North American Terrestrial Vegetation
Second Edition

Edited by

Michael G. Barbour
William Dwight Billings

CAMBRIDGE UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, United Kingdom   www.cup.cam.ac.uk
40 West 20th Street, New York, NY 10011-4211, USA   www.cup.org
10 Stamford Road, Oakleigh, Melbourne 3166, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain

First published 1988
Second edition 1999

Printed in the United States of America

Typeface, 9/11 Palatino pt.   *System* DeskTopPro$_{/UX}$ [RF]

A catalog record for this book is available from the British Library.

Library of Congress Cataloging-in-Publication Data
North American terrestrial vegetation / edited by Michael G. Barbour,
William Dwight Billings. – 2nd ed.
p. cm.
Includes bibliographical references (p.) and index.
ISBN 0-521-55027-0 (hardbound)
1. Plant communities – North America. 2. Plant ecology – North
America. 3. Phytogeography – North America. I. Barbour, Michael G.
II. Billings, W. D. (William Dwight), 1910–1997.
QK110.N854 1999
581.7'22'097 – dc21   97-29061
CIP

ISBN 0 521 55027 0 hardback
ISBN 0 521 55986 3 paperback

Contents

	Contributors	*page vii*
	Preface to the First Edition	*ix*
	Preface to the Second Edition	*xi*
CHAPTER 1	**Arctic Tundra and Polar Desert Biome** *Lawrence C. Bliss*	*1*
CHAPTER 2	**The Taiga and Boreal Forest** *Deborah L. Elliott-Fisk*	*41*
CHAPTER 3	**Forests and Meadows of the Rocky Mountains** *Robert K. Peet*	*75*
CHAPTER 4	**Pacific Northwest Forests** *Jerry F. Franklin and Charles B. Halpern*	*123*
CHAPTER 5	**Californian Upland Forests and Woodlands** *Michael G. Barbour and Richard A. Minnich*	*161*
CHAPTER 6	**Chaparral** *Jon E. Keeley*	*203*
CHAPTER 7	**Intermountain Valleys and Lower Mountain Slopes** *Neil E. West and James A. Young*	*255*
CHAPTER 8	**Warm Deserts** *James A. MacMahon*	*285*
CHAPTER 9	**Grasslands** *Phillip L. Sims and Paul G. Risser*	*323*
CHAPTER 10	**Eastern Deciduous Forests** *Hazel R. Delcourt and Paul A. Delcourt*	*357*
CHAPTER 11	**Vegetation of the Southeastern Coastal Plain** *Norman L. Christensen*	*397*
CHAPTER 12	**Freshwater Wetlands** *Curtis J. Richardson*	*449*
CHAPTER 13	**Saltmarshes and Mangroves** *Irving A. Mendelssohn and Karen L. McKee*	*501*
CHAPTER 14	**Alpine Vegetation** *William Dwight Billings*	*537*
CHAPTER 15	**Mexican Temperate Vegetation** *Alejandro Velázquez, Victor Manuel Toledo, and Isolda Luna*	*573*
CHAPTER 16	**The Caribbean** *Ariel E. Lugo, Julio Figueroa Colón, and Frederick N. Scatena*	*593*
CHAPTER 17	**Tropical and Subtropical Vegetation of Mesoamerica** *Gary S. Hartshorn*	*623*

CHAPTER 18 **Vegetation of the Hawaiian Islands** *661*
Lloyd L. Loope

Subject Index *689*
Species Index *695*

Chapter 1

Arctic Tundra and Polar Desert Biome

L. C. BLISS

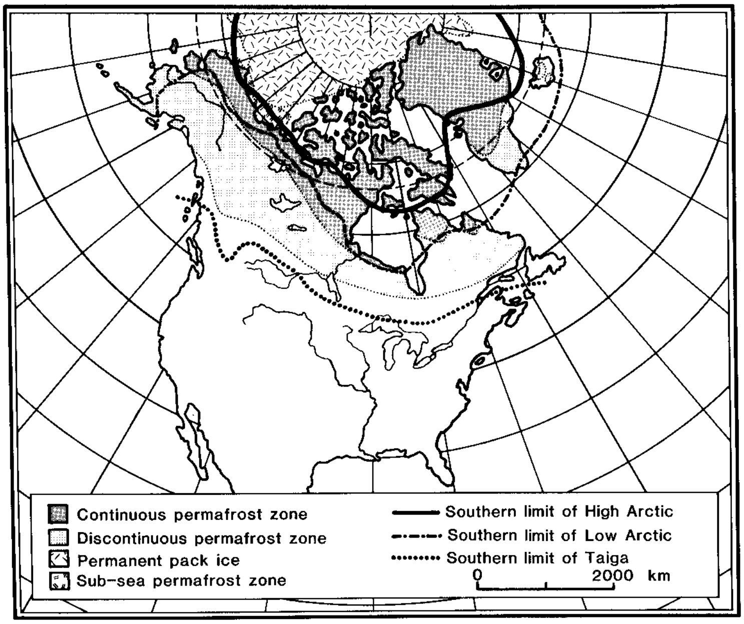

Figure 1.1. Major subdivisions of the North American and Greenland arctic.

INTRODUCTION

The Arctic is often viewed as a monotonous landscape with a limited number of vascular plants and an abundance of cryptogams. In reality, the arctic tundra and polar desert biome is as diverse in its vegetation types and soils as are the grassland biomes and the coniferous biomes of the western mountains and the taiga. The Arctic constitutes about 20% of North America (Fig. 1.1, general map of biomes), about 2.5 M km^2 in Canada, 2.0 M km^2 in Greenland, and 0.3 M km^2 in Alaska. Over this large area there are considerable variations in climate, ice cover, soils, sizes of the flora (cryptogam and vascular), and plant communities.

As used here, ''Arctic'' refers to those areas beyond the climatic limit of the boreal forest and treeline. There are often small pockets of trees, usually *Picea glauca*, in protected mesohabitats (south-facing slopes, river terraces) beyond the treeline, but the uplands are dominated by arctic tundra vegetation. Throughout these cold-dominated landscapes, soils are permanently frozen (permafrost) with only the upper portion (20–60 cm, except 100–200 cm along rivers), the active layer, thawing in summer. The Circumpolar Arctic is divided into the Low and High Arctic (Fig. 1.1) based on many ecological characteristics (Table 1.1). Tundras predominate in the Low Arctic, and polar semideserts and polar deserts dominate the High Arctic. ''Tundra'' is a generic term that includes vegetation types that range from tall shrub (2–5 m high) to dwarf shrub heath (5–20 cm high) and graminoid-moss. These landscapes have a total plant cover of 80–100%, including an abundance of cryptogams in most sites.

PHYSICAL ENVIRONMENT

Climate

The macroclimate of the Arctic is characterized by continuous darkness in midwinter, with a nearly continuous cover of snow and ice for 8–10 mo and by continuous light in summer, with a short growing season of 1.5–4 mo. In winter a large semipermanent high-pressure system of intensely cold dry air occurs over the Yukon Territory and the western Northwest Territories (N.W.T.). The average southern position of these anticyclonic systems parallels the southern boundary of the taiga in winter. However, outbreaks of cold arctic air periodically extend into the midwestern and southern states during severe storms. In summer, the arctic high-pressure system is weaker, with its southern limit paralleling the arctic–boreal forest boundary over 50% of the time (Bryson 1966). Low-pressure systems in the Gulf of Alaska and between Baffin Island and Greenland bring increased precipitation to the Arctic in summer, when these storm systems move across Alaska, into the Canadian Arctic Archipelago and Greenland. Winter penetration of low-pressure systems into the Arctic seldom occurs

Table 1.1. Comparison of environmental and biotic characteristics of the Low and High Arctic in North America

Characteristics	Low Arctic	High Arctic
Environmental		
Length of growing season (months)	3–4	1.5–2.5
Mean July Temperature (°C)	8–12	3–6
Mean July soil temperature at − 10 cm (°C)	5–8	2–5
Annual degree days above 0°C	600–1400	150–600
Active-layer depth (cm)		
fine-textured soils	30–50	30–50
coarse-textured soils	100–300	70–150
Botanical/vegetational		
Total plant cover (%)		
Tundra	80–100	80–100
Polar semidesert	20–80	20–80
Polar desert	1–5	1–5
Vascular plant flora (species)	700	350
Bryophytes	Common	Abundant
Lichens	Fruticose and foliose growth forms common	Frutcose growth form minor, crustose and foliose common
Growth-form types	Woody and graminoid common	Graminoid, cushion, and rosette common
Plant height (cm)		
Shrubs	10–500	5–100
Forbs	5–30	2–10
Sedges	10–50	5–20
Shoot : root ratios (alive)		
Shrubs	1:1	1:1
Forbs	1:1–2	1:0.5–1
Sedges	1:3–5	1:2–3

except in southern Baffin Island and southern Greenland, regions with much higher annual precipitation (Table 1.2).

Whether the positioning of the Arctic Front (leading edge of polar air) in summer along the treeline results from changes in surface albedo, evapotranspiration, and surface roughness of vegetation, as suggested by Hare (1968), or from an assemblage of climatic variables, as suggested by Bryson (1966), is not known. However, both the vegetation limits of forest and tundra and the air-mass systems are responding to the basic solar radiation controls of net radiation (Hare and Ritchie 1972). Annual net radiation averages 1000–1200 MJ m^{-2} yr^{-1} in the northern boreal forest, 750–800 MJ m^{-2} yr^{-1} across Canada, and about 670 MJ m^{-2} yr^{-1} across Alaska at treeline. In the High Arctic it averages 200–400 MJ m^{-2} yr^{-1} over much of the land and drops to near zero in northern Ellesmere Island and northern Greenland. A similar pattern of reduced summer temperature, mean annual temperature, and precipitation occurs northward (Fig. 1.2). These dramatic shifts in summer climate and length of the growing season explain much of the change in vegetation from the Low Arctic to the High Arctic. Winter snow cover averages 20–50 cm over many upland areas, whereas in the Low Arctic, lee slopes and depressions may have snowbanks 1–5+ m. In the High Arctic, with greatly reduced winter precipitation, many uplands have only 10–20 cm snow and some areas even less. Deep snowbanks (1–3+ m) occur in protected slopes and in depressions. With a lower sun angle and lower summer temperatures many of these snowbanks do not melt until late July or August, whereas in the Low Arctic nearly all snow is melted by mid-June. The time of snowmelt greatly influences the distribution of species, especially north of 74° latitude. There is also a very strong correlation between shrub height and average snow depth, especially in the Low Arctic. This explains why tall shrubs (2–5 m) are confined to river bottoms, steep banks, and drainages in uplands.

Global climate change is a major subject of cur-

Table 1.2. Climatic data for selected stations in the Low and High Arctic

Station and latitude	Temperature (0° C) Mean monthy June	July	August	Mean annual	Degree-days (>0° C)	Precipitation (mm) Mean monthly June	July	August	Mean annual
Low Arctic									
Frobisher Bay, N.W.T., 64°	0.4	3.9	3.6	−12.7	610	38	53	58	425
Baker Lake, N.W.T., 65°	3.2	10.8	9.8	−12.2	1251	16	36	34	213
Tuktoyaktuk, N.W.T., 70°	4.7	10.3	8.8	−10.4	903	13	22	29	130
Kotzebue, AK, 67°	8.2	12.4	8.5	−4.3	1462	22	44	37	246
Umiat, AK, 69 °	9.1	11.7	7.3	−11.7	993	43	24	20	119
Angmagssalik, Greenland, 65°	5.8	7.4	6.6	−0.4	793	44	35	62	770
Godthaab, Greenland, 64°	5.7	7.6	6.9	−0.7	809	46	59	69	515
Umanak, Greenland, 71°	4.8	7.8	7.0	−4.0	682	12	12	12	201
High Arctic									
Barter Island, AK, 70°	1.8	4.6	3.7	−11.6	368	10	18	25	124
Barrow, AK, 71°	1.3	3.8	2.2	−12.1	288	8	22	20	100
Cambridge Bay, N.W.T., 69°	1.5	8.1	7.0	−14.8	579	13	22	26	137
Sacks Harbour, N.W.T., 72°	2.2	5.5	4.4	−13.6	458	8	18	22	102
Resolute, N.W.T., 75°	−0.3	4.3	2.8	−16.4	222	13	26	30	136
Isachsen, N.W.T., 79°	−0.9	3.3	1.1	−19.1	161	8	21	22	102
Eureka, N.W.T., 80°	2.2	5.5	3.6	−19.3	318	4	13	9	58
Alert, N.W.T., 83°	−0.6	3.9	0.9	−18.1	167	13	18	27	156
Scoresbysund, Greenland, 70°	2.4	4.7	3.7	−6.7	333	26	38	33	248
Nord, Greenland, 81°	−0.4	4.2	1.6	−11.1	202	5	12	19	204

Source: Data from various sources

rent research, especially in relation to boreal and arctic regions. Plant and animal communities and ecosystems have changed greatly in the past and no doubt will respond significantly to future climate changes (Warrick, Shugart, Antonovsky, Tarrant, and Tucker 1986). Arctic ecosystems are likely to be the most altered with climate warming (Maxwell and Barrie 1989; Maxwell 1992, 1995); there is a potential for a 2–5° C increase in summer temperatures. Variations in surface ocean temperatures are believed to play a major role in governing terrestrial climate (Lowe et al. 1994). Recent ice-core data from Greenland (Taylor et al. 1993) indicate that these climate changes have been abrupt in the past (as brief as one to two decades).

Data for 65 arctic stations from 1881–1981 (Kelley and Jones 1981) indicate that 1881–1920 was a cool period, followed by warming until the early 1950s. Climate warming has continued in Alaska and the western Canadian Arctic in the 1980s and 1990s, whereas areas in the eastern Canadian Arctic are cooling (Chapman and Walsh 1993; Maxwell 1995). Other indications of warming are the earlier melt of snow, especially at Barrow compared with the central Canadian Arctic (Foster 1989), the 2° C rise in permafrost temperature in the past few decades in northern Alaska (Lachenbruck and Marshall 1986), and the more recent data from the Toolik Lake, Alaska, site. The mean July–August water temperature of Toolik Lake has risen about 3° C from 1975 through 1991 (Hobbie et al. 1994) and air temperatures at Barrow by AK $\simeq$ 1.5° C since 1971 (Oechel, Vourlitis, Hastings, and Bochkarev 1995). However, on Devon Island N.W.T., where lakes thawed completely in the early 1970s and 1980s, only 30–50% of the ice has melted in 1991–1996. The overall indications are that there is a warming trend that is within the range of historic variability yet that also appears to be a response to increased levels of CO_2.

Permafrost

''Permafrost'' refers to those areas of soil, rock, and sea floor where the temperature remains below 0° C for 2+ yr. In coarse gravels and frozen rock there is little ice; a dry permafrost predominates. Ice, however, is generally an important component of permafrost, reaching 80–100% by volume in massive ice wedges and ice lenses. Permafrost underlies all of the Arctic and extends into the boreal forest, tapering off as discontinuous permafrost where mean annual temperature in the atmosphere ranges from −8.5° C at the northern limit of discontinuous permafrost to about −1° C at its southern limit. The depth of the permafrost depends on mean annual temperature, thermal conductivity of soil and rock, proximity to the sea, and topographic position. Permafrost is

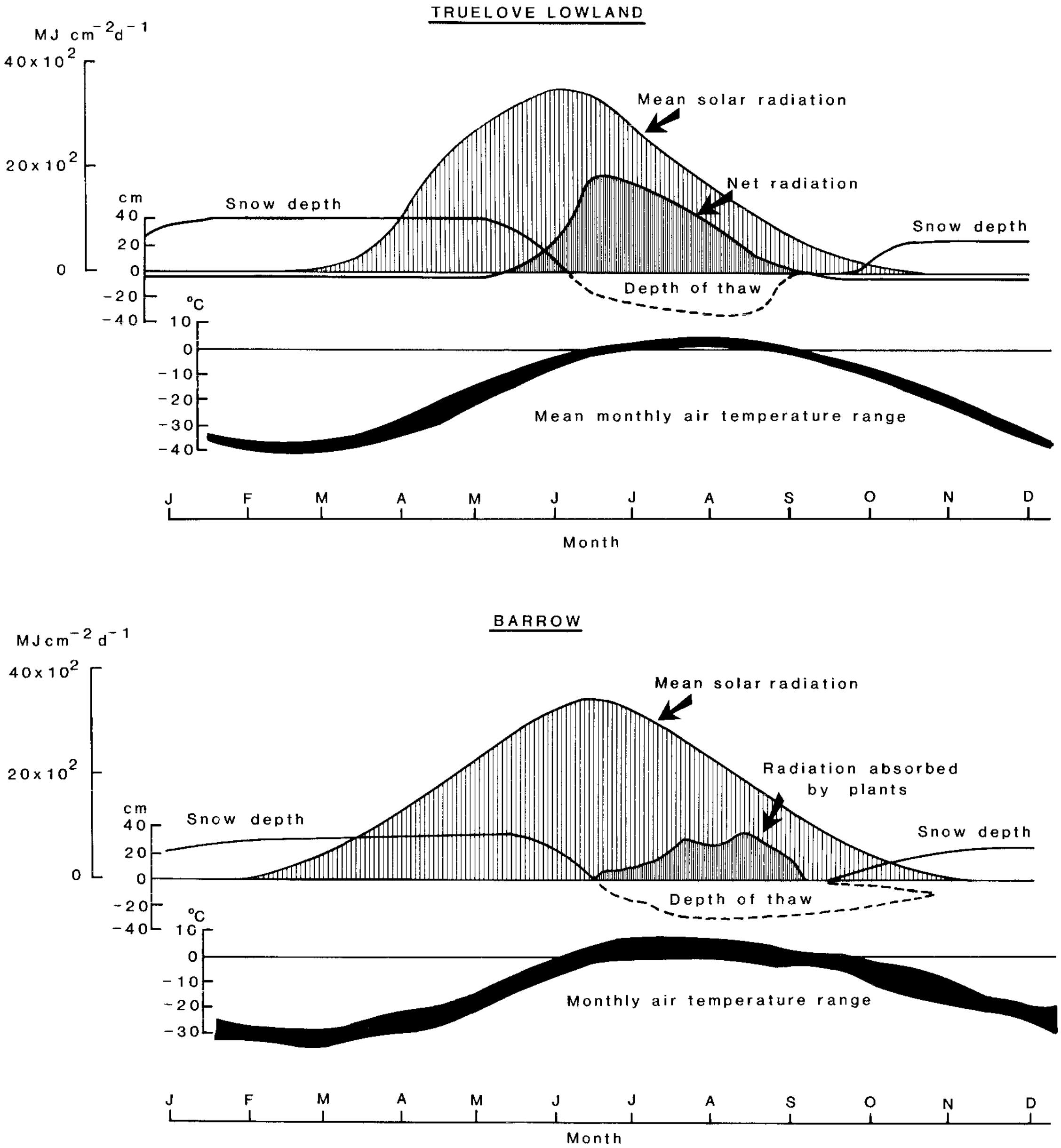

Figure 1.2. Diagram of mean maximum and mean minimum temperatures, snow depth, active-layer depth, and solar radiation at Truelove Lowland (from NATV, 1st edition) and Barrow (From Chapin, F. S. III and G. R. Shaver 1985, Arctic, pp. 16–40 in B. F. Chabot and H. A. Mooney (ed.), Physiological ecology of North America plant communities, Chapman & Hall, New York; with kind permission of Kluwer Academic Publishers.

about 320 m thick at Barrow, 500–600 m in the Mackenzie River Delta region, and 400–650+ m throughout the High Arctic. Mean annual temperature near the top of the permafrost table has risen 2° C in parts of the Arctic in the past 30–100 yr, an indication of climate warming.

Permafrost and the dynamic processes of the annual freeze–thaw cycle result in many surface features. Ice-cored hills (pingos) (Fig. 1.3), and small ice mounds (palsas) occur in the Low Arctic but are more limited farther north. The most common features, which are not restricted to the Arctic, are sorted and nonsorted circles and stripes, polygons, earth hummocks, and solifluction steps. The circles, stripes, and polygons may be 10–25 cm across each unit, but many polygons are 3–10 m, even 50–100 m in diameter. Raised and depressed-center polygons, sorted and nonsorted circles, soil hummocks, and

Figure 1.3. Pingo (ice-cored hill) east of the Mackenzie River Delta. These form in old lake basins when permafrost invades formerly unfrozen soils.

terraces all influence the distribution of plants and the development of soils (Fig. 1.4A–C). Large soil polygons (>1 m) are common in lowlands, whereas stone nets and stripes are typical of uplands. Polygonal patterns occur on lands that are level or have gentle slopes (1–3°); elongated polygons, stripes, and solifluction steps are common on slopes >3–5° (Washburn 1980). Cushion plants often predominate on the step (tread), with taller herbs and shrubs predominating on the riser where winter snow cover is deeper and continuous.

Not all patterned ground features result from ice formation. In the High Arctic, many small polygonal patterns (10–30 cm) result from desiccation cracks (Fig. 1.4D) that form as the silty to sandy soils dry each summer. Vegetated soil hummocks probably result from plant establishment, desiccation crack formation, and the slow accumulation of organic matter as plants grow on the hummocks and they become more defined (see Fig. 1.4C). Needle ice is another important feature in finer-textured soils. This ice forms in many soils, especially in the fall, and the resulting lifting of surface soils greatly inhibits seedling establishment in some sites.

Soils

Plant communities and soils are interrelated in the Arctic, as they are in all biomes. Because of reduced plant cover, a short growing season, and the short time since ice retreat (<12,000 yr) or emergence from the sea, the soils are less well developed than in temperate regions. The presence of permafrost, which limits the vertical movement of water and the churning of some soils (cryoturbation), further restricts soil and plant development. Consequently, chemical decomposition, release of nutrients, and synthesis of minerals from weathering of clay all progress very slowly.

The early concepts that arctic soils form under processes quite different from those in temperate regions have been replaced by the realization that the same soil-forming processes occur but at greatly reduced rates. The process of podzolization is limited in the Arctic to well-drained soils with a deep active layer. Where dwarf shrub heath species and dwarf birch predominate, weakly developed podzols (Spodosols) are found. Soils of uplands and dry ridges that are less well developed are arctic brown soils (Inceptisols). Cushion plant and heath shrub communities occur in these areas. The most common group of soils in the Low Arctic includes the tundra soil (Inceptisols) of cottongrass–dwarf shrub heath and some sedge communities of imperfectly drained habitats. These soils form under the process of gleization. Poorly drained lowlands, where soils remain saturated all summer, accumulate both sedge and moss peats. These bog and half-bog soils (Histosols) are dominated by sedge-moss or grass-moss plant communities (Fig. 1.5).

The arctic podzols (Spodosols) and arctic browns (Inceptisols) show some translocation of humus and iron, with iron-enriched B_2 horizons and weakly eluviated A_2 horizons in the podzols. The surface layers tend to be quite acidic (pH 6–4) and low in available nutrients but quite well drained above the perma frost layer. Inceptisols of imperfectly drained lands (arctic tundra soils) are acidic (pH 6.5–4.5), contain B horizons that have subangular to angular structures, are grayish in color with iron oxide mottles, and are low in available nutrients. Histosols of poorly drained lands are acidic (pH 6.5–5.0) and are similar to the arctic tundra soils in having limited translocation of minerals into the B horizon.

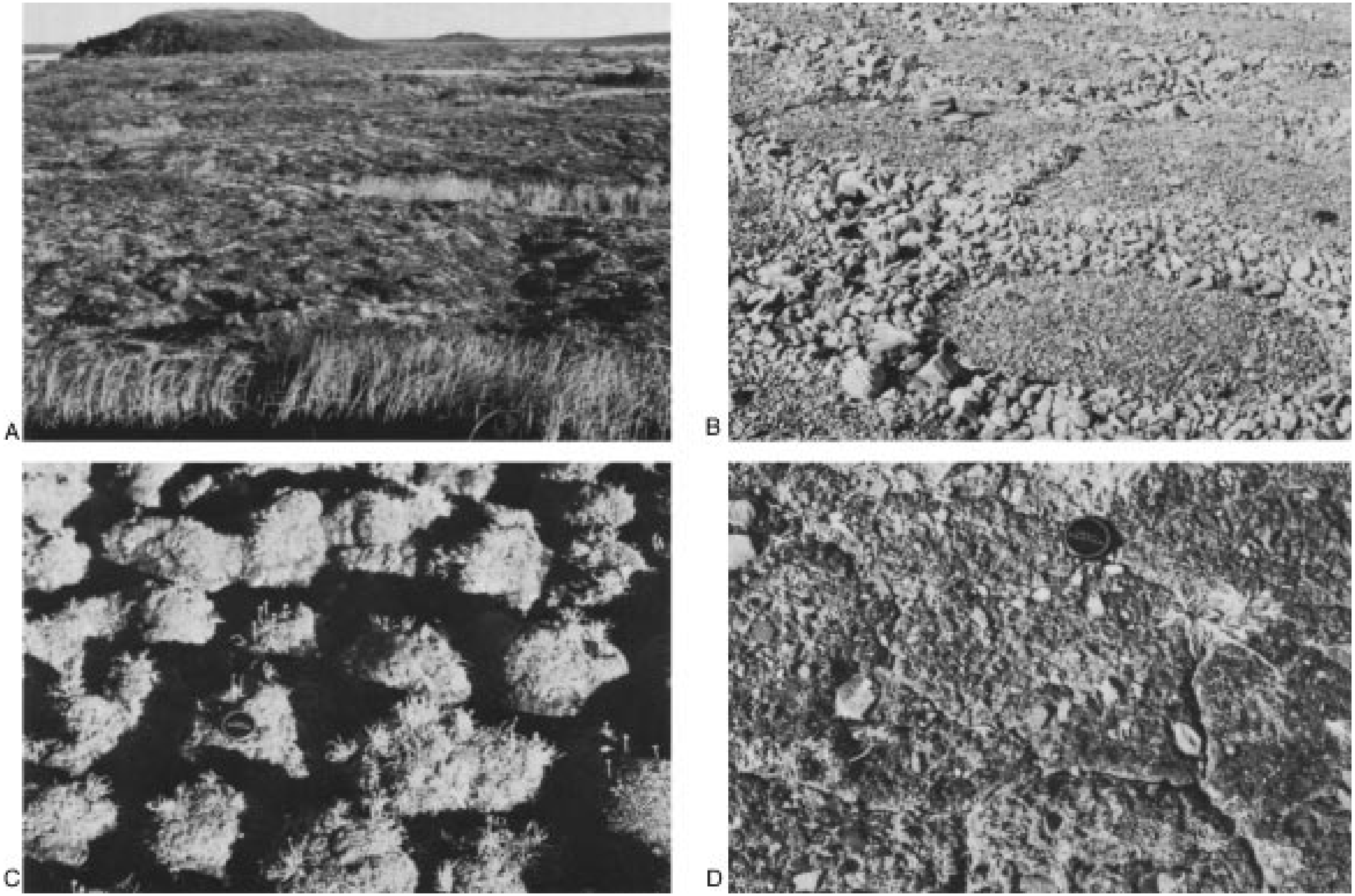

Figure 1.4. Patterned ground features in the Arctic: (A) raised-center polygons in the Mackenzie River delta area with sedges in the troughs and heath shrubs and lichens on the top; note the pingo beyond; (B) sorted polygons on Cornwallis Island within a polar desert landscape; (C) soil hummocks with Dryas integrifolia, *Banks Island; and (D) desiccation cracks, with the development of mosses and ''safe sites'' for vascular plants to grow, King Christian Island.*

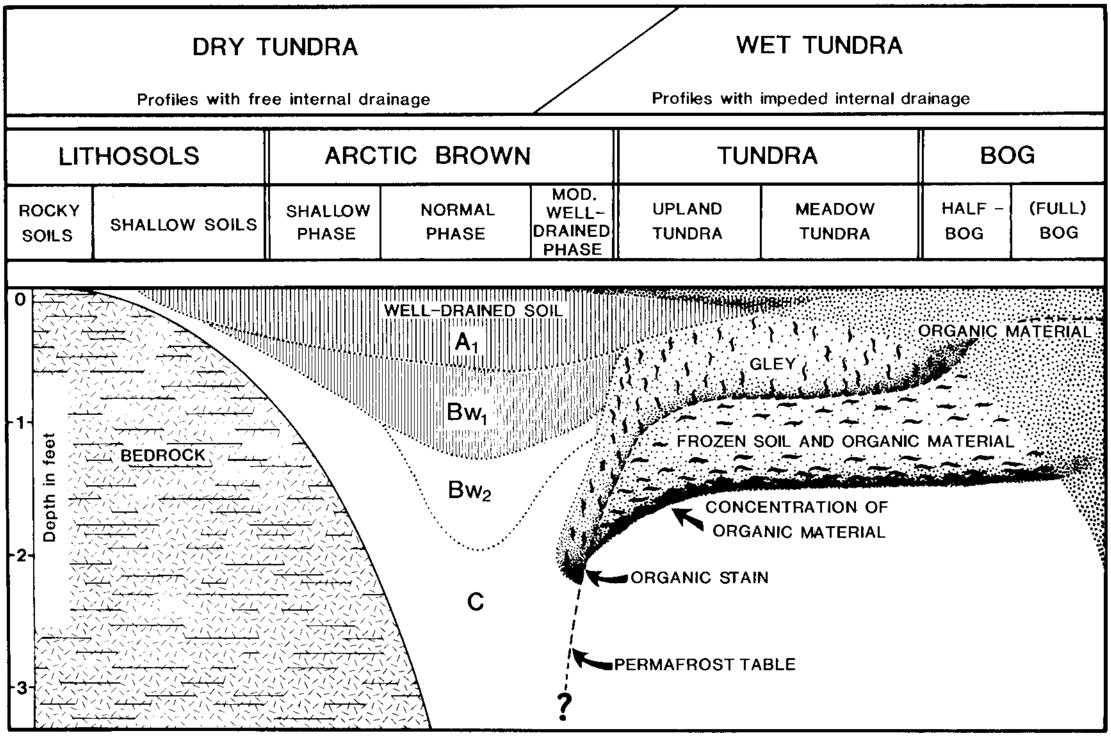

Figure 1.5. Generalized diagram of major soils in the Arctic (modified from Tedrow 1977).

Within the High Arctic, soil-forming processes are further reduced. The very limited lowlands of sedge-moss or grass-moss communities have thin peats, 2–20 cm thick overlying gleyed (arctic tundra) soils. Many slopes covered with cushion plant–cryptogam communities overlie well-drained soils of the arctic brown group (Inceptisols). Within the barren polar deserts, soils develop under the process of gleization or calcification. These soils are generally basic (pH 7.5–8.5), contain very little organic matter, and are base saturated, but they are very deficient in nitrogen and phosphorus. There are some areas where free carbonates are released from sedimentary rocks or from recently uplifted marine sediments along coastal areas. In these habitats, calcium and magnesium salts effervesce on the soil surface during the brief warm and drier periods in summer. Halophytic species predominate in these sites, as they often do in the extremely depauperate salt marshes in some coastal areas. For a detailed discussion of arctic soils, see Tedrow (1977).

PALEOBOTANY

On a geological basis, arctic ecosystems are relatively young. The fossil record from Cook Inlet, Alaska, indicates that tropical, subtropical, and warm temperate forests predominated in Eocene time (≃ 55 M yr BP) (Wolfe 1977). In Miocene time (≃ 22 M yr BP) there were mixed coniferous-deciduous forests on Devon Island at what is now 75 ° N (Whitlock and Dawson 1990), and comparable forests occupied uplands in central Alaska (≃ 18–15 M yr BP) (Wolfe 1969). By Pliocene time (≃ 6–3 M yr BP), coniferous forests still predominated, along with insects typical today of southern British Columbia and northern Washington (Hopkins, Matthews, Wolfe, and Silberman 1971). The Beaufort Formation, extending from Banks Island (71° N) to Meighen Island (80° N) and estimated to be of middle Miocene to Pliocene age, contains fossils of mixed coniferous-deciduous forests (Hills, Klovan, and Sweet 1974). An amazing group of fossil seed plants, mosses, and invertebrates from Meighen Island indicates a forest-tundra vegetation in late Miocene to early Pliocene time on a land surface that is now polar desert. Tundra probably occurred farther north and at higher elevations on Axel Heiberg and Ellesmere islands and in northern Greenland. Much of the arctic flora and fauna is believed to have evolved in the highlands of Central Asia (Hoffman and Taber 1967; Yurtsev 1972) and to a more limited degree in the central and northern Rocky Mountains (Billings 1974;

Packer 1974). From these centers of origin, plants and animals spread north and across Beringia to enrich the biota on both continents.

A circumpolar flora of perhaps 1500 species developed prior to the onset of Pleistocene glaciations (Löve and Löve 1974). Glacial advances and retreats, with accompanying climatic changes, reduced both the flora and fauna of these northern lands. The result is a truly Circumpolar Arctic vascular plant flora of 1000–1100 species, with about 700 of these species occurring in the North American Arctic.

The evolution of arctic ecosystems in Beringia (the land connection between Alaska and Siberia during the Late Pleistocene) and the northern Yukon Territory has been discussed by Hopkins et al. (1982) and Ritchie (1984). The pollen record from the Bering Strait region from the Duvanny Yar Interval (30,000–14,000 yr BP) was interpreted as a fairly uniform herbaceous tundra in which upland sedges, grasses, and *Artemisia* predominated (Colinvaux 1964, 1967; Matthews 1974). It was assumed that this vegetation was similar to that of the steppe tundra of eastern Siberia and that it occupied much of northern Alaska and the Yukon Territory. More recent studies by Ager (1982), Anderson and Brubaker (1986, 1994), Anderson, Reanier, and Brubaker (1988) in Alaska, and Cwynar and Ritchie (1980), Ritchie (1984, 1987), and Ritchie, Cwynar, and Spear (1983) in the Yukon indicate that more mesic graminoid communities typified the western Alaskan lowlands and that more xeric herbaceous communities dominated eastern Alaska and the Yukon Territory. Ericaceous heath shrubs probably have been underestimated because of their low pollen production. Spruce became extinct, and balsam poplar and aspen became more restricted during that period. Willow scrub was confined to river bottoms, as today.

Although many fossils remains of large mammals have been found in central Alaska, most have been reworked by rivers, so that accurate carbon dates are difficult to determine. Earlier studies by Guthrie (1972) indicated that an arctic grassland must have predominated to support these mammals. However, more recent studies and summaries of various research indicate little basis for this belief (Ritchie 1982, 1984; Ritchie and Cwynar 1982; Schweger 1982). Relict examples of this ''mammoth steppe'' exist in Alaska today on steep south-facing river bluffs. Dominants include *Artemisia frigida, Agropyron spicatum*, and *Calamagrostis purpurascens* (Wesser and Armbruster 1991).

The Birch Zone (14,000–12,000 yr BP) was a warmer period during which a rapid rise in the sea level drowned the Bering land bridge. The increase in birch pollen indicates a rise in shrub tundra along with the entrance of cottongrass and cottonwood pollen. The large mammal fauna changed with the loss of woolly mammoth at about 14,000 yr, bison at about 13,000 yr, and horse and wapiti at about 10,000 yr BP. Ritchie (1984) has presented new data from the Bluefish Cave site in the northern Yukon indicating that large changes occurred in vegetation from herb tundra (15,000–12,000 yr BP) to closed and open woodlands at low elevations and to herb tundra in the uplands (9,000 BP to the present). The Late Pleistocene fauna of woolly mammoth, horse, Dall sheep caribou, bison, wapiti, and musk-ox shifted to caribou and moose with major changes in vegetation. This is one of the very few records in the north that conclusively documents simultaneous changes in mammal and vegetation patterns. The extinction and reduction of large mammal species over a 4000 yr period probably resulted from a combination of climate change that induced major changes in vegetation and from overhunting by humans (Martin 1974, 1982). Grayson (1991) presents evidence that the extinction of 35 genera of mammals occurred over several thousand years and that the overkill hypothesis alone does not adequately explain the large number of extinct mammals.

Studies indicate that a warmer period prevailed across northern Alaska, the central Yukon, and the adjacent N.W.T. from 10,000–6500 yr BP (Ritchie 1984, 1987; Anderson et al. 1988; Cwynar and Spear 1991). Balsam poplar formed gallery forests and localized groves. Open stands of white spruce dominated uplands from 9400–5000 yr when climate cooled and shrub and tussock tundra again became dominant.

VEGETATION

Given the diversity of arctic landscapes (mountains, Precambrian Shield, low-elevation lands) and their great latitudinal extent (55° along Hudson Bay to 83° at northern Ellesmere Island and Greenland), with associated climatic changes, it is not surprising that there are diverse patterns of plant communities. Although arctic vegetation has a general structure and pattern of herbaceous species and (often) low scattered shrubs, not all of it has the same appearance.

The major types include (1) tall shrub tundra (*Salix, Alnus, Betula* 2–5 m high) along river terraces, stream banks, steep slopes, and lake shores; (2) low shrub tundra (*Salix, Betula* 40–60 cm high) on slopes and uplands beyond the forest tundra; (3) dwarf shrub heath tundra (5–20 cm high) and cottongrass–dwarf shrub heath tundra (tussock tundra) on rolling terrain with soils of intermediate drainage; (4) graminoid-moss tundra (20–40 cm high) on poorly drained soils; and (5) cushion plant–herb–cryptogam polar semidesert (2–5 cm high) on wind-exposed slopes and ridges with limited snow cover. This last vegetation type is more typical of the High Arctic.

There are general reductions in total plant cover, plant height, and woody and vascular plant species and increases in lichens and mosses from the Low Arctic to the High Arctic. At the final limit of plant growth in the polar desert barrens, the ultimate restriction to plant growth appears to be soils which are saturated in the spring but of which the upper 1–2 cm bakes hard later in some summers, preventing seedling establishment. These soils lack nitrogen and phosphorus and have few safe sites in which vascular plants can become established because of the lack of cryptogamic crusts that provide sites with more water and nutrients. These bare soils also favor an abundance of needle ice in autumn. Plant limits are not caused by temperature alone, because vascular plants grow to within a few meters of glaciers and ice caps at elevations of 650–720 m on Ellesmere and Devon islands (Bliss et al. 1994).

A vegetation classification system that follows Russian concepts of the Arctic and an associated circumpolar vegetation map are still under development (Walker et al. 1995).

Forest Tundra

Throughout northern Alaska and Canada there is a relatively narrow zone, 10–50 km wide, of forest tundra. This vegetation consists of scattered clumps of trees in more protected sites where snow accumulates within a matrix of low shrub tundra. An added factor in the role of climate (position of the Arctic Front) is the role of soils. In Canada, where the forest tundra lies farther north, the transition zone is narrower and the soils tend to be more nutrient-rich and of finer texture. Where the transition zone lies south of the climatic potential for forest, the zone is wider and the soils are nutrient-poor and more droughty (Timoney, LaRoi, Zoltai, and Robinson 1992, 1993; Timoney 1995).

In many places, the transition from forest tundra to shrub tundra consists only in loss of stunted trees. Because of this patterning, earlier Russian ecologists considered shrub tundra a part of the Subarctic rather than the Arctic (Aleksandrova 1980), for they believed that fire had eliminated the trees in many places. Repeated fires within these Subarctic communities have little effect on the understory vascular plants, for they easily resprout. However, lichens and mosses are slow to return. In the Mackenzie River delta region, it takes about 200+ yr for an extensive lichen cover to develop on the fine-textured soils (Black and Bliss 1978). On sandy soils to the southeast, where shrubs are minor, a lichen cover developed in 60–120+ yr in the Abitan Lake region (Maikawa and Kershaw 1976). Studies conducted near Inuvik, N.W.T., indicate that there is a period of only 5–8 yr following fire during which seedlings of *Picea mariana* have a chance to become established, because of a short period of seed viability, rapid seed release from surviving cones, and seed destruction by rodents and insects (Black and Bliss 1980). Massive fires within the forest tundra could drive the treeline 50–100 km south should they occur during a cool climatic period, for the seeds germinate only when temperatures are >15° C. Chapter 2 describes this vegetation and the role of fire in more detail.

Low Arctic Tundra

The general appearance of most landscapes within the Low Arctic is that of a grassland in which low to dwarf shrubs are common, except in the wetter habitats. The vascular flora in an area of 100–200 km^2 may total 100–150 species, although any single plant community may have only 10–50 species of vascular plants and 20–30 species of mosses and lichens.

Tall shrub tundra. The rivers that flow across the tundra have sandbars and gravel bars, islands, and terraces with well-drained soils that are relatively warm, have a deep active layer (1–1.5 m), and contain higher nutrient levels than do adjacent uplands. These habitats and steeper slopes above lakes and rivers that have a deep snow cover in winter (2–5 m) are generally covered with various mixtures of *Salix*, *Betula*, and *Alnus*. In arctic Alaska, the Yukon, and the northwestern Northwest Territories, *Salix alaxensis* predominates on the coarser-textured alluvium, dune sands, and slopes (Fig. 1.6). Associated shrubs, 1–2 m high, of lesser importance and of varying abundance from site to site, include *S. arbusculoides*, *S. glauca* ssp. *richardsonii*, *S. pulchra*, and *Alnus crispa* (Table 1.3) (Bliss and Cantlon 1957; Drew and Shanks 1965; Johnson, Viereck, Johnson, and Melchior 1966; Gill 1973; Komarkova and Webber 1980). There is often a rich understory of grasses and forbs in these shrub communities.

Depauperate outliers of the *Salix alaxensis*, *S. lanata* ssp. *richardsonii*, *S. pulchra* shrub community, with sedges and forbs, occur along rivers and steep slopes on southern Banks and Victoria islands (Kuc

Figure 1.6. Tall shrub tundra dominated by Salix alaxensis *with lesser amounts of* S. glauca *ssp.* desertorum, S. arbusculoides, *and herbaceous plants including* Lupinus arcticus, Hedysarum mackenzii, Deschampsia caespitosa, *and* Agropyron sericeum, *on river gravels along the Colville River, Umiat, Alaska.*

1974) within the southern High Arctic. *Salix alaxensis* is usually only 0.5–1.5 m tall, and the stands look similar to those in the upper river drainages on the north slope of the Brooks Range.

Low shrub tundra. Plant communities dominated by varying combinations of dwarf birch, low willows, heath species, scattered forbs, and graminoids are common on rolling uplands beyond the forest tundra in Alaska and northwestern Canada (Hanson 1953; Corns 1974). Open forest and forest tundra may have occupied these lands in northwestern Canada in the past, but fires and changing climate have forced the treeline south (Ritchie and Hare 1971; Ritchie 1977).

The open canopy of shrubs is 40–60 cm high and is dominated by *Betula nana* ssp. *exilis, Salix glauca* ssp. *acutifolia, S. planifolia* ssp. *pulchra,* and *S. lanata* ssp. *richardsonii,* with the combinations of species varying from place to place (Fig. 1.7). Ground cover includes *Carex lugens* and *C. bigelovii* in Alaska (*C. bigelowii* alone in the Northwest Territories), *Eriophorum vaginatum,* and numerous forbs, grasses, and heath shrubs (10–20 cm high). Varying combinations of *Vaccinium uliginosum, V. vitis-idaea* ssp. *minus, Empetrum nigrum* ssp. *hermaphroditum, Ledum palustre* ssp. *decumbens, Arctos (Arctostaphylos) alpina, A. rubra, Rubus chamaemorus,* and dwarf species of *Salix* occur along with an abundant ground cover of lichens and mosses (Table 1.3). Where snow lies late into June, the heaths are often dominated by *Cassiope tetragona.* The most common mosses include *Aulacomnium turgidum, Hylocomium splendens,* and *Polytrichum juniperinum.* Important fruticose lichens are *Cetraria nivalis, C. cucullata, Cladonia gracilis, Cladina mitis, C. rangiferina,* and *Thamnolia vermicularis.*

In much of the northeastern mainland of Canada, low shrub tundra is minor, probably because of limited winter snow and abrasive winter winds (Savile 1972). In the Chesterfield Inlet of Hudson Bay, northern Quebec, and southern Baffin Island, the dominant shrubs are *Betula glanulosa, Salix glauca* ssp. *callicarpaea,* and the aforementioned heath species, graminoids, and cryptogams (Polunin 1948).

In Greenland, low shrub tundras occur in the inner fjord regions that are warmer in summer. These shrub communities, dominated by *Salix glauca* ssp. *callicarpaea, Betula nana,* and *B. glandulosa* predominate on steep slopes and along streams and rivers from Disko Island (69°N) and Sønder Stromfjord (67° N) southward. The shrubs (>1 m in height) are associated with herbs and dwarf heath shrubs (Böcher 1954, 1959; Hansen 1969).

Dwarf shrub heath tundra. As used here, ''heath'' refers to species within the Ericaceae, Empetraceae, and Diapensiaceae. Some authors have broadened the concept to include *Dryas* and dwarf species of *Salix.* A characteristic feature of these heath plants is the evergreen leaf, although deciduous-leaved species also occur (*Vaccinium uliginosum, Arctosataphylos alpina, A. rubra*). Heath-dominated communities occur on well-drained soils of river terraces, slopes, and uplands where winter snows are at least 20–30 cm deep. Heath tundra occupies relatively small areas, a few hundred meters square, rather than the many hectares or square kilometers of other tundra vegetation types.

In western Alaska (Hanson 1953; Churchill 1955; Johnson et al. 1966), the northern Yukon (Hettinger et al. 1973), and the Mackenzie River

Table 1.3. Prominence values (cover × square root of frequency) for plant communities in the Low Arctic at Umiat, Alaska. Sampling area for each stand was 10 m⁻².

	Plant communities				
Species	Tall shrub	Low shrub	Cottongrass-heath	Cushion plant	Graminoid-moss
Eriophorum vaginatum	—	—	90	—	—
Arctagrostis latifolia	29	27	19	—	27
Carex lugens	—	30	27	—	—
Carex glacialis	—	—	—	27	—
Luzula confusa	—	—	19	—	—
Dryas integrifolia	—	—	—	90	—
Ledum palustre ssp. *decumbens*	9	30	30	—	—
Vaccinium vitis-idaea	9	29	70	—	—
Vaccinium uliginosum	14	23	—	—	—
Arctostaphylos alpina	—	21	27	19	—
Rhododendron lapponicum	—	—	—	9	—
Cassiope tetragona	—	14	29	9	—
Empetrum nigrum ssp. *hermaphroditum*	—	21	27	—	—
Rubus chamaemorus	—	—	25	—	—
Salix planifolia ssp. *pulchra*	80	14	9	—	—
Salix glauca ssp. *acutifolia*	9	29	—	25	—
Betula nana ssp. *exilis*	9	30	30	—	—
Alnus crispa	375	23	—	—	—
Pedicularis lanata	—	—	—	25	—
Lupinus arcticus	—	—	—	29	—
Saussurea angustifolia	—	14	—	—	—
Saxifraga punctuta	—	14	19	—	—
Saxifraga cernua	14	—	—	9	29
Polemonium acutiflorum	—	14	—	—	—
Petasites frigidus	9	—	19	—	—
Polygonum bistorta	—	23	16	—	—
Pyrola grandiflora	21	25	—	—	
Stellaria longipes	—	—	—	—	27
Caltha palustris	—	—	—	—	23
Carex aquatilis	—	—	—	—	375
Eriophorum angustifolium	—	—	—	—	21
Cardamine pratensis	—	—	—	—	16
Hedysarum alpinum	—	—	—	19	29
Mosses	29	190	625	30	90
Lichens	—	90	375	—	—
Total vascular species	13	20	17	17	9

Source: Churchill (1955)

Delta region (Corns 1974), communities of heath species (10–20 cm high) are quite common. The species occur in various combinations including *Ledum palustre* ssp. *decumbens, Vaccinium uliginosum, V. vitis-idaea, Empetrum nigrum* ssp. *hermaphroditum, Loiseleuria procumbens, Rhododendron lapponicum, R. kamschaticum*, and *Cassiope tetragona. Betula nana* ssp. *exilis* and one or more species of dwarf *Salix* are commonly associated, along with abundant lichens and mosses.

In the Keewatin District, N.W.T, west of Hudson Bay, dwarf shrub heath predominates on north exposures, fellfields, and gravel summits. Here, the heaths are less rich floristically, with *Ledum palustre* ssp. *decumbens, V. uliginosum, V. vitis-idaea, Empetrum nigrum* ssp. *hermaphroditum*, and *Cassiope tetragona* dominating (Larsen 1965, 1972). Where snow is deep, *Betula glandulosa* and highly deformed *Picea mariana* (60–90 cm high) occur near the treeline at Ennadai.

At Chesterfield Inlet along the west coast of Hudson Bay, at Wakeham Bay in northern Quebec, and at Lake Harbour, Baffin Island, heath vegetation is common. The dominant species include *V. uliginosum, Ledum palustre* ssp. *decumbens, Empetrum nigrum* ssp. *hermaphroditum, Phyllodoce caerulea*, and the sedge *Carex bigelovii*. Where snow lies into July, *Cassiope tetragona* dominates, with *Salix reticulata, S. herbacea, Dryas integrifolia, Carex misandra, Luzula nivalis*, and numerous lichens and mosses (Polunin 1948).

In southeast and west Greenland, heath vege-

Figure 1.7. Low shrub tundra dominated by Salix planifolia *ssp.* pulchra, Salix glauca *ssp.* acutifolia, Betula nana *ssp.* exilis, Vaccinium uliginosum, V. vitis idaea, Empetrum nigrum *ssp.* hermaphroditum, Ledum palustre *ssp.* decumbens, *and* Carex lugens *in the Brooks Range.*

Figure 1.8. Cottongrass–dwarf shrub heath tundra in the Caribou Hills, northeast of Inuvik, N.W.T.

tation is found on steep, moist slopes, usually in inland valleys, which have a warmer and drier continental climate as compared with the moist maritime climate along the coast and outer fjords (Böcher 1954). Species dominating in various combinations include *Cassiope tetragona, Vaccinium uliginosum* ssp. *microphyllum, V. vitis-idaea* ssp. *minus, Ledum palustre* ssp. *decumbens, Rhododendron lapponicum, Phyllodoce caerulea, Empetrum nigrum* ssp. *hermaphroditum*, and *Loiseleuria procumbens* (Sørensen 1943; Böcher 1954, 1959, 1963; Böcher and Laegaard 1962; Hansen 1969; Daniels 1982). *Betula nana* is a component of the more southern heaths. *Ledum, Phyllodocae*, and *Loiseleuria* drop out in the Melville Bugt region (72–75° N). At Thule (78° N) the dominant species of the limited heaths include *Cassiope tetragona, Vaccinium uliginosum* ssp. *microphyllum*, and *Salix arctica* (Sørensen 1943), as they do on Ellesmere in the High Arctic.

Cottongrass–Dwarf shrub heath tundra. Large areas of rolling uplands between the mountains and the wet coastal plain in Alaska and the Yukon Territory are dominated by tussocks of *Eriophorum vaginatum*, dwarf shrubs, lichens, and mosses (Hanson 1953; Churchill 1955; Britton 1957; Johnson et al. 1966; Hettinger et al 1973; Wein and Bliss 1974; Komarkova and Webber 1980). This vegetation type is of limited occurrence in the Northwest Territories, except in the Mackenzie River Delta region (Corns 1974), where it is common (Fig. 1.8), and it is absent from most of the eastern Canadian Arctic, with the exception of southern Baffin Island and northern Quebec (Polunin 1948).

Historically, these landscapes have been called cottongrass tussock tundra or tussock–heath tundra because of the conspicuousness of the cottongrass tussocks. However, the phytomass, net annual production, and cover of heath and low shrub species often are greater than for cottongrass. The Alaskan and western Canadian cottongrass is *E. vaginatum* ssp. *vaginatum*, whereas the subspecies *spissum* occurs in the eastern Arctic.

The predominant heath species are *V. vitis-idaea* ssp. *minus, V. uliginosum* ssp. *alpinum, Ledum palustre* ssp. *decumbens*, and *Empetrum nigrum* ssp. *hermaphroditum*. Scattered low shrubs of *Betula nana* ssp. *exilis* and *Salix pulchra* are common, along with *Carex bigelovii, C. lugens*, and several species of forbs (Table 1.3). The cryptogam layer is well developed and includes the mosses *Dicranum elongatum, Aulacomnium turgidum, A. palustre, Rhacomitrium lanuginosum, Hylocomium splendens, Tomenthypnum nitens*, and several species of *Sphagnum*. The most common lichens include *Cetraria cucullata, C. nivalis, Cladina rangiferina, C. mitis, Cladonia arbuscula, Dactylina arctica*, and *Thamnolia vermicularis* (Bliss 1956; Johnson et al. 1966).

Graminoid-moss tundra. The concept of arctic tundra is often associated with treeless wetlands in which species of *Carex, Eriophorum*, and sometimes the grasses *Arctagrostis, Dupontia, Alopecurus*, and *Arctophila* predominate, along with an abundance of bryophytes, but few lichens. In northern and western Alaska, arctic wetland meadows are of minor extent in the mountain valleys, but they increase in importance in the Foothill Province and dominate the Coastal Plain Province (Churchill 1955; Britton 1957; Webber 1978; Komarkova and Webber 1980). Arctic wetlands are again minor in the Yukon mountains, but they increase in importance on the coastal plain and eastward to the Mackenzie River region (Hettinger, Janz, and Wein 1973; Corns 1974).

The dominant sedges are *Carex aquatilis, C. rariflora, C. rotundata, C. membranacea, Eriophorum angustifolium, E. scheuchzeri*, and *E. russeolum* (Table 1.3). The grasses *Arctagrostis latifolia, Dupontia fisheri, Alopercurus alpinus*, and *Arctophila fulva* occur along a gradient from drier sites to saturated soils and standing water. In shallow waters of lakes and ponds (50–60 cm deep), *Menyanthes trifoliata, Equisetum variegatum*, and *Arctophila fulva* predominate, with *Potentilla palustris* and *Hippuris vulgaris* 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 (Fig. 1.9) in low-center polygons and in the troughs of high-center polygons (Britton 1957; Hettinger et al. 1973; Corns 1974). The nearly continuous cover of mosses includes species of *Aulacomnium, Ditrichum, Calliergon, Drepanocladus, Sphagnum, Hylocomium splendens*, and *Tomenthypnum nitens* (Britton 1957; Johnson et al. 1966).

Studies of plant succession in the thaw-lake cycle of northern Alaska have shown that high-center polygons form in drained lake basins from the melting of ice wedges and postdrainage thermokarst erosion. Pioneer plants include the moss *Psilopilum cavifolium* on dry peaty sites and the graminoids *Arctophila fulva* in wet sites, and *Eriophorum scheuchzeri* and *Dupontia fisheri* in the moist swales. *Eriophorum angustifolium* and *Carex aquatilis* enter somewhat later, but in time they predominate (Britton 1957; Billings and Peterson 1980).

Sedge-dominated wet meadows are found in the Ennadai area (Larsen 1965), Chesterfield Inlet, northern Quebec, and Lake Harbour (Polunin 1948). Common species include *Eriophorum angustifolium, E. scheuchzeri, Carex rariflora, C. membranacea*, and *C. stans* (Polunin 1948).

In Greenland, graminoid-moss tundra is present, but as with large areas of eastern Canada, the marshes are less common. Important species include *Carex rariflora, C. vaginata, C. holostoma, Eriophorum angustifolium*, and *E. triste* (Böcher 1954, 1959).

Other graminoid vegetation. With thousands of kilometers of arctic shoreline, one might assume that salt marshes, coastal dune complexes, and other coastal vegetation would be common. Such is not the case, for favorable habitats are limited. Factors that restrict arctic salt marshes are the limited areas of fine sands and silts, the annual reworking of shorelines by sea ice, a modest tidal amplitude, the low salinity of coastal waters, a very short growing season, and low soil temperatures. Coastal salt marshes have been described from subarctic Alaska (Vince and Snow 1984), northern Alaska (Jefferies 1977; Taylor 1981), Tuktoyaktuk (Jeffries 1977) and Hudson Bay, N.W.T. (Kershaw 1976; Bazely and Jefferies 1986a), the west-central part of southern Greenland (Søorensen 1943; Vestergaard 1978), and Devon, Ellesmere, and Baffin islands (Polunin 1948; Jefferies 1977; Muc, Freedman, and Svoboda 1989; Bliss and Gold 1994). See also Chapter 13 of this volume.

Many of these marshes have only a 5–20% plant cover, with plant heights of 1–5 cm. Floristically, most salt marshes have only three to five herba-

Figure 1.9. Graminoid-moss tundra in the High Arctic dominated by Dupontia fisheri *on Melville Island.*

ceous species, none of which is woody or belongs to the Chenopodiaceae, a family of plants common in temperate and tropical latitudes. The most common species are *Puccinellia phryganodes* on mud, with scattered clumps of *Carex ursina, C. ramenskii, C. subspathacea, Stellaria humifusa*, and *Cochlearia officinalis*. In many ways it is quite amazing that there are any species at all adapted to living in these harsh coastal environments, in contrast with the extensive and highly productive salt marshes of temperate regions.

The *Puccinellia* marshes along Hudson Bay are heavily grazed by lesser snow geese. Grazing in summer increases the aboveground net primary production of these marshes by 40–100% because the geese produce so many droppings that accelerate nitrogen cycling (Bazely and Jefferies 1986b; Jefferies 1988) in what are nitrogen-limited systems.

Beach and dune grasslands are minor features in the Arctic. *Elymus arenarius* ssp. *mollis* often dominates, with small amounts of the semisucculents *Honckenya peploides, Mertensia maritima*, and *Cochlearia officinalis* ssp. *groenlandica*, along with *Festuca rubra* and *Matricaria ambigua* (Barbour and Christensen 1993).

Small areas of grassland are found in the inner fjords of east-central Greenland, dominated by *Calamagrostis purpurascens, Arctagrostis latifolia, Poa arctica*, and *P. glauca* (Seidenfaden and Sørensen 1937; Oosting 1948). In west Greenland, larger areas (1–5 ha) of grassland occur that are dominated by *Calamagrostis neglecta, Poa pratensis*, and *P. arctica* (Böcher 1959). Similar small grasslands are found in the eastern Canadian Arctic of Baffin Island (Polunin 1948) and northern Keewatin (Larsen 1972).

Low Arctic Semidesert: Cushion Plant–Cryptogam

From the Rocky Mountains of Montana north to the Yukon Territory and Alaska, windswept slopes and ridges are often dominated by cushions or mats of *Dryas integrifolia* and *D. octopetala*. This vegetation type, often called *Dryas* fellfield or *Dryas* tundra, is limited in areal extent within the western Low Arctic but increases in importance in the large areas of barren rock and lag gravel surfaces in the eastern Arctic. In the Mackenzie District and Keewatin District, N.W.T., where acidic soils derived from granites predominate, *Dryas* is less prominent. Other cushion plants include *Silene acaulis, Saxifraga oppositifolia*, and *S. tricuspidata*. The lichens *Alectoria nitidula, A. ochroleuca, Cetraria cucullata*, and *C. nivalis*, along with the moss *Rhacomitrium lanuginosum*, are common in the Repulse Bay, Peely Lake, and Snow Bunting Lake areas (Larsen 1971, 1972).

Within the ecotone between forest and tundra in the Campbell–Dolomite uplands near Inuvik, N.W.T., mats of *Dryas integrifolia* and *Cladonia stellaris* cover the limestone and dolomite rocks. Where small pockets of soil occur, open stands of *Picea glauca* predominate (Ritchie 1977). In the Brooks Range (Spetzman 1959) and northward along exposed ridges within the Foothill Province, *Dryas*-lichen vegetation is common. *Dryas integrifolia* or *D. octopetala* and their hybrids often comprise 80–90% of the vascular plant cover. Associated species include *Silene acaulis, Carex rupestris, C. capillaris, Kobresia myosuroides, Anemone parviflora*, and *Polygonum viviparum*. Cushions of *Dryas* are often 0.5–1.0 m across, and they seldom reach a height greater than 2–5 cm. The ground cover of herbs, lichens, and mosses is generally sparse. As a result, there is often much bare rock and soil, although crustose lichens are often common.

High Arctic Tundra

In contrast with the Low Arctic, the High Arctic is characterized by herbaceous rather than woody species, and there is generally much less plant cover, especially of vascular plants. Lichens and mosses contribute a much larger percentage of total cover and biomass than in the Low Arctic. Vast areas are dominated by lichens and mosses, with only a 5–25% cover of flowering plants. Equally large areas of polar deserts have almost no cryptogams (0–3% cover) and only a 0.1–4% cover of vascular plants (Table 1.1). Vascular plants are much smaller in size (3–10 cm) than those of the same species (10–30 cm) in the Low Arctic, and their root systems are also smaller.

Based on vegetation types, the High Arctic can be divided into small areas of tundra (tall shrub, dwarf shrub heath, cottongrass tussock, and graminoid-moss), vast areas of cushion plant–cryptogam and cryptogam-herb polar semidesert, herb barrens, and very limited snowflush herb-moss vegetation of the polar deserts. With the exception of a few locations, woody species other than dwarf willows and semiwoody *Dryas* and *Cassiope* are very minor components.

Graminoid-moss tundra. Of the common vegetation types in the Low Arctic, only the graminoid-moss tundra is ecologically important farther north. It occupies 5–40% of the lands on the southern islands, with the exception of Baffin Island, which is mountainous. In the Queen Elizabeth Islands, $<2\%$ of the area contains this vegetation, yet it provides the major grazing habitat for musk-ox and breeding grounds for waterfowl and shore birds.

In the eastern and southern islands, *Carex stans* (*C. aquatilis*) and *C. membranacea* are the dominants, with lesser amounts of *Eriophorum scheuchzeri*, *E. triste*, *Dupontia fisheri*, and *Alopecurus alpinus*. Small clumps of *Salix arctica* and *Dryas integrifolia* are restricted to moss hummocks or rocky areas within the wet meadows – the best-drained and best-aerated microsites. Plant communities of this vegetation type occur where drainage is impeded along river terraces, small valleys, and coastal lowlands (Beschel 1970; Bird 1975; Muc 1977; Thompson 1980; Sheard and Geale 1983; Freedman et al. 1983; Bliss and Svoboda 1984; Muc et al. 1989; Schaefer and Messier 1994). In the northwestern islands, including northern Melville Island, the grass *Dupontia fisheri* dominates (Fig. 1.9), with lesser amounts of *Juncus biglumis* and *Eriophorum triste* in wetlands. Where there are shallow ponds, *Pleuropogon sabinei* occurs – the ecological equivalent of *Arctophila fulva* to the south (Savile 1961; Bliss and Svoboda 1984).

Bryophytes are abundant in the various wetland plant communities, including *Orthothecium chryseum*, *Campylium arcticum*, *Tomenthypnum nitens*, *Drepanocladus revolvens*, *Ditrichum flexicaule*, and *Cinclidium arcticum*. Cyanobacteria are abundant, including species of *Nostoc* and *Oscillatoria*. Lichens are minor in these wetlands.

Dwarf shrub heath tundra. Compared with the Low Arctic, these heaths have few species, and they are almost always in snowbed sites that melt by early July. The heaths of central and northern Baffin Island are richer floristically than elsewhere. *Cassiope tetragona* is the dominant and characteristic species and is commonly associated with *Vaccinium uliginosum* ssp. *microphyllum*, *Salix herbacea*, *S. arctica*, *Carex bigelovii*, *Luzula nivalis*, and *L. confusa*. Important lichens and mosses include *Cladina mitis*, *Dactylina arctica*, *Aulacomnium turgidum*, *Drepanocladus uncinatus*, *Hylocomium splendens*, and *Rhacomitrium lanuginosum* (Polunin 1948).

Heath vegetation is sparse in western Greenland in terms of species and areal extent. *Cassiope* dominates, with lesser amounts of *Salix arctica*, *Dryas integrifolia*, and *Luzula confusa* (Sørensen 1943). Small areas of heath with *Cassiope*, *Dryas*, and *Salix* occur in northern Greenland at 81–83; dg N (Holmen, 1957).

Farther north and west in the Queen Elizabeth Islands, the depauperate heaths are dominated by *Cassiope*, *Dryas*, and *Luzula*. Only in the warmer eastern High Arctic is *Vaccinium uliginosum* ssp. *microphyllum* present (Fig. 1.10) (Beschel 1970; Brassard and Longton 1970; Bliss, Kerik, and Peterson 1977; Reznicek and Svoboda 1982; Muc et al. 1989). Lichens and mosses are also common in these heaths.

Other tundra vegetation types. Cottongrass tussock and tall shrub tundra occupy small areas on Banks and Victoria islands, the northern limits for these common vegetation types of the Low Arctic. Tussock tundra is dominated by *Eriophorum vaginatum* ssp. *vaginatum*, with scattered plants of *Vaccinium vitis-idaea* ssp. *minus*, the only heath species, and a few other vascular species and cryptogams. Along some of the rivers and near the lakes of these same southern islands, there are small willow thickets (0.5–1.5 m), with *Salix alaxensis* and *S. pul-*

Figure 1.10. Dwarf shrub heath tundra dominated by Cassiope tetragona *with lesser amounts of* Dryas integrifolia, Vaccinium uliginosum *ssp.* microphyllum, *and* Luzula parviflora. *Note the wet sedge-moss meadows beyond, Truelove Lowland, Devon Island.*

chra (Kuc 1974) and in southeastern Victoria Island *S. lanata* ssp. *richardsonii* (Schaefer and Messier 1994).

High Arctic Semidesert

Arctic vegetation and plant communities included within this landscape unit have generally been considered polar desert (Aleksandrova 1980; Andreyev and Aleksandrova 1981). However, in terms of plant cover, plant and animal biomass, species richness, and soil development, the High Arctic semidesert is so different from barren polar deserts that the two have been separated for North America (Bliss 1975, 1981). Areas of polar semidesert cover about 50–55% of the southern islands and about 25% of the northern islands. The two major vegetation types include cushion plant–cryptogam and cryptogam–herb.

Cushion plant–cryptogam vegetation. Large areas of the southern islands and the Boothia and Melville peninsulas are covered with large mats of *Dryas integrifolia*. Associated species include *Salix arctica, Saxifraga oppositifolia, S. caespitosa, S. cernua, Draba corymbosa, Papaver radicatum*, and two to three species each of *Minuartia* and *Stellaria*. Graminoids are always present as scattered plants, including *Carex rupestris, C. nardina, Luzula confusa*, and *Alopecurus alpinus* (Table 1.4). Lichens and mosses provide 30–60% of the total plant cover; vascular plants provide 5–25% of the cover (Fig. 1.11).

This vegetation is common on rolling uplands, gravelly raised beaches, and river terraces that are drier and warmer than surrounding lands in summer. Plant communities of this type have been described from Victoria Island (Schaefer and Messier 1994), Devon Island (Svoboda 1977), Ellesmere Island (Brassard and Longton 1970; Freedman et al. 1983; Muc et al. 1989), Bathurst Island (Sheard and Geale 1983; Bliss, Svoboda, and Bliss 1984), Cornwallis and Somerset islands (Bliss et al. 1984), and South Hampton Island (Reznicek and Svoboda 1982). These landscapes are the major habitats for Peary's caribou, collared lemming, ptarmigan, and several species of passerine birds.

Cryptogam–herb vegetation. This vegetation type is common on the western Queen Elizabeth Islands, where the previous vegetation type is minor or totally lacking. Cryptogam–herb vegetation covers low rolling uplands with sandy to silty and clay loam soils. Vascular plants contribute 5–20% cover and cryptogams 50–80%.

Alopecurus alpinus, Luzula confusa, and *L. nivalis* are the common graminoids, along with three to five species of *Saxifraga, Papaver radicatum, Draba corymbosa, Cerastium alpinum*, and *Juncus albescens* (Table 1.4). Abundant bryophytes include the mosses *Rhacomitrium lanuginosum, R. sudeticum, Aulacomnium turgidum, Polytrichum juniperinum, Pogonatum alpinum, Ditrichum flexicaule, Dicranoweisia crispa, Tomenthypnum nitens*, and *Schistidium holmenianum*, and in wetter soils, the liverwort *Gymnomitrion corallioides*. Common lichens include crustose *Lecanora epibryon, Lepraria neglecta*, and *Dermatocarpon hepaticum*, and fruticose *Cladonia gracilis, Parmelia omphalodes, Cetraria cucullata, C. delisei, C. nivalis*, and *Dactylina ramulosa*. There is often a black cryptogamic crust of lichens, mosses, cyanobacteria, and fungi on soils (Bliss and Svoboda 1984). Seeds of vascular plants germinate at random on a variety of microsite surfaces, but their survival to adult plants is strongly favored by moss mats or desiccation cracks where mosses are also

Table 1.4. Prominence values (cover × square root of frequency) for plant communities in the High Arctic. Sampling area for each stand was 40 m^{-2}.

	Plant communities				
Species	Cushion plant 31S	Cryptogam-herb 4M	Graminoid-steppe 27ER	Snowflush 12C	Herb barrens 19C
Dryas integrifolia	28	—	—	—	—
Saxifraga oppositifolia	8	—	—	4	—
Saxifraga caespitosa	—	11	—	1	—
Saxifraga hieracifolia	—	9	—	—	—
Saxifraga cernua	—	10	—	1	—
Saxifraga flagellaris	—	17	—	9	—
Phippsia algida	—	—	—	—	—
Papaver radicatum	—	14	—	6	2
Cerastium alpinum	—	4	—	—	—
Oxyria digyna	—	7	—	—	—
Ranunculus sulphureus	—	4	—	—	—
Minuartia rubella	—	3	—	—	—
Stellaria crassipes	—	6	—	—	—
Draba corymbosa	—	2	—	5	9
Draba subcapitata	—	1	—	—	—
Festuca brachyphylla	—	14	—	—	—
Alopecurus alpinus	—	37	20	—	—
Puccinellia angustata	—	—	—	—	6
Luzula confusa	—	6	81	—	—
Luzula nivalis	—	5	2	—	—
Mosses	—	116	76	66	—
Lichens	22	41	24	14	—
Total vascular species	6	19	4	14	5

Note: Sampling area for each stand was 40 m^2.
Source: Data from Bliss and Svoboda (1984) and Bliss et al. (1984).

Figure 1.11. Cushion plant–cryptogam vegetation of the polar semideserts. Dryas-dominated community with lesser amounts of Saxifraga oppositifolia, *and* Salix arctica *with* Cassiope tetragona *in the small depressions, Thomson River, Banks Island.*

important (Sohlberg and Bliss 1984). Plant communities within this vegetation type have been described from Axel Heiberg Island (Beschel 1970), Melville, Cameron, King Christian, and Ellef Ringnes islands (Bliss and Svoboda 1984), Laugheed Island (Edlund 1980), and Prince Patrick Island (Bird 1975).

Graminoid steppe. Large areas of fine sand to clay loam soils are dominated by *Luzula confusa* and *Alopecurus alpinus* on Ellef Ringnes and King Christian islands which is seen in Figure 1.12. Other areas on Melville, Laugheed, King Christian, and Ellef Ringnes islands are dominated by *A. alpinus*

Figure 1.12. Luzula confusa *and* Alopecurus alpinus *dominate this graminoid steppe on Ellef Ringnes Island.*

on black soils derived from shales of the Lower Cretaceous age. There are very few herbs or cryptogams associated with *Alopecurus* (Bliss and Svoboda 1984). This great reduction in species richness may result from soil churning, which is so common in these dark soils, as well as low nutrient status. *Alopercurus* is rhizomatous and can tolerate soil movement.

High Arctic Polar Desert

Herb barrens. Landscapes that are almost totally devoid of plants occupy thousands of square kilometers, especially in the Queen Elizabeth Islands (Fig. 1.13A). These landscapes occur from near sea level (10–20 m) to upland plateaus at over 200–300 m. The basic controls appear to be the geologic substrate (which influences soil development), the very low amount of soil nutrients, formation of needle ice in autumn, surface soil drying (1–2 cm) in many summers, and a very short growing season (1–1.5 mo). Soil texture ranges from medium-grained sands to silt loams. In many areas there is a thin veneer of rocks that covers much of the surface, reducing the area of safe sites for plant establishment. In other areas there is at least 30–70% open soil.

Woody or semiwoody species are very rare in these barren landscapes, where rosette (*Draba*), cushion (*Saxifraga*), and mat-forming (*Puccinellia*) species predominate. In a study of 23 barren sites on six islands, a total of 17 vascular species and 14 species of cryptogams were found, with a mean species richness of 9 per site (60 m^2). Vascular plant cover averaged 1.8% and cryptogams 0.7%; the remaining 97.5% was bare soil, frost-shattered rocks, and pebbles (Fig. 1.13B). Most vascular plants were found in desiccation cracks or adjacent to stones within the polygonal patterns (sorted nets and stripes). Cryptogams were seldom present in close association with vascular plants, in contrast to polar semidesert and snowflush habitats within this barren landscape, where moss mats and cryptogamic crusts are preferred sites for vascular plants. Of the vascular plants recorded, *Draba corymbosa, D. subcapitata, Papaver radicatum, Minuartia rubella, Saxifraga oppositifolia,* and *Puccinellia angustata* were most commonly present (Table 1.4). The most important cryptogams were *Hypnum bambergeri, Tortula ruralis, Thamnolia subuliformis, Dermatocarpon hepaticum,* and *Lecanora epibryon* (Bliss et al. 1984). The lack of lichens on rocks and the very depauperate flora and plant cover suggest that these lands, especially uplands, may have become vegetated only since the Little Ice Age (130–430 yr BP) (Svoboda 1982).

Not all uplands in the High Arctic constitute true polar deserts. The uplands above Alexandra Fiord, Ellesmere Island, are much richer in vascular (37), bryophyte (22), and lichen (23) species than other comparable sites (Batten and Svoboda 1994). *Saxifraga oppositifolia, Luzula confusa,* and *L. nivalis* dominated at 520–920 m elevation with three sites having limited amounts of *Salix arctica.* Large mats of *S. arctica* were sampled at 525–530 m on the western plateau (Batten and Svoboda 1994; Bliss, Henry, Svoboda, and Bliss 1994) as well as populations of *Cassiope tetragona* and *Dryas integrifolia* above 500 m. Cryptogamic crusts indicating higher surface moisture levels in some sites and higher temperatures due to dark rock surfaces receiving reflected radiation off the nearby glaciers (Labine 1994) are important factors that account for the presence of woody species and a richer flora than is typical of most polar deserts (Bliss et al. 1984; Bliss et al. 1994).

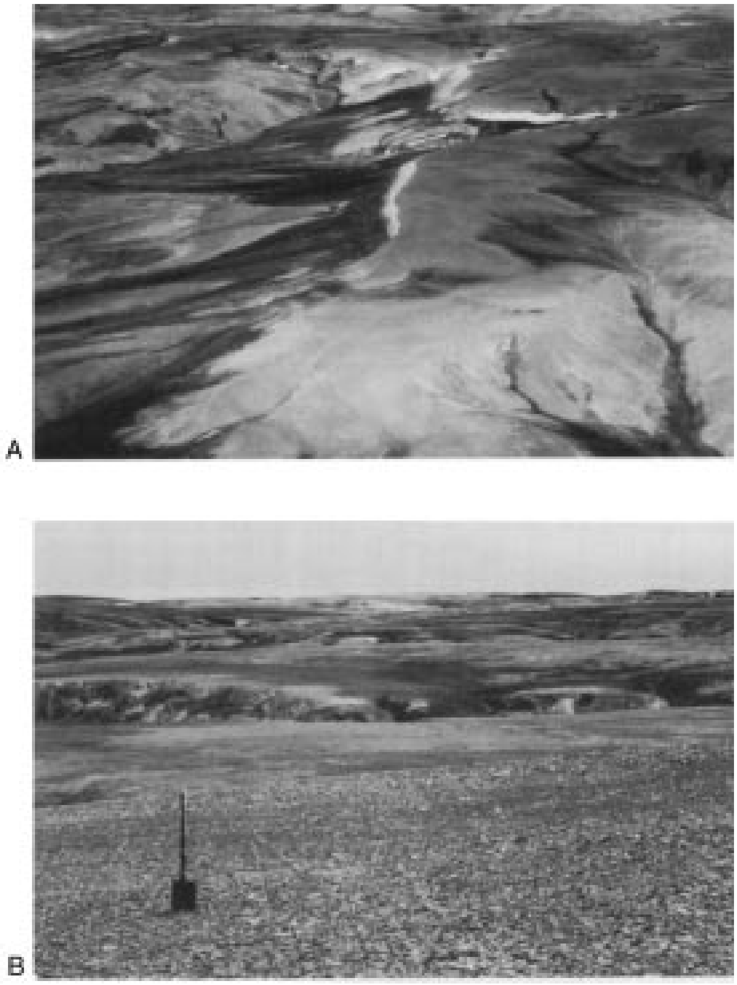

Figure 1.13. (A) Aerial view of a polar desert landscape on Prince Patrick Island. The darker areas are snowflush communities with an abundance of mosses and a few vascular plants. (B) Polar desert barrens on Ellef Ringnes Island, with 1–2% cover of Papaver radicatum *and* Puccinella angustata.

Snowflush community. Within the polar barrens, the only habitats that have significant plant cover are those below large snowbanks and snowfields. The meltwaters, present part of the summer, enable the development of cryptogamic crusts and moss mats in which flowering plants become established. Although snowflush communities occupy only 3–5% of the landscape, they are very conspicuous features when present. Species richness was found to be much greater in these habitats (30 species of vascular plants and 27 species of cryptogams) at 12 sites (60 m^2) on three islands (Bliss et al. 1984). Plant cover was also much greater in these habitats (vascular plants 9.5%, bryophytes 18.5%, and lichens 8.2%) than in the herb barrens (Table 1.4).

Plant composition can be quite variable, with graminoid-dominated meadows in some sites (*Eriophorum triste, Alopecurus alpinus*) and herbs (*Saxifraga oppositifolia, S. cernua, Papaver radicatum, Draba corymbosa, Minuartia rubella*, and *Stellaria longipes*) in others. The polygonal troughs and stripes contain *Orthothecium chryseum, Ditrichum flexicaule*, and *Drepanocladus revolvens*, and nearly all vascular plants are restricted to these moss mats or cryptogamic crusts (Fig. 1.14). These microsites always contain cyanobacteria and thus have the ability to fix nitrogen. Few species other than *Phippsia algida, Alopecurus alpinus, Papaver radicatum, Cerastium alpinum*, and *Stellaria longipes* occur in the large areas of bare soil.

PLANT COMMUNITY DYNAMICS

Succession–Low Arctic

Primary succession. Plant succession has received less attention in the arctic literature, for it is not a conspicuous feature. Natural disturbances (fire, massive erosion, permafrost melt, glacier retreat)