes by sedge–moss tundra meadows (Fig. 19.46). This is an important grazing range for Peary's caribou (*Rangifer tarandus pearyi*) and musk-oxen, and the wetlands produce many waterfowl and shore birds each year. Even larger landscapes of this type are found in the southern part of the island. The flora of Banks Island is richer (≃190 spp) than in the northern islands.

The rolling uplands of the Thomsen River area are dominated by large mats of *Dryas integrifolia* with lesser amounts of *Carex rupestris, Salix arctica,* and *Saxifraga oppositifolia.* Small amounts of *Astragalus alpinus* and *Oxytropis arctica* occur. Species of these genera are found only on southern Melville Island within the Queen Elizabeth islands. Where there is stone striped ground, *Cassiope tetragona* occurs in the troughs, microsites that have deeper winter snows (Fig. 19.47).

Slopes in the lee of prevailing winds develop large snowbanks, and in these habitats dwarf-shrub heath is found. The dominant species is *Cassiope tetragona.* Associated species include *Dryas integrifolia, Pedicularis hirsuta, Polygonum viviparum, Salix arctica* and *S. niphoclada.* The major bryophyte species are *Ditrichum flexicaule, Hypnum bambergeri,* and *Tomenthypnum nitens* and the lichen *Thamnolia subuliformis* is also present (Bliss et al., 1994a).

Valley bottoms, benches on slopes, and flat areas contain graminoid–moss tundra meadows. Most of these are dominated by *Carex stans* and *Salix arctica* with smaller amounts of *Dryas integrifolia* and *Pedicularis hirsuta.* On the raised rims of polygons low clumps (~50–60 cm) of *Salix lanata* ssp. *richardsonii* occur. Sites such as this are the northern limit for the complex of taller shrubs. The

Fig. 19.47 Cushion-plant–cryptogam vegetation dominated by *Dryas integrifolia* with *Cassiope tetragona* in small depressions, Banks Island, N.W.T.

mosses include *Drepanocladus revolvens, Orthothecium chryseum,* and *Tomenthypnum nitens* in wetter sites and *Bryum pseudotriquetrum* in drier ones.

On lower benches near the Thomsen River, mats of *Dryas integrifolia* predominate on the sands and small sand-dunes. Intermixed are scattered clumps of *Astragalus alpinus, Carex nardina, C. subspathacea, Oxytropis arctica, Pedicularis lanata, Polygonum viviparum* and *Salix arctica* (Bliss et al., 1994a).

Truelove Lowland, Devon Island. Of the several areas studied in the High Arctic, this one is best known due to the International Biological Program (IBP) ecosystem study conducted in the early 1970's. This lowland (43 km^2) and three adjacent lowlands (125 km) along the northeast coast of Devon Island are ecologically particularly rich because of their diverse mesotopography of rock outcrops, raised beach ridges, wet meadows, ponds, and lakes (Fig. 19.48). These landscapes have been called polar oases. Other major environmental factors include a higher incidence of radiation and therefore air and soil temperature, higher precipitation, closeness to the sea, and a slow release of snowmelt waters because of the sequence of raised beaches across the Lowland (Bliss, 1977b). These beaches are old shoreline features resulting from the slow rise of land following ice retreat 8000–10,000 yr. B.P. (Barr, 1971).

The plateau to the east and south rises about 300 f m above the lowland, a barren landscape (polar desert) covered with large sorted and non-sorted polygons (1–3 m) on level land with sorted stone stripes on gentle slopes (>3°). Mosses are more important within 1–2 km of the plateau edge than further inland. These include *Distichum capillaceum, Ditrichum flexicaule, Hypnum bambergeri,* and *Mnium lycopodioides.* Small mats of lichens occur on the soils of the desiccation polygons including *Alectoria nigricans, Dermatocarpon hepaticum, Lecanora epibryon,* and *Pertusaria dactylina.* Vascular plants are more common in the shallow troughs of the polygons. The species include *Cerastium alpinium, Draba corymbosa, Minuartia rubella, Papaver radicatum Phippsia algida, Saxifraga caespitosa, S. cernua,* and *S. oppositifolia* (Muc and Bliss, 1977; Bliss et al., 1994b). Total plant cover averages 5–7%, with vascular plants comprising 1–3%. Of the many polar desert sites studied to date by the author, this one is the richest floristically.

About 43% of the Lowland is covered with graminoid–moss tundra, consisting of hummocky sedge–moss meadows (21%), frost-boil sedge–moss meadows (19%), wet sedge–moss meadows (2%), and minor amounts of salt marsh (0.5%) and

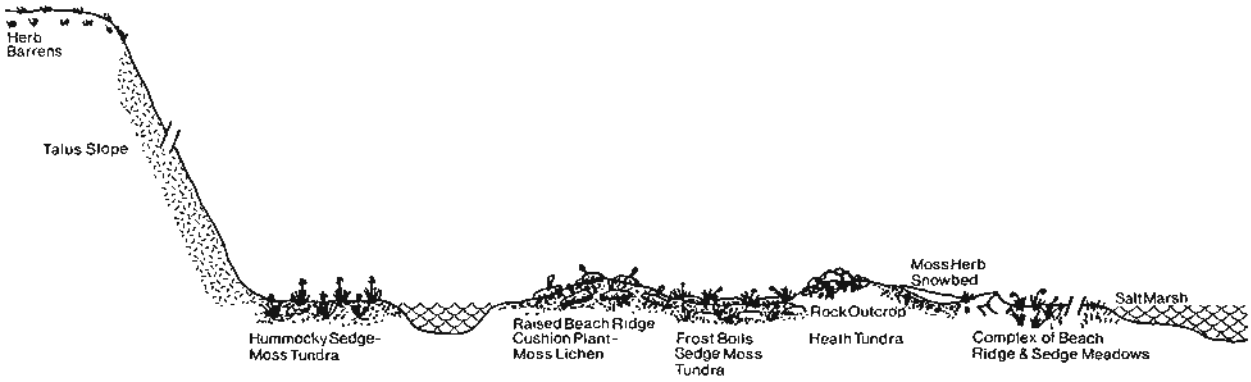

Fig. 19.48. Mesotopographic profile of vegetation types, Truelove Lowland, Devon Island, N.W.T.

hummocky graminoid–moss meadows (0.2%). A total of 38 vascular plant species were sampled in these meadows. The hummocky sedge–moss meadows (Fig. 19.49) are dominated by *Carex membranaceae, C. stans,* and *Eriophorum angustifolium* with *Salix arctica* on the moss hummocks. Bryophytes include *Campylium arcticum, Cinclidium arcticum, Distichium capillaceum, Drepanocladus brevifolius, D. revolvens, Meesia triquetra, Orthothecium chryseum,* and *Riccardia pingius* (Muc and Bliss, 1977; Vitt and Pakarinen, 1977). These meadows are covered with water after snowmelt and are moist throughout the summer.

The frost-boil meadows (Fig. 19.50) consist of about 50% soil boils, some active but most covered with cyanobacteria, some mosses, and scattered sedges. The dominant vascular plants are *Carex membranacea* and *Eriophorum triste* with lesser amounts of *Arctagrostis latifolia, Carex stans*, and *Salix arctica.* Bryophytes include *Bryum pseudotriquetrum, Campylium arcticum, Catoscopium nigritum, Cinclidium arcticum, Distichum capillaceum, Ditrichum flexicaule, Drepanocladus revolvens, Orthothecium chryseum,* and *Seligeria polaris* (Vitt and Pakarinen, 1977).

The wet sedge meadows occur along streams

Fig. 19.49. Hummocky sedge–moss meadow (mire) in wetter habitats dominated by *Carex stans* and *Eriophorum angustifolium*, with polar desert on plateau, Truelove Lowland, Devon Island, N.W.T.

Fig. 19.50. Frost-boil–moss meadow dominated by *Carex stans, C. membranacea,* and *Eriophorum triste*, Truelove Lowland, Devon Island, N.W.T.

and are totally dominated by *Carex stans,* all other graminoids being minor. These sites are inundated with water all summer. The frost-boil sedge–moss meadows occur in older portions of the Lowland and on better drained soils than do the hummocky sedge–moss meadows (Muc, 1977; Muc and Bliss, 1977). There is no indication that one type is successional to the other. This is in contrast with the Russian literature where the frost-boil meadows (spot medallion) are considered successional to the hummocky sedge meadows with their nearly complete cover of vascular plants.

The raised beach ridges are old shoreline features that result from isostatic rebound following ice retreat. Radiocarbon dating from sea shells and whale bones on the beach ridges shows that the ones nearer the sea are about 2,900 yr B.P., those in the center of the Lowland 6,100–7,500 yr B.P. and the oldest ones near the base of the cliff about 9,450 yr B.P. at a height of 109 m above sea level (Barr, 1971). The beach ridges are typically 30–100 m wide, 3–10 m higher than the surrounding lowlands below the foreslope, and are 500–1,500 m in length. Drainage across the Lowland is impeded by the sequence of beach ridges and periodic rock outcrops; only four small creeks drain the larger lakes. The creeks are so small that the arctic char remain land-locked in the deeper lakes. Lakes and ponds account for 22% of the Lowland, beach ridges and their cushion-plant–cryptogam vegetation an additional 11% (Bliss, 1977b).

Cushion-plant–lichen communities dominate the crest and upper slopes where winter snow is 10–50 cm in depth (Fig. 19.51). Dominant vascular plants include *Carex nardina, Dryas integrifolia, Salix arctica,* and *Saxifraga oppositifolia.* Dominant lichens are *Alectoria ochroleuca, A. pubescens, Lecanora epibryon, Thamnolia subuliformis,* and *Umbilicaria arctica.* Common bryophytes include *Distichum capillaceum, Ditrichum flexicaule, Encalypta rhaptocarpa, Hypnum bambergeri,* and *Mnium lycopodioides.* The lower slopes and transition to the sedge meadows, those habitats with deeper snow (1–3 m) and longer-lasting snow (1–2

Fig. 19.51. Cushion-plant–lichen vegetation on a raised beach ridge, Truelove Lowland, Devon Island, N.W.T. The dominant species include *Carex nardina, Dryas integrifolia, Salix arctica, Saxifraga oppositifolia,* and numerous lichen species. Sedge–moss meadows beyond in wetter sites.

wk), have a great cover of *Dryas, Salix,* and *Saxifraga. Carex misandra* and *C. rupestris* replace *C. nardina; Cassiope tetragona* occurs where snow melts last. Bryophyte cover is greater than on the upper slopes, and is dominated by *Oncophorus wahlenbergii, Rhacomitrium sudeticum* and *Tortella arctica*; important lichens include *Cetraria cucullata, C. nivalis, Lecanora epibryon, Physcia muscigena*, and *Thamnolia subuliformis* (Svoboda, 1977; Muc and Bliss; 1977; Richardson and Finegan, 1977; Vitt and Pakarinen, 1977).

The granite rock outcrops (12% of area) heat up more in summer, are well drained, and in winter have deep snow, some of which melts later in early July. As a result dwarf-shrub heath communities dominated by *Cassiope tetragona* are common. Other species include *Carex misandra, Dryas, Salix* and *Saxifraga oppositifolia.* The most abundant bryophytes include *Dicranum elongatum, Ditrichum flexicaule, Hylocomium splendens, Hypnum revolutum, Polytrichum juniperinum, Rhacomitrium lanuginosum,* and *Tomenthypnum nitens.* The common lichens, all fruticose forms, include *Alectoria ochroleuca, Cetraria cucullata, C. laevigata, C. nivalis, Dactylina arctica,* and *Thamnolia subuliformis* (Bliss et al., 1977).

Small communities of graminoids and mosses (3–5 m^2) occur in the rocks and are dominated by *Hierochloë alpina* and *Luzula confusa* with lesser amounts of *Festuca brachyphylla, Poa arctica* and *Potentilla hyparctica. Rhacomitrium lanuginosum* dominates the mosses and the lichens *Alectoria ochroleuca* and *Umbilicaria vellea* occur on the rocks. Where snow lies latest, herb–moss communities occur with *Alopecurus alpinus, Luzula nivalis, Oxyria digyna, Papaver radicatum, Phippsia algida, Saxifraga cernua, S. nivalis,* and *S. tenuis.* Important bryophytes include *Bryum cryophilum, B. pseudotriquetrum, Catoscopium nigritum* and *Cinclidium arcticum* (Bliss et al., 1977).

Flat areas next to the sea, contain silts and organic matter from mats of marine algae and cyanobacteria, and include small salt marshes, often a fringe only 10–30 m wide (Fig. 19.52). *Puccinellia phryganodes* forms a solid turf in which scattered plants of *Carex ursina, Cochlearia officinalis* ssp. *groenlandica* and *Stellaria humifusa* occur. Upslope from these marshes are small meadows of *Alopecurus alpinus*, grading into sedge meadows in some areas. In others the gradient is into cushion-plant communities of *Salix arctica* and *Saxifraga oppositifolia.*

Rea Point, Melville Island. This portion of Melville Island is quite well vegetated compared with

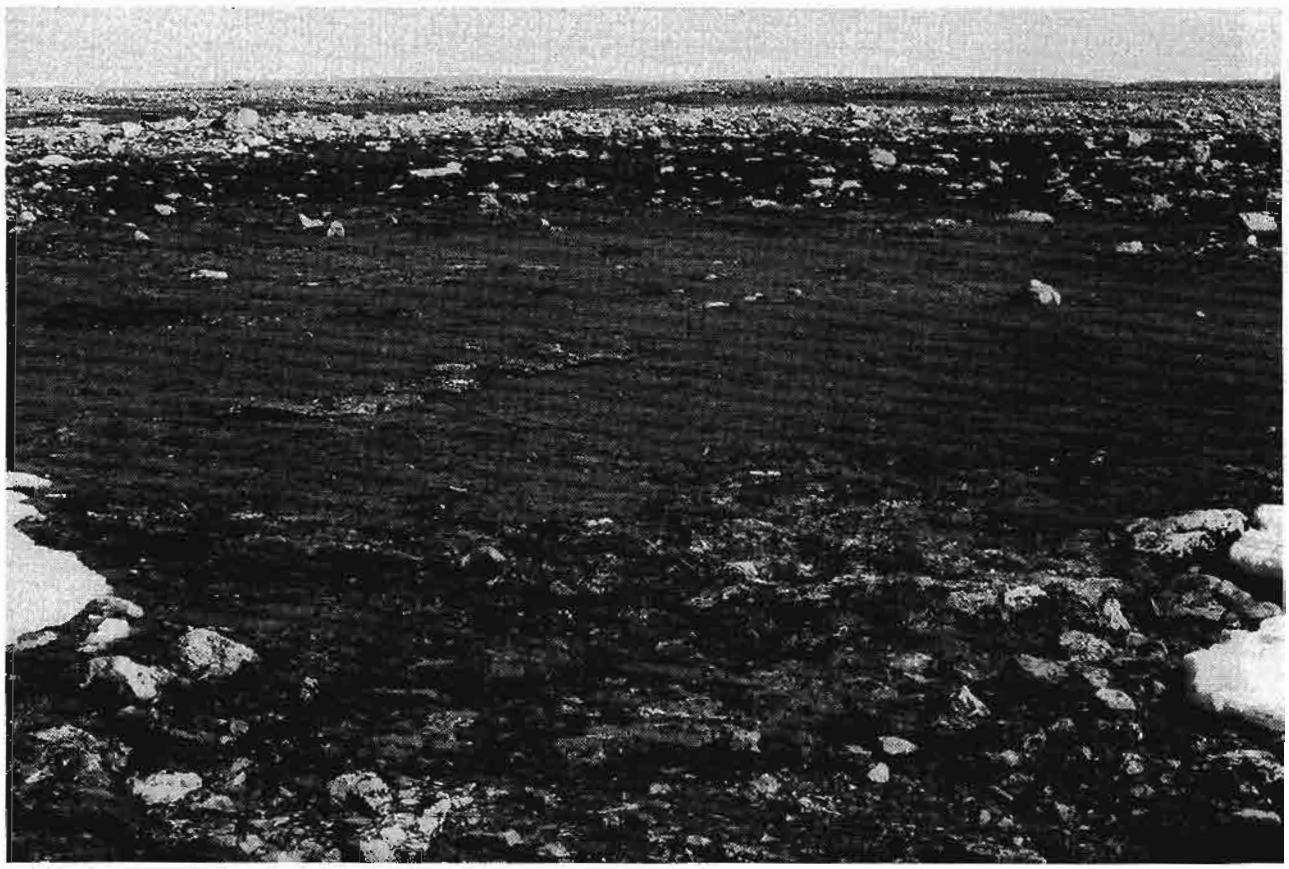

Fig. 19.52. Small salt marsh along a brackish-water lagoon, dominated by *Puccinellia phryganodes* and marine algal mats in the foreground, Truelove Lowland, Devon Island, N.W.T.

the central uplands and northern peninsulas. The vascular plant flora of Melville Island is one of the larger in these northern islands (≈115 spp). The Rea Point area does not include barren uplands (polar desert) within 10–15 km of the coast (Fig. 19.53).

The rolling uplands and slopes are part of the polar semidesert, cryptogam–herb vegetation. The uplands with their silty loam and loam soils are dominated by *Alopecurus alpinus* and *Luzula confusa* with varying amounts of *Oxyria digyna, Papaver radicatum, Salix arctica* and *Saxifraga oppositifolia*. Important mosses include *Ditrichum flexicaule, Polytrichum juniperinum,* and *Tortula ruralis* and the lichens *Dermatocarpon hepaticum, Lepraria neglecta,* and *Thamnolia subuliformis*. On some slopes and upland areas, non-sorted soil polygons and soil stripes are abundant. On the moss mats in the troughs *Luzula confusa, Papaver radicatum, Salix arctica* and *Saxifraga oppositifolia* predominate (Fig. 19.54) (Bliss and Svoboda, 1984).

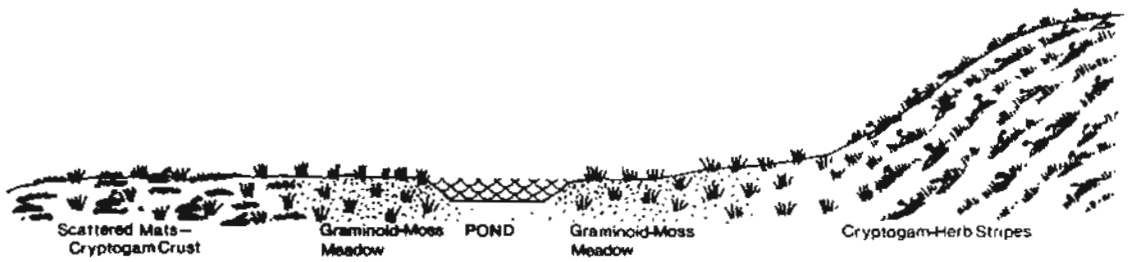

Fig. 19.53. Mesotopographic profile of vegetation types, Rea Point, Melville Island, N.W.T.

Fig. 19.54. Patterned ground with mosses, cushion plants, and graminoids in troughs and bare soil stripes between, Rea Point, Melville Island, N.W.T.

In gullies where snow remains until mid or late July, scattered plants of *Alopecurus alpinus, Luzula nivalis, Phippsia algida,* and *Saxifraga cernua* occur along with crustose lichens and a few mosses.

On the sandy lower slopes and benches, large mats of *Salix arctica* and *Saxifraga oppositifolia* predominate along with scattered clumps of *Juncus albescens, Papaver radicatum,* and *Saxifraga caespitosa.* Crustose lichens are very prominent including *Dermatocarpon hepaticum, Lepraria neglecta, Pertusaria dactylina,* and *P. octomela. Thamnolia subuliformis* and the mosses *Bryum algovicum* and *Polytrichum juniperinum* are also common (Fig. 19.55). In early July these slopes appear purple with the abundant flowering of *Saxifraga oppositifolia.*

On warmer slopes and local meso-sites, small patches of *Dryas integrifolia* occur; where snow lasts longer, small (10 × 20 m) snowbed communities of *Cassiope tetragona* dominate along with limited amounts of *Luzula nivalis, Papaver radicatum, Salix arctica, S. reticulata,* and numerous lichens and mosses.

Where streams from the uplands discharge their waters onto a nearly level bench, small ponds and graminoid–moss meadows occur. The dominant plant is *Dupontia fisheri* with lesser amounts of *Carex stans, Eriophorum scheuchzeri* and *E. triste.* In these latitudes, *Pleuropogon sabinei* replaces *Arctophila fulva* in the shallow pond waters. Mosses are abundant including *Aulacomnium turgidum, Campylium arcticum, Orthothecium chryseum, Philonotis fontana,* and *Polytrichum juniperinum.* Mats of *Nostoc commune* are common as they always are in northern arctic mires.

On the long, sandy slopes to the sea, where shifting sand is common, the rhizomatous grass *Alopecurus alpinus* is common along with clumps, often on sand pedestals, of *Oxyria digyna, Papaver radicatum, Salix arctica,* and *Saxifraga oppositifolia* (Fig. 19.56).

Cape Abernethy, King Christian Island. King Christian Island is a small island (≃1000 km^2) with a low domal profile; the highest point is only 110 m. There are numerous intermittent streams that carry large volumes of water during snowmelt, but none flow all summer and there are no ponds or permanent lakes. The total vascular plant flora is about 45 species, reflecting the limited habitat diversity and general biological barrenness of these northwestern islands.

Herb barrens (Fig. 19.57) on King Christian Island are restricted to the higher-elevation outcroppings of the Isachsen Formation and their sandy to silty loam soils. Vascular plants include *Draba corymbosa, D. subcapitata, Papaver radica-*

Fig. 19.55. Cryptogam–herb vegetation type on sandy soils, Rea Point, Melville Island, N.W.T.

Fig. 19.56. Scattered mats of *Luzula confusa*, *Salix arctica*, and *Saxifraga oppositifolia* with a well-developed cryptogamic crust, Rea Point, Melville Island, N.W.T.

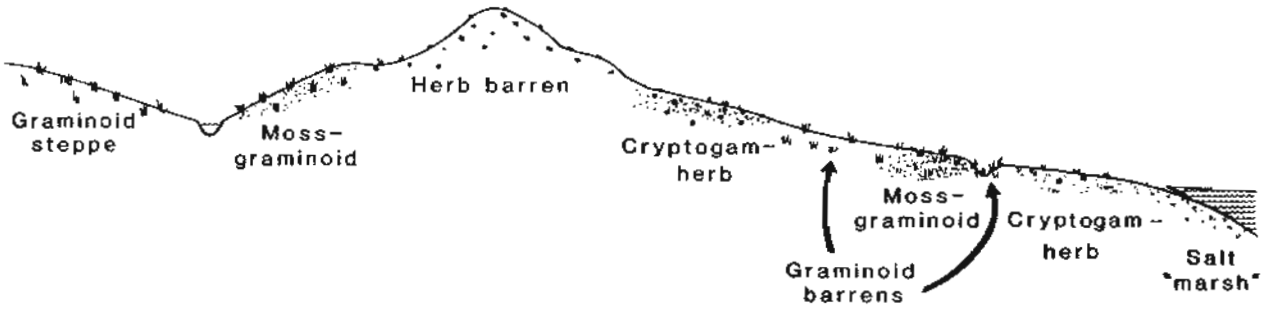

Fig. 19.57. Mesotopographic profile of vegetation types on King Christian Island, N.W.T.

tum, and *Saxifraga oppositifolia* on sandy well-drained soils and *Puccinellia angustata* and *Papaver radicatum* on silt and hard-packed clay loam surfaces. Lichens and mosses are very minor; total plant cover is 0.1–3% (Bliss et al., 1984).

Where Christopher shale has weathered to form silty loam soils that are dark in color, *Alopecurus alpinus* dominates with a few scattered plants of *Cerastium arcticum, Draba alpina, D. corymbosa, Papaver radicatum, Saxifraga cernua, S. nivalis,* and *Stellaria longipes.* Lichens and mosses are minor, in large measure the result of active "soil boils" and their highly plastic nature in spring and fall. The surface is always hummocky, the result of the abundance of soil boils.

Where silty loam to clay loam silts occur, derived from the coastal marine sediments or shales at inland sites, bryophytes predominate including *Aulacomnium turgidum, Ditrichum flexicaule, Polytrichum juniperinum, Rhacomitrium lanuginosum, Schistidium holmenianum,* with the liverwort *Gymnomitrion corallioides* where the soils are fine textured and remain wetter all summer. The most common lichens are *Cetraria islandica, Lepraria neglecta* and *Parmelia omphalodes. Alopecurus alpinus, Luzula confusa,* and *L. nivalis* generally dominate the vascular-plant flora with lesser amounts of *Draba alpina, Papaver radicatum,* and *Saxifraga cernua.* Total species richness (20–25) and plant cover (70–80%) are quite high for these communities (Bliss and Svoboda, 1984).

On soils that are generally a bit coarser (sandy to silty loams), lichens, mostly crustose species, increase in importance and bryophytes are less important. These are termed cryptogam–herb communities. Dominant species include the lichens *Dermatocarpon hepaticum* and *Lepraria neglecta* with lesser amounts of *Cetraria islandica, Dactylina arctica* and *Thamnolia subuliformis.* Vascular plants include *Alopecurus alpinus, Cerastium arcticum, Draba corymbosa, Luzula confusa, Minuartia rubella,* and *Papaver radicatum* (Fig. 19.58).

Near the contact of the Isachsen sandstones and the thin marine sediments, the surfaces are subject to severe sheet erosion, soil churning, and needle-ice formation in spring and fall. On these surfaces there are often large bare soil areas with only a few scattered plants of *Phippsia algida* and small "islands" of former vegetated surfaces with *Dermatocarpon hepaticum, Gymnomitrion corallioides, Lepraria neglecta, Pertusaria dactylina, P. octomela* and some *Alopecurus alpinus* (Fig. 19.59). The gullies (coulees) fill with snow in winter (2–4 m) and melt out in early to late July. In these sites there is often a nearly complete plant cover, mostly of the crustose lichens listed above for the eroded sites. *Phippsia algida* is the dominant vascular plant with lesser amounts of *Cerastium arcticum, Cochlearia officinalis, Saxifraga cernua,* and *S. nivalis.* Mosses dominate and there are large areas of cryptogamic crust including cyanobacteria and crustose lichens (Fig. 19.60).

Within 50–100 m of the seashore there are small patches of *Puccinellia phryganodes* and *Stellaria humifusa,* often only 1–3 m^2 in extent. They are the northern remnant of the subarctic and arctic salt marshes.

Hoodoo Dome, Ellef Ringnes Island. Ellef Ringnes Island is a much larger island (13,310 km^2), but its vascular plant flora is small (≈50 spp), a reflection of its cold, bleak climate and limited habitat diversity. Lakes and ponds are limited to the Isachsen area (Savile, 1961). The Hoodoo area is an upland region in the southern central part of the Island. In contrast with King Christian Island, there are rivers that flow all summer. Polar semi-desert and polar desert vegetation predominate (Fig. 19.61).

Uplands with coarse-textured soils are more extensive than on King Christian Island, and

Fig. 19.58. Cryptogam–herb vegetation with scattered rosette plants of *Draba*, *Ranunculus*, *Saxifraga*, and the graminoids *Alopecurus* and *Luzula*, King Christian Island, N.W.T.

Fig. 19.59. Eroded surfaces with small "patches" of mosses, lichens, *Alopecurus* and *Papaver*, King Christian Island, N.W.T.

Fig. 19.60. Cryptogamic crusts of cyanobacteria, crustose lichens (at knife) with clumps of mosses, and scattered plants of *Alopecurus*, King Christian Island, N.W.T.

consequently herb barrens of the polar deserts are more common. Total plant cover is only 1–3%, characterized by scattered plants of *Papaver radicatum, Puccinellia angustata*, and the lichen *Thamnolia subuliformis* (Fig. 19.62).

On slopes where soils are developed from Christopher shale, *Alopecurus alpinus* is the major species. Soil slumping, following unusual summer rains, frequently occurs in these soils. Associated herbs include *Cerastium arcticum, Saxifraga cernua*, and *Stellaria longipes.*

Floristically poor moss–herb communities develop on gentle slopes where soils are sandy loam to silty loam in texture. The dominant vascular plants are *Alopecurus alpinus, Draba corymbosa, Luzula confusa, L. nivalis, Papaver radicatum, Saxifraga cernua, S. tenuis, S. caespitosa,* and *Stellaria longipes.* Mosses include *Ditrichum flexicaule, Polytrichum juniperinum* and *Rhacomitrium lanuginosum,* with the lichen *Dermatocarpon hepaticum.* There are small level or depression habitats that contain higher levels of sodium salts, sites that are white when dry. These contain *Cochlearia officinalis, Puccinellia phryganodes*, and *Stellaria humifusa.*

On river terraces where there is abundant water

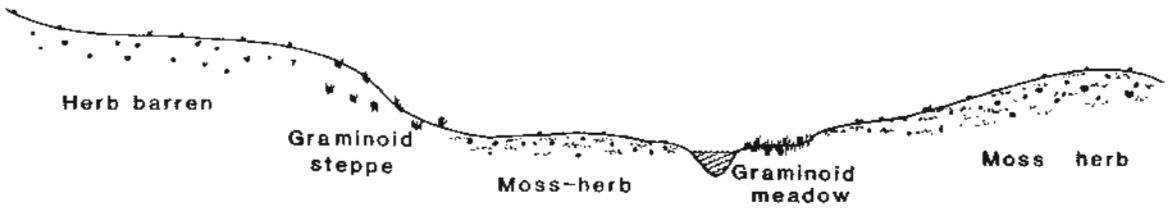

Fig. 19.61. Mesotopographic profile of vegetation types, Hoodoo Dome, Ellef Ringnes Island, N.W.T.

Fig. 19.62. Polar desert barren on uplands, Hoodoo Dome, Ellef Ringnes Island, N.W.T. The only vascular species are *Papaver radicatum* and *Puccinellia angustata*.

from large snowbanks at the base of adjacent uplands, meadows of *Dupontia fisheri* are found. There are essentially no other vascular plant species. Bryophytes include *Cinclidium arcticum, Drepanocladus revolvens*, and *Orthothecium chryseum* (Fig. 19.63) (Bliss and Svoboda, 1984).

Polar deserts in High Arctic

Vegetation types

Herb barrens. Since the previous vegetation types and plant communities have generally been termed polar desert, the truly barren landscapes have not been described until recently (Bliss et al., 1984). Porsild (1951) recognized ice deserts, rock deserts, and tundra based upon floristics, as did Young (1971) with his arctic floristic zones. As stated earlier, the present author believes that zones cannot be recognized, except those based upon species. If ecological characteristics are used (vegetation structure, role of dominant species including cryptogams, species richness of plants and animals, and soil development) a mosaic pattern emerges. This pattern does not lend itself to simple zonal lines on a map.

Bliss et al. (1984) studied seven sites in detail on six islands and 14 additional sites on 10 islands including the original six islands. The sites range from sea level (10–20 m) to over 200–300 m on upland plateaus. In the 23 stands of vegetation sampled, the vascular plant flora averaged 4–9 species (total of 17 spp) with an average plant cover of 1.8% (Fig. 19.64). Cryptogam species averaged 3–5 with an average plant cover of only 0.7%; the remaining 98% was bare soil and frost-shattered rock and pebbles. The limited role of cryptogams is in sharp contrast with the polar semideserts where cryptogams dominate. These landscapes dominate thousands of square kilometers, especially in the Queen Elizabeth islands of Canada.

The vascular plants include *Draba corymbosa, D. subcapitata, Minuartia rubella, Papaver radicatum, Puccinellia angustata*, and *Saxifraga oppositi-*

Fig. 19.63. Small *Dupontia fisheri* meadow with mosses in a wetland near a large snowbank, Hoodoo Dome, Ellif Ringnes Island, N.W.T.

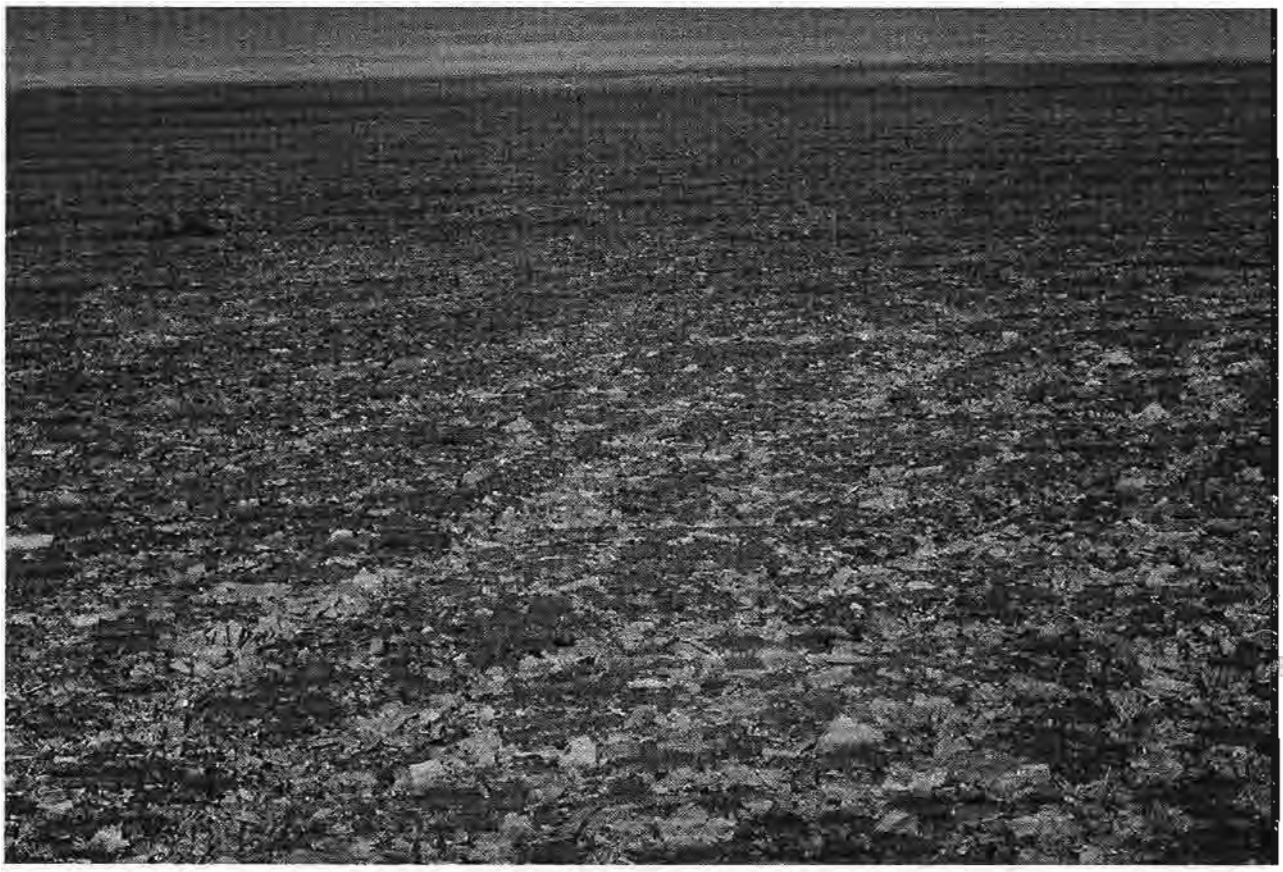

Fig. 19.64. Herb barren with only 2 to 4% total plant cover in a polar desert, Devon Island.

folia. All of these are rosette, cushion, or mat-forming species, including the prostrate grass *Puccinellia.* There are no woody or semi-woody species in these barren landscapes, although *Salix arctica* occupies high-elevation sites near permanent ice and snow on Ellesmere Island and on protected slopes on Devon Island where snow-flush waters occur (Bliss et al., 1994b). These latter sites are relatively warm in summer, which indicates that the lack of water and nutrients are more important than temperature in limiting plant cover in these barren lands. The lack of lichens on rocks and the very depauperate flora suggest that these lands may have become vegetated only since the Little Ice Age (130–430 yr B.P.) (Svoboda, 1982). Further research is required to determine if this is a controlling factor in the barrenness of these lands.

Snow-flush communities. Within the polar barrens, the only habitats that have any significant plant cover are those resulting from snowmelt waters. Species richness was much greater, averaging 13 species per site; a total of 30 species of vascular plants were sampled in 12 sites. Lichens and mosses averaged 12 species per site; a total of 27 species were recorded with mosses most prominent. Total plant cover averaged 36% (Bliss et al., 1984). The limited extent of these communities demonstrates the importance of water and the ability of cyanobacteria and bacteria to fix nitrogen in these sites.

Plant communities are variable in species composition, ranging from small graminoid meadows dominated by *Alopecurus alpinus,* or *Eriophorum triste* to many in which *Saxifraga oppositifolia* dominates along with *Alopecurus alpinus, Minuartia rubella, Papaver radicatum, Phippsia algida,* and *Saxifraga cernua.* Mosses are abundant in the polygon troughs, especially *Ditrichum flexicaule, Drepanocladus revolvens* and *Orthothecium chryseum* (Bliss et al., 1984).

Although these habitats generally cover only 3–5% of the landscape, they are conspicuous features, especially from the air because of dark streaks of bryophytes and cryptogamic crusts.

Other arctic plant communities

Vegetation types

Salt marshes. Although there are thousands of kilometers of arctic shoreline, salt-marsh communities are a very minor feature. Along many shorelines, boulder or sandy beaches or sea cliffs occur (Bliss, 1993). In a few locations there are coastal marshes developed on fine sands and silts with a highly specialized, yet a very small, group of species. Other factors that limit development of coastal marshes are the annual reworking of shorelines by sea ice, limited tidal amplitude, low salinity of coastal waters, a short growing season, and low soil temperatures.

Floristically there is little difference between these low and high arctic salt-marsh communities, although plant height, plant cover, and areal extent are reduced northward. The most common species are *Puccinellia phryganodes*, usually on muds and found furthest to seaward along with patches or clumps of *Carex ramenskii, C. subspathacea, C. ursina, Cochlearia officinalis,* and *Stellaria humifusa.* Coastal marshes have been described from northern Alaska (Jefferies, 1977; Taylor, 1981), Tuktoyaktuk (Jefferies, 1977) and Hudson Bay, Canada (Kershaw, 1976; Jefferies et al., 1979; Jefferies, 1988), southwestern and southeastern Greenland (Böcher, 1933; 1954; Molenaar, 1974), central western Greenland (Sørensen, 1943, Vestergaard, 1978), Devon, Ellesmere, and Baffin Islands (Polunin, 1948; Jefferies, 1977; Dawson and Bliss, 1987). In many of these marshes vascular plant cover is only 15–25% and plant height 1–5 cm. Floristically most marshes have only 3–5 species. These characteristics are in sharp contrast with the extensive and highly productive coastal marshes of temperate regions. Arctic salt-marshes and rocky shorelines have been summarized by Bliss (1993).

Grasslands. Grasslands, in the sense of those in temperate regions, are lacking, although grasses are often a component of wetland and upland communities. Small areas of grassland occur in the inner fjords of central eastern Greenland (Seidenfaden and Sørensen, 1937; Oosting, 1948) dominated by *Arctagrostis latifolia, Calamagrostis purpurascens, Poa arctica,* and *P. glauca.* In west Greenland larger areas (1–5 ha) of grassland dominated by *Calamagrostis neglecta, Poa arctica,* and *P. pratensis* occur (Böcher, 1959). Similar grasslands, but usually of small extent, occur in the eastern Canadian arctic of Baffin Island (Polunin, 1948) and northern Keewatin (Larsen, 1972).

Hanson (1951, 1953) described rather extensive areas of grassland in western Alaska. Major grass species include *Agrostis scabra, Calamagrostis canadensis,* and *Festuca altaica* in more arctic–alpine

locations. Grassland communities in the upper Matanuska Valley near Palmer that include *Artemisia frigida, Bromus, pumpellianus, Calamagrostis purpurascens, Poa glauca, Potentilla pennsylvanica* and *Rosa acicularis* are somewhat similar in structure, if not species, to what is considered to have been a dominant vegetation in central Alaska during the Late Pleistocene. Some authors have referred to this as the mammoth-steppe biome of Beringia. This is discussed elsewhere in this chapter (p. 646 *ff*).

Walker et al. (1991) have shown that south-facing slopes of pingos on the coastal plain in Alaska have plant communities dominated by grasses and forbs. They present this as evidence for steppe vegetation in the Duvanny Yar interval (30,000 to 12,000 yr B.P.).

SUCCESSION

Plant succession, the replacement of species with time leading to a more stable community with increased community structure and complexity, is a universal phenomenon. However in the Arctic, with increasing latitude and environmental severity, succession changes from species replacement to species establishment and survival. Three models of arctic succession were developed by Svoboda and Henry (1987) (Fig. 19.65). Directional change with species replacement occurs in the Low and High Arctic, but appears to be less common than directional change with nonreplacement of species (Bliss and Peterson, 1992). A third model of nondirectional change and nonreplacement of species characterizes the polar deserts.

Directional change with species replacement

Major rivers in the Low Arctic have meandering channels and river terraces that support a diversity of plant communities. Tall shrubs are typical along river channels, often with an understory of herbs and shorter *Salix* shrubs. On older sand and gravel bars and on lower terraces, the taller *Salix alaxensis* shrubs are replaced with shorter greenleaf willow species. With time, a decrease in active-layer depth and an increase in organic matter, dwarf-heath shrubs and often *Dryas* replace the taller shrubs (Bliss and Cantlon, 1957; Peterson and Billings, 1980). At Atkasuk, Alaska, where there are large sand dunes, *Elymus mollis* is an

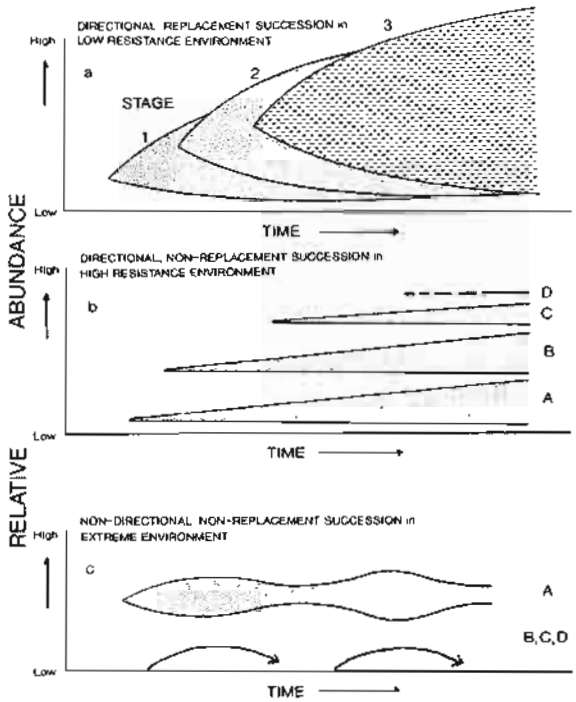

Fig. 19.65 Model of plant succession in diverse arctic environments (from Svoboda and Henry, 1987). Directional-replacement model (a) within low-resistance environments characteristic of some low arctic communities. Directional-nonreplacement model (b) within many low arctic and semi-desert communities of the High Arctic. Nondirectional and nonreplacement model (c) within some polar semidesert and polar desert communities. Invading species (A, B, C, D) establish successfully in type b, but species B, C, D fail in type c.

important pioneer species because of its rhizome development. Cottongrass tussock tundra with scattered dwarf-shrubs, lichens, and mosses appears to be the stable, climax community along the Meade and Colville rivers. The mechanisms for species replacement include facilitation and plant competition for nutrients and soil water.

Sedge–moss meadows or mires also develop as a result of directional change with species replacement. The thaw–lake cycle near Barrow, Alaska demonstrates this pattern (Britton, 1957; Billings and Peterson, 1992). Mosses are the first to establish, followed by the graminoids *Arctophila fulva, Dupontia fisheri,* and *Eriophorum scheuchzeri.* With time *Carex aquatilis* and *Eriophorum angustifolium* replace *Dupontia fisheri.* Physical environment changes include decreased available phosphorus, pH, and active-layer depth, and increased depth of organic matter (Billings and Peterson, 1992).

Coastal lowlands, which are biological oases in the High Arctic, appear to develop in a similar way. On the Truelove Lowland, Devon Island of Canada, marine algae often wash into shallow lagoons, and with the gradual isostatic rebound of these shorelines, the algae become elevated. They are invaded with cyanobacteria and the brackish marsh grass *Puccinellia phryganodes*. If the landscape forms a concavity with snow-flush waters from upslope, *Dupontia fisheri* establishes a graminoid meadow because of its rhizomatous reproduction. With time, *Carex stans* replaces *Dupontia fisheri* to form nearly pure stands of mire vegetation where soils remain wet all summer. Physical and biological changes include decreased available phosphorus, pH and rate of nitrogen fixation, increased depth of organic matter, and maintenance of wet soils throughout the summer. On the margins of these basins, succession ends in a cushion-plant–moss community where soils are shallow (2–5 cm) and much drier by mid-summer (Bliss et al., 1990; Bliss and Gold, 1994).

Directional change with nonreplacement of species

While this process of succession no doubt occurs in the Low Arctic, it has only been studied in the High Arctic. On King Christian Island and others within the western Queen Elizabeth Islands of Canada, cryptogam–herb vegetation predominates. It appears that cryptogam crusts of mosses, crustose and foliose lichens, and cyanobacteria establish. With time vascular plants invade, almost always on these cryptogam mats rather than in bare soil (Sohlberg and Bliss, 1984). The cryptogams are not replaced, nor is there evidence that a replacement sequence occurs with the vascular plants: only an increase in cover of vascular plants. The important environmental factors are surfaces kept moist throughout the summer, the limited role of cyanobacteria in fixing nitrogen, and the development of a thin organic mat at the surface.

In the eastern Queen Elizabeth islands and the islands to the south, cushion-plant–cryptogam vegetation dominates uplands, whereas mires in lowlands are kept wet all summer. The raised beach ridges on the Truelove Lowland, Devon Island, have less plant cover than older beach ridges (3000–6000 vs 6000–9000 yr) (Svoboda, 1977). The very young beach ridges along Rocky Point have even less plant cover and fewer species (Svoboda, 1977; Leggett, 1990; Bliss and Gold, 1994). The development of a cryptogamic mat of mosses and lichens appears central to the establishment of vascular plants in these "upland" habitats, for areas without cryptogams have few vascular plants, except in the dark soils derived from shales that support the rhizomatous grass *Alopecurus alpinus* (Bliss et al., 1984).

Nondirectional change with nonreplacement of species

Large areas within the High Arctic are almost devoid of cryptogams and vascular plants, the polar deserts. These barren lands result from a combination of limited available soil moisture in surface soils after mid-summer, very low soil nutrients, abundant needle ice in fall, a very short growing season, and for upland sites many areas covered with permanent snow during the Little Ice Age (Svoboda, 1982; Bliss et al., 1994a). Under these extreme conditions there are only a few species that can grow in these barrens, unless snow-flush or soil water seepage habitats are present. Only in snow-flush habitats is there any indication of plant succession. There is little indication of directional change and no indication of species replacement within these polar deserts.

Morphological and physiological adaptations of the plant species studied to date help to explain why they occupy the ecological niches that they do (Bliss and Peterson, 1992). Many species of climax communities maintain wintergreen or evergreen leaves; this enables them to initiate photosynthesis with snowmelt and to conserve the limited nutrient pools. Pioneer herbs and deciduous shrubs grow rapidly, produce large amounts of seed that is often highly viable, and have high rates of photosynthesis. Some of these factors will be discussed in greater detail in the section on plant adaptations.

From the previous material, it should be apparent that the vegetation of arctic landscapes is very diverse. The northward reduction in kinds of vegetation, height of plants, and floristic richness is very dramatic. In general, moving from the Low to the High Arctic results in the loss of all major vegetation types of the southern region except for graminoid–moss mires. Within the High Arctic, there is a shift from polar semidesert vegetation of cushion–plant–cryptogam and cryptogam–herb to the polar-desert vegetation of the herb barrens.

TABLE 19.15

Mean daily, monthly, and annual environmental data for selected arctic and alpine sites

Parameter	Barrow, Alaska 71°N[a]	Truelove Lowland, N.W.T. 75°N[b]	King Christian Island, N.W.T. 78°N[c]	Mt. Washington, New Hampshire 1840m[d]	Niwot Ridge, Colorado 3500m[e]	Piute Pass, California 3540m[f]
Radiation (MJ $m^{-2}d^{-1}$)						
July mean global solar	18.5	20.2	12.5	15.4	20.1	28.3
July mean daytime global solar	0.77	0.84	0.52	0.96	1.30	1.89
Maximum photoperiod (h)	24	24	24	16	15	15
Temperature (°C)						
July mean air (0.5–1.5m)	3.7	3.9	3.1	9.3	12.5	10.5
January mean air	−26.4	−30.8	−31.2	−14.7	−10.1	–
July mean soil (−10 cm)	2.1	2.0	4.5	8.8	14.3	22.0
Thaw depth, mean max. (cm)	35–60	30–40	45–60	–	–	–
Precipitation (mm)						
June–Aug.	40	42	51	183	207	7
Annual	170	185	130	1880	1020	–
Atmospheric moisture, June-Aug. (VPD in kPa)	0.08	0.11	0.04	0.13	0.61	
Wind, July mean ($m\ s^{-1}$ at 50–60 cm)	3.1	4.8	3.5	3.7	5.8	2.3

[a]Dingman et al. 1980, Hobbie 1980; [b]Courtin and Labine 1977, Bliss 1975; [c]Addison and Bliss 1980, Grulke 1983, [d]Bliss 1966; [e]Barry 1973; [f]Chabot and Billings 1972

Associated with these major changes in plant species and plant cover are changes in soils and wildlife, all basically controlled by climate changes and especially solar radiation, length of the growing season, and effective soil moisture.

ADAPTATIONS OF PLANTS TO ARCTIC ENVIRONMENTS

Arctic species, like those of desert and saline habitats, have received much attention because they grow in stressful environments. Plants of tundra and polar-desert habitats are subjected to low air and soil temperatures, often to too low nutrient availability, and to extremes in atmospheric and soil moisture. Some species grow in cold, water-saturated soils with low oxygen tensions, and others in soils that are wet after snowmelt, yet dry considerably in summer. Plant responses are further controlled by a short growing season that limits growth and sexual reproduction.

The major objectives of this section are to discuss the morphological and physiological responses of plants adapted to the stressful environments of these high latitudes. This will be done in the context of the life history of species and the major morphological life forms of species (annuals, graminoids, forbs, cushion and rosette species, and shrubs).

Environments

Although the climatic and soil environments of arctic tundras and polar deserts were discussed earlier, it seems appropriate to summarize some of the major factors in a comparison of arctic and alpine environments. Global (short-wave) radiation can be quite similar in mid-summer in sunny alpine and arctic environments, yet the radiation per daylight hour and the hours of daylight are very different (Table 19.15). Air and soil temperatures are generally low, yet they are considerably lower in the Arctic than in most alpine sites in summer because permafrost is seldom present in the mountains, and the soils are better drained. Precipitation is also much greater in alpine environments on an annual basis, but the western mountains have very dry summers (Sierra Nevada, California). This is also illustrated by mean daily atmospheric moisture expressed as vapor pressure deficits (VPD). They are low throughout the Arctic

and in the foggy alpine environment of the Presidential Range, New Hampshire. Vapor pressure deficits on warm, sunny days range from 1.00 to 2.2 kPa at Umiat, Alaska; Mount Washington, New Hampshire; and the Snowy Range, Wyoming (Bliss, 1956, 1962a, 1966). Soils in most alpine environments are much better drained than in the Arctic and therefore drought stress is a more important factor in the water economy of alpine plants. The exceptions in the High Arctic are the polar deserts, and elsewhere during those rare summers with limited precipitation, higher levels of sunshine, and daily winds. Under these conditions, soil water potentials (ψ_s) can approach values of dry alpine sites (−3.0 to −5.0 MPa). Both arctic and alpine environments are windy, with wind velocity greatest on exposed sites including ridges and mountain cols. This greatly influences the distribution pattern of plant growth forms, with those of low stature (cushion and rosette) predominantly in the windy and well-drained sites throughout all of these cold-dominated regions.

There are considerable differences between some arctic and alpine environmental parameters, parameters that have a profound influence on plant development and ecotypic differentiation. Photoperiod, or length of the night, best typifies this, with the ecotypes of *Oxyria digyna* (Mooney and Billings, 1961; Billings et al., 1971) and *Trisetum spicatum* (Clebsch and Billings, 1976) adapted to arctic environments with continuous light and to alpine environments with photoperiods of 15 to 18 hours. Ultraviolet radiation is also very different (7-fold) between arctic and tropical alpine environments (Caldwell et al., 1980), yet this is not reflected in significant differences in the transmittance of UV-B to leaf mesophyll (Robberecht et al., 1980). The concentration of carbon dioxide is much greater in the air near sea level (Arctic) than in high alpine sites. This is reflected in a more efficient use of carbon dioxide and thus higher rates of photosynthesis for alpine than for arctic populations of *Oxyria digyna* (Billings et al., 1961). A final point is the significant difference in soil temperature and drainage induced by permafrost in the Arctic compared with most alpine environments. Major reviews on the physiological ecology of arctic and alpine plants include those of Bliss (1962a, 1971, 1985), Billings and Mooney (1968), Savile (1972), Billings (1974a), Lewis and Callaghan (1976), Chapin and Shaver (1985a), and Chapin et al. (1992).

Life-history patterns

Reproduction and plant establishment

Arctic species are generally long-lived, although aging them is a difficult task. There are very few annuals or short-lived perennials in these environments. On average, plants of tundra environments probably live 20 years or more. Basal stems of *Betula* and *Salix* and the massive root and rhizome systems of sedges may live for a minimum of 200–400 years. Plants of *Luzula confusa* can live 90–130 years (Addison and Bliss, 1984), *Puccinellia vaginata* 30–70 years and *Phippsia algida* 20–40 years (Grulke and Bliss, 1988) at 78°N, and *Dryas integrifolia* 80–120 years (Svoboda, 1977) at 75–76°N. Ages of mature tussocks of *Eriophorum vaginatum*, from six sites in Alaska, ranged from 120 to 190 years (Mark et al., 1985). Most of these graminoids were aged by knowing the number of leaves produced per year, how long they live, the number of leaves per tiller, and the number of tillers per plant. Forbs are much more difficult to age because of annual die-back and the loss of old leaves that seldom leave leaf scars.

Many graminoids depend upon tillering (*Alopecurus, Carex, Dupontia, Eriophorum, Luzula*) and shrubs on branch-layering (*Betula, Empetrum, Ledum, Salix, Vaccinium*), yet most of these species flower and fruit abundantly and produce viable seed. The exceptions seem to be species of *Luzula*; they produce seed, but seedlings are very rare and germination tests show no seed viability (Bell and Bliss, 1980).

Seed dormancy mechanisms including chilling, after-ripening, light requirements (Bliss, 1958; Densmore and Zasada, 1983) and seed-coat inhibition (Amen, 1966; Bell and Amen, 1970; Rocow, 1970) are evident in 20–40% of alpine and arctic species. One might predict that seeds of most species would require cold treatment (stratification) and would then germinate rapidly with snowmelt. Seeds of many species ripen only in late fall, and often are dispersed over the snow (Grulke and Bliss, 1983). Germination percentages are low for most high arctic species and the germination rates are slow (2–3 weeks for full emergence of root and shoot), the opposite of what might be expected with cool, short summers. It is believed that the small numbers of seedlings and slow rates of germination (2–3 weeks) are a response to low temperatures. If germination occurs over an extended period of time and in limited numbers in

cool summers, this may favor seedling establishment in those rare summers that are warm (Bell and Bliss, 1980). Optimum temperature for germination is quite high (15–30°C) for most species, but a small percentage of species germinate below 10°C (Billings and Mooney, 1968; Bell and Bliss, 1980).

There are two kinds of seed dispersal and germination patterns in arctic and alpine willows. Some species (*Salix alaxensis, S. arbusculoides, S. lanata, S. planifolia*) disperse their seeds in summer; they have a high rate of germination initially, but a short period of viability. Other willow species disperse their seeds in fall, and they germinate the next spring (*S. arctica, S. brachycarpa, S. glauca, S. reticulata*). For this latter group, almost no germination occurred at 5° or 10°C, but germination was maximum at 25°C (Densmore and Zasada, 1983). Species with fall seed ripening and spring germination appear best adapted to environments with a short growing season.

Although seedlings are generally rare in arctic vegetation, some species germinate abundantly in bare soil in northern Alaska and northwestern Canada (*Carex bigelowii, Eriophorum vaginatum*) (Wein and MacLean, 1973; Chester and Shaver, 1982a; b) and the High Arctic (*Juncus biglumis, Phippsia algida*) (Sohlberg and Bliss, 1984; Bliss and Grulke, 1988; Grulke and Bliss, 1988). Seedlings of some species are found in established vegetation (McGraw and Shaver, 1982; Wager, 1938). Disturbed gravelly soils or raised beach ridges on Devon Island contain many young plants of *Cerastium alpinum, Draba* spp., *Minuartia* spp., and *Saxifraga oppositifolia*. The microsite patterning of seedlings and adult plants within "safe sites" of moss turf and crustose lichen patches in cryptogam–herb meadows, and in desiccation cracks with mosses in more barren sites, seems directly related to more favorable soil moisture and nutrient conditions (Sohlberg and Bliss, 1984).

Flowering in arctic plants is variable from year to year, and so is the production of viable seed (Bell and Bliss, 1980; Chester and Shaver, 1982a). In spite of this and the fact that many species reproduce by vegetative means, the soils contain large seed banks (Leck, 1980; McGraw 1980; Freedman et al., 1982; Gartner et al., 1983; Sohlberg and Bliss, 1984). Generally these are species that can serve as both pioneer and climax. This differs from temperate ecosystems where seed banks are dominated by pioneer (weedy) species. The abundance of flowering and fruiting, the production of large amounts of seed, (many of which are viable), and the large seed banks confirm that many arctic species allocate large amounts of carbon to reproduction (Maessen et al., 1983; Grulke and Bliss, 1985), even though these stressful environments are not conducive to seedling establishment. It is evident that both sexual and asexual reproduction are important, even in these most stressful environments where herbaceous plants live many years.

Plant growth

The patterns of growth and development of tundra species are very similar to those of temperate plants. However, tundra species grow at low temperatures and put on their growth in a shorter period of time. Buds, both flower and leaf, overwinter in an advanced stage of development, and growth begins as soon as there are a few hours per day of temperatures above freezing. Forbs and deciduous shrubs have rapid, near synchronous growth of shoots and flowering, with most growth occurring in 2–4 weeks. Graminoids, however, initiate leaves throughout the growing season, those produced late in the season completing their growth early the next summer (Bliss, 1956; Johnson and Tieszen, 1976; Muc, 1977; Tieszen, 1978). Leaves of deciduous species remain functional until August–September when nutrients and carbohydrates are translocated to stems and rhizomes (Johnson and Tieszen, 1976; Campbell, 1983). Going north, the number of deciduous and evergreen woody species is greatly reduced (Table 19.16) but the percentage of the herbaceous flora with wintergreen (leaves function into the second summer) or evergreen leaves (function two or more years) increases (Bell and Bliss, 1977). The ability to carry some green leaves over winter, even in the graminoids, permits plants to initiate photosynthesis as soon as snow melts. Many of these high arctic species have a limited root system and thus are not able to store large amounts of carbohydrates (Bell and Bliss, 1977, 1978). As will be discussed in more detail later, arctic plants with evergreen or wintergreen leaves have lower growth rates, and lower rates of photosynthesis and transpiration, than graminoids and deciduous forbs. The latter species put on a new leaf surface each summer, which is an energy-expensive process.

Some arctic species have a periodic growth

TABLE 19.16

Selected arctic floras and their number of deciduous and evergreen woody species

Location	Latitude °N	Number of Species			Author
		Total Vascular	Deciduous	Evergreen	
Cape Thompson, Alaska	68	305	16	7	Johnson et al., 1966
Reindeer Station near Inuvik, N.W.T.	69	420	26[2]	10	Cody, 1965
Umiat, Alaska	69	82[1]	17	6	Churchill, 1955
Barrow, Alaska	71	139	10	3	Murray and Murray, 1978
Rea Pt., Melville Isl., N.W.T.	75	49	2	1	Bliss (unpublished data)
Truelove Lowland, Devon Isl., N.W.T.	75	96	3	2	Bliss, 1977c
King Christian Isl., N.W.T.	78	35	1	0	Bliss (unpublished data)
Northern Ellesmere Isl., N.W.T.	81	119	2	2	Brassard and Beschel, 1968

[1]incomplete flora
[2]includes three tree species

pattern — that is, they cease growth at a given time regardless of current environmental conditions. This is a well-developed process in high arctic species (Bell and Bliss, 1977; Addison and Bliss, 1984). Growth-chamber studies, utilizing continuous light, alternating "day" and "night" temperatures, and high humidity, resulted in plants of eight species going dormant after a growing season of 50–55 days, although these summer conditions were maintained. Non-periodic growth patterns have been observed in some eastern Greenland species (Sørensen, 1941) and in Alaskan species from different habitats (Murray and Miller, 1982). The synchronous flowering and fruiting of diverse species is typical of some habitats (Bliss, 1956), while in others these phenological stages are asynchronous (Murray and Miller, 1982).

The relative growth rates (mg $g^{-1}d^{-1}$) of arctic and alpine species and communities are comparable with those of temperate grasslands as summarized by Chapin and Shaver (1985a). Tundra species appear to grow close to the maximum that can be attained under the limitations imposed by nutrients and in some environments by available soil water, rather than by the low levels of air and soil temperature that prevail. However, other studies have shown that temperature is a key factor limiting the growth of arctic plants.

There are great differences in rates of plant growth imposed by growth form in tundra plants. Forbs and deciduous shrubs grow most rapidly, evergreen shrubs most slowly, and graminoids at an intermediate rate (Bliss, 1956; Johnson and Tieszen, 1976). In general, plant communities and individual species with relatively rapid rates of growth occur on nutrient-rich sites, and species and communities with slow growth rates occur on nutrient-poor sites (Chapin, 1980). Miller (1982) studied the pattern of plant communities across a snowbed in relation to plant responses. He concluded that availability of nitrogen and phosphorus rather than length of the snowfree season, pH, or soil moisture best explained these plant community patterns. Much of this correlation may be explained by the fact that evergreen species have low rates of photosynthesis and respiration, yet maintain relatively high levels of tissue nutrients in sites with low available soil nutrients. Deciduous species, graminoids and forbs grow rapidly, have higher rates of photosynthesis and respiration, and often lower levels of tissue nutrients, on sites with higher available nutrients (see Chapin, 1980).

Root growth generally begins as soon as soils thaw and warm above 2–4°C. However, growth of lateral roots is usually greater later in the season, often continuing when shoot growth has slowed (Shaver and Billings, 1975; Bell and Bliss, 1978; Dawson, 1987). Decrease in root growth has been correlated with reduction in photoperiod (Shaver and Billings, 1977; Kummerow and Russell, 1980). The separation of most shoot growth early in the growing season from root growth later in the season reduces competition for carbohydrates and enables growth of each plant part to make the best use of more favorable environmental conditions.

Various studies have concluded that plant growth rates and plant community net production are more closely correlated with availability of soil

nutrients, soil moisture, soil aeration, and soil temperature, than with air temperature (Bliss, 1956; Warren Wilson, 1957; Shaver et al. 1979; Miller, 1982). Shoots and roots of arctic plants are capable of growing at low temperatures (0–5°C) (Shaver and Billings, 1977; Bell and Bliss, 1978; Billings et al., 1978; Dawson, 1987). However, recent field studies with small greenhouses show that growth of low arctic graminoids, forbs, and deciduous shrubs is enhanced by temperatures of 10- 20°C (Chapin and Shaver, 1985b). *Carex stans* in the High Arctic increased its growth only 8 to 10% with a three-fold increase in degree-days (above 0°C) in the warmest and sunniest summer (Bliss, 1977b; Muc, 1977). However, flowering rates were depressed 80% after a cooler summer in this same species. The use of small plastic greenhouses raised air temperature by an average of 7°C, increased flowering 110%, and plant growth about 30% compared with adjacent control plants of *Carex* (Muc, 1977). Further north (79°), Henry (1987) reported that small greenhouses raised air temperatures by about 5°C which significantly increased growth of graminoids.

Carbon allocation

As discussed in the previous section, arctic plants are adapted to a rapid burst of growth following snowmelt. Rapid growth has been correlated with the translocation of root and rhizome carbohydrates into shoot primordia (Shaver and Billings, 1976; Muc, 1977; McCown, 1978; Chapin et al., 1980a). Other more detailed studies have shown that graminoid shoots become self-sufficient in carbohydrates with the initiation of photosynthesis (Allessio and Tieszen, 1975; Tieszen, 1978a). Computer simulations indicate that the decline in root and rhizome reserves is being used primarily for growth of belowground parts at a time when most photosynthetic carbon is being used for leaf growth (Stoner et al., 1978). In the fall, carbohydrates are translocated to belowground parts. A comparative study of three graminoids found that *Carex aquatilis* stores most of its reserves in the rhizome, *Eriphorum angustifolium* stores carbohydrates in the stem base, and *Dupontia fisheri* about equally in stem base and rhizome. In all three species, total sugars and nonstructural carbohydrates are concentrated in the growing tips of shoots and roots (Shaver and Billings, 1976). The pattern appears different in evergreen and deciduous shrubs, where ^{14}C studies indicate substantial translocation of carbohydrates from roots and stems to growing shoots early in the season (Campbell, 1983). Carbohydrate concentrations were highest in stem tissues closest to buds in *Salix arctica* – an indication of their use for rapid spring growth and cold hardiness (Dawson, 1987).

There appears to be a link between these nonstructural carbohydrates (sugars and starches) and cold resistance in arctic species (Muc, 1977; Svoboda, 1977). The high concentrations of oligosaccharides are believed to be associated with freezing tolerance. Total non-structural carbohydrates increace in plants of colder climates (Mooney and Billings, 1961; McCown, 1978; Dawson, 1987; Sakai and Larcher, 1987; Dawson and Bliss, 1993). This suggests that low temperatures reduce carbon utilization relative to photosynthesis (Warren Wilson, 1966). Carbohydrates are translocated to roots in arctic plants (Allessio and Tieszen, 1975) at root temperatures of 2°C or less. Haag (1974) found that low temperature acts to inhibit incorporation of phosphorus into nucleoproteins, although the uptake of phosphorus was not inhibited by low temperature. Chapin et al. (1980a) reported that stored nutrients are used in spring leaf growth as well as newly absorbed nutrients (Chapin and Bloom, 1976). The movement of nutrients into rhizomes and stems in late summer helps to explain why fertilizer treatments generally affect plant growth more than one year after addition (Chapin et al., 1980a).

Arctic graminoids have high living root:shoot ratios, generally 7:1 to 20:1, but they are somewhat lower in forb and shrub communities (3:1 to 17:1) (Dennis and Johnson, 1970; Svoboda, 1977; Muc, 1977; Maessen et al. 1983). The root systems of herbaceous high-arctic plants in the polar semideserts are much smaller, and consequently the root:shoot ratios are much lower (0.4:1 to 1:1) (Bell and Bliss, 1978; Bliss and Svoboda, 1984). The continuous arctic day permits rather high rates of daily photosynthesis, much of which is translocated belowground where it is used to produce large root systems and maintain quite high rates of respiration in addition to storage, especially in graminoids. Root systems of graminoids appear to be long-lived and have rather low turnover rates (10–25 years) (Dennis and Johnson, 1970). Although not discussed in detail, the overall patterns of resources (carbohydrates, nutrients) correlate with patterns of phenology (Mooney and

TABLE 19.17

Protein, lipid, total non-structural carbohydrate (TNC), and crude fiber content of arctic plants (shoots only)

Species	% Content of dry matter				Author
	Protein	Lipid	TNC	Crude fiber	
Carex stans	17–22	1.5–2.5	–	20–30	Muc, 1977
Carex nardina	3.7–5.0	4.1–6.2	3.0–6.0	–	Svoboda, 1977
Dupontia fisheri	-	6–16	1.3–2.2	–	McCown, 1978
Sedge meadow	8–10	–	–	29–31	Haag, 1974
Arctagrostis latifolia	5–9	8.6	–	45	Scotter, 1972
Eriphorum vaginatum	10–13	1.0–1.3	–	24–34	Scotter, 1972
Dryas integrifolia	7.2–7.5	2.5–3.4	0.5–3.0	33–42	Svoboda, 1977
Saxifraga oppositifolia	5.0–6.0	5.7–6.8	0.5–5.0	41–43	Svoboda, 1977
Betula nana	12–13	–	–	20–21	Haag, 1974
Salix glauca	10–11	2.9–4.1	–	12–14	Scotter, 1972
Ledum palustre	8–10	10.2–10.5	–	24–30	Scotter, 1972

Billings, 1961; Chapin et al., 1980a; Dawson, 1987; Dawson and Bliss, 1993).

Protein, lipids, and fiber

The protein content of tundra plants is often quite high; *Carex stans* averaged 19% in summer and a relatively high value of 9.6% in dead material. These high protein levels in winter are, no doubt important in maintaining musk-oxen in what is a very energy-limiting climate. Protein values of a *Carex–Eriophorum* sedge meadow near the Mackenzie River Delta, N.W.T., were lower, as were measurements for shrub communities in the same area (Table 19.17).

Lipid concentrations are also quite high in arctic species. Some have hypothesized that their high energy value may be important for rapid growth (Bliss, 1962b; Svoboda, 1977). Others postulate that high lipid concentrations relate to membranes necessary for high metabolic capacity (Kedrowski and Chapin, 1978) or to the production of resins in antiherbivore defense (Jung et al., 1979). Subarctic vertebrates avoid feeding on plant tissues that contain high concentrations of secondary chemical compounds. They do not select winter forage on the basis of nutrient content (Bryant and Kuropat, 1980). *Salix* species utilized in the subarctic are the same species utilized in the shrub communities in the Low Arctic. *Salix arctica*, in the High Arctic, is an important food, both summer and winter, for musk-oxen, arctic hares, and ptarmigan. Crude fiber content of evergreen shrub species is generally much greater than for graminoids (Table 19.17). Similar patterns are found in plants of the temperate region.

Rates of soil mineralization and microbial respiration were studied along a topographic gradient in northern Alaska ranging from upland tussock tundra, hilltop dwarf-heath shrub to wet sedge tundra, and riparian willow (Nadelhoffer et al., 1991). It was found that microbial respiration and nitrogen mineralization were insensitive to temperatures between 3 and 9°C. Between 9 and 15°C rates of mineralization of carbon and nitrogen doubled. The quality of organic matter probably has a greater effect than temperature on microbial activity.

Physiological responses

Photosynthesis

Arctic species photosynthesize by the C_3 pathway (Tieszen and Sigurdson, 1973; Teeri and Stowe, 1976; Stowe and Teeri, 1978). Utilizing the C_3 system, arctic species show the following patterns: 1) they possess low temperature requirements for photosynthesis with rather large Q_{10} responses (2–3); 2) they have relatively low light compensation and saturation points; 3) many arctic species have relatively high photosynthetic rates in spite of high rates of photorespiration; 4) they have relatively high mesophyll resistance (r_m) to compensate for lower efficiency of water use; and 5) they have higher chlorophyll levels than alpine species, and there is a relatively lower ratio of chlorophyll a to b in arctic species.

TABLE 19.18

Photosynthetic rates of arctic species from field studies

Species	Photosynthetic rates (mg CO_2 g^{-1}dw h^{-1})		Optimum Temperature (°C)	Author
	average	maximum		
Graminoids				
Carex aquatilis	7–10	19	14	Tieszen, 1975
Carex stans	11–15	22	10–15	Mayo et al., 1977
Dupontia fisheri	10–15	17	16	Tieszen, 1975
Eriophorum angustifolium	10–14	17	16	Tieszen, 1975
Luzula confusa	5–8	16	15–25	Addison and Bliss, 1984
Deciduous Shrubs				
Betula nana	7–12	14	20	Limbach et al., 1982
Salix pulchra	12–18	24	10	Limbach et al., 1982
Evergreen Shrubs				
Dryas integrifolia	2–3	7	10	Mayo et al., 1977
Vaccinium vitis-idaea	0.5	1	=	Limbach et al., 1982
Mosses				
Calliergon sarmentosum	1–2	3	10	Oechel and Sveinbjørnsson, 1978
Pogonatum alpinum	0.5–1	4	10–20	Oechel and Sveinbjørnsson, 1978
Lichens				
Alectoria nitidula	0.5–0.1	0.2	15–20	Kershaw, 1975
Cetraria cucullata	0.2–0.4	0.7	10–12	Lechowicz, 1981
Cladonia alpestris	0.1–0.2	0.3	10–12	Kershaw, 1975

The general pattern of photosynthesis in arctic species is quite similar to that of plants in more temperate environments. However, the shortness of the growing season, low air and soil temperatures, and low nutrient content of most soils greatly limit total plant growth. Tundra plants reach maximum photosynthetic rates at temperatures (10 to 15°C), which are considerably lower than in temperate grasslands and forests. Positive carbon gain in some species is maintained at 0 to 4° (Tieszen, 1973, 1975; Hartgerink and Mayo, 1976). Photosynthetic rates are highest in forbs, intermediate in graminoids and deciduous shrubs, and lowest in evergreen shrubs and wintergreen rosette species. Cryptogams have lower photosynthetic rates than flowering plants, lichens having rates lower than mosses (Table 19.18).

Tundra plants begin growth rapidly following snowmelt. Depending upon the species, flowering may precede leaf and shoot elongation (cushion plants, e.g. *Saxifraga oppositifolia, Silene acaulis;* some deciduous shrubs, e.g. *Salix alaxensis, S. arctica*) or may follow shoot elongation (graminoids and forbs). Early in the season, whole plant or shoot rates of net assimilation (photosynthesis) may be low or even negative, due to high rates of respiration in relation to rapid shoot development. With reduced shoot growth, respiration rates drop and net assimilation increases. This pattern was found in dwarf-heath shrubs, evergreen cushion plants, graminoids and forbs in the alpine zone of Mt. Washington, New Hampshire (Hadley and Bliss, 1964a). *Dryas integrifolia*, an evergreen species characteristic of the High Arctic, took 3–5 days to become photosynthetically active following snowmelt (Mayo et al., 1977), and typically reached its highest assimilation rates early in the season. This species can maintain positive rates of photosynthesis at temperatures down to −5°C (Hartgerink and Mayo, 1976). There is a considerable reduction in net assimilation prior to plant senescence in arctic species (Tieszen, 1975; Mayo et al., 1977; Tieszen et al., 1980; Addison and Bliss, 1984). Solar radiation and temperature also decrease dramatically during August. Older leaves of evergreen shrubs (2–3 yr) may still contribute to

carbon gain of the plant, as in *Ledum palustre* ssp. *decumbens* and *Vaccinium vitis-idaea* ssp. *minus* in Alaska (Johnson and Tieszen, 1976).

Alpine populations of *Oxyria digyna* (Mooney and Billings, 1961) and *Thalictrum alpinum* (Mooney and Johnson, 1965) have photosynthetic optima at higher temperatures than do the arctic populations of the same species. Maximum photosynthetic rates were higher in the arctic populations of *Oxyria digyna*, but the alpine populations of *Thalictrum alpinum* had higher rates when grown under controlled environment conditions.

Billings and his students (Billings et al., 1971) analyzed the photosynthetic and respiratory responses of seventeen populations of *Oxyria digyna* from arctic and alpine environments. Maximum rates of photosynthesis were reached at lower temperatures in arctic than in alpine populations. Alpine populations showed a greater degree of homeostasis in net assimilation when compared with arctic ecotypes. Maximum rates of net assimilation were lowered by higher temperature acclimation in the arctic populations, but not in the alpine ones. Alpine plants are preadapted to alternating diurnal temperature fluctuations, in contrast with the arctic ecotypes which grow in a more temperature-stable environment. Studies on *Oxyria digyna* show that the alpine ecotypes are physiologically adapted to these lower levels of carbon dioxide in terms of photosynthetic efficiency compared with their arctic counterparts (Billings et al., 1961).

A recent study on plants grown from seed has shown some differential photosynthetic inhibition under supplemental solar UV-B irradiation in the field. Some, but not all, species and ecotypes from arctic Alaska showed photosynthetic inhibition from UV-B enhanced irradiation. However, alpine plants from equatorial regions showed no damage induced by UV-B in either light-saturated or light-limited photosynthesis (Barnes et al., 1987).

Field and laboratory (controlled environment chambers) studies have shown that plants acclimate to the conditions under which they have been grown (Mooney and West, 1964; Billings et al., 1971). These findings must be considered when evaluating results from plants grown in growth chambers or greenhouses. Yet, these studies that permit one to manipulate environmental factors such as temperature, light, CO_2, and soil water potential, add greatly to understanding of plant responses.

The relatively low temperature optima for photosynthesis in arctic and alpine plants seem to result from high concentrations of the enzyme ribulose bisphosphate (RuBP) carboxylase (Berry and Björkman, 1980). This permits higher photosynthetic rates at lower temperatures. However, RuBP carboxylase reacts with oxygen, resulting in high rates of photorespiration, thus reducing net photosynthesis at higher temperatures leading to lower temperature optima for tundra species (Chabot et al., 1972; Chabot, 1979).

Rates of respiration are also higher in alpine than in arctic populations (Mooney and Billings, 1961; Billings et al., 1971) and in alpine populations than in those from lower elevations (Mooney, 1963; Mooney et al., 1964). Rates of mitochondrial activity are genetically based and are higher in arctic than alpine populations of *Oxyria digyna* (Billings et al., 1971). Mitochondrial oxidative activity is increased by cold acclimation in both arctic and alpine populations of *Oxyria*. These studies help to explain the high rates of respiration of tundra plants at low temperatures.

In summary, arctic vascular plants have several physiological mechanisms (resistance of chloroplast and mitochondrial membranes to low temperature changes, high enzymatic levels of RuBP carboxylase, and high mitochondrial oxidative rates) that enable various species to cope remarkably well with these low-temperature environments.

Photosynthetic rates are, generally, much lower in mosses and lichens than in vascular plants (Table 19.18). The longevity of bryophyte leaves and lichen thalli enables them to become photosynthetically active as soon as temperature, light, and moisture become favorable. Temperature optima are quite low and there is little resistance to water loss; thus, as soon as these plants begin to dry, photosynthetic rates drop dramatically. Arctic mosses are resistant to frost and thus carry on a net carbon gain to 0°C (Oechel and Sveinbjörnsson, 1978). The broad range of temperature responses of arctic bryophytes permits relatively high rates of photosynthesis from 0° to >20°C. This enables them to gain carbon over a broad range of arctic conditions and to remain photosynthetically active in August when many vascular plants have become dormant. Measured Q_{10} rates are highest (4.2) between 0 and 10°C, but drop to 1.9 at temperatures of 20 to 30°C (Oechel, 1976). Photosynthetic measurements of *Poly-*

trichum alpinum from drier habitats and *Calliergon sarmentosum* from wetter habitats at Barrow, Alaska showed that *C. sarmentosum* from semi-aquatic habitats required a higher water content (450% dry wt) compared with *P. alpinum* (200% dry wt) to reach maximum rates of photosynthesis.

Lichens, even more than mosses, are exposed to large environmental extremes of water content and temperature. Lichens growing on rocks and bare soil are subjected to long periods of unfavorable conditions. The most favorable conditions for assimilation and growth are moist periods with moderate temperature and light, conditions that prevail with frequent fog and showers.

Assimilation rates are very low in lichens (Table 19.18); they generally reach optimal photosynthetic rates at 15–20°C. When a thallus dries, photosynthetic rates tend to drop more rapidly than respiratory rates (Hadley and Bliss, 1964b; Kershaw, 1975; Larson and Kershaw, 1975a; b). Net photosynthesis of *Cladina rangiferina* and *C. stellaris* at Anaktuvuk Pass, Alaska was restricted to days with rain or fog. When thallus water content dropped to 20–30% of oven-dry weight, there was no net photosynthesis, clearly demonstrating the critical nature of thallus water content (Moser et al., 1983).

Temperature acclimation for photosynthesis but not respiration has been shown for *Alectoria nitidula, A. ochroleuca,* and *Cetraria nivalis* collected at different times of the year (Kershaw, 1975; Larson and Kershaw, 1975a; b). The rates of photosynthesis in *Alectoria ochroleuca* were not significantly different in plants collected from the tops and the bases of beach ridges at Pen Island, Ontario, just north of the tree line. However, when this material was compared with lichens from Melville Island (75°N), photosythetic rates were 0.33 mg CO_2 $g^{-1}hr^{-1}$ at 14°C (optimum temperature) while the high arctic plants reached their maximum rates of only 0.05 mg CO_2 $g^{-1}hr^{-1}$ at 7°C. Maximum photosynthetic rates were reached (radiation of 150 μE $m^{-2}s^{-1}$) at ~85% thallus water content and the rates dropped sharply at 200% thallus water content (Larson and Kershaw, 1975b). In contrast, *Cetraria nivalis* reached its maximum photosynthetic rates at 250 μE $m^{-2}s^{-1}$ at 14°C, and at 160% thallus water content. Plants collected in July and August from the beach ridge base had higher photosynthetic rates than plants from ridge tops (Larson and Kershaw, 1975c). Both species acclimated to temperature and light conditions when sampled from June through October. *Cetraria nivalis* is more characteristic of protected habitats and both species of *Alectoria* of more exposed sites. These data demonstrate that lichens function quite differently in contrasting mesohabitats in southern compared with northern regions, and at different times of the year.

Water relations

One might expect that plants adapted to growing in cold, moist to wet soils, and high atmospheric moisture levels (low leaf-to-air vapor pressure gradient) would show little water stress. An earlier study in Alaska supported this hypothesis (Billings and Mooney, 1968), yet more recent studies there (Miller et al., 1978; Oberbauer and Miller, 1979, 1981), and in the Canadian Arctic (Addison, 1977), show that plants growing in graminoid–moss meadows (wet habitats) are subjected to some water stress, especially on sunny days with moderate wind velocity. Plants growing in better-drained soils (xeric habitats) are subjected to greater stresses.

Water stress is measured as a negative water potential; the lower the water content of leaf, stem, or root tissues, the lower or more negative is the water potential. Where there is no water stress, water potential is 0 MPa, while a moderate stress may result in −0.2 to −0.4 MPa (−2 to −4 bars in the earlier literature).

Plants growing in ponds, wet meadows, and polygon troughs (*Arctophila fulva, Dupontia fisheri, Eriophorum angustifolium*) generally developed leaf water potentials (ψ_l) of −0.2 to −0.8 MPa while *Potentilla hyparctica* and *Salix pulchra*, more typical of polygon tops, developed ψ_l of −0.5 to −1.0 MPa (Stoner and Miller, 1975). *Carex aquatilis* occurs from wet to drier sites, and it maintained intermediate ψ_l of −0.3 to −0.7 MPa (Table 19.19). Those species typical of the wetter sites began to close their stomates at −0.4 to −0.6 MPa while *Carex, Potentilla* and *Salix*, characteristic of the more exposed sites with better-drained soils, closed their stomates at −0.8 to −1.4 MPa (Stoner and Miller, 1975). These measurements, and the simulation models developed, indicate that water stress can limit photosynthesis in *Arctophila, Dupontia,* and *Potentilla* and therefore influence the topographic distribution of these species, *Arctophila* and *Dupontia* being restricted to wet sites and *Potentilla* to polygon tops.

Diurnal measurements of ψ_l at Barrow showed

that *Arctophila, Dupontia,* and *Carex* reached minimum values of −0.7 to −0.8 MPa at 1200–1300 hr and maximum values of −0.1 MPa from 0000–0200 hr. *Eriophorum angustifolium* also had a small diurnal range (−0.7 to −0.05 MPa) but *Potentilla hyparctica* and *Salix pulchra*, restricted to better-drained soils on the more exposed polygonal tops, showed greater water stress (−1.0 to −1.2 MPa at midday and −0.2 to −0.25 MPa early in the morning) (Stoner and Miller, 1975).

Near Eagle Summit in central Alaska, water stress is a factor in the mesotopographic position of species. *Dryas octopetala* growing in an exposed fellfield, and heath shrubs growing in slightly more protected habitats, developed ψ_1 of −0.5 to −1.0 MPa; in late summer *Cassiope tetragona* maintained ψ_1 of −1.0 to −3.0 MPa, while *Eriophorum vaginatum*, growing on lower mesic slopes, developed ψ_1 of only −0.2 to −0.3 MPa throughout the summer (Oberbauer and Miller, 1979).

A major reason that water stress occurs in wet sedge (mire) and cottongrass tussock tundras is that low soil and root temperatures affect stomatal conductance (Grulke and Bliss, 1988; Dawson and Bliss, 1989a,b). Reduced stomatal conductance is influenced by root membrane permeability or by changes in root–shoot hormone balance (Kramer, 1942). Water stress does not appear to be a limiting factor for plant production in cottongrass tussock–shrub and graminoid–moss (mire) tundras in northern Alaska (Stoner and Miller, 1975; Oberbauer and Miller, 1979; Miller, 1982; Chapin and Shaver, 1985b).

Soil moisture conditions and plant water stress are somewhat different in the High Arctic, for here most plants maintain lower water potentials and soil moisture is often more limiting (Addison, 1977; Addison and Bliss, 1984; Grulke and Bliss, 1988; Dawson and Bliss, 1989a; b). Many habitats have coarse-textured soils that are well drained in mid to late summer, although permafrost with saturated soils occurs at the bottom of the active layer.

Dryas integrifolia dominates the raised beach habitats on Devon Island and similar habitats on other islands in the southern, central, and eastern Canadian Arctic Archipelago (see 604). Soil water potential averaged −2.0 MPa (−20 bars) within the rooting zone and ψ_1 ranged from −1.0 to −3.5, dropping to −4.0 to −5.0 MPa for short periods during two summers (Addison, 1977). Laboratory studies showed that net photosynthesis approached zero at ψ_1 of −2.0 to −3.0 MPa (Hartgerink and Mayo, 1976). Using different methods, Teeri (1973) reported ψ_1 of −1.0 to −2.5 MPa over much of the summer for *Saxifraga oppositifolia* growing in these same habitats. In the adjacent wet sedge–moss meadows, *Carex stans* also maintained low transpiration rates and relatively high ψ_1 of −0.5 to −1.5 MPa, but dropped as low as −4.0 MPa with stomatal closure on sunny days (Addison, 1977; Table 19.19). Although root resistance was not measured in *Dryas* or *Carex*, it is assumed that resistance to water entering the roots in these cold, saturated meadow soils is a major factor, especially for *Carex*.

Dryas plants are well adapted to the extreme environmental conditions under which they grow. The leaf cuticle reduces cuticular transpiration from the upper surface. The densely tomentose lower surface reduces sensible heat flux, thus conserving water but permitting the leaves to reach high temperatures (40–45°C) on sunny days with little wind (Addison, 1977). *Carex stans* grows in soils with abundant water, but low oxygen tensions and low soil temperatures reduce root permeability to water absorption, and these plants also develop low plant water potentials. However, *Carex* leaves are better able to dissipate energy, and thus leaf temperatures are seldom above 5° to 10°C (Addison, 1977).

In the northwestern islands, typified by King Christian Island, there is less sunshine, lower temperatures and less precipitation during the growing season. During most summers there is little soil and plant water stress, but drought periods do occur in some summers. In the cool, wet summers of 1973 to 1975 soil water potentials (ψ_s) did not go below −0.03 MPa at 0–5 cm soil depth and were generally −0.03 to −0.6 MPa at −5 to −10 cm. Some plants are sensitive to soil moisture stress, for net photosynthesis of *Luzula confusa* dropped to 25% of maximum at ψ_s of −0.7 MPa (Addison and Bliss, 1984). These data help to explain why this species is confined to sites with high soil moisture levels – sites with a considerable cover of lichens and mosses.

Phippsia algida is a ruderal species that colonizes disturbed, bare soils in mesic habitats, and *Puccinellia vaginata* is a stress-tolerant species, characteristic of xeric habitats with little soil disturbance on King Christian Island and other high arctic islands. Leaf water potentials often ranged from −1.5 to −2.5 MPa, yet these potentials did not

TABLE 19.19

Plant water relations of arctic species

Species	Leaf water potential (MPa)		Authors
	Average	Minimum	
Graminoids			
Arctophila fulva	−0.7 to −1.2	−1.5	Stoner and Miller, 1975
Carex aquatilis	−0.7 to −1.0	−1.5	Stoner and Miller, 1975
Carex stans	−0.8 to −1.2	−4.0	Addison, 1977
Dupontia fisheri	−0.4 to −0.6	−1.5	Stoner and Miller, 1975
Eriophorum angustifolium	−0.3 to −0.6	−0.7	Stoner and Miller, 1975
Eriophorum vaginatum	−0.1 to −0.4	−1.5	Oberbauer and Miller, 1981
Luzula confusa	−0.4 to −0.7	−1.0	Addison and Bliss, 1984
Phippsia algida	−0.3 to −3.0	−4.9	Grulke and Bliss, 1988
Forbs and shrubs			
Dryas integrifolia	−1.0 to −3.0	−4.2	Mayo et al., 1977
Potentilla hyparctica	−0.7 to −1.0	−1.2	Stoner and Miller, 1975
Salix arctica	−0.1 to −1.1	−1.5	Dawson and Bliss, 1989a
Salix pulchra	−0.6 to −1.0	−1.2	Stoner and Miller, 1975
Vaccinium vitis-idaea	−0.8 to −1.5	−3.5	Oberbauer and Miller, 1979

indicate drought stress for they were not accompanied by low turgor or stomatal closure (Grulke and Bliss, 1988). Field studies showed that leaf-to-air vapor pressure gradient, soil moisture, and leaf and root temperature were limiting to leaf conductance, but wind and photosynthetically active radiation were not limiting to it. Drought stress and low temperatures reduced whole plant biomass of *Phippsia algida* at all ages, but affected only seedlings of *Puccinellia*. *Puccinellia* developed lower water potentials earlier in the season than *Phippsia algida*, but the latter species developed the lowest ψ_l (−4.8 vs −2.9) later in the season. These data help to explain why these species grow in different habitats, and why *Phippsia* is relatively successful in producing large numbers of seedlings and adult plants compared with *Puccinellia vaginata* and the closely related *P. angustata*, characteristic of the polar deserts.

As a last example of the important role of soil–plant–air water relations and the distribution of a species one can consider the data for *Salix arctica* (Dawson and Bliss, 1989a,b, 1993). Sex ratios of this dioecious, deciduous shrub, sampled in 144 sub-populations on five arctic islands, showed that the sex ratio is female-biased (1.9:1). Female plants are more common in wet habitats with higher nutrients, but lower soil temperatures (6:1). Male plants predominate in xeric habitats with lower nutrients, and higher soil temperatures (1.5:1). In wet habitats (sedge–moss meadows), female plants maintained higher rates of stomatal conductance and higher ψ_l than male plants in cold soils (<4°C). In contrast, male plants maintained higher stomatal conductance and lower ψ_l at low soil water potentials (ψ_s) and a higher leaf-to-air vapor pressure gradient (w) than female plants. Male plants demonstrated lower osmotic potentials in tissue at the turgor-loss point and a higher tissue elasticity than female plants. These sex-specific habitat differences and their ecophysiological characteristics are well correlated with greater plant growth and sexual reproduction for male plants in xeric habitats and for female plants in wet habitats (Dawson and Bliss, 1989a,b, 1993).

These data demonstrate that plants of typically dry sites adjust physiologically (more elastic cell walls, more rapid adjustment of stomata and osmotic content of the leaf tissue) more rapidly than plants of mesic sites. These mesic plants often adjust more slowly to initial water stress, then close their stomata rapidly, reducing both water loss and carbon gain by photosynthesis. Many arctic species of moist to wet habitats develop much lower leaf and shoot water potentials than what one might predict, based on the abundant supply of water. A contributing factor is a greater root resistance to the entry of water (Miller et al., 1978).

Lichens and mosses are very tolerant of severe drought stress because of their ability to rapidly reduce photosynthesis and respiration with the loss of water, and thus to reduce biological activity to a low level. Consequently, they are often found in the most stressful environments, even though they have little ability to control water loss.

When lichens take up water following a rain, their respiratory metabolism is activated more rapidly than their photosynthetic mechanism. This results in a negative carbon balance (Lechowicz, 1981). The length of time that lichens remain moist before redrying becomes important in maintaining a positive carbon balance. Thus, the daily and seasonal cycles of wetting and drying become important (Moser and Nash, 1979), and help to explain why lichens are more abundant in number of species and biomass where rains or dew/fog are more frequent.

Mosses are somewhat better able to resist water losses through infolding and leaf-roll. Mosses from wetter habitats have less resistance to water loss at low water content, and photosynthetic rates are somewhat higher in mosses from wet sites (Oechel and Collins, 1976; Oechel and Sveinbjørnsson, 1978). This pattern also occurs in many flowering plants.

Mineral nutrition

Arctic and alpine soils are infertile when compared with temperate grasslands and some forest systems. Consequently, tundra species have a general set of characteristics that are common to plants of infertile soils. These include: (1) low absorption rates of nutrients per plant, and only small increases in absorption with increased nutrient concentration; (2) many species have a high root:shoot ratio; (3) many species retain all or part of their leaves for more than one year; (4) plant growth rates are generally lower, yet shoots often maintain rather high concentrations of nutrients; (5) seasonal storage of minerals and carbohydrates is important; and (6) nutrient losses are reduced through less leaching and increased translocation from senescing leaves. A detailed review on the mineral nutrition of wild plants has been given by Chapin (1980) and Chapin et al. (1992).

In arctic environments phosphorus and nitrogen in the form of ammonium are the two most limiting elements. Where soil and plant nutrient analyses have been made, their concentrations are adequate for normal plant growth. There are few if any examples of soils with toxic levels of aluminum, iron or magnesium. However, local areas of saline soils in Greenland and the Canadian Archipelago limit the species present and their growth rates.

Tundra plants are adapted to absorb phosphorus more efficiently at low soil temperatures than are temperate species (Chapin and Bloom, 1976; McCown, 1978; Chapin, 1980). Efficient absorption at low temperatures is due in part to membranes that maintain their fluidity and function at low temperature (McCown, 1978).

The seasonal movement of nutrients differs considerably with plant growth form. Evergreen species continue growth and accumulation of nitrogen and phosphorus throughout the growing season and appear to have no large storage of nutrients in stems and roots. Deciduous species (forbs, graminoids, shrubs) accumulate biomass, nitrogen and phosphorus in new leaves and twigs until midseason. Approximately 50% of the maximum amount of nitrogen and phosphorus are withdrawn before leaf senescence, regardless of growth form (Chapin et al., 1980a; Chapin and Shaver, 1989). The continued growth and nutrient accumulation in shoots of evergreen species may reflect less dependence upon stored reserves and greater dependence upon current nutrient uptake and photosynthesis (Chapin and Shaver, 1989). The high nutrient-use efficiency of the evergreen species is advantageous to plants growing in infertile soils (Vitousek, 1982). In contrast, species with low use efficiency have higher tissue nutrient concentrations, and they have higher rates of photosynthesis and related metabolic processes (Schulze and Chapin, 1987).

In *Eriophorum vaginatum*, spring production of leaves and roots depletes rhizome nitrogen reserves (Chapin et al., 1980b). In a separate study Chapin and Tryon (1982) reported that *E. vaginatum* required 30–40 days to absorb the quantity of phosphorus necessary to produce the annual roots and an additional 5–6 days to provide the net phosphorus required for the remainder of the plant. *Carex stans* in the High Arctic begins to reduce its total amount of nitrogen, phosphorus and potassium before peak biomass is achieved, indicating that net translocation to belowground organs begins well before leaf senescence (Muc, 1977). There are indications that much of the potassium may be leached rather than translocated

(Chapin et al., 1980b). While most nutrients are stored belowground in winter, the overwintering green shoots of the graminoids have the highest concentrations of any time in the year. This is of great importance to lemmings in the Low Arctic and lemmings, caribou, and musk-oxen in the High Arctic; herbivores that are very dependent upon nutrient-rich vegetation for winter survival (see pp. 654–658).

Many of the high arctic rosette and cushion plants have limited root systems, and their ability to store nutrients as well as carbohydrates below ground is more limited (Bell and Bliss, 1978; Maessen et al., 1983; Grulke and Bliss, 1985). An important adaptation is the presence of wintergreen leaves for nutrient and carbohydrate storage in addition to facilitating early photosynthesis following snowmelt.

These various studies indicate that graminoids, forbs, and deciduous shrubs that have higher growth rates also have higher rates of nutrient absorption and utilization, as well as higher photosynthetic rates. Evergreen shrubs and some of the cushion plants have much lower growth rates, lower rates of nutrient utilization and lower photosynthetic rates. They are more conservative species in many ways; these are true stress-tolerators.

Rhizosphere relationships

Because arctic plants grow in stressful environments, one might predict that rhizosphere relationships, especially the role of mycorrhizae, would be very important. The limited data from the North American Arctic indicate that ectomycorrhizae are present in the roots of species of *Salix* and the woody species *Cassiope tetragona, Dryas integrifolia, Ledum palustre* ssp. *decumbens,* and *Vaccinium vitisidaea,* as well as the herbs *Cochlearia officinalis* and *Pedicularis kanei* at Barrow, Alaska (Miller and Laursen, 1978). Inland tundras (Meade River) contain a greater diversity of vascular species and also a greater number of mycorrhizal fungi compared with the coastal plain at Barrow. Ectomycorrhizae are also found on roots of *Cassiope tetragona, Dryas integrifolia, Potentilla hyparctica, Salix arctica,* and *Vaccinium uliginosum* in the High Arctic on Devon Island (Bledsoe et al., 1990). These fungi develop a sheath from which hyphae radiate into the soil. These sheaths hold phosphate and carbohydrates, necessary for the development of large fruiting bodies that are often associated with these woody species.

The endomycorrhizae observed at Barrow are sparingly septate and they produce hyphae called vesicular-arbuscular mycorrhizae (VAM). These mycorrhizae are found in a greater range of vascular species including the Poaceae in arctic Alaska (Miller and Laursen, 1978). On Devon, King Christian, and Ellesmere Islands, true VAM endomycorrhizae are rarely found, although fungal hyphae are often present in the roots of vascular species (Bledsoe et al., 1990). At these latitudes, mycorrhizae were seldom found until mid or late summer, indicating that low soil temperatures slow the growth rates of the fungi. The lack of true VAM mycorrhizae in the High Arctic again illustrates that these low-temperature environments deficient in nutrient and water are more limiting than in the Low Arctic.

Nitrogen fixation

Nitrogen is a major limiting nutrient in ecosystems of the world, and the Arctic is no exception. The importance of the biological fixation of nitrogen for plant growth and ecosystem function is well established for the Low Arctic (Alexander and Schell, 1973; Chapin et al., 1975; Shaver and Chapin, 1980) and for the High Arctic (Babb and Whitfield, 1977; Henry and Svoboda, 1986; D.M. Chapin and Bledsoe, 1992; D.M. Chapin et al., 1991). Cyanobacteria are the major nitrogen fixers in arctic ecosystems, although soil bacteria (Stutz and Bliss 1975; Jordan et al., 1978a) and legumes (Karagatzides et al., 1985) contribute to total fixation in some systems.

Rates of acetylene reduction are greatest in early summer when soil moisture levels are highest. Soil moisture and temperature are major factors controlling these rates, with phosphorus availability appearing secondarily (D.M. Chapin et al., 1991). Light levels appear to be seldom limiting, except for cyanobacteria within moss mats and in the upper 0.5 cm of soil.

Based upon the high arctic studies on Ellesmere Island (Henry and Svoboda, 1986), Cornwallis Island (Bliss, 1990), and Devon Island (D.M. Chapin et al., 1991), there are very large spatial differences in rates of acetylene reduction (Table 19.20). The highest rates are on marine algae in brackish-water lagoons, the margin of ponds, and wet sedge–moss mires. The lowest rates are on well-drained beach ridges and rock outcrops that support cushion and rosette vascular plants, and in polar deserts with their cryptogamic crusts (Jordan

TABLE 19.20

Rates of nitrogen fixation ($\mu gN_2\ m^{-2}\ h^{-1}$) based upon acetylene reduction by cyanobacteria and other bacteria in low and high arctic ecosystems

Location and habitat	N-fixation ($\mu g\ N_2\ m^{-2}\ h^{-1}$)	Author
Polar barrens		
Devon Island plateau (320 m)	1.9	Jordon et al., 1978a
Resolute, Cornwallis Isl - beach ridge	1.2	S. Bambrough, unpubl.
Resolute, Cornwallis Isl - snowflush with moss	6.4	S. Bambrough, unpubl.
Resolute, Cornwallis Isl. - snowflush bare soil	3.0	S. Bambrough, unpubl.
Polar semidesert		
Devon Island - beach ridge	7.2	Stutz, 1977
Devon Island - beach ridge	4.8	Jordon et al., 1978a
Devon Island - Wolf Hill	1.5	Stutz, 1977
Low and high arctic mires		
Barrow, Alaska - inland, sedge–moss	16.5	Alexandra et al., 1978
Devon Island, Truelove Lowland - inland, sedge–moss	53	Jordon et al., 1978a
Devon Island, Truelove Lowland - inland, sedge–moss	25	Stutz, 1977
Devon Island, Trulove Lowland - coastal, sedge-meadow	352	D.M. Chapin et al., 1991
Devon Island, Truelove Lowland - coastal saltmarsh	1370	D.M. Chapin et al., 1991
Ellesmere Island, Alexandra Fiord, sedge-meadow	59	Henry and Svoboda, 1986
Ellesmere Island, Sverdrup Pass, sedge-meadow	51	Henry and Svoboda, 1986

et al., 1978; Bliss et al., 1990; D.M. Chapin et al., 1991; Dickson and Lennihan, unpublished data).

The exceptionally high rates of acetylene reduction in the brackish lagoons and salt-marsh communities are believed to result from higher biomass of cyanobacteria, a more constantly wet surface, and higher levels of phosphorus (D.M. Chapin et al., 1991). It is interesting that these pioneering plant communities (primary succession) have the highest rates of nitrogen fixation, as they often do in other major biomes, and that there is a decline in fixation rates as systems develop (Gorham et al., 1979; Reiners, 1981). However, cyanobacteria appear ubiquitous in plant communities of the High Arctic, and thus there is a minimal input of nitrogen in all of them; controlled mainly by soil moisture and biomass of the cyanobacteria. The loss of fixed nitrogen into the permafrost as the permafrost table rises and the slow release of mineral nitrogen from soil organic matter, means that nitrogen is always low in the Arctic, even in well-developed systems (D.M. Chapin and Bledsoe, 1992).

Although species of *Nostoc* appear to be the major fixers, species of *Anabaena, Fischerella, Hapalosiphon, Scytonema, Stigonema,* and *Tolypothrix* are also important. *Calothrix, Chlorogloea,* and *Gleocapsa* are often present, but their lack of heterocysts makes their ability to fix nitrogen questionable (D.M. Chapin and Bledsoe, 1992). Lichen genera that also fix nitrogen include *Lobaria, Nephroma, Peltigera, Placopsis, Solorina,* and *Stereocaulon* (Kallio and Kallio, 1975; Stutz and Bliss, 1975; Waughman et al., 1981). Two species of *Oxytropis* and *Astragalus alpinus* fixed nitrogen at Scarpa Lake in the eastern Canadian Arctic, while *Dryas integrifolia* and *D. octopetala* are sometimes nodulated (Alexander et al., 1978; Karagatzides et al., 1985).

From the above discussion, it is evident that most arctic ecosystems fix at least some nitrogen; however, rates of nitrogen fixation are generally <10% of annual uptake by vascular plants. Thus decomposition processes must be a major source for plant growth, considering that arctic plants have relatively high tissue concentrations of nitrogen (Alexander et al., 1978; Chapin et al., 1980a; D.M. Chapin and Bledsoe, 1992).

Pollination biology

Early arctic biologists were impressed with the size and color diversity of arctic flowers, but they often reported the lack of pollinating insects. They

concluded that insect pollination was of minor importance, and that self-pollination for seed production and vegetative reproduction were the two most important mechanisms. Russian biologists reported the importance of insect pollinators in the 1960s. Peter Kevan, working in the Arctic, and Walter Macior working in the alpine, have added much to our knowledge of plant–insect interactions. Insects are attracted to flowers by their color, size and shape, flower temperature (basking sites), nectar guides, and pollen (Kevan, 1973).

Kevan (1972a) examined most of the vascular plant species at Lake Hazen, Ellesmere Island (81°49′N) in relation to pollination biology. He found that *Dryas integrifolia, Pedicularis capitata, P. langsdorfii, Salix arctica, and Saxifraga oppositifolia* are very dependent upon insects for seed set. Species independent of insects for seed set include *Cassiope tetragona, Papaver radicatum, Saxifraga tricuspidata*, species of *Potentilla*, and the Brassicaceae. White flowers (insect yellow) are unattractive to insects, while purple flowers (insect blue and green) and yellow flowers (insect red) are very attractive. Insects, in these high arctic species, can see 15 different colors and color combinations, but humans can detect only 12 of them (Kevan, 1972b). The leaves of arctic plants reflect relatively little visible light (≃15%), while many flowers have high reflectivity (45–80%). The relatively dull backgrounds of soil and vegetation enable insects to see flowers more readily, especially yellow ones.

Arctic flowers frequently have elevated temperatures. *Salix* catkins can be 7–10°C warmer than ambient air, heather flowers that hang down and trap longwave reradiation may be 4°C warmer. The parabolic-shaped, solar tracking (heliotropic) flowers of *Dryas* and *Papaver* may be 8–10°C warmer than adjacent air and thus provide basking sites for flies, midges, and other groups of insects (Kevan, 1972c). The higher temperatures also speed maturation of fruits and seeds, an important adaption where the growing season is so short.

Nectar is an important fuel for insect flight, but its production is less in high arctic than in low arctic species. Hocking (1968) found that plants at Lake Hazen, Ellesmere Island produce less nectar than plants at Churchill, Manitoba, but that the nectar yield in mg. of sugar per flower per day was greater further north. Nectar yields increased about 0.5 mg of sugar per flower for every 400 J cm^{-2} increase in solar radiation.

Mosquin and Martin (1967) reported that Diptera were more important pollinators than Hymenoptera in the Arctic. Kevan (1972a) reported the same for Lake Hazen, and he stressed the obligatory flower constancy in pollination which facilitates seed set. Empidid and syrphid flies are the most important pollinators. Bumblebees pollinate the zygomorphic flowers of *Pedicularis* spp. as well as many other species.

Growth form and physiological adaptation

From the previous discussion it should be clear that there are relationships between plant form and function. The intent of this section is to summarize this information and to demonstrate how and why certain growth forms often predominate in certain habitats.

Annuals

Annuals are a very minor component of tundra floras, although there are more species in alpine than in arctic environments. The North American alpine flora numbers about 55 annual species of which 47 species are in the high subalpine–low alpine in the Sierra Nevada, 10 species in the Rocky Mountains and only 2 species in the New England mountains. There are few if any endemic arctic annual species, but at least 10 species have a North American arctic–alpine distribution.

Tundra annuals have a rather unique set of morphological and physiological attributes compared with their perennial counterparts. They have very low root to shoot ratios, an indeterminate growth pattern so that they can produce flowers and seeds until killed by drought or low fall temperatures, they regulate water balance by stomatal control until the soils dry completely in mid to late summer, they have quite high rates of photosynthesis, and seeds germinate rapidly and at relatively low temperatures (Jackson and Bliss, 1984; Reynolds, 1984).

The early initiation of flowering when the plants have only a few leaves, coupled with high photosynthetic rates and a small root system, enables these species to maximize reproductive effort. Reynolds (1984) reported that *Koenigia islandica* has a lower optimal temperature for photosynthesis (27°C) than do *Polygonum confertiflorum* and *P. douglasii* (32°C). This helps to explain their origins, for *Koenigia islandica* is common in the Arctic and the Himalayan region while the *Poly-*

gonum species and their close relatives are common in western mountains in dry montane and foothill habitats.

Forbs

Broad-leaved herbaceous plants are found in many arctic habitats. Of the forb species that have been studied none is better understood than the arctic–alpine sorrel *Oxyria digyna*. This herb is rather long-lived, and a very widely distributed circumpolar species with many ecotypes. Seeds of *Oxyria digyna* and other herbs have optimal germination temperatures at surprisingly high levels (15–30 °C) for alpine plants (Mooney and Billings, 1961; Amen, 1966; Chabot and Billings, 1972). Germination occurs at somewhat lower temperatures for arctic species and ecotypes (Mooney and Billings, 1961; Bell and Bliss, 1980). Relatively few species have special seed dormancy requirements and all germinate more readily at oscillating than at constant temperatures. Growth rates of forbs following snowmelt are quite rapid: the result of stored reserves in belowground roots and rhizomes (Mooney and Billings, 1960).

Temperature optima for photosynthesis were generally 5 to 15°C, and rates declined above 20° to 25 °C. The earlier studies of Mooney and Billings (1961) and Billings et al. (1971) showed that alpine ecotypes of *Oxyria digyna* have photosynthetic optima at higher temperatures and also higher rates of respiration than arctic ecotypes of the same species. Maximum photosynthetic rates were higher (6–8 mg CO_2 $dm^{-2}hr^{-1}$) in all arctic populations than in alpine populations (2–5 mg CO_2 $dm^{-2}hr^{-1}$), higher rates resulting from cold treatment (12°C day, 4°C night) than with medium temperature treatment (21° and 10°C) (Billings et al., 1971). These authors concluded that temperature acclimation is genetically controlled. As a group, forbs allocate considerable carbon to reproduction and many species have large showy flowers. These species generally produce considerable seed, but seedlings are quite rare.

Graminoids

Sedges and grasses are often the most conspicuous group of tundra plants, and consequently they have received considerable attention. As a group they range from wet soils (*Arctophila fulva, Carex aquatilis, C. stans, Dupontia fisheri, Eriophorum angustifolium*), through mesic-site species (*Carex bigelowii, Deschampsia caespitosa, Eriophorum vaginatum, Phippsia algida*) to species of well-drained sites (*Carex nardina, Kobresia bellardii, Puccinellia vaginata*).

Wet-site species. The studies of *Carex aquatilis, C. stans, Dupontia fisheri,* and *Eriophorum angustifolium* from the Arctic all show the same basic adaptive characteristics. These species have rapid growth rates of shoot growth in spring as a result of large carbohydrate reserves and high photosynthetic rates with new leaf production (Allessio and Tieszen, 1975; Tieszen, 1975, 1978a; Muc, 1977; Henry, 1987). These wetland species carry a 5–10% biomass of green tissue over winter, and the tissues have a high concentration of nitrogen, phosphorus and potassium (Chapin, 1979). *Carex aquatilis* and *Dupontia fisheri* at Barrow and *Carex stans* on Devon Island grow in nutrient-deficient soils, are able to use either ammonium or nitrate ions and have levels of nitrogen and phosphorus in shoot tissues about twice those of plants in temperate regions. These species have large rhizome and root systems that function for several years (roots 4–8 years). Carbohydrates are maintained at high levels throughout the year. Starches are a relatively small component and simple sugars, important in cold-hardiness, comprise a high percentage of the total.

These species grow in saturated or near-saturated soils and are seldom subjected to significant water stress. Consequently, leaf conductances are higher than in upland species, although rather low leaf water potentials can develop. With low leaf resistances to fluxes of water vapor and carbon dioxide, net assimilation rates are relatively high. These graminoid species and others are adapted to carrying on maximum photosynthetic rates at 10° or 15°C, and to reach light saturation at relatively low light levels. Consequently these species and many others are able to maintain a positive carbon gain for 24 hours/day, provided the "nights" do not have heavy cloud (Mayo et al., 1977; Tieszen 1978a). Flowering and seed production are limited in most arctic graminoids, but these species spread by rhizomes and tillers.

Eriophorum scheuchzeri is a summer-green, strongly rhizomatous species that has a limited growing season and limited allocation to reproduction because the plants grow in wet, peaty soils that are nutrient-poor (Mark and Chapin, 1989).

In the Low and High Arctic most graminoids of wet sites have upright culms and display leaves at a high angle. *Carex aquatilis and Dupontia fisheri*

have leaf angles that average 72° in northern Alaska (Caldwell et al., 1974; Miller et al., 1980). These high leaf and culm angles enable species to intercept solar radiation continuously, even at the prevailing low sun angles (daily average of 25° to 19° above the horizontal during the growing season). Although not measured, *Carex stans* in the High Arctic has the same leaf and culm display as do graminoids in the Low Arctic.

Mesic- to dry-site species. Some of the most successful tundra plants are the grasses and sedges of uplands. These include *Arctagrostis latifolia, Carex bigelowii,* and *Eriophorum vaginatum* of the Low Arctic, and *Alopecurus alpinus, Luzula confusa,* and *Phippsia algida* of the High Arctic.

The tussock-tundra sedge or cottongrass *Eriophorum vaginatum* has received the most attention because of its importance in the Low Arctic and its ease of growth. This species flowers and begins leaf elongation within a few days of snowmelt. New tillers are produced intravaginally next to the parent tiller, and therefore tussocks are formed. The tussock form ameliorates both temperature and the nutrient regime immediately around and below each tussock (Chapin et al., 1979; Addison and Bliss, 1984; Mark and Chapin, 1989). On natural disturbances (soil boils) and man-induced disturbances, seedlings of *Eriophorum* develop more readily than in closed, undisturbed tundra. On disturbed sites, tillering rate was greater and the minimum size of flowering tussocks was lower than in undisturbed sites (Fetcher and Shaver, 1982). *Eriophorum* is about average (3.5%) among tundra plants (0.4–21.9%; mean 5.4%) in its total reproductive allocation, and seedling survival is quite high due to early establishment in the growing season, production of tillers, and relatively high growth rates (Chester and Shaver, 1982 a,b).

Photosynthetic rates of *Eriophorum vaginatum* are low (3.4 mg CO_2 $g^{-1}hr^{-1}$) compared with many other graminoids in the Arctic (10–20 mg CO_2 $g^{-1}hr^{-1}$). In part a positive carbon gain in cottongrass is maintained by low rates of shoot and root respiration, and by a longer growing season due to earlier snowmelt on the elevated tussocks (Limbach et al., 1982; Mark and Chapin, 1989). Leaf nitrogen content is also low in this species. Although tundra plants grow in nutrient-poor soils, adding fertilizer depressed maximum photosynthetic rates in *Carex bigelowii* but had no effect on *Eriophorum vaginatum* (Bigger and Oechel, 1982). While additional nitrogen stimulates shoot growth more than added phosphorus (Shaver and Chapin, 1980), phosphorus reduced photosynthetic rates more than nitrogen fertilizer (Bigger and Oechel, 1982). The reasons for reduced photosynthetic rates with fertilization are not known.

In a major modeling effort (Miller et al., 1984), a computer-based simulation model of *Eriophorum vaginatum* tussock tundra was developed called ARTUS. In the simulations that were run, a temperature increase of 4 °C increased thaw depth 50%, decomposition increased 45%, and net production 40%. An increase in solar radiation (shortwave) of 20% increased net production by only 3%, yet a 50% reduction in solar radiation reduced net production by 37%; decomposition changed little with an increase or decrease in radiation. Changes in the thickness of the organic layer and the rates of mineralization also produced profound changes in rates of decomposition and net primary production. Increasing photosynthesis by 50% resulted in little change to respiration, net production and decomposition (Table 19.21). These results show how powerful a tool simulation modeling can be for understanding basic plant and ecosystem processes.

There are many arctic and alpine dry-site graminoid species, and several of these have been studied in detail. For brevity, only *Kobresia bellardii*, a representative arctic–alpine species, is discussed here. This species has narrow, wintergreen leaves, and is capable of limited shoot development in spring and fall when soils are frozen and roots are essentially dormant. Shoot growth occurs rapidly with soil thaw. Growth results from sugars stored in partially expanded leaves. Root carbohydrates change little during spring growth and onset of fall dormancy, indicating they contribute little to shoot development (Bell and Bliss, 1979).

Kobresia maintains high photosynthetic rates in summer, and the rates drop little with summer drought (–2.4 MPa) (Johnson et al., 1973). Minimum ψ_l measurements of −2.2 to −2.9 MPa have been reported (Johnson and Caldwell, 1974; Bell and Bliss, 1979). *Kobresia* is well adapted to sites with shallow snow cover, such as raised beach ridges in the Arctic and uplands in the alpine. Fellfields with strong abrasive winter winds and little or no snow cover inhibit this species.

The leaf angle of high arctic graminoids is significantly lower than for low arctic species (Grulke and Bliss, 1985). With lower sun angles

TABLE 19.21

Analysis of simulation modeling resulting from changing climatic, soil, and physiological processes in *Eriophorum vaginatum* tussock tundra[1]

Variables	Standard case	Temperature		Solar Radiation		Organic mat thickness		Mineralization		Photosynthesis		Respiration	
		−4°C	+4°C	−50%	+20%	−50%	+50%	−100%	+100%	−50%	+50%	−50%	+50%
Water Evaporation (mm yr^{-1})	180	147	187	147	190	148	197	180	180	180	180	180	180
Gross primary production (g $m^{-2}yr^{-1}$)													
Respiration	116	74	170	106	119	118	113	114	117	115	117	69	162
Net vascular plant production	99	51	139	77	103	99	96	87	106	97	105	104	96
Net moss production	117	115	116	91	117	117	117	116	117	117	117	117	117
Net ecosystem production	120	100	118	75	123	101	90	203	46	118	127	125	117
Decomposition	95	66	138	93	97	55	122	0	178	95	95	95	95
Nitrogen (g $m^{-2}yr^{-1}$)													
Mineralization	1.85	1.27	2.67	1.80	1.87	1.06	2.37	0	3.45	1.85	1.85	1.85	1.85

[1] From Miller et al. (1984).

(daily average is 21° on the solstice, declining to 17° in mid August), one would predict that plants would maintain upright culms and high leaf angles to intercept more radiation. Leaf angle averaged 32° in eight species, with *Alopecurus alpinus, Puccinellia phryganodes*, and *P. vaginata* averaging only 10° above a horizontal surface. When small plastic greenhouses were placed over *Phippsia algida* and *Puccinellia vaginata*, their leaf angles increased in one growing season from 45° to 60° and from 10° to 25° respectively. Growth form in these two grasses seems to be controlled primarily by environmental factors (soil moisture, temperature, VPD, and wind speed) rather than selection to maximize leaf and culm orientation to a low sun angle (Grulke and Bliss, 1985).

Cushion and rosette

Cushion and rosette species are typical of wind-exposed sites with well-drained soils. In the Low Arctic these sites are more typical of ridge tops and mountain slopes, while in the High Arctic vast areas are dominated by species with these growth forms. The cushion form results from a compact, vigorous branching system with few nodes and leaves produced per year, and with very short internodes. Representative species include *Cerastium* spp. *Draba* spp. *Dryas integrifolia, D. octopetala, Papaver radicatum, Saxifraga caespitosa*, and *S. oppositifolia* from the Arctic.

Cushion, rosette, and mat-forming species generally have wintergreen or evergreen leaves (Bell and Bliss, 1977; Svoboda, 1977), grow slowly, and are long-lived. Spomer (1964) believed that the cushion form resulted more from reduced temperatures than from reduced soil water or increased wind in these exposed sites. Other studies point to high leaf and stem temperatures in cushion plants (Salisbury and Spomer, 1964; Courtin, 1968; Addison, 1977), resulting from boundary-layer conditions. Wind velocities are higher at 2 cm in fellfields where cushion plants predominate than in meadows; the differences are most pronounced in winter (Bell and Bliss, 1979). Periods in winter with little or no snow cover severely limit the sedge *Kobresia bellardii* but favor cushion plants. Thus, it is probably winter and spring environmental conditions that are most critical in determining where the cushion form is favored.

Slow growth rates of these species is favored by the very low rates of photosynthesis and respiration, low carbohydrate reserves, and low leaf

conductances. Most of these rosette and cushion species produce 2–5 leaves per shoot per year and they invest relatively little carbon in reproduction, although abundant seed is produced in some species (*Dryas, Saxifraga, Silene*). Root systems are generally large, with many alpine species having deep tap roots.

Shrubs

Shrub species of the Betulaceae, Ericaceae and Salicaceae are a common feature of low arctic environments, but are very minor in the High Arctic except for *Salix arctica*. Both evergreen and deciduous species are found together in many habitats, although deciduous shrubs are more common on well-drained slopes and river terraces where the active layer is deeper and where soil nutrients are greater. Evergreen shrubs are more common in poorly-drained to medium-drained, nutrient-poor soils.

Evergreen shrub species. Evergreen shrub species are conservative, slow- growing plants. Nutrients are conserved with leaves that function for two or more years and consequently they grow well on nutrient-poor, acid soils. The low photosynthetic rates support a limited carbon base and consequently shoot and root growth is often limited. Aboveground carbon allocation to reproduction averages 2–5% (Johnson and Tieszen, 1976; Campbell, 1983). Photosynthetic rates are low in all arctic and alpine evergreen shrubs, but leaves 2–3 years old often have positive rates and are not a carbon drain (Hadley and Bliss, 1964a; Johnson and Tieszen, 1976; Limbach et al., 1982; Oberbauer and Oechel, 1989). These species appear to have limited carbon reserves, for their roots and rhizomes are usually small. However, *Vaccinium vitis-idaea* maintains relatively high rates of root respiration (Limbach et al., 1982).

Nutrient levels are low in the leaves of evergreen shrubs and the addition of nitrogen does not appear to increase photosynthetic rates in *Empetrum nigrum* spp. *hermaphroditum, Ledum palustre* ssp. *decumbens*, and *Vaccinium vitis-idaea* (Bigger and Oechel, 1982).

Deciduous species. This growth form, with large amounts of carbon devoted to roots and woody stems, necessitates a very different suite of physiological characteristics compared with the evergreen species. As soon as snow melts, these species break dormancy and within 2–3 weeks have a full complement of leaves. Respiration rates are initially high as the new leaf surface is added, then drop while photosynthesis is maintained at high levels (Hadley and Bliss, 1964a; Dawson, 1987). Under field and experimental conditions, leaves typically go dormant within 50–60 days. Photosynthetic rates are generally higher in species with this life form than the other growth forms. It is believed that the short growing season, low air and soil temperatures, and limited nutrient availability are the major factors limiting deciduous shrubs to the warmest and most protected habitats.

Nutrient requirements appear to be greater in these shrubs — at least leaf nitrogen contents are higher (Limbach et al., 1982); but fertilizer addition reduced photosynthetic rates in *Betula nana* and *Vaccinium uliginosum* (Bigger and Oechel, 1982). Tundra deciduous shrubs translocate considerable amounts of nutrients into leaves from underground storage each year, in contrast with evergreen shrubs (Chapin, 1979; Chapin et al., 1980b). The deciduous shrubs also have higher rates of phosphorus absorption than evergreen species, and at relatively low temperatures (10°C) (Chapin and Tryon, 1982).

From the above information, it is evident that most species are conservative in growth and reproduction; there are very few ruderal (weedy) species. These stressful environments select against species that grow rapidly and are competitive. Resources of thermal energy, carbon gain and nutrients are too limiting to permit that luxury. Yet arctic plants are well adapted to these most stressful environments, for they function quite well at 3 to 10°C, have rather high Q_{10} rates for physiological processes, and they take full advantage of the limited growing season. However, the expenditure of carbon for large, showy flowers seems wasteful, considering the longevity of most species and the general rarity of seedlings. Most high arctic species have a biological clock that ushers in dormancy after 45–55 days, even though they are given favorable summer growing conditions.

The growth forms represented by arctic plants enable them to grow successfully in habitats ranging from exposed, dry, and windy ridges and uplands with little winter snow cover to snow-protected slopes, and habitats with deep snow accumulation. The patterns and processes of tundra plants are more easily observed and studied than in temperate and tropical forests, yet the processes are very similar.

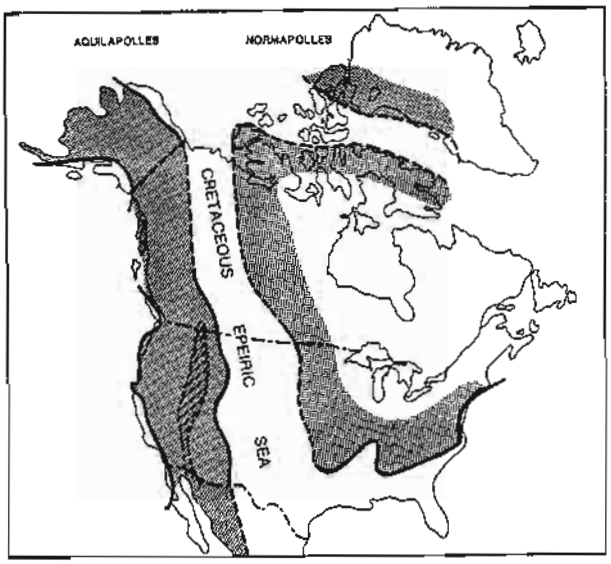

Fig. 19.66. Cretaceous Epeiric Sea during Late Cretaceous time. After Leopold and MacGintie (1972).

ECOSYSTEMS

Origins of arctic ecosystems

The paleoecological history of northern North America is a fascinating story that to date is only partially unraveled. It is known from the fossil record that past vegetation and climates were very different from those of today. Only broad generalizations can be made here, yet this information will help to explain the evolution of arctic systems. The brief general history of mountain building and the evolution of forest vegetation is given as background to discussing the evolution and spread of mountain biota adapted to cold climates. Beringia, the former land bridge connecting Asia with North America, is then discussed for the role it played in the evolution of arctic ecosystems.

Mountain building

During the Late Mesozoic some 100 Ma (100×10^6) years B.P., a large sea, the Cretaceous Epeiric Sea, extended from Mexico and the Gulf States to the northern Yukon Territory, dividing the continent into two land masses (Fig. 19.66). Based upon plant fossils, three distinct floristic provinces were developing: an Eastern region, a Rocky Mountain region, and a West Coast floristic region. Over time, the deep sediments that accumulated in this inland sea were folded and faulted to form the Rocky Mountain Cordillera System that extends from the Brooks Range in Alaska to the Sierra Madre Oriental in eastern Mexico. This mountain-building period, known as the Laramide Orogeny, occurred during the Late Cretaceous and Early Tertiary, from about 70 to 60 Ma B.P. (Table 19.22). These mountain ranges were low during the Early Tertiary, then rose to their present elevations late in the Tertiary. The eastern mountains of the Appalachian System are much older. They developed over a long period of time, the middle to late Paleozoic Era, from about 350 to 200 Ma B.P. The mountain ranges of the Great Basin developed in the Middle Tertiary, during the Basin and Range Orogeny from about 35 to 20 Ma B.P. The Sierra Nevada, the Cascade Ranges, the Coastal Ranges, and their associated volcanoes are much younger. They formed in the Pliocene and Pleistocene Epochs, 5 to 1 Ma B.P. (King, 1977). Thus there was a general progression of mountain building through time from east to west across the continent. Prior to the rise of the Sierra Nevada, the Cascade Ranges, and the further rise of the Rocky Mountains, precipitation was relatively uniform across the continent and mean annual temperature appears to have been higher than today.

Evolution of floras and vegetation

Although the angiosperms (flowering plants) began to evolve from the gymnosperms (cone-bearing plants) in the Late Mesozoic Era, the fossil record is much more complete for the past 65 Ma, the Tertiary Period. Fossils from the Gulf States, Wyoming, and California indicate that a temperate deciduous forest, the so-called mixed mesophytic forest with its many tree species, was developing in the Paleocene and Eocene Epochs. These early fossil floras, typified by the Lower Eocene Wilcox Flora of Tennessee, contain a warm-temperate to tropical element of evergreen species and a cool-temperate element of deciduous species (Graham, 1972). During the Middle Tertiary (Upper Oligocene and Miocene) the fossil record shows widespread development of deciduous forests across the continent to relatively high latitudes (50–60°N). The fossil record across central and eastern Canada is minimal, for the older rocks were eliminated by the continental ice sheets of the Pleistocene. Although broad-leaved species predominated in these Early Tertiary epochs, conifer genera were present and they became more abun-

TABLE 19.22

Geologic time and the development of major vegetation

Period	Epoch	Time before present (10^6 yr)	Dominant vegetation	
			Central U.S.	Alaska
Quaternary	Pleistocene	2.0	Forests and grasslands	Coniferous forests and tundra
Tertiary	Pliocene	7	Grasslands	Coniferous forests
	Miocene	26	Deciduous forests and grasslands	Coniferous and deciduous forests
	Oligocene	37	Deciduous forests	Deciduous forests
	Eocene	53	Warm temperate and tropical forests	Warm temperate and tropical forests
	Paleocene	65		Tropical and temperate forests
Cretaceous	Late	100		
	Early	136		
Jurassic		190		
Triassic		225		
Permian		280		
Pennsylvanian		325		
Mississippian		345		
Devonian		395		
Silurian		430		
Ordovician		500		
Cambrian		570		
Precambrian				

dant in Miocene and Pliocene time with further rise of ranges within the Rocky Mountains (Leopold and MacGinitie, 1972). This provided cooler environments more favorable for the development of coniferous forests.

In early Tertiary times, the macrofossil and pollen record from 60 to 65°N latitude in Alaska indicate a tropical to subtropical vegetation with evergreen trees with entire leaf margins. A Late Paleocene flora from the Cook Inlet (61–62°N) included evergreen and deciduous species, and two species of palms. An Early Eocene flora from the Gulf of Alaska (60°N) contained about 70 species, the modern relatives of which occur in tropical forests of Malaysia! Even the Middle Eocene floras (ca 50 Ma B.P.) of Alaska contained deciduous and evergreen-leaved species, most with entire margins. Comparable modern floras are the evergreen oak–laurel forests of southern China (Wolfe, 1972).

By the Oligocene Epoch the fossil floras appear more like present-day floras of central China and Japan. Deciduous forests appear to have dominated by Late Oligocene time, and a diverse conifer flora was also present, based upon collections from 40 locations.

The Wrangell Mountains of Central Alaska contain a Middle Miocene (18 to 15 Ma B.P.) flora with abundant conifers including species of fir (*Abies*), spruce (*Picea*), pine (*Pinus*), cedar (*Thuja*), and hemlock (*Tsuga*). These conifer or mixed conifer–deciduous forests must have occupied uplands (Wolfe, 1969). At the same time fossil pollen from rocks on the Seward Peninsula (65–66°N) shows a dominance of genera within the Pinaceae, but also the deciduous genera *Carya* (hickory), *Fagus* (beech), *Ilex* (holly), *Pterocarya* (wingnut) and *Ulmus* (elm). Even at 70°N coniferous forests of *Abies, Larix* (larch), *Picea, Pinus, Pseudotsuga* (false fir) and *Tsuga*, predominated, but with some *Pterocarya, Ulmus* and *Zelkova* present (Wolfe, 1972). The Haughton Formation on Devon Island

contains fossils of a conifer–hardwood forest of early Miocene age (22 Ma B.P.) (Whitlock and Dawson, 1990).

The Pliocene Epoch in Alaska (6 to 3 Ma B.P.) is not well represented in the fossil record. The limited material suggests that coniferous forests still predominated but that climatic cooling continued. Species of fir had disappeared from Cook Inlet and hemlock from western Alaska. A Pliocene flora and insect fauna (5.7 Ma B.P.) from the Seward Peninsula contained 10 species of conifers and seeds of *Symphoricarpos* and *Vaccinium*, shrubs typical of a flood-plain forest. The insects, mostly beetles and ants, appear typical of forests of present-day southern British Columbia and northern Washington (Hopkins et al., 1971).

The western islands of the Canadian Arctic Archipelago also contain fossil evidence of late Tertiary and early Pleistocene forests, a dramatic contrast in climate and vegetation with the present. The unconsolidated sands and gravels with organic sediments of the Beaufort Formation extend from Banks Island at 71°N to Meighen Island at 80°N. Although these freshwater sediments have not been precisely dated, indications are they date from late Miocene to late Pliocene time, about 7 to <3 Ma B.P. (Matthews and Ovenden, 1990; Fyles, 1990). Pollen and megafossils of cones, fruits, leaves and seeds from southwestern Banks Island indicate that mixed coniferous–deciduous forests of *Juglans* (walnut), *Larix*, *Metasequoia* (dawn redwood), *Picea*, *Pinus*, and *Tsuga*, dominated in middle Miocene time (Hills et al., 1974). Megafossils and pollen from the Beaufort Formation on northwestern Banks Island and from Ellef Ringnes Island far to the north (78–79°N) probably date from Late Miocene to Early Pliocene time (6 to 4 Ma B.P.). This is an amazing group of species, characteristic of present-day northern hardwood and coniferous forests of the upper Great Lake States and New England. The genera include *Alnus*, *Betula*, *Carpinus*, *Carya*, *Corylus* (hazelnut), *Picea*, *Pinus*, *Populus*, *Pterocarya*, *Salix*, *Tsuga*, ferns (*Osmunda*) and club moss (*Lycopodium*) (Hills and Ogilvie, 1970). The Upper Beaufort Formation of Banks Island is characterized by a dominance of *Larix*, *Picea banksii*, *Pinus strobus*, and *Tsuga* needles and cones, and *Alnus* cones, along with an abundance of pollen from heath species. Thirteen species of moss are represented; all presently occur in the boreal coniferous forests and tundra (Kuc and Hills, 1971).

A diverse group of fossil seed plants (Hills and Matthews, 1974), mosses (Kuc, 1974b), and invertebrates (Matthews, 1974) comes from the Beaufort Formation on Meighen Island (80°N). The vascular plants include *Abies*, *Betula nana* or *B. glandulosa*, *B. papyrifera*, *Carex*, *Cassiope tetragona*, *Empetrum*, *Hedysarum*, *Larix*, *Ledum palustre*, *Picea banksii*, *Pinus albicaulis*, *Potentilla palustris*, *Salix*, and *Vaccinium*. The invertebrates include ground, diving, rove, carrion, and click beetles (Coleoptera) as well as weevils, midges, and mites. The mosses were very similar to those from northwestern Banks Islands. These fossils indicate that a forest–tundra vegetation and insect fauna must have occurred there in Miocene–early Pliocene time. It is assumed that tundra was at higher elevations then, and further north on Axel Heiberg and Ellesmere Islands and northern Greenland, at least in the more mountainous areas. An open larch forest with abundant wetland mosses and sedges occurred at Beaver Pond near the head of Strathcona Fjord, Ellesmere Island in late Pliocene time (3 Ma B.P.) (Matthews and Ovenden, 1990).

Bennike and Böcher (1990) have reported forest–tundra and heathlands in Peary Land, Greenland (82°30′N) at the Pliocene–Pleistocene transition (2.0 to 2.5 Ma B.P.). This fossil record includes 120 species of Coleoptera, yet only 33 species of beetles occur in all of Greenland today and only two species in northern Greenland. No ants occur today, yet three are in this fossil record.

There is also evidence for the evolution of an arctic fauna and flora in the highlands of Central Asia (Hoffman and Taber, 1967; Yurtsev, 1972) and subsequent spread of species north and east into Eastern Siberia and Alaska and west into Eurasia with continental cooling and land formation in Late Tertiary time. Further evolution of plant and animal groups occurred within Beringia (Kontrimavichus, 1984). Enrichment of cold-adapted floras and faunas also resulted from evolution of species in the central and northern Rocky Mountains with their uplift in the Late Tertiary (Packer, 1974; Billings, 1974a). Unfortunately, there is a lack of fossil evidence from the predominantly herbaceous plants with only soft parts and small seeds. With major climatic cooling of polar regions (Wolfe, 1969, 1972) and the possible northward drift of the tectonic plates (Löve and Löve, 1974) into higher latitudes already possessing an arctic or near-arctic climate, there was rapid evolution of plants and animals adapted to arctic and

high-mountain (alpine) environments.

A circumpolar flora of perhaps 1500 species developed prior to the onset of Pleistocene glaciations (Löve and Löve, 1974). Glacial advances and retreats in temperate regions triggered concomitant southward and northward migration of species. Alpine regions were enriched with arctic species during glaciations, and the northward migrations during interglacial periods enriched the arctic biota with alpine species. The Rocky Mountain Cordillera was especially important as a migration route. With glacial advances the tundra vegetation and probably the invertebrate fauna were isolated, resulting in populations of species that are evident today as morphologically distinct species or subspecies in arctic and alpine areas. Ice did not totally cover the Arctic, for the North Slope of Alaska, central and much of western Alaska, and the western and central islands of the Canadian Arctic Archipelago remained largely unglaciated and thus could have served as refugia. Pleistocene glaciation greatly reduced the floras and faunas of northern oceanic islands and the alpine "islands" of mountains in more temperate regions. The modern circumpolar flora contains about 900 species (Polunin, 1959).

While it is generally accepted that alpine and arctic species have evolved from nontundra species of open forests and scrub vegetation at lower elevations and latitudes (Billings, 1974), an interesting set of questions relates to their mechanisms of adaptation. One mechanism for the adaptation of arctic species appears to result from the evolution of polyploids, species with a duplication of chromosomes through hybridization of closely related species or doubling of the existing number of chromosomes. Polyploidy occurs at a low frequency in all plant populations in all climates, but through natural selection it becomes more frequent at higher latitudes. Löve and Löve (1974, 1975) reported that in the Low Arctic 60% of the vascular plants are polyploid, as against 70% of those in the High Arctic and 80% for the endemic species of the High Arctic. Although Packer (1974) found no significant increase of polyploidy within the Canadian Arctic Archipelago flora, he did demonstrate an increase in polyploidy with increased climatic severity in the northwestern arctic islands. Earlier, Johnson and Packer (1967) presented data from Cape Thompson, Alaska, to show that polyploids were more abundant in cold, wet soils with high frost action than in uplands with warmer soils where frost action was less. If environmental severity does play a role in polyploidy, one can better understand this process when the observed degree of ploidy is related to ecological information by using environmental data. The hypothesis that polyploids are preadapted to more extreme environments has its counterpart in considering these species better adapted because of their greater genetic variability and thus their ability to occupy new habitats (Löve and Löve, 1974).

From several studies it is now evident that the physiological and, often, morphological adaptations are quite different in arctic and alpine ecotypes of the same species [*Oxyria digyna* (Mooney and Billings, 1961; Billings et al., 1971); *Trisetum spicatum* (Clebsch and Billings, 1976); and *Thalictrum alpinum* (Mooney and Johnson, 1965)]. General adaptations of arctic species have already been discussed (pp. 621–639).

In summary, the early Tertiary period was warmer and wetter than at present, there were no high mountains in western North America, and subtropical and tropical floras and vegetation occurred throughout much of the conterminous United States and northwest to Central Alaska. Eocene time saw extensive development of deciduous forests across the continent into Alaska. There was rapid cooling during the Oligocene Epoch which resulted in expansion of the cool-temperate deciduous forests in Alaska and the extirpation of the evergreen subtropical species. By Miocene time, forests equivalent to the northern hardwoods of the Upper Great Lakes region and New England predominated in Alaska, and mixed conifer–hardwood forests in the arctic islands. With further cooling in Pliocene time coniferous forests dominated in Alaska and at least to Ellef Ringnes Island, followed by evolution of tundra biota in the Miocene and early Pleistocene as mountain and continental glaciers become more dominant with higher precipitation and continued cooling. Open larch forests indicate that southern Banks Island was roughly 10°C warmer in late Pliocene time than today (Vincent, 1990). The Arctic appears to be a dead end in the evolution of woody plants. While some lineages did adapt to the Arctic, there has been little subsequent diversification at a low taxonomic level. Origins of genera and higher taxa appear to have been in middle and low latitudes (Spicer et al., 1987). As stated by Wolfe (1972), the available geologic data indicate

that theories of continental drift, sea-floor spreading, and pole wandering do not adequately explain the existence of these fossil vegetation records in rocks that today are at 60–65°N, let alone the assemblages in the Beaufort Formation northward to 80°. We have much yet to learn.

Evolution of mammals

It has been recognized for some time that the mammalian faunas of northeastern Siberia, Alaska, and Canada are very similar (Baker, 1920; Colbert, 1937; Zeuner, 1959; Flerow, 1967; Repenning, 1967; Hoffman and Taber, 1967; Vereshschagin and Baryshnikov, 1982). The interesting questions are: how did this happen? and what role did Eurasia vs. North America play in this? During the Early Tertiary, mammals spread rapidly to temperate regions from tropical and subtropical regions. Both the fossil record and present-day zoogeography are central to unravelling the history and migration patterns of mammals. Where a biota is richer in genera and species, it is believed to be older and possibly the region of origin. Hoffman and Taber (1967) used these criteria to state that the plateau region of central Asia, especially the Tibet Plateau, was important in the origin of alpine and arctic tundra animals because of the great diversity of its fauna. There are a greater number of mammal and bird species native to this region than elsewhere (Table 19.23). There are also specialized alpine amphibians and reptiles, the only place in the world where alpine species of these groups are found.

A more direct method of analysis is the paleontological record of mammals for the Old World or Palearctic and the New World or Nearctic across the "land bridge" of Beringia. The last major exchange of vertebrate groups across this region occurred in Pliocene and Pleistocene time. By using morphological features of bones it is possible to determine the taxonomic relationships of organisms in time and to piece together the evolutionary history of species within different genera.

The fossil record shows there have been four periods of major mammal migration between Asia and North America, and that each has been progressively shorter (Table 19.24). The evidence presented indicates that a much larger number of genera and species evolved in Eurasia and spread to North America than the reverse (Repenning, 1967). It is believed that many of these mammal groups evolved in the grasslands of south-central

TABLE 19.23

Faunistic richness of mammals, passerine and non-passerine birds for various alpine areas in the world[1]

Region	Number of Species		
	Mammals	Birds	
		Passerine	Non-passerine
Europe	11	23	12
Western North America	22	22	13
Eastern Siberia	20	41	21
Central Asia	51	120	34
Total	90	145	47

[1]After Hoffman and Taber (1967).

Eurasia and moved into Siberia prior to the development of massive coniferous forests. The limited extent of Pleistocene glaciation in Siberia also favored the evolution and geographic extension of mammals, compared with the massive Laurentide and mountain ice sheets of North America that greatly reduced or eliminated north–south migration avenues. The species listed in Table 19.24 show that the mammals migrating to North America in the Late Pleistocene (Rancholabrean) time were either tundra or taiga species, and that they were often considered better adapted to colder climates than the Pliocene and Early Pleistocene immigrants. Repenning (1967) reported that 11 of the 23 mammal species considered to have migrated from Eurasia to North America in the Late Pleistocene were correlated with the late Wisconsin glaciation (14,000–10,000 yr B.P.). This indicates that the earlier mammal migrations also occurred during earlier Wisconsian glacial advances because of the land bridge created by the fall in sea level.

Beringia and its role in tundra ecosystems

One of the most fascinating aspects of northern paleoecology is the role that Beringia has played in the evolution of tundra ecosystems. Beringia was first postulated by Hultén (1937) as the land bridge connecting Alaska with Siberia to account for the distribution of certain groups of arctic plants in eastern Asia and Alaska. This was before modern techniques of radiometric dating were available and before methods of palynology, paleobotany, and paleontology had been applied to fossil evidence in the region. The land bridge developed

TABLE 19.24

Dispersal of Palearctic and Nearctic mammals in the Late Cenozoic[1]

Mammalian Age	Duration (Ma) yr	Number genera represented, oldest fossil record			Examples	
		Holarctic	Palearctic	Nearctic	Palearctic	Nearctic
Mid Pliocene (Hemphillian)	6	24	9	5	*Agriotherium* bearlike carnivore *Castor* spp. beaver *Lutravus* otterlike carnivore *Ochotona* pika *Prosimomys minus* meadow mouse	*Dipoides* beaver *Eutamias* chipmunk *Hypolagus schreuderi* rabbit *Sirohippus zitteli* browsing horse
Late Pliocene (Blancon)	2	29	14	4 - 5	*Canis* wolf *Panthera leo* lion *Marmota* marmot *Paracamelus* camel *Plesippus* zebra	*Enhydriodon* weasel *Lynx* lynx *Notiosorex* shrew *Ursus* bear
Early Pleistocene (Irvingtonian)	1	-	11	2	*Alopex* fox *Dinobastis* saber-toothed cat *Equus* horse *Euceratherium* shrub ox *Mammuthus* mammoth *Smilodon* saber-toothed cat *Spermophilus* ground squirrel	*Dinobastis* saber-toothed cat *Equus* horse *Euceratherium* shrub ox *Microtus* meadow mouse *Mammuthus* mammoth
Late Pleistocene (Rancholabrean)	<1	-	23	0	*Alces* moose *Bootherium* extinct musk-ox *Lemmus* lemming *Lepus* hare *Ovibos* musk-ox *Rangifer* caribou	*Alopex* fox *Dicrostonyx* lemming *Bootherium* extinct musk-ox *Lemmus* lemming *Lepus* hare *Mammuthus primigenius* mammoth *Ovibos* musk-ox *Rangifer* caribou

[1]After Repenning (1967).

following a drop of 100–200 m in sea level as water was tied up in continental ice sheets and huge mountain glaciers. The concept of Beringia was given a spatial and temporal frame by Hopkins (1959), and since then many papers and two books have been published dealing with the past history of this region (Hopkins, 1967; Schweger et al., 1982). The region includes Siberia east of the Kolyma river, central Alaska and the Yukon Territory to the Mackenzie River, N.W.T., and the continental shelf where present water depths are <200 m (Fig. 19.67). The history of Beringia, as discussed here, spans the time from the Sangamon Interglacial (120,000 yr B.P.) to the Wisconsin full-glacial period (~18,000 yr B.P.), the last Wisconsian Glaciation (Hopkins, 1982), although most of the discussion is for the last 40,000 yr, a period of ice advance and retreat.

Beringia is central to understanding present-day arctic and alpine ecosystems because of the role this land bridge served for the migration of cold-adapted animals and plants throughout the Pliocene and Pleistocene, including the entrance of people into North America in the last 50,000 to 12,000 years. The region is also important because of the paradox of having supported a diverse fauna

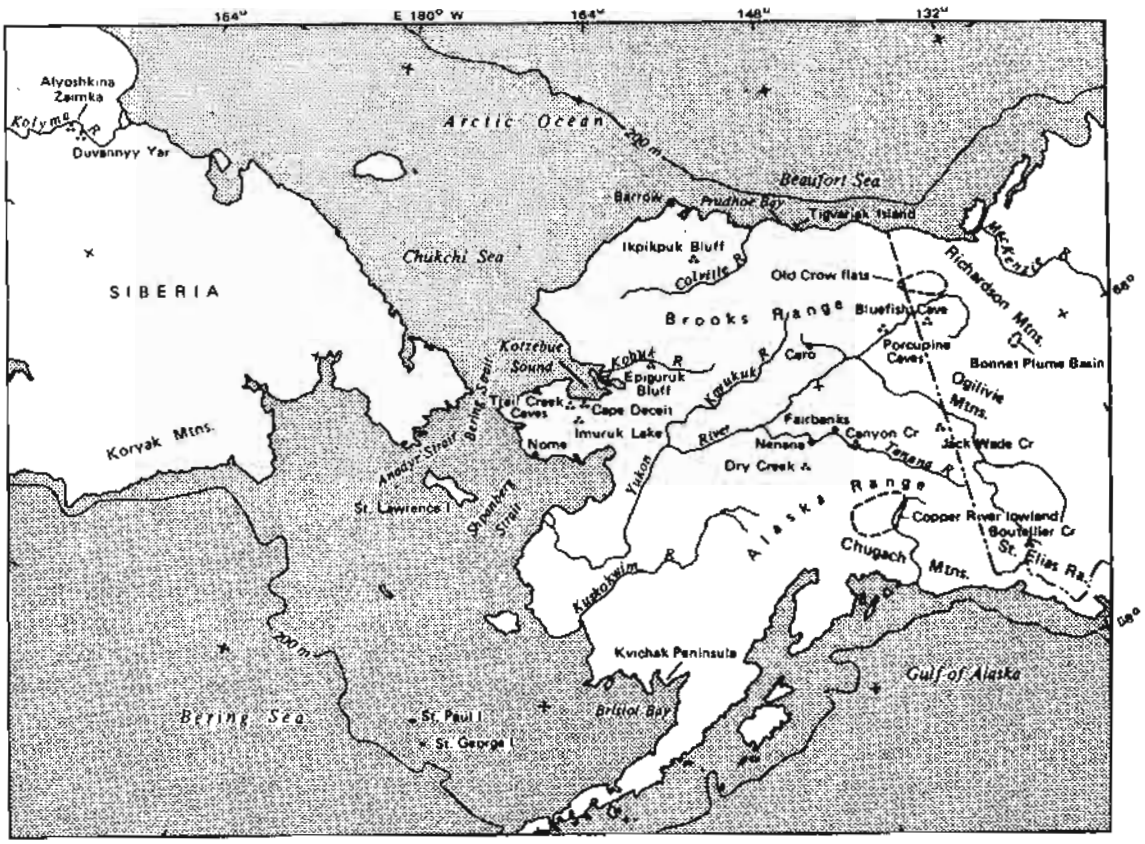

Fig. 19.67. Map of Beringia showing locations given in the text. From Hopkins (1982).

of large and small mammals in the past, at a time when the overall arctic climate is believed to have been colder and drier than at present. The pioneering studies by Hopkins (1959) on the Cenozoic history of Beringia, as viewed by a geomorphologist–paleoecologist, and the early palynological study by Colinvaux (1964) on the past vegetation and climate, set the stage for many studies that led to a 1979 symposium held at Burg Wartenstein, Austria. The book *Paleoecology of Beringia*, its summary (Schweger et al., 1982), and a few related papers serve as the basis for this discussion.

Boutellier interval (65,000–30,000 yr B.P.). The name Boutellier interval was first applied to an interglacial soil and nonglacial alluvium in the foothills of the St. Elias Range of southwestern Yukon Territory (Denton and Stuiver, 1967). Since then Hopkins (1982) has applied the concept to all of Beringia, suggesting a period when climate was cooler than today. Sea level was lower but the land bridge was probably reduced to a narrow isthmus. Pollen records from late in the Boutellier interval indicate that open forests of spruce and shrub thickets occupied river floodplains, and extensive meadows of forbs and graminoids probably dominated the uplands. Alder (*Alnus*) was absent and heath shrubs may have been limited, but were present. Insect faunas were a mixture of mesic and xeric species characteristic of treeless areas. Bone, antler, and ivory artifacts have been recovered from reworked sediments in the Old Crow River valley, northern Yukon, but the material does not come from undisturbed strata and thus positive proof of human presence in Beringia at this time is lacking. These artifacts contain butchering marks and bone flakes interpreted as evidence of early man in the area at about 40,000 yr B.P. (Morlan and Cinq-Mars, 1982). An *in situ* fauna at Jack Wade Creek, in east-central Alaska, is believed to be of this same general age (Porter, 1979). The remains indicate a diverse large-mammal fauna including woolly mammoth (*Mammuthus primigenius*), horse (*Equus* sp.), bison (*Bison*), caribou (*Rangifer tarandus*), mountain sheep (*Ovis* sp.), steppe antelope (*Saiga* sp.), and moose (*Alces alces*) throughout Beringia. The

woolly rhinoceros (*Coelodonta antiquitatis*) was present in western Beringia and the camel (*Camelops hesternus*) in eastern Beringia. A diverse mammalian fauna at Lost Chicken Creek, Alaska, included moose at 1400 yr B.P., down to ptarmigan, the Yukon wild ass (*Equus lambei*), caribou, the helmeted musk-ox (*Symbos cavifrons*), the bison, and the woolly mammoth at >45,000 yr B.P. (Porter, 1988). However, these fossil remains are almost always within reworked sediments of undated age and they give no realistic idea of the number of species, or individuals per species, within a given area. The presence of a few well-preserved large mammal carcasses in redeposited loess and stony colluvium suggest winter death and burial by spring flooding. Accumulating loess and sand-dunes on these landscapes indicate the influence of a dry and probably a cold climate. Late in this period (ca 30,000 yr B.P.) sea level dropped and the land bridge became more extensive.

Duvanny Yar interval (30,000–14,000 yr B.P.). The type locality for this period is along the Kolyma river in eastern Siberia where there are thick loess deposits nearly devoid of organic matter, indicating a dry and cold climate. The pollen record from several cores in the Bering Strait region led Colinvaux (1964, 1967) to state that herbaceous tundra, similar to the arctic coast at Barrow today, occupied the region. The abundance of *Artemisia* pollen led him to suggest a steppe tundra similar to that in Siberia. Other studies by Matthews (1974) and Ager (1982) in western Alaska and by Ritchie (1977, 1982) and Ritchie and Cwynar (1982) in the Yukon and N.W.T. all indicate that an herbaceous tundra dominated by grasses and sedges with *Artemisia* was widespread in Beringia during this period of maximum Wisconsin glaciation. Ericaceous heath species appear to have been present throughout the area, but due to their low pollen production their importance in the vegetation may be underestimated. The macrofossil evidence indicates that spruce became extinct in the region, and that cottonwood and possibly aspen may have persisted, but in limited numbers (Ritchie and Cwynar, 1982). Willow scrub was no doubt common along the valleys. Young (1982) referred to Beringia as a polar desert, although this terminology is questionable if one considers polar desert in the context of high arctic landscapes today with their very limited plant cover and even less wildlife. The earlier concept of a steppe tundra or an herb tundra seems more appropriate. The climate is believed to have been characterized by dry and sunny summers, longer than at present, and by dry and windy winters with limited snow cover. The Polar Front may have been displaced southward with a southerly and southeasterly air-mass circulation predominating. Air-mass movement would have been controlled by a high-pressure cell over the Laurentide ice sheet and a low-pressure cell over the northwest Pacific Ocean (Barry, 1982).

Mammal remains, all from reworked sediments along rivers, indicate the presence of mammoth, bison, horse, caribou, mountain sheep, steppe antelope, and musk-ox in Beringia sometime during the Duvanny Yar period. However, there is no evidence to indicate what species occurred in a given area and at a given time. Schweger et al. (1982) stated that it is probably wrong to consider a single community of herbivores and carnivores densely clustered on the landscapes, as presented by Guthrie (1982). No doubt the mammals occurred in more specialized habitats. Since grass and sedge pollen cannot be identified to species, it is not possible to determine whether they occupied wet, mesic or dry habitats, although it is assumed they dominated in uplands, based upon the presence of grazing mammals. A recent paper by Guthrie and Stoker (1990) reported that horse-hoof fossils from along the Titaluk River, northern Alaska, indicate from hoof wear that these animals lived in an environment with little winter snow cover. The dominance of horse fossils on the North Slope of Alaska indicate that these animals, rather than bison, were favored as grazers in a cold, dry arctic environment.

In spite of the lack of hard evidence from *in situ* mammal remains, rather meager plant macrofossil and insect data, and limited evidence of people prior to about 15,000 yr B.P., Hopkins (1959), Guthrie (1968) and Matthews (1976) hypothesized that an arctic grassland with a large and diverse mammal fauna dominated Beringia. This early arctic ecosystem with its assumed rich biota must have contained sufficient numbers of people to have resulted in the extinction of numerous species by hunting (Martin, 1974, 1982). This grassland–large mammal ecosystem and the reasons for its demise have been questioned by Schweger and Habgood (1976), Ritchie (1977, 1980, 1984), Ritchie and Cwynar (1982), and Colinvaux (1981) among others.

The early discussions at the Burg Wartenstein

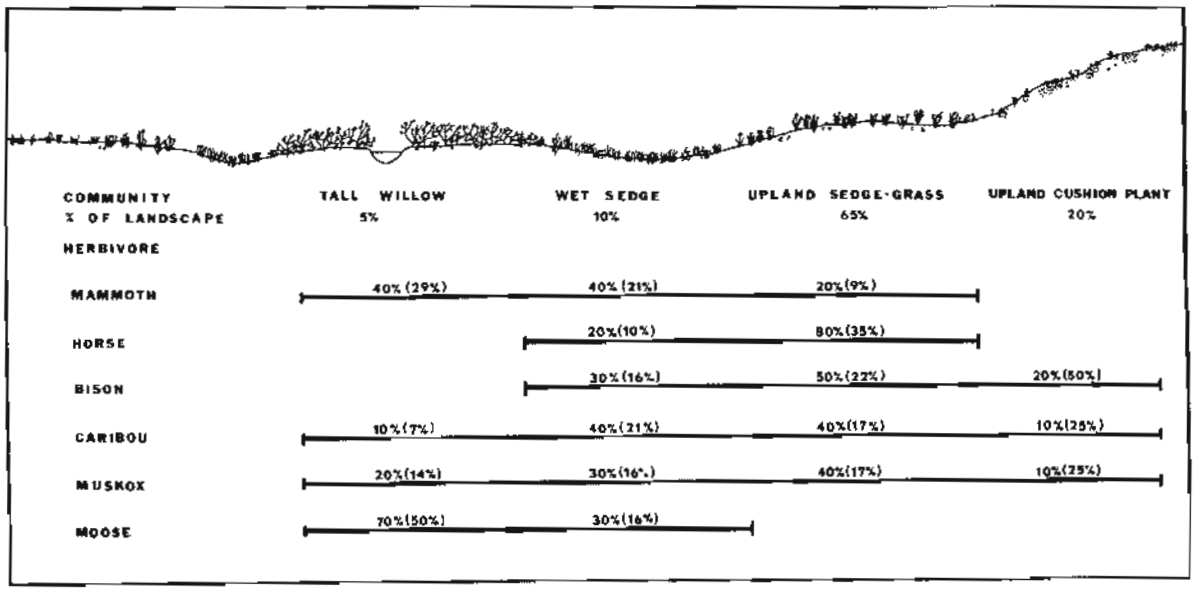

Fig. 19.68. Theoretical ecosystem of Beringia, 25,000 yr B.P., showing major plant communities and major large herbivores. The first number is the assumed percentage of the total forage that a given herbivore obtains from a given plant community (add across). The second number is the percentage contribution that a given community contributes to the diet of an herbivore (add down). The percentage of forage taken in each community contributes by each herbivore is based upon feeding strategies of its modern analogue. From Bliss and Richards (1982).

Conference centered upon the dominance of a relatively lush arctic or subarctic grassland with its highly diverse fauna. The evidence presented by Ritchie and Cwynar (1982) on the pollen record in eastern Beringia and by Redmann (1982) and Bliss and Richards (1982) on temperate grassland and arctic-tundra ecosystems resulted in acceptance of the proposition that landscapes in Beringia had diverse vegetation types. While graminoid–herb meadows may have predominated in uplands, cushion-plant vegetation would have occurred on higher, more exposed mountain slopes. Wet sedgelands occupied poorly drained lowlands, and shrub vegetation occurred along rivers. It is presumed that only in this way could a diverse large-mammal fauna, with each species having somewhat different forage requirements, be accommodated (Fig. 19.68). The discussions that followed and the final papers in the book reflect the recognition of a greater diversity of vegetation and niche-partitioning of mammals across these little-known landscapes (Guthrie, 1982; Schweger, 1982).

Fossils of the large mammals reveal that some had adaptive features not present today in arctic animals. Their body size was greater than in modern species, they had larger horns and antlers, probably for sex display, and their hoofs were smaller, presumably because of fewer wetlands to traverse. Horses and steppe antelopes were unable to paw through snow deeper than 20 cm for forage. The same is believed to be true of the woolly mammoth. Most of the large mammals were grazers rather than browsers, as evidenced by their high-crowned teeth (Guthrie, 1982).

Based upon data from many sources, and discussions with participants at the meetings, a theoretical Beringian ecosystem was developed (Fig. 19.69). This was based upon a landscape model from river bottom to surrounding highlands with four major types of vegetation supporting six species of large mammals. By assigning percentages of the landscape to each vegetation type, assuming that each herbivore obtained a given percentage of its annual forage requirements from the appropriate vegetation types (Table 19.25), and assuming rates of annual plant production, sustainable harvest rates of vegetation types and assumed rates of daily forage consumption for each herbivore species, it was possible to calculate live biomass for each animal species (Table 19.26). By assuming mean body weights for the "average" animal of each species, it was also possible to calculate herbivore numbers and animal density

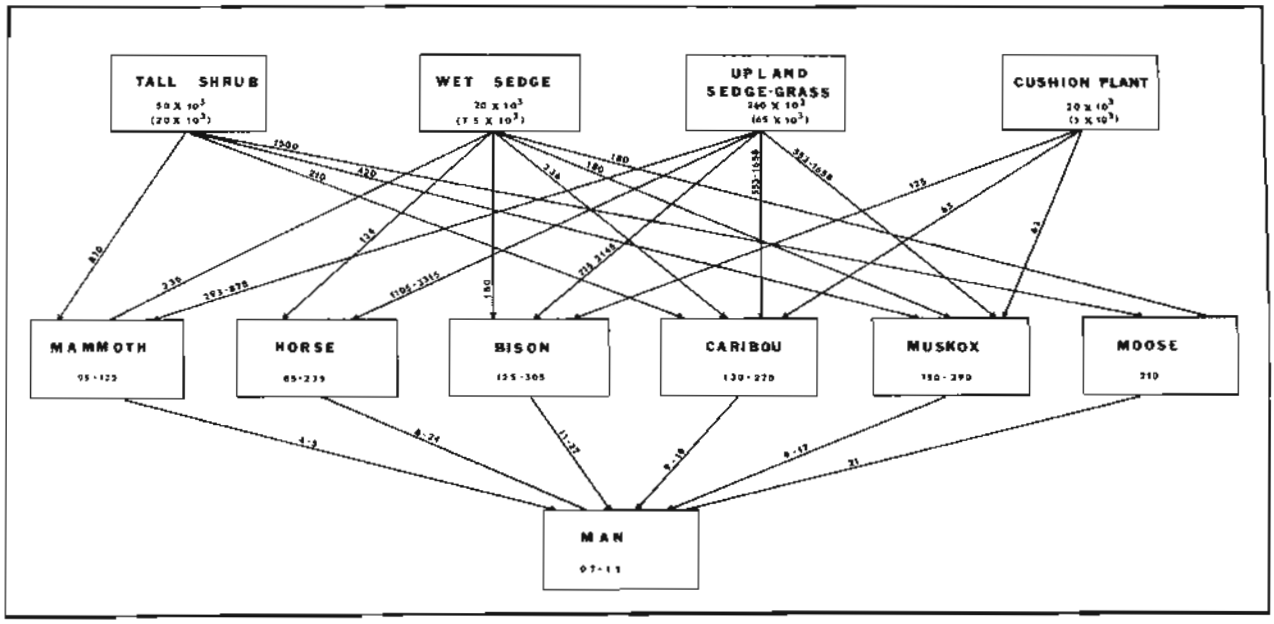

Fig. 19.69. Energy flow within a theoretical Beringian landscape, depicting aboveground biomass and net annual production () for major plant communities, the living biomass of six major large herbivores, and the biomass of people the system can support. All data are metric tons per 1000 km^2 with transfers expressed on an annual basis. From Bliss and Richards (1982).

for a landscape of 1000 km^2.

The calculated densities were similar to modern animal densities for caribou and musk-oxen in the Arctic, and for moose and bison in aspen parkland. The herbivore biomass estimated for this Beringian ecosystem (800 to 1450 kg km^{-2}) is significantly greater than for modern arctic ecosystems (300 to 400 kg km^{-2}). Herbivore biomass estimates based upon 12 studies, for East African ecosystems, range from 3000 to 5500 kg km^{-2} or 3.4 to 4.0 times greater (Coe et al., 1976). A final step added an estimate for the number of native people this paleoecosystem could support. By knowing the living biomass of herbivores and assuming an annual sustainable harvest of 4% for woolly mammoth and 6–10% for the other five species, it was possible to calculate the annual harvestable biomass for the area of 1000 km^2 (60 to 115 t). Then assuming that 50% of the harvestable biomass was actually meat, that only 50% of this meat was consumed (rest to dogs, other carnivores and spoilage), and that an average person ate 1.1 t of meat per year (3 kg d^{-1}) based upon modern data for Inuit living on country food, meat, and fat (Spencer, 1959), the system could have supported 15 to 25 people. This model is intended as a first approximation to the density of people and large herbivores in Beringia. It can no doubt be refined as more accurate data become available.

Birch time (14,000–12,000 yr B.P.). Based upon the pollen record from many cores and mammal remains, there was a major climatic change in Beringia about 13,000 ± 500 yr B.P. A rapid sea-level rise drowned the land bridge connecting the continents. The rise in birch pollen, the entrance of *Eriophorum* pollen, and the macrofossil and pollen evidence of cottonwood indicate a warming trend accompanied by significantly higher precipitation. The fossil insect assemblages were mixtures of mesic and dry-ground species, including species present today in the arctic tundra such as dung beetles (*Aphodius*) (Matthews, 1982). The climate was characterized as having snowy winters, a rapid spring melt, and warm, dry, and cloudless summers.

The large mammal fauna changed over a 4000 year period with the disappearance of the woolly mammoth about 14,000 yr B.P., the bison about 13,000 yr B.P., and the horses about 10,000 yr B.P. Wapiti (*Cervus elaphus*) reappeared about 15,000 yr B.P. and then disappeared again about 10,000 yr B.P., possibly in response to more browse being available during the Birch time, followed by its decline as forest replaced tundra and the tundra

TABLE 19.25

Estimated forage production and percentage consumed by large herbivores in central Beringia 25,000 yr B.P. (after Bliss and Richards, 1982) (see also Fig. 19.69)

Vegetation type	Area (km^2)	Net primary production ($t\ km^{-2}yr$)	Total net production ($t\ yr^{-1}$)	Harvested by herbivores (%)	Forage consumed ($t\ yr^{-1}$)
Tall shrub	50	400	20,000	15	3,000
Wet sedge–grass	100	75	7,500	15	1,125
Upland grass–herb	650	100	65,000	5–15	3,250–9,750
Upland cushion plant	200	25	5,000	5	250
Total	1000	-	97,500	-	7,625–14,125

became wetter. Mountain sheep (*Ovis* sp.) remained in the mountains until approximately 10,000 yr B.P., to be replaced by Dall sheep (*Ovis dalli*). Caribou and musk-oxen remained important components of the western and northern Alaskan tundra ecosystems (Schweger et al., 1982).

The final chapter in this saga, and a most contentious one, is: why did the large mammal fauna change rather abruptly, and when did humans become important in the North? Three scenarios are presented on this lively topic. Martin (1974, 1982) has argued, based upon archaeological evidence of animal-kill sites, and the chronology of extinction, that big-game hunters of the Late Pleistocene so reduced the numbers of mammals that they could not survive. Large mammals became extinct, not only in Beringia, but also in the southwestern United States and in South America between 12,000 and 10,000 yr B.P. Similar waves of extinction occurred in Australia with the loss of 12 genera of marsupials between 40,000 and 20,000 yr B.P. Mammal reductions were much less in Europe and Asia from 20,000 to 10,000 yr B.P. It is known that humans have been present in North America for at least 11,000 years. Fluted projectile points of the Clovis culture found *in situ* with large extinct mammals between 11,200 and 10,800 yr B.P. (Haynes, 1982) give some support to the theory of "overkill" by Martin (1982). One difficulty of this theory is the extinction of small mammals and birds (Grayson, 1977) during this same period. It is difficult to believe that people could have effectively hunted these groups to extinction. Secondly, the extinction of large mammals over a period of 4,000 years in Beringia does not support the "overkill" theory of rapid extinction by human overpredation.

The second mechanism used to explain these megafaunal changes is that of climate. This theory was also hotly debated at the symposium in 1979 and is yet unresolved. The decline of the steppe-tundra and the rise of muskeg and taiga, coupled with wetter tundra landscapes, has been used to explain the demise of large mammals. The mechanism advanced by Guthrie (1982) and Guthrie and Stoker (1990) assumes more winter snow and

TABLE 19.26

Forage consumption, mean body weight, and numbers of large herbivores within a 1000 km^2 ecosystem in central Beringia, 25,000 yr B.P.[1]

Species	Mean body weight (kg)	Mean daily food consumption (% body wt.)	Annual % body wt.	Forage harvested ($t\ yr^{-1}$)	Herbivore biomass ($t\ 1000\ km$)	Numbers in 1000 km^2
Mammoth	2230	4	1460	1400–1985	96–136	43–61
Horse	150	4	1460	1230–3440	84–236	650–1573
Bison	450	2.2	803	1020–2450	127–305	282–678
Caribou	100	2.2	803	1060–2170	132–270	1320–2700
Musk-oxen	180	2.2	803	1215–2320	151–289	840–1605
Moose	300	2.2	803	1680	209	697
Total	–	–		7600–14,000	800–1445	3830–5895

[1]After Bliss and Richards (1982). See also Fig. 19.69.

increased summer precipitation resulting in more swampy ground (wet sedge–moss tundra), and an increase in plant species having strong defenses against ungulate herbivory. Guthrie believes that, with increased moisture, evergreen woody species were favored. Few mammals can tolerate a diet of alder, dwarf birch, mature larch, and spruce. Probably of greater importance were warmer summers that favor woody species. While antiherbivory compounds (tannins, alkaloids, anthraquinones and terpenes) are present in the heath shrubs *Cassiope, Empetrum,* and *Ledum*, and to a lesser extent in *Alnus* and *Betula*, the greatest biomass in most arctic vegetation types consists of the palatable graminoids and deciduous shrubs of *Salix*. Thus antiherbivory compounds would appear to play a minor role, except where coniferous forests of *Larix, Picea*, and abundant heath shrubs occur. During this same period, *Eriophorum* tussock vegetation became important in the pollen record (Colinvaux, 1964); *Eriophorum* is a prefered species for caribou today. The lands north of the Brooks Range and Yukon mountains contained a broad expanse of tundra that large herbivores could occupy, lands dominated by sedge, grass, and cottongrass species.

A third mechanism is a combination of climate change with a probable increase in hunting pressure by northern people. The climate change led to changes in vegetation with an increase in coniferous forests. For eastern Beringia, Ritchie (1977) interpreted the pollen record as a general successional sequence over time, rather than a change in climate forcing a change in vegetation types. Cwynar and Ritchie (1980), Ritchie and Cwynar (1982), and Ritchie (1983) have concluded, based upon their pollen analyses and the evaluation of other studies, that the vegetation during the postglacial maximum was a sparse herb tundra rather than an arctic or subarctic grassland. The botanical evidence from the Bluefish Cave site in the northern Yukon indicates a major change in vegetation from herb tundra (15,000 to 12,000 yr B.P.) to closed and open woodland at low elevations and herb tundra in the uplands (9000 yr B.P. to present). The Late Pleistocene fauna of woolly mammoth, horse, dall sheep, caribou, bison, musk-ox, and elk shifted to the modern fauna of caribou and moose with the major changes in vegetation. This site is one of the very few in the North where there is conclusive dated documentation of people, vegetation and wildlife. Ritchie (1983) calculated, using the same basic method of Bliss and Richards (1982), that in the Bluefish Caves area, a 1000 km^2 landscape of sedge–grass marsh (4.5%), willow shrub (9.5%), herb tundra (65%), and cushion-plant (21%) vegetation types would have supported 18 mammoth, 130 horses, 80 bison, 290 musk-ox, 460 caribou, and 390 elk, or about 1–1.5 animals per km^2. He used a lower rate of plant production for this landscape and thus estimated lower animal densities. The arrival of open coniferous forest would have reduced the utilizable vegetation from 75% to 15%, a 5-fold reduction in forage and no doubt in animal density as well. Grayson (1991) has provided a detailed summary of the above mechanisms, and presented evidence that the extinction of 35 genera of mammals occurred over a longer period of time than between 12,000 and 10,000 yr B.P. He concluded that the "overkill" hypothesis does not adequately explain the large number of extinct groups of mammals, and that these arctic landscapes must have been more diverse in vegetation than hypothesized by Guthrie (1982) and Guthrie and Stoker (1990).

Before leaving the subject of Beringia, it is important to point out, as did Ritchie (1983, pp. 164–65), that Russian botanists use the term "steppe" to describe grasslands as in central North America. These grasslands occupy the rolling uplands and slopes, the so-called "zonal" communities, that dominate the grassland biome. The terms "tundra steppe" or "arctic steppe" are used by them to describe azonal communities that occupy well-drained slopes, usually south- or west-facing slopes, in the Siberian Arctic and subarctic. The Russians refer to these as relict tundra steppes, while North American ecologists recognize them as specialized plant communities occupying specialized habitats. While these grasses, dry-site sedges, and forbs physiographically resemble a grassland, the species are not representative ecologically or geographically of grasslands or prairies. Thus I concur with Ritchie (1982, 1983) and Colinvaux (1981) that the term "steppe tundra" and especially "mammoth–steppe–tundra", as proposed by some paleoecologists, have relatively little supporting evidence. Clearly the final word on Beringia is yet to be written. Much remains to be learned of the diversity and life history of large and small mammals, the timing of their presence, the patterns of tundra vegetation, and the chronology of arrival and density of humans. The detailed

TABLE 19.27

Environmental data for Barrow, Alaska and the Truelove Lowland, Devon Island[1]

Site	Radiation (MJ m^{-2})		Temperature	Precipitation
	June–Aug	Year	Annual (°C)	Annual (mm)
Barrow 71°N	1677	3207	−13.1	175
Truelove Lowland 75°N	1823	3539	−18.8	185

	Mean Monthly Temperature (°C)			Mean Monthly Precipitation (mm)		
	June	July	Aug.	June	July	Aug.
Barrow	0.8	4.8	2.4	2	10	15
Truelove Lowland	0.8	3.1	2.5	11	17	21

[1]From Bliss (1975); Bunnell et al. (1975), Barry et al. (1981).

archaeological and paleoecological data from *in situ* dated sites that are needed to clarify these contrasting, yet interesting hypotheses are at present lacking.

Modern arctic terrestrial ecosystems

Present-day arctic ecosystems, like those of the past, include plants the producers (algae, lichens, mosses, herbs, and shrubs), herbivores that consume plants (soil worms and insects, microtines, geese, caribou), carnivores that consume herbivores (spiders, soil worms, numerous bird species, wolves, and foxes), and decomposers (bacteria and fungi). All of these biotic groups (trophic levels) fix carbon into living biomass, a process termed net production. Ecosystems are generally studied by trophic levels and by the contribution of each level to the flow-through of energy and the cycling of nutrients within the system. All of these dynamic processes are controlled by factors of the environment such as solar and net radiation, air and soil temperature, precipitation, air and soil moisture, wind, and soil nutrients.

During the International Biological Program (I.B.P.) detailed terrestrial ecosystem studies were conducted at Barrow, Alaska (Tieszen, 1978b; Brown et al., 1980) and the Truelove Lowland, Devon Island, N.W.T. (Bliss, 1977d).

The ecosystems at Barrow and the Truelove Lowland are quite similar in structure and function. This is not surprising, since both sites are dominated by wetland sedge–moss (mire) plant communities on organic soils. Arctic ecosystems have evolved in stressful environments with short, cool summers, very limited soil nutrients, and, in some sites, limited soil moisture for at least part of the summer; all of which limit carbon gain. In general there is a limited flora and fauna, and the vegetation structure is low (<50 cm) in most areas away from steep banks, rivers, and streams with their tall shrubs (only in the Low Arctic). Compared with temperate and tropical areas, these ecosystems are relatively simple, often with only 1–2 dominant species at each trophic level.

Abiotic environment

Detailed information on soils, hydrology, meso- and microclimate are presented in earlier sections for these locations. Thus only major summary points are given here (Table 19.27). Solar radiation is higher on Devon Island than at Barrow because of more hours of sunshine and a longer period of 24-hr days because of its more northerly location. Snow does not melt until late June or early July, and consequently the sun is beyond the summer solstice before net radiation is available for plant growth, soils melt, and herbivores begin to feed on new forage. The growing season averages 50 days (wet meadows), or 60 days (raised beaches) on the Truelove Lowland and 70 days at Barrow; precipitation is similiar at both sites. Soils in the wet meadows are organic (Histic Pergelic Cryoquepts). At Barrow, soils are more acid (pH 5.3 vs. 6.5), lower in organic matter (33% vs. 38%) and contain less nitrogen (0.1% vs. 3.1%) than on Truelove Lowland. On the gravelly raised beaches, Arctic Brown soils occur (Pergelic Cryochrepts) at both locations. The water budgets are dominated by snow (70–85%) rather than rain. In the small

TABLE 19.28

Plant biomass and net annual production (g m^{-2}) for three arctic ecosystems[1]

Component	Barrow, Alaska Sedge–moss		Truelove Lowland, Sedge–moss		Devon Island Cushion plant	
	Biomass	Net production	Biomass	Net production	Biomass	Net production
Vascular plants						
Above-ground						
Graminoids	129	41	61	32	2	1
Forbs and Shrubs	21	4	25	12	87	14
Below-ground	4366	142	1085	104	57	3
Bryophytes	40	22	908	33	30	2
Lichens	5	T[2]	0	0	49	2
Algae	N.D.[3]	N.D.	4	4	<1	T
Total	4561	209	2083	185	226	22

[1] From Bliss (1977a); Miller et al. (1980).
[2] T = trace, [3] N.D. = no data

catchments at each location 80–90% of the annual runoff occurs within 2–3 weeks. Evapotranspiration and precipitation are generally in balance each summer. Consequently the soils are recharged with water each autumn prior to refreezing of the active layer. In the poorly-drained organic soils, the active layer is 20–30 cm thick, but the well-drained Arctic Brown soils of the raised beaches thaw to 80–120 cm by early August.

Primary production

Plant communities. The vascular plant floras are relatively low in species at Barrow and the Truland Lowland (139 and 96 spp. respectively), but are rather high in cryptogam species (122 and 162 spp. bryophytes, 70 and 120 spp. lichens). The landscape at the Barrow site is quite flat with small ponds and numerous low-center and raised-center polygons. *Carex aquatilis, Dupontia fisheri, Eriophorum angustifolium,* and *E. russeolum* dominate the wetter sites with *Arctophila fulva* in the ponds. *Arctagrostis latifolia, Carex bigelowii, Luzula arctica, Poa arctica,* and species of *Saxifraga* and dwarf *Salix* occupy better drained flats, high-center polygons, and raised beaches. Bryophytes in wet sites include *Calliergon sarmentosum, Campylium stellatum, Drepanocladus brevifolius,* and *Oncophorus wahlenbergii* (Webber, 1978).

Carex stans dominates the hummocky sedge meadows on the Truelove Lowland, with lesser amounts of *Arctagrostis latifolia, Carex membranaceae* and *Eriophorum angustifolium.* Common bryophytes include *Campylium arcticum, Cinclidium arcticum, Drepanocladus brevifolius* and *D. revolvens.* Vascular plant cover averaged 86% and moss cover 98% in the hummocky sedge meadows (Muc, 1977). Dry tops and slopes of the raised beaches are dominated by *Dryas integrifolia* with *Carex nardina, Salix arctica* and *Saxifraga oppositifolia* as common associates. Important lichens are *Alectoria pubescens, Cetraria cucullata, Lecanora epibryon,* and *Thamnolia subuliformis.* The mosses *Distichum capillaceum, Hypnum bambergeri, Oncophorus wahlenbergii,* and *Tortella arctica* are common. Vascular plant cover averaged 20%, mosses 2%, and lichens 38% on the top of the raised beaches and 35%, 7%, and 33% respectively on the slopes (Svoboda, 1977).

Plant biomass and net production. Data on biomass (living material only) and net production show that graminoids (sedges and grasses) dominate the wetlands and that bryophytes are a major component (Table 19.28). Forbs (broad-leaved herbs) are minor and lichens are rarely present. In contrast, the raised beaches with their cushion plants are dominated by sub-shrubs (*Dryas, Salix*) with minor amounts of graminoids. Lichens are more abundant than bryophytes.

There is a greater amount of biomass and net production below ground than above in the wet sedge–moss meadows at both sites. The opposite is true for plants in the drier raised beach systems (Table 19.28). Daily plant production averaged 3–4 g m^{-2} for much of the short growing season,

rates similar to those of many grass- and shrub-dominated systems in temperate regions. The limited carbon gain per unit area results from the short growing seasons. In all of these systems total annual plant production is 4–9% of the total plant biomass. This is a low percentage compared with more temperate ecosystems.

Soil algae are an especially important component of the wetland systems. They are important producers of carbon, and the cyanobacteria are major fixers of nitrogen. Nitrogen fixation at Barrow averaged 70 mg N $m^{-2}yr^{-1}$ (Gersper et al., 1980) and on the Truelove Lowland 120–380 mg N $m^{-2}yr^{-1}$ in the meadows and 7–30 mg N $m^{-2}yr^{-1}$ on the drier raised beaches (Stutz, 1977). At these high latitudes there are no legumes to fix nitrogen, and the *Dryas* is not nodulated, unlike many populations in the Low Arctic. Due to their very slow growth, lichens contribute very little carbon per year.

Secondary production

Grazing herbivores. In the Arctic the dominant grazers are the mammals and to a lesser extent birds, and of least importance are aboveground invertebrates. Few groups of insects are adapted to life above ground. At Barrow the brown lemming (*Lemmus sibericus*) is the dominant grazer, feeding on graminoids and mosses in the wetter habitats. Collared lemming (*Dicrostonyx groenlandicus*) is a minor species. It feeds on forbs and dwarf-shrubs in the drier habitats. Populations of *Lemmus* have fluctuated over a 20-year period from 150–225 animals ha^{-1} in a "high" (high population) to only <1–5 animals ha^{-1} in a "low" (low population). The cycles are 3–6 years in length. Lemmings increase their numbers rapidly in the spring following with deep snow, high-quality forage, and low winter predator density [snowy owl (*Nyctea scandiaca*), fox (*Vulpes*), weasel (*Mustela*)]. The gestation period of the lemming is 21 days with a maximum of nine litters per year and an average litter size of seven. Lemmings can reproduce very rapidly, although their average life span is only 35–110 days with a maximum age of 1.5 year (Batzli et al., 1980). The radical declines in population are attributed to overgrazing and a rise in predator populations. The earlier concept of a reduction in nutrient content of the vegetation (nutrient-recovery hypothesis) following a high population density and a slow 2–4 year recovery of vegetation and animal numbers (Schultz, 1964) does not appear to explain the cycles adequately. In a lemming "high" there is excessive clipping of graminoids, the moss layer is disrupted as the animals dig for sedge rhizomes, and there is a large manuring effect. This results in stimulated plant growth, increased decomposition rates, an increased depth of the active layer, and an increase in mineral cycling (Batzli et al., 1980). A lower nutrient content of graminoids does appear to reduce winter reproduction of lemmings. Krebs and Myers (1974) found no evidence that physiological stress plays a significant role in microtine cycles. *Lemmus* generally reaches higher densities where there are high- and low-centered polygons. Winter grazing is concentrated in the polygon troughs where plant density is greater and winter snow is deeper. Early summer grazing is concentrated on the high-center polygons that melt out and dry out earlier. Later in the summer the low-centered polygons are grazed (Batzli et al., 1980). In a "high", lemmings can consume 40 g m^{-2} of aboveground biomass but <1 g m^{-2} during a "low".

MacLean et al. (1974) found that snow conditions at the surface in winter are critical for lemmings. They concentrate where temperatures are higher under deep snow cover. In the winter of 1970–71, surface temperatures ranged from −20 to −26° under 30 cm of snow, but dropped to −32° under only 15 cm of snow. MacLean et al. found that winter reproduction was inhibited in years of shallow snow. Research has also shown that the structure of the snowpack is as critical to lemmings as is snow depth. Once the snowpack accumulates, an upper fine-grained, wind-packed layer of high density develops with a large-grained layer of low-density snow ("depth hoar") at the ground surface. A thick layer of depth hoar facilitates animal movement and grazing, while a thin layer, or its absence, increases the energy cost of foraging. Even worse, fall rains that freeze produce ice layers in the snow. If these form at the ground surface the vegetation is locked in ice, preventing foraging. This is also a serious problem for large and small mammals in the High Arctic (see below).

The herbivore community at Prudhoe Bay, Alaska, includes more species than at Barrow, in part because of the presence of more diverse habitats. Caribou (*Rangifer tarandus*), willow ptarmigan (*Lagopus lagopus*), and arctic ground squirrels (*Spermophilus parryii*) are added to the two species of lemming. The density of brown lemmings is much lower (0.01 to 10 animals ha^{-1}) than

at Barrow, but collared lemmings reach similar densities (0.01–10 vs. 0.01–25 at Barrow). The much larger caribou have a low density (0.001 to 0.01 animals ha^{-1}) compared with lemmings, yet a high density for the species. The biomass of caribou at Prudhoe Bay was greater than the combined biomass of the two species of lemming and ground squirrels (Batzli et al., 1980). Ground squirrels, like collared lemmings, prefer warmer and drier soils that permit deep burrows, such as sand-dunes, pingos, and stream banks.

In the High Arctic, typified by the Truelove Lowland, the only microtine species is the collared lemming. Over a four-year period their density ranged from 0.1 to 2.1 animals ha^{-1}, and the low and high numbers were in consecutive years. Their numbers are more controlled by snow depth, winter snow conditions (fall icings, depth hoar), and speed of spring snowmelt than by predation or forage quality (Fuller et al., 1977). Lemming numbers were highest where raised-center polygons predominate (7 to 10 animals ha^{-1}) with their deep snow (1–1.5 m) in the troughs. Litter size averaged 5.7 animals, with only one or two litters in summer. Most breeding occurs from April to June when temperatures and light are higher, yet with deep snow. Summer burrows are on the raised beaches, rocky areas, and high-center polygons, whereas winter nests are in the transition between raised beaches and meadows where snow averages 1–2 m in depth. These animals feed almost exclusively on *Dryas, Salix,* and *Saxifraga oppositifolia.* Lemmings are the dominant grazers in these drier habitats, although a few arctic hares (*Lepus arcticus*) are preent. Their prefered food is *Salix arctica.*

Musk-oxen are the dominant grazers within the sedge–moss meadows. Animal density averaged 0.0005–0.001 animals ha^{-1} during the four years of observation. In summer these animals range over the landscape, often feeding in habitats with less vegetation. In early July they concentrate feeding on *Salix arctica* when present. Winter feeding is confined to the sedge meadows and their abundant vegetation. Summer feeding cycles were 4–6 hr, with considerable time spent resting, usually on the warmer and drier raised beaches or comparable sites. Winter grazing cycles were somewhat shorter. These animals effectively paw through ("crater") 50 cm of snow for forage, and they often return to the same area to crater for forage later in winter (Hubert, 1977). In 1972 six meadows were sampled in early July to estimate winter foraging. At that time the darker green areas of new shoots without old standing-dead material were clearly visible. In these meadows 19% of the total area was grazed and 15% of the potential aboveground biomass of the meadow was harvested. Almost regardless of microsite, 80% of the estimated total forage (adjacent control plots) had been consumed in each crater (Bliss, 1975). Similar sampling in 1973 showed that 24% of the sampled meadows had been grazed and that 85% of the biomass had been consumed (Hubert, 1977). Summer forage had a high protein content (17–21%), and the winter forage was reasonably nutritious (6–9%).

Although musk-oxen remove only 1–2% of the total aboveground forage per year in the meadows, this tells little of the grazing dynamics. In select meadows the animals remove 15–20% of the total forage. A 12-month study in 1972–73 showed that 17% of the 243 animals in the 5 lowlands in northeastern Devon Island utilized the Truelove Lowland and adjacent Truelove Valley throughout the year. The Lowland and Valley comprise 16% of the potential range-lands below 200 m (30 km^2), but 36% of the total meadow habitat available to the animals. The population consisted of 86 adult females, 73 adult males, 8 three-year males, 6 two-year animals, 34 yearlings, and 36 calves. If the animals were distributed at random, one would expect a 16% occupancy of the area. Year-round studies showed that they used the area 17% of the total musk-ox-days. However the pattern differed greatly throughout the year. The Lowland and Valley provide a 30–40% musk-ox-day occupancy from January through March, 26% in April, but only 6–10% from June through November. This demonstrates the importance of these few lush habitats for the critical winter months when obtaining forage is so difficult. In summer the animals can forage in marginal lands (Hubert, 1977).

Detrital herbivores. Although invertebrate herbivores within the soil are inconspicuous, their species richness and numbers can be awesome. Included here are organisms that feed upon organic matter (detritivores) and upon microbial tissue (microbivores). Each year 95–99% of the annual plant production enters the pool of dead organic matter and is available directly or indirectly to these organisms. Major groups of organisms important in the detrital component of temperate and tropical ecosystems are totally lacking in these arctic ecosystems (earthworms, isopods,

TABLE 19.29

Biomass, net production and maturation time for various invertebrate groups in the cushion–plant and sedge moss meadow systems, Truelove Lowland, Devon Island (from Ryan, 1977; Addison, 1977; Procter, 1977)

Invertebrate Taxon	Cushion-plant			Sedge–moss meadow		
	Biomass (mg m^{-2})	Net production (J m^{-2} yr^{-1})	Maturation (yr)	Biomass (mg m^{-2})	Net production (J m^{-2} yr^{-1})	Maturation (yr)
Protozoa	–	–		300	35,563	0.2
Nematoda	263	13,958	1.8	95	1,707	6.6
Annelida						
Enchytraeidae	180	8075	0.9	590	12,987	0.9
Arachnida						
Araneida	–	96	7.0	–	5	3.0
Acarina	57	255	2.6	40	146	5.0
Insecta						
Collembola	97	2,310	1.4	43	448	2.8
Diptera						
Tipulidae	–	18	3.5	46	105	4.3
Chironomidae	11	883	2.0	95	5045	4.3

millipedes, ants, termites), others are poorly represented (beetles, stoneflies). Other groups are well represented (mites, nematodes, enchytraeid worms, springtails, flies and midges).

At Barrow, species of nematodes (Nematoda) and springtails (Collembola) are most numerous (24,000 to 724,000 animals m^{-2}). Because of their small size, the biomass of Collembola and Nematoda is only 0.02 to 0.7 g m^{-2}, not as great as that of the enchytraeid worms (0.7 to 4.1 g m^{-2}). Mites are also limited in numbers and biomass. Of the five major groups of invertebrate detritivores, 85% of the net production results from the enchytraeid worms and 10% from the springtails (MacLean, 1980). The nematodes are herbivores on plant roots as well as microbial feeders on bacteria, algae, and fungi. The mites are mainly detritus feeders or carnivores. The enchytraeids are mostly fungal and bacteria feeders, but some are detrital feeders. Springtails are mainly detrital and microbial feeders, but a few are herbivores and others carnivores. The flies (Diptera) are diverse feeders. The larva of one cranefly species is carnivorous on the Enchytraeidae, other species are detritivores or microbivores (MacLean, 1980). Arctic invertebrates are slow to mature as a result of the low temperatures and short summers. The enchytraeid species take one or two years to complete their life cycle, while the craneflies (Tipulidae) require at least four years.

On Truelove Lowland the enchytraeid worms dominate in biomass within the cushion-plant and the sedge–moss mire ecosystems. Protozoa are the most productive in the wet sedge meadows due to their numbers and shorter life cycle. Other important groups are the Nematoda, Enchytraeidae, and Diptera. On the raised beaches the nematodes are the most productive, followed by the enchytraeids, springtails, and flies (mostly midges) (Ryan, 1977). The feeding habits of these organisms are similar to those at Barrow. The Protozoa, Rotifera, Nematoda, Enchytraeidae, Acarina, Collembola and Diptera are mostly detritivores or microbivores. Some of the mites (Acarina), Protozoa, Nematoda, Collembola, Diptera, and Hymenoptera are carnivores.

On the raised beaches nematodes account for 60% of the total invertebrate energy flow and the Protozoa account for 70% within the sedge meadows. All of the invertebrates assimilate about 5% of the net plant production, four times the combined assimilation of all of the vertebrates (small and large mammals and birds) (Ryan, 1977). Most of the invertebrates are within the detritus–herbivore trophic level, although, as shown above, a few are carnivores. Only detailed studies enable one to determine the feeding roles of this most complex component of an ecosystem, the belowground mass of invertebrates.

Ryan (1977) developed models to calculate energy flow and to estimate maturation time and adult life span for major invertebrate groups.

Biological functioning of each group was based upon (1) death rate; (2) respiration rate; (3) growth rate; and (4) ratio of respiration/production. The predicted rate of development to maturity and the adult lifespan for each invertebrate group were based upon the known growth rate of that group in relation to accumulated degree-days. There were on average (1971–1973 seasons) 621 degree-days above 0 °C at −1 cm on the raised beach and 313 degree-days on the meadow. The data in Table 19.29 include biomass, production, and maturation time for some of the invertebrate groups on the Truelove Lowland. These data show the importance of soil invertebrates compared with those above ground, the differences of major invertebrate groups between the two ecosystems, and the length of time for organisms to reach maturity in these environmentally severe high arctic habitats.

Tertiary production

Vertebrates. Arctic ecosystems are no different from those of temperate regions in that carnivores are minor in terms of biomass and net production, yet there are relatively many species, especially during a peak in lemming populations when more food is available. This is especially true for the avian fauna.

Predators are conspicuous at Barrow during the summer of a lemming "high". Snowy owls (*Nystea scandiaca*) are the first birds to return in late winter (April), followed by jaegers (*Stercorarius* spp.), glaucous gulls (*Larus hyperboreus*) and short-eared owls (*Asio flammeus*) at snowmelt (Batzli et al., 1980). Pomarine jaeger (*S. pomarinus*) is the most important species of jaeger, although small numbers of parasitic jaeger (*S. parasiticus*), and long-tailed jaeger (*S. longicaudus*) are present when more food is available. In winter the only predators are least weasel (*Mustela nivalis*) short-tailed weasel (*M. erminea*), and arctic fox (*Alopex lagopus*). These latter species move out of the coastal tundra in a lemming "low". The densities of all these carnivores are low, except during a lemming "high". The least weasel has the ability greatly to increase the number of young embryos carried by females (average 10.5) and thus to produce large litters when more food is available. The weasel population was estimated to be 25 animals km^{-2} (Thompson, 1955), during a lemming "high" in 1953, yet near zero during a "low".

Other important predators at Barrow include the sandpipers (*Calidris alpina, C. hairdii, C. melanotos*, and *C. pusilla*). These shorebirds are important insectivores along the shores of the numerous lakes and ponds. The passerine species Lapland longspur (*Calcarius lapponicus*) and snow bunting (*Plectrophenax nivalis*) are also very important. In spring and fall they are seed-eaters but concentrate on invertebrates during the growing season (Bunnell et al., 1975). Seven species of shore birds and the two passerine species collectively have nesting densities of 80–100 pairs km^{-2}. Their densities are greater than those of the mammalian predators, and again this illustrates the relative magnitude of the invertebrate vs. vertebrate component of these systems.

Vertebrate carnivores are much lower in species richness, numbers, and net production within the Truelove Lowland ecosystems, due to a greatly reduced number of lemmings (a lemming "high" here is equal to a "low" at Barrow!), and fewer nesting birds whose eggs are also prey. Avian predators are more abundant than are mammalian predators. Of the 15 species that regularly breed on the Lowland, 13 species are predators. Based upon data from four summers, mean post-breeding bird density averaged 53.6 birds km^{-2} (Pattie, 1977). With an assumed recruitment of 35% for all species, there were on average a total of 17 pairs km^{-2} of breeding birds on the Lowland (based upon 15 species). A summary of 16 years of data from this Lowland shows that 18 species bred regularly on or adjacent to the Lowland, 10 other species were occasional breeders and 15 other species were visitors. From 1970 to 1973, adult birds averaged 23.1 birds km^{-2} and from 1978 to 1989 adults averaged 33.8 birds km^{-2} (Pattie, 1990). The Lowland supported an average of 40 long-tailed and parasitic jaegers per year, yet on average only 2–4 pairs of jaegers nested each year in the area of 43 km^{-2} (Pattie, 1977). At Barrow nine of the common species averaged 80–100 pairs km^{-2} (7 species of shorebirds and the 2 species of passerines). These much higher densities of birds reflect the much larger population of insects, which most species depend upon.

The Arctic fox and short-tailed weasel are the only predator mammals of any importance on Devon Island. Arctic wolves (*Canis lupus*) are rarely seen. Foxes seldom breed successfully on the Lowland due to an inadequate food supply. The 3–5 foxes that occupy the Lowland in summer must range over a much larger area in order to obtain adequate food. Gut and scat analyses

showed that foxes prey or scavenge on at least 12 species of birds and mammals (Riewe, 1977). Foxes predated 42% of lemming nests in 1972, a year in which 63% of all observed bird nests were predated (Pattie, 1977). Weasels predated an average 12% of winter lemming nests (Riewe, 1977). In winter, foxes spend most of their time on sea ice following the kills of seals by polar bear (*Thalarctos maritimus*).

Invertebrates. As indicated earlier, relatively few invertebrate groups are predators at these northern latitudes. At Barrow the larvae of craneflies are the most important group (72%), although spiders, several species of beetles, and mites are also predators (MacLean, 1980). On the Truelove Lowland, carnivory is found in all spider species (10) and in some of the Nematoda, Tardigrada, Crustacea, Acarina, Collembola, Diptera, and Hymenoptera.

Decomposers

Arctic and alpine ecosystems are very dependent upon fungi, yeasts, and bacteria, the decomposers, to recycle elements tied up in plant and animal tissues and animal wastes. Organic matter is decomposed through the synthesis of microbial tissues, tissue which then decomposes, producing more substrate for microbial activity. Soil invertebrates and Protozoa indirectly influence decomposition rates by directly feeding upon organic-matter fragments and by grazing upon bacteria and fungal hyphae. Rates of decomposition are influenced by soil temperature and moisture, oxygen levels, pH, organic substance, and the kinds and numbers of microbes present. Given the diversity of physical, chemical, and biological processes involved in decomposition, a diversity of methods has been used to investigate this most complex trophic level of ecosystems. Measurements include estimates of biomass and net production of microbial groups, production yield per gram of substrate consumed, chemical analyses of substrate composition and weight loss to estimate the rate of cellulose degradation, respiration rates of key organisms, weight loss of litter bags, and rates of release of carbon dioxide from soils (Flanagan and Bunnell, 1980). These and other measurements require both field and laboratory studies.

Organic substances utilized by decomposers can be divided into two groups based upon their chemical composition. Substrates with low molecular weight that are soluble in water and/or alcohol (simple sugars, citric and succinic acids) are decomposed more rapidly and by more organisms, whereas substances with a large molecular weight (starch, cellulose, hemicellulose, lignin, pectin) are decomposed more slowly. At Barrow about 25% of aboveground plant products are more soluble, and this fraction contains most of the leaf nitrogen, phosphorus, and potassium (Flanagan and Bunnell, 1980). The microflora is greatly reduced in the Arctic, as is the vascular flora and the herbivore fauna. Bacteria are more numerous in wetter soils, and fungi are more abundant in better drained and warmer soils. Microbial biomass is less in soils of poorly drained meadows and polygonal troughs, the result of cold soils with low oxygen levels (Widden, 1977; Bunnell et al., 1980).

Bacteria. The genera *Arthrobacter, Bacillus, Flavobacterium* and *Pseudomonas* were found in soils at both Barrow and the Truelove Lowland. Species of the first two genera are more common in drier soils (Widden, 1977; Bunnell et al., 1980). Species of *Bacillus, Clostridium, Beijerinchia,* and *Klebsiella* may contribute to nitrogen fixation on the Truelove Lowland (Jordon et al., 1978a), but *Azotobacter* at Barrow has not been shown to fix nitrogen. The denitrifying bacterium *Pseudomonas* is present at both locations, as are species of *Cytophaga* which utilize cellulose. Bacteria that reduce sulfates and iron, and those that oxidize sulfides, are rare or absent at Barrow and at most arctic sites. The dominant species are facultative psychrophiles in terms of temperature range for growth. Optimum growth temperatures were above 20°C, but these bacteria are capable of growth at 5°C (Nelson, 1977; Jordon et al., 1978b). The wet, acid soils are not favorable for nitrogen-fixing bacteria, but denitrifiers are common. Bacteria, although small in size and biomass, are well represented in the wetter soils of meadows and polygon troughs. The microbial flora declines rapidly with soil depth and shifts to a dominance of anaerobic bacteria. Numbers of bacteria appear higher in the Truelove wet meadow (98×10^7 g^{-1} dw soil) than at Barrow wet meadows (8×10^6 g^{-1} dw soil) (Nelson, 1977; Bunnell et al., 1980).

Fungi. Sterile forms, Basidiomycetes, and Fungi Imperfecti are the most common fungi, although Ascomycetes, yeasts, and aquatic fungi are also present at these arctic locations. The abundance of Basidiomycetes (species and biomass) reflects their role as mycorrhizal symbionts at Barrow (Laursen and Miller, 1977; Miller and Laursen, 1978) but

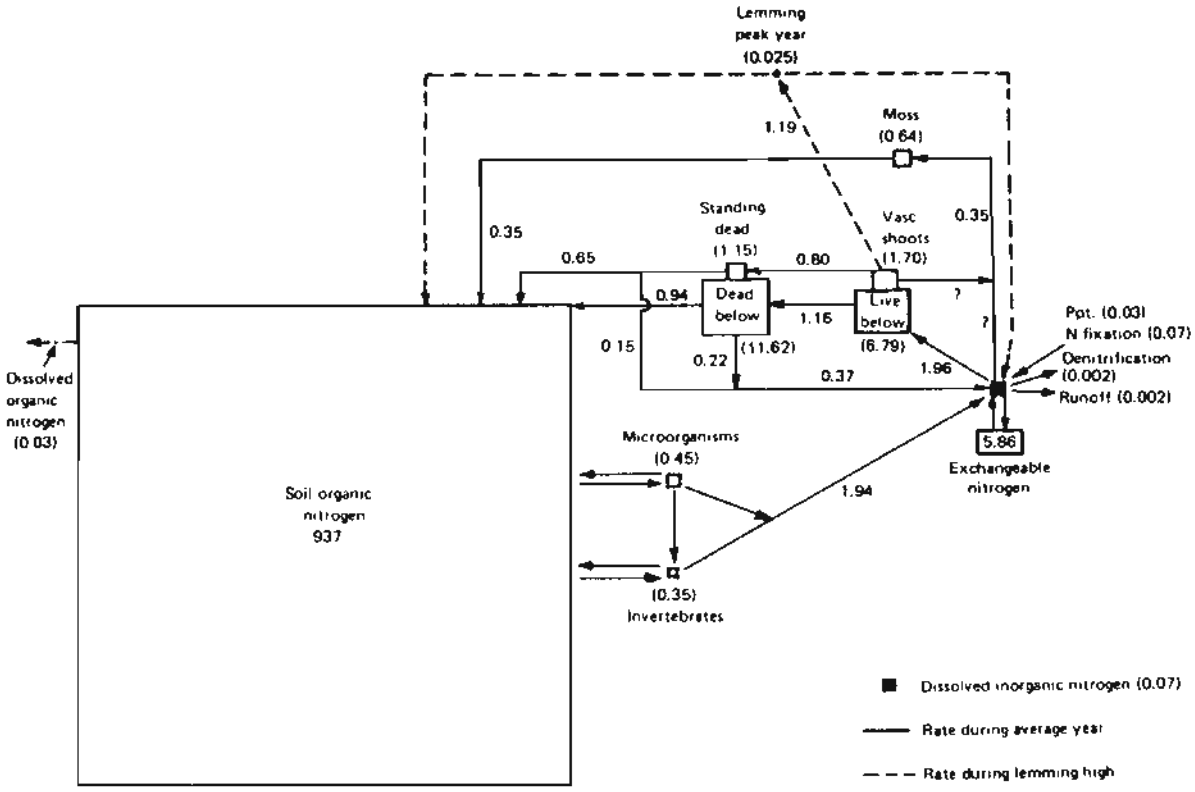

Fig. 19.70. Annual budget for nitrogen in a sedge–moss meadow at Barrow, Alaska. Values within boxes and next to arrows are g m^{-2} From Chapin et al. (1980).

not at the Truelove Lowland in the High Arctic. Wood-rotting fungi are rare. Fungi appear to be more important early in summer, a possible response to a nutrient flush with snowmelt (Bunnell et al., 1980). A second peak in biomass late in the season is probably associated with senescence and death of plant parts.

On the Truelove Lowland, fungi remain important although mycelium biomass is low compared with other tundra sites (1000 m g^{-1} soil in wet meadows and 100 m g^{-1} in soils from beach ridges (Widden, 1977). Data for other tundra sites are often between 1000 and 5000 m g^{-1} soil (Dowding and Widden, 1974). There was a relatively high frequency of Actinomycetes in the raised-beach soils, probably the result of high pH. Although mycelium biomass is higher earlier in the season (Widden, 1977), the quantity of mycorrhizae and mycorrhizal structures peaks only in mid to late season, presumably related to warmer soils in late July (Bledsoe et al., 1990).

Biomass and net production. The total microbial biomass ranged from 12 to 20 g m^{-2} in the upper 7 cm of soil at Barrow. The lower biomass reflects the drier microhabitats of polygonal rims and basins of low-centered polygons, whereas the higher values were found in wet meadows and polygonal troughs. Within the wetter habitats, bacteria account for about 75% of the total biomass (Bunnell et al., 1980). Minimal annual production was estimated to be 7 g m^{-2} in the wet meadow. Bacterial production was 11 g m^{-2} on polygon rims. On the Truelove Lowland, microbial annual production was estimated to be 17 g m^{-2} in the sedge meadow (mostly fungi), but only 2 g m^{-2} on the dry beach ridge (Widden, 1977).

Soil and litter respiration has been measured at −6.5°C, and considerable fungal biomass was measured at 0 to 2°C. However, optimal temperature for growth and respiration occurred at 20–30 °C (Flanagan and Bunnell, 1980). Nelson (1977) reported that three species of bacteria (*Arthrobacter* sp., *Bacillus* sp., *Pseudomonas* sp.) were efficient in utilizing low levels of carbon and were tolerant of low temperatures, and *Pseudomonas* was resistant to starvation stress. These results indicate that microbial species are well adapted to arctic conditions.

Nutrient budgets

A very limited pool of soil nutrients is one of the major environmental stresses imposed on arctic ecosystems. The shallow active layer (20 to 40 cm) at most sites effectively limits mineralization of frozen peats and limits weathering of mineral soil and rock. There is limited nutrient input from the atmosphere because of limited precipitation, distance from urban and agricultural areas, and presence of sea ice. Consequently the most significant source of nutrients comes from release by decomposition, from lateral transfer with meltwater, and from dung deposition by birds and mammals. Nitrogen and phosphorus are usually the nutrients most limiting in arctic systems.

At Barrow, nitrogen input by fixation (0.07 g m^{-2}) and precipitation (0.03 g m^{-2}) is greater than the amount lost through spring runoff (0.03 g m^{-2}). The inputs constitute 5% of the nitrogen that cycles annually through the vegetation (1.96 g m^{-2}). The cycling of nitrogen is dependent upon litter decomposition. The estimated turnover time for nitrogen in the soil organic matter (based upon total and input) is 480 yr (Chapin et al., 1980; Fig. 19.70). In the Truelove Lowland the hummocky sedge–moss meadow fixes more nitrogen (0.25 g m^{-2}) and there is more input from precipitation (0.06 g m^{-2}). This constitutes about 13% of the nitrogen that cycles annually through the vegetation (2.35 g m^{-2}) (Fig. 19.71a). The turnover time for nitrogen in the living and dead plant material is 11 yr at Barrow and 16 yr on the Truelove Lowland. At both locations the annual input of nitrogen is only 0.01 to 0.02% of the total nitrogen within each ecosystem (Babb and Whitfield, 1977: Chapin et al., 1980).

There is considerably less nitrogen in the cushion-plant system on the raised beach on Devon Island, but the turnover time is much greater, 1060 yr. The turnover time for nitrogen in the living and dead plant material is also much greater (31 yr). This system has an input of only 0.08 g m^{-2} and an annual uptake by plants of 0.21 g m^{-2} (Fig. 19.71b).

The cycling of phosphorus is even more limiting in these ecosystems. In the Truelove Lowland sedge–moss meadows, the annual input accounts for only 2% of that which cycles annually through the vegetation and only 0.005% of the total phosphorus in the system. The comparable figures for the Barrow wet meadow are 0.6% and 0.002% respectively. Within the Devon Island cushion-plant system, the annual input is 36% of the phosphorus that cycles annually and 0.03% of the total phosphorus within the system. Turnover time for phosphorus in the soil organic matter averaged 225 years at Barrow, 410 years at the Devon Island sedge-moss meadow and 1500 years in the cushion-plant community. These nutrient-deficient systems are very dependent upon the slow rates of recycling the existing pool of nutrients, rather than on large inputs per year. Low soil temperatures, the short growing season, a shallow active layer with much of the organic matter locked in permafrost, and soils with low oxygen levels are the controlling factors (Chapin et al., 1980)

At Barrow 82% of the potassium content of litter leaches during snowmelt, but little calcium is released in this way. Chapin et al. (1980) concluded that calcium must recycle from litter decomposition. They also calculated that 80% of the nitrogen and 60% of the phosphorus in the litter must be recycled through decomposition. All of this points to the need for relatively efficient decomposition processes and relatively nutrient-conservative species if these nutrient-limited systems are to function. A further constraint is the sponge effect of mosses in filtering nutrients out. All of this is in contrast with temperate systems (grasslands and forests) where mosses are minor and leaching of litter is of much greater importance.

These ecosystems add relatively little carbon per year although there is a large accumulation of carbon in the soils, again indicating slow rates of decomposition. Tundra ecosystems are quite different from many other ecosystems where much of the carbon and relatively large amounts of nutrients are tied up in the vegetation (Schlesinger, 1977). At Barrow 1.6% of the carbon, 0.9% of the nitrogen, and 1.3% of the phosphorus are found in the vegetation. Comparable figures for the Truelove Lowland systems are 4.7%, 2.0% and 2.3% respectively for the sedge–moss meadow and 1.2%, 1.4%, and 1.0% for the cushion-plant community (Babb and Whitfield, 1977; Chapin et al., 1980).

Energy flow

One of the most difficult aspects to calculate is the flow of energy. It requires detailed bioenergetic studies of all the major groups of organisms, including estimates of the energy available, the amount consumed and assimilated, and an estimate of the net annual production. Plants differ from animals in lacking rejecta and excreta.

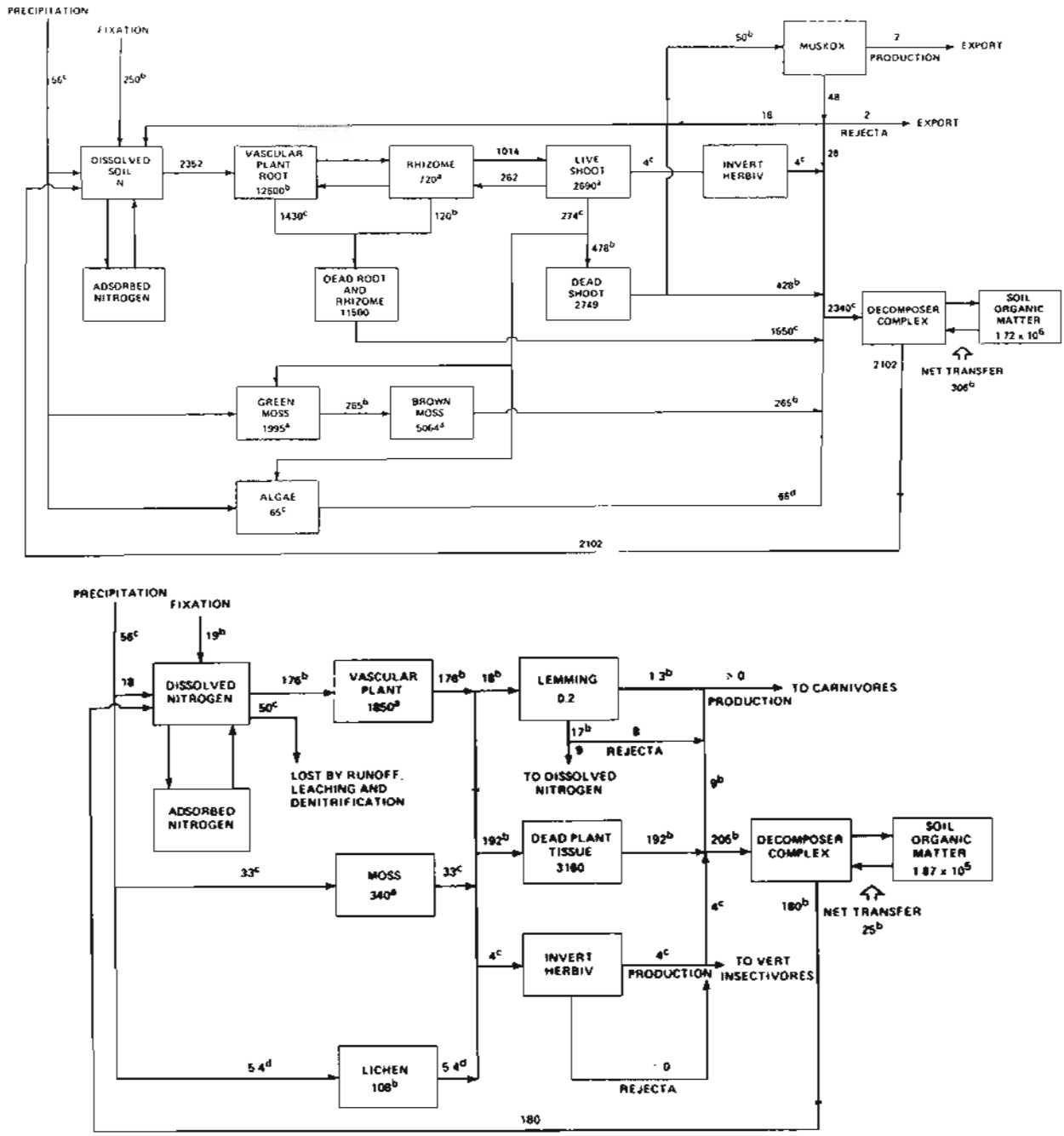

Fig. 19.71. Annual nitrogen budget within a hummocky sedge–moss meadow (top) and within a cushion-plant system (bottom) on the Truelove Lowland, Devon Island, N.W.T. Values are in mg m^{-2} for both standing crop in boxes and annual fluxes next to arrows. From Babb and Whitfield (1977).

The two subsystems on the Truelove Lowland were very different in terms of the dominant plant and animal species and vegetation structure. However, the pattern of energy flow was very similar in each subsystem (Figs. 19.72a,b). In each subsystem, plants contribute 98–99% of the total standing crop (live + dead material) and 90% of the total ecosystem net production (Table 19.30). The microflora, dominated by bacteria in the sedge–moss meadow and fungi in the cushion-plant system,

TABLE 19.30

Percentage contribution to the standing crop (live + dead) and net production of the major components of the Truelove Lowland, Devon Island (T.L.) cushion-plant and sedge–moss systems and the Barrow, Alaska (B.) sedge–moss system (based upon Figs. 19.72-19.73)

System component	Standing crop (%)	Net production (%)
Herbivores and Carnivores (vertebrates)		
Cushion-plant (T.L.)	+	1.9
Sedge–moss (T.L.)	0.1	0.2
Sedge–moss (B.)	+	0.5
Primary Producers		
Cushion-plant (T.L.)	97.8	90.1
Sedge–moss (T.L.)	98.9	90.0
Sedge moss (B.)	98.7	74.1
Microflora		
Cushion-plant (T.L.)	0.7	4.4
Sedge–moss (T.L.)	0.9	8.3
Sedge- moss (B.)	1.1	24.2
Saprovores		
Cushion-plant (T.L.)	0.6	3.3
Sedge–moss (T.L.)	0.1	1.4
Sedge–moss (B.)	0.1	0.7
Herbivores (Invertebrates)		
Cushion-plant (T.L.)	0.1	0.2
Sedge–moss (T.L.)	+	+
Sedge–moss (B.)	0.1	0.4
Carnivores (Invertebrates)		
Cushion-plant (T.L.)	+	0.1
Sedge-moss (T.L.)	+	0.1
Sedge–moss (B.)	+	0.1

accounts for 0.9% and 0.7% of the total standing crop and 8.3% and 4.8% of the net annual production respectively. The saprovores, so diverse in species of invertebrates, contribute 0.1% and 0.6% of the total standing crop and 1.1% and 2.7% of the total net production in the cushion-plant and meadow subsystems respectively. Aboveground herbivores and carnivores (mostly vertebrates) constitute a larger component of the net production of the system (0.3% and 1.6%) than do the belowground invertebrate herbivores and carnivores (0.1%) (Table 19.30). The saprovores (Collembola, Crustacea, Diptera, Enchytraeidae, Rotifera, Tardigrada) feed upon the microflora and partially decomposed organic matter (Ryan, 1977). Invertebrates as a group (saprovores, herbivores, carnivores) assimilate about 5% of the total production in each ecosystem, roughly four times that of all vertebrates! Invertebrates are the dominant animal group in these cold-dominated and nutrient-deficient systems, systems that are frozen for 10 months each year.

The structure and function of the sedge–moss meadow at Barrow is similar to that on the Truelove Lowland (Fig. 19.73). Plants provide 97.8% of the total system biomass, followed by the microflora (decomposers) at 1.1%. The invertebrate saprovores and herbivores provide only 0.2% of the total (Table 19.30). The microflora, mostly bacteria, contribute 24.2% of the total annual production of the system, vascular plants and mosses 74.1%, and all invertebrates 1.2%. Although the invertebrate biomass is 14 times greater than for the vertebrates, net production is only 4 times greater for the invertebrates. This reflects the efficiency of food consumption and the rapid rate of reproduction of lemmings compared with the invertebrates at Barrow.

All three systems divert most of the energy to the detritus component. The major compartments are solar and net radiation → plants → decomposers → organic-matter storage. In the Barrow and Truelove Lowland ecosystems 92–98% of the total net plant production is utilized by the decomposer complex (Figs. 19.72a,b and 19.73). Herbivores and carnivores are of great interest to people and are the most appropriate trophic levels for human harvest. These data and the energy-flow diagrams explain why large and small herbivores are restricted to those parts of the Arctic where plant cover and net annual production are greater.

Assimilation efficiency of species and production efficiency of ecosystems

Organisms have the ability to assimilate energy and to produce new tissue (net production). Their efficiency in these biochemical processes is critical to their survival, especially in cold-dominated environments. It is no accident that arctic animals are quite efficient in assimilating (digesting) energy. However, there is a considerable range in assimilation efficiency in different animal groups (Table 19.31). Invertebrates are least efficient, vertebrate herbivores intermediate and vertebrate carnivores appear most efficient. Efficiency is controlled by many factors including the energy value of the food and the adaptations each species has for controlling assimilation and heat loss.

Plants are very inefficient at energy conversion, although a relatively large amount of net production is added to all terrestrial ecosystems by the

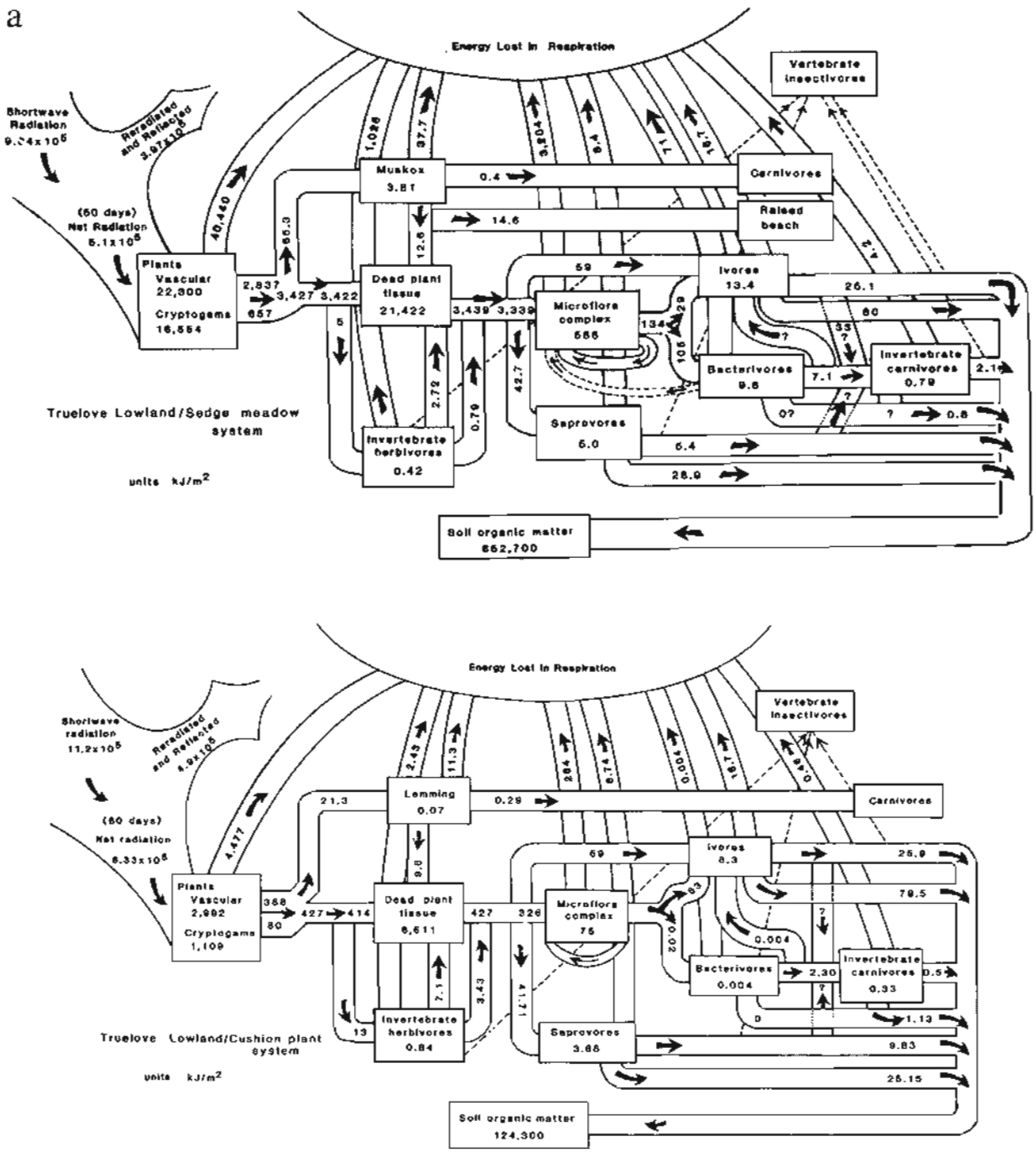

Fig. 19.72. Energy flow within a hummocky sedge–moss meadow (top) and a cushion-plant community (bottom) on the Truelove Lowland, Devon Island, N.W.T. Standing crop (boxes) and energy flow (arrows) are expressed in kJ m^{-2}. From Bliss (1986) modified from Whitfield (1977).

action of photosynthesis. Photorespiration consumes a large percentage of gross photosynthesis because arctic plants use the C_3 pathway.

Since plants account for 74 to 91% of the total production of these ecosystems, it is not surprising that ecosystem production and net plant produc-

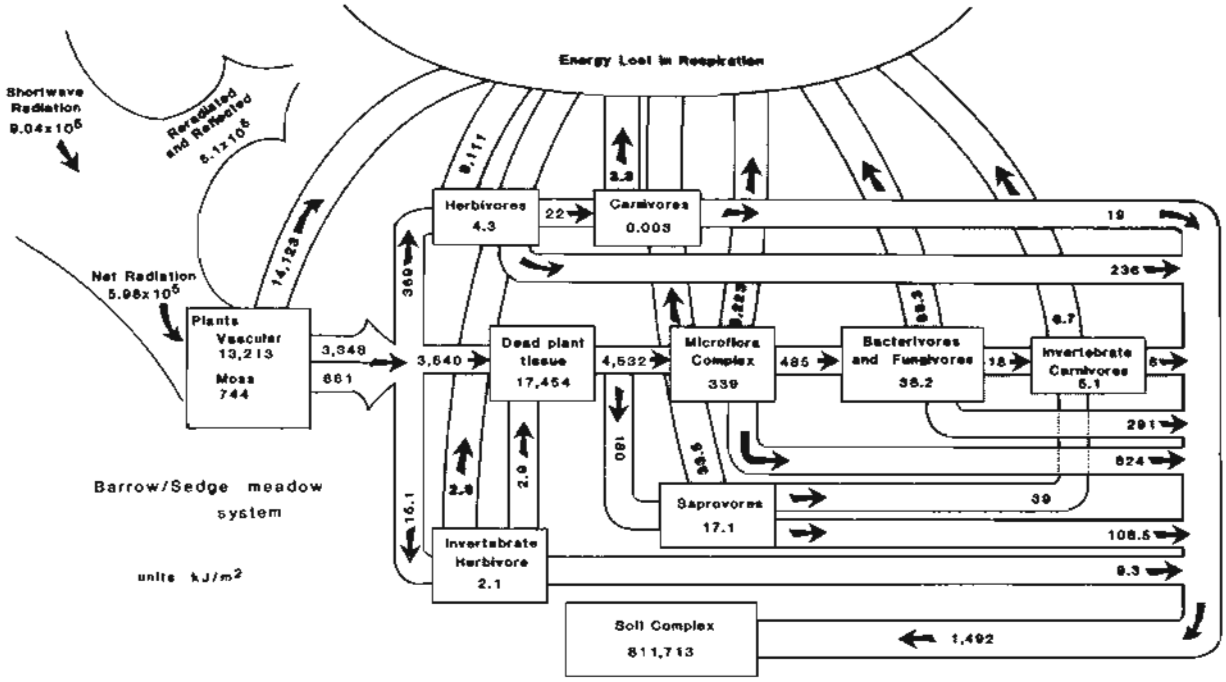

Fig. 19.73. Energy flow within a sedge–moss meadow at Barrow, Alaska. Standing crop (boxes) and energy flow (arrows) are expressed in kJ m^{-2}. From Bliss (1986), modified from MacLean (1980) and Chapin et al. (1980).

tion constitute only a small percentage of the net radiation available to each system for production (Table 19.32).

Arctic aquatic ecosystems

Aquatic systems that have been studied in the Arctic include ponds and lakes, with limited data from streams and rivers. Polar limnology has been dealt with elsewhere in this series (Hobbie, 1984), but a brief account here of ponds and lakes in arctic North America will serve to highlight the links and relationships between these and the terrestrial systems of the surrounding tundra.

Research on arctic lakes and ponds is made easier by the low species richness of dominant plants and animals, but the long, cold winters limit the season of detailed studies to 1–3 months. Earlier studies of deep arctic lakes revealed that most of the early primary production by flagellated algae and diatoms occurred prior to ice-melt. When snow depth is less than 10 cm, short-wave radiation penetrates the ice and the non-turbulent conditions beneath the ice permit large algal blooms (Hobbie, 1973). A shallow lake near Barrow, Imikpuk, was studied in terms of its chemis-

TABLE 19.31

Assimilation efficiency of animals in arctic ecosystems

Species	Assimilation efficiency (%)	Author
Invertebrates		
Lepidoptera larvae	24	Ryan and Hergert, 1977
Nematoda	40	MacLean, 1980
Enchytraeidae	40	MacLean, 1980
Collembola	40	MacLean, 1980
Tipulidae	40	MacLean, 1980
Vertebrate herbivores		
Lemmus sibericus	35	Melchoir, 1972
Lepus articus	50	Smith and Wang, 1977
Dicrostonyx groenlandicus	55	Fuller et al., 1977
Ovibos moschatus	65-75	Hubert, 1977
Rangifer tarandus	57-63	White, 1979
Chen caerulescens	69	Pattie, 1977
Corvus corax	63	Pattie, 1977
Plectrophenax nivalis	40 (seeds), 74 (arthropods)	Pattie, 1977
Vertebrate carnivores		
Alopex lagopus	86	Riewe, 1977
Calidris bairdii	75	MacLean, 1980
Mustela erminea	74	Riewe, 1977

TABLE 19.32

Efficiency of net annual plant production for three arctic ecosystems[1]

Ecosystem	Growing season (days)	Net production (kJ m^{-2})	Total radiation (kJ m^{-2})	Net radiation (kJ m^{-2})	Efficiency Total radiation (%)	Net radiation (%)
Cushion-plant (Devon I.)	60	448	11.20×10^5	6.3×10^5	0.04	0.07
Sedge–moss (Devon I.)	50	3494	9.04×10^5	5.1×10^5	0.39	0.69
Total Lowland (Devon I.)[2]	53	1920	9.62×10^5	5.2×10^5	0.20	0.37
Sedge–moss (Barrow)	70	4009	9.04×10^5	6.0×10^5	0.44	0.67

[1] From Bliss (1975, 1986).
[2] Weighted average based upon aerial extent of the two ecosystems

try, productivity, zooplankton, and microbiology (Edmondson, 1955; Comita, 1956; Boyd and Boyd, 1963; Kalff, 1967; Howard and Prescott, 1973).

The arctic I.B.P. ecosystem studies concentrated on ponds at Barrow, Alaska (Hobbie, 1980a) and lakes at Resolute (Rigler, 1975) and at the Truelove Lowland (Minns, 1977) in Canada. The latter study was much less detailed and was conducted only for one year.

More recently detailed studies are being conducted at Saqvaqjuac, northwest Hudson Bay (63°N) (Welch et al., 1989; Welch, 1991). Arctic lakes and ponds seldom warm above 8–10 °C, high arctic lakes seldom above 2–5°C. These lakes are generally unstratified in summer, and are covered with 1–2 m of ice for 9–11 months. Ponds and shallow lakes freeze solid and support no fish. Runoff occurs over a short period, and the meltwater from snow is low in nutrients. Thus arctic lakes and ponds are cold, oligotrophic systems with minimal diversity of organisms.

Ponds

The ponds studied near Barrow are small (30×40 m), shallow (about 0.5 m), and were formed by the melting of ice wedges that developed in previously drained lake basins. The surrounding vegetation consists of graminoid–moss meadows. Although mean water temperature in summer is about 6°C, water temperatures can reach 10–16°C on sunny days with little wind. Phosphorus levels are low in the pond waters (0.001–0.002 mg P l^{-1}) and rain provides only 0.008 mg P l^{-1}, yet the top 10 cm of sediments contain 25,000 mg P m^{-2}. Based upon a phosphorus flow diagram, the dissolved reactive phosphorus (DRP) cycles (turns over) 50 times per day! Most of the DRP is tied up in hydrous iron complexes in the sediments. Hobbie (1980c) concluded that the chemical reactions involving iron set the concentrations of the DRP and that the amount of phosphorus controls pond production.

Nitrogen does not appear to limit primary production. Rain contributes 11.5 mg N $m^{-2}yr^{-1}$ and nitrogen fixation adds 28 mg N $m^{-2}yr^{-1}$. The estimated annual accumulation of nitrogen (80 mg m^{-2}) is a small fraction of the 38,400 mg N m^{-2} stored in the upper 5 cm of sediments. Nitrogen uptake by plankton is slow, giving an estimated turnover rate of 30–100 days for inorganic nitrogen. *Carex aquatilis* roots remove ammonia as fast as it is released by bacteria in the surface sediments and water column.

The graminoids *Arctophila fulva* and *Carex aquatilis* are abundant in the shallow water of the pond margins; they contribute 63% of the total primary production of the ponds. Arctic lakes have few if any emergent macrophytes; thus their presence in arctic ponds and very shallow lakes sets these systems apart from larger and deeper bodies of water. Benthic algae, mostly green algae and cyanobacteria, are important contributors to production (Table 19.33). A total of 45 species were identified (Alexander et al., 1980). Phytoplankton is a minor component in these pond ecosystems, consisting of small flagellated green and golden-brown algae and other groups: a total of 105 species. Their populations do not build up for they are heavily grazed by herbivorous Crustacea: *Daphnia* and two species of fairy shrimp (Anostraca). These zooplankton species are fed upon by the predatory Crustacea *Cyclops, Diaptomus,* and *Heterocope*. The lack of fish permits the presence of large species of zooplankton not found in lakes with planktivorous fish (Stross et

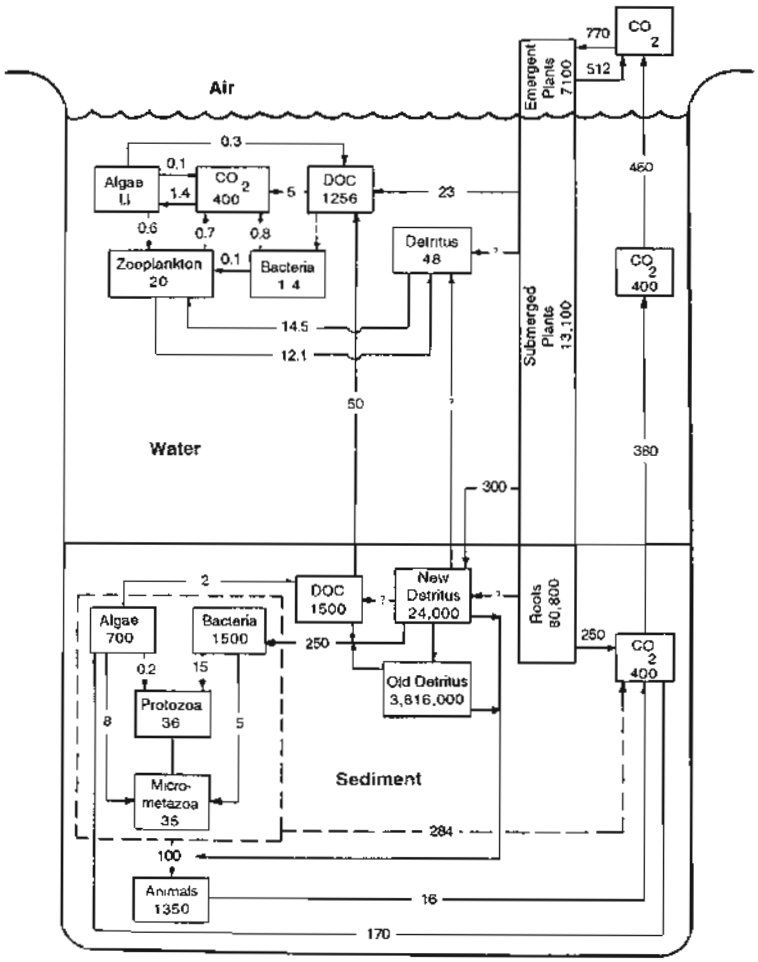

Fig. 19.74. Energy flow within ponds at Barrow, Alaska. Standing crop (boxes) and energy flow (arrows) are expressed in kJ m^{-2}. From Hobbie (1980a).

TABLE 19.33

Annual production of arctic ponds and lakes in gC m^{-2} yr^{-1}.

Ecosystem component	Barrow Ponds	Char Lake	Immerk Lake
Macrophytes (*Carex*, *Arctophila*)	16.4	–	–
Benthic algae	8.4	17.9	n.d.[1]
Phytoplankton	1.1	4.1	4.3
Zooplankton	0.2	0.2	n.d
Benthic animals	1.9	0.7	n.d.
Benthic bacteria	8.6	n.d.	n.d.
Arctic char (*Salvelinus alpinus*)	–	0.03	n.d.
Lake metabolism ($CO_2 m^{-2} yr^{-1}$)	n.d.	43.6	69.2

[1] n.d. = no data available.

Data are from Hobbie (1980b) for Barrow, Alaska; Rigler (1975) for Char Lake, Cornwallis Island; and Minns (1977) for Immerk Lake, Devon Island

al., 1980). Nine species of Crustacea were found in the ponds, but the five species of rotifers and fairy shrimps are present in low numbers. The large fairy shrimps provide relatively more biomass and carbon gain than their low densities would indicate. All of the Crustacea except *Daphnia* produce only one generation per year.

The high rates of production of macrophytes and benthic algae, but low production by planktonic algae, shift organic carbon to the sediments where it enters the detritus compartment (Fig. 19.74). Benthic algae, bacteria, and zooplankton grazers predominate here in these ecosystems. The biomass of organisms is about 150 times greater per square meter of sediment than for the water column. The detritus pool provides nutrients for the algae and macrophytes, but most of the organic matter and nutrients remain tied up in sediments.

Bacteria comprise a major component of the total carbon gain of these systems, and 99% of this is contributed by benthic bacteria. The planktonic bacteria are a minor component as are the phytoplankton. The production of bacteria is controlled by the amount of compounds of low molecular weight, mostly released by decomposing sedge leaves and stems. The flagellated and ciliated protozoans are the major bacterivores (Hobbie et al., 1980). Chironomid larvae also feed on bacteria and benthic algae in addition to decaying plant parts.

The grazing food chain in these ponds is unimportant relative to the detritus food chain (Hobbie, 1980b). This parallels the findings for arctic terrestrial ecosystems.

Lakes

Char Lake, Cornwallis Island, is representative of small (53 ha) but deep lakes (mean 10.2 m) that are in a polar-desert catchment. Water temperature varies from 0°C in winter to only 4°C in summer. In cold summers the ice never totally melts. Biologically the lake is very simple in species richness and in production of carbon. Temperate lakes may have 10–15 species of fish, most high arctic lakes have only one. Temperate lakes may have 10–15 species of zooplankton, Char Lake has two. Midges (Chironomidae) may number 200–300 species in temperate lakes, here only six species. However there are about 100 species of benthic diatoms and 21 species of roundworms (nematodes) (Rigler, 1975).

Char Lake is very deficient in nutrients, receiving only 16 mg P $m^{-2}yr^{-1}$ from the catchment-shed. Nitrogen fixation results from cyanobacteria. In contrast with the Barrow ponds, there are no emergent macrophytes in this lake or the lakes on the Truelove Lowland. However, Char Lake has a broad zone of mosses (*Drepanocladus*) growing at a depth of 4–15 m. This is not typical of high arctic lakes. Planktonic algae contribute 20% of the total plant production (Table 19.34). The zooplankton are less important than the benthic animals, the same pattern as in the ponds at Barrow.

There are many small arctic char (*Salvelinus alpinus*) in Char Lake. This is a landlocked population and thus they are of small size due to the constant low temperatures and a limited food supply. The fish spawn on the rock delta formed by the largest inflowing stream. Eggs are laid in autumn and hatch the following April under the thick ice. The young fish, 0–3 years old, stay in the shallow waters, while older fish move to deeper water. Midge pupae provide the major food in July and August. Fish caught at other seasons feed on midge larvae and other small benthic organisms. Large fish (>20 cm) here and on Devon Island are cannibals. These larger fish are 15 to 20+ years old, and the size-frequency data indicate two size–age groups in three lakes on the Truelove Lowland (Minns, 1977).

TABLE 19.34

General characteristics of high arctic lakes[1]

Characteristic	Cornwallis I. Char Lake	Truelove Lowland, Devon Island		
		Loon Lake	Immerk Lake	Fish Lake
Area (ha)	53	16	96	101
Mean depth (m)	10.2	2.9	3.2	3.1
Catchment	Polar Desert	Polar Desert	Sedge Tundra	Sedge Tundra
Surrounding vegetation (% cover)	1–3	1–5	100	100
Mean summer chlorophyll (mg m^{-2})	0.4	0.3	0.7	1.3
Zooplankton (No. m^{-3})	2500	141	1740	4784
Lake metabolism (CO_2 m^{-2} yr^{-1})	43.6	33.7	69.2	54.2
Age of Arctic char at 20 cm (yr)	14+	17+	10+	10+

[1] Data from Minns (1977).

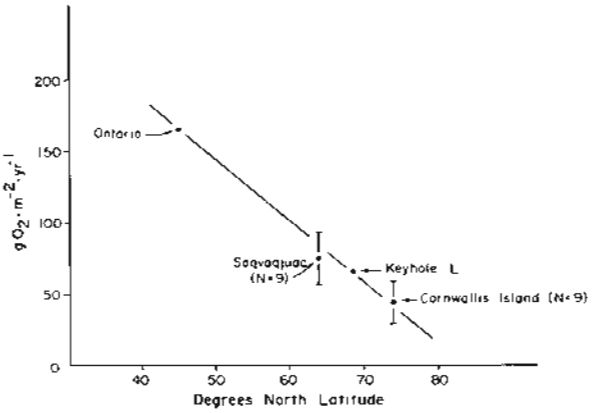

Fig. 19.75. Annual respiration in 19 oligotrophic arctic lakes and one Ontario lake in relation to latitude. From Welch and Bergmann (1985).

An integrative measure of lake productivity can be obtained by measuring the total oxygen metabolism (Welch, 1974; Welch and Bergmann, 1985). At fall freeze-up almost all of the oxygen freezes out and enters the water column, saturating it. Since the long polar night and snow-covered ice eliminate photosynthesis from November through March, whole-lake respiration can be measured independently of photosynthesis. Because carbon storage in sediments and outflow are low, measurements of lake respiration are good estimators of lake production (Welch, 1991). Table 19.34 gives data for Char Lake at Resolute and three lakes on the Truelove Lowland. One may note that Char and Loon lakes, with their drainage basins in a polar-desert landscape, have much lower levels of chlorophyll (measure of algal biomass) and lake metabolism, and a greater estimated age of char at 20 cm length compared with Immerk and Fish lakes, surrounded by sedge–moss meadows. Thus the general productivity of these lakes is closely coupled with that of the surrounding lands.

More recently, winter metabolism of 11 lakes has been measured near Saqvaqjuac, N.W.T. (63°N). The lakes are surrounded by shrub tundra and wet meadows of *Carex* and *Eriophorum*, with heath species, *Dryas*, and legumes at upland sites (Welch, 1985). Thus the drainage basins are more typical of the Low Arctic. Annual rates of lake respiration ranged from 53 to 109 g $O_2m^{-2}yr^{-1}$, averaging 77 g $O_2m^{-2}yr^{-1}$ for all of the lakes. Thus the general range of lake respiration is about 30 to 100 g $O_2m^{-2}yr^{-1}$ (Welch, 1991). Including oligotrophic lakes in Ontario, there is a reduction of 4–5 g $O_2m^{-2}yr^{-1}$ per degree of latitude (Welch and Bergmann, 1985; Fig. 19.75). In spring, photosynthesis of benthic and planktonic algae begins about 1 April at 63°N and about 1 May at 75°N. This results in changes in the oxygen budget. Roughly 3 to 6 weeks later when snowmelt begins, the lakes produce more oxygen than they consume. In years of low snow, plankton blooms appear before snowmelt, and up to 75% of total annual phytoplankton production can occur before ice melt (Welch et al., 1989).

All of these data point to the low levels of production of arctic lakes and ponds, levels controlled by cold water, low levels of phosphorus, and a very short summer season (although much of the algal growth occurs before ice melt). Another important factor is the amount of vegetation that occupies the catchment. There appear to be few special adaptations of the organisms that occupy these cold waters. Their rates of growth and respiration are no higher than for the same

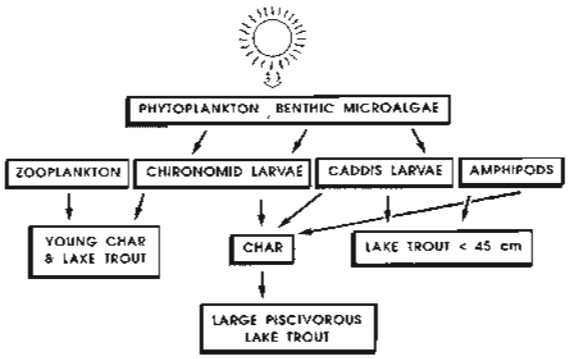

Fig. 19.76. Trophic structure of oligotrophic lakes near Saqvaqjuac along Hudson Bay (64°N). From Welch (1991).

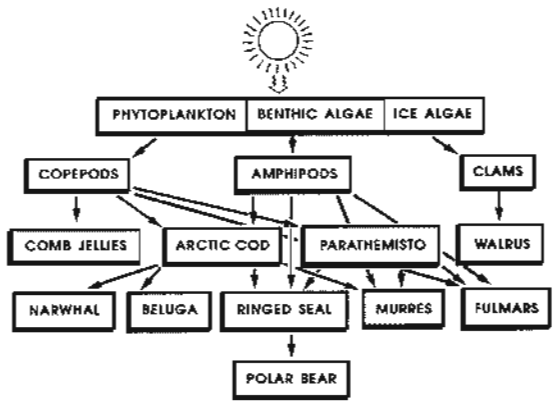

Fig. 19.77. Trophic structure of marine waters of Lancaster Sound, N.W.T. From Welch (1991).

TABLE 19.35

Comparison between arctic lakes and seas in winter[1]

Characteristic	Lakes	Seas
Winter temperature	0 to 3°C	−1.8°C
Salinity	0.01 to 0.2 g l^{-1}	32 to 34 g l^{-1}
Ice structure	crystals large, frazil ice uncommon	crystals small, frazil ice common
Respiration rates	30 to 100 g $O_2 m^{-2} yr^{-1}$	100 to 200 g $O_2 m^{-2} yr^{-1}$
Biomass	1 to 2 g dry wt m^{-2} of benthos and zooplankton, fish high 1 to 4 g m^{-2}	500 g dry wt m^{-2} of benthos, fish low 0.1 g m^{-2}
Species diversity	low, insects important	high, no insects, mammals important
Trophic structure	4 trophic levels, lake trout or char top carnivore	4 to 5 trophic levels, polar bear top carnivore
Mammals and birds	absent in winter	present in winter
Antifreeze properties	absent	present

[1] From Welch (1991).

species living in more temperate lakes when water temperatures are 2–4°C (Rigler, 1975).

The trophic structure of arctic lakes is relatively complex, considering their low annual production. Char Lake (75°N) has three trophic levels, while lakes near Saqvaqjuac (63°N) have large lake trout (*Salvelinus namaycush*) that feed on smaller char (Fig. 19.76). Although this book does not address arctic marine systems [but see another volume in this series (Postma and Zijlstra, 1988) and particularly the chapter by Dragesund and Gjøsœter (1988)], it is interesting to note that the trophic structure for Lancaster Sound includes five levels, capped by the polar bear (Fig. 19.77). A further comparison of arctic lakes and seas in winter is presented in Table 19.35. The biological differences resulting from physical differences include no ice communities, fewer trophic levels, lower species diversity, lower benthic but higher fish biomass, and lack of birds and mammals in lakes in winter compared with arctic seas (Welch, 1991). As Welch concluded, the frozen lakes and the sea remain biologically active in winter, a constant temperature oasis, compared with the terrestrial ecosystems that possess minimal activity except for the limited numbers of birds and mammals.

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