Chapter 7

Arctic Tundra and Polar Desert Ecosystems

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Summary

The dominant response of current arctic species to climate change, as in the past, is very likely to be relocation rather than adaptation. Relocation possibilities vary according to region and geographic barriers. Some changes are occurring now.

Some groups such as mosses, lichens, and some herbivores and their predators are at risk in some areas, but productivity and number of species is very likely to increase. Biodiversity is more at risk in some ACIA regions than in others: Beringia (Region 3) has a higher number of threatened plant and animal species than any other ACIA region.

Changes in populations are triggered by trends and extreme events, particularly winter processes.

Forest is very likely to replace a significant proportion of the tundra and this will have a great effect on the composition of species. However, there are environmental and sociological processes that are very likely to prevent forest from advancing in some locations.

Displacement of tundra by forest will lead to a decrease in albedo, which will increase the positive feedback to the climate system. This positive feedback is likely to dominate over the negative feedback of increased carbon sequestration. Forest development is very likely to also ameliorate local climate, for example, by increasing temperature.

Warming and drying of tundra soils in parts of Alaska have already changed the carbon status of this area from sink to source. Although other areas still maintain their sink status, the number of source areas currently exceeds the number of sink areas. However, geographic representation of research sites is currently small. Future warming of tundra soils is likely to lead to a pulse of trace gases into the atmosphere, particularly from disturbed areas and areas that are drying. It is not known if the circumpolar tundra will be a carbon source or sink in the long term, but current models suggest that the tundra is likely to become a weak sink for carbon because of the northward movement of vegetation zones that are more productive than those they displace. Uncertainties are high.

Rapid climate change that exceeds the ability of species to relocate is very likely to lead to increased incidence of fires, disease, and pest outbreaks.

Enhanced carbon dioxide concentrations and ultraviolet-B radiation levels affect plant tissue chemistry and thereby have subtle but long-term impacts on ecosystem processes that reduce nutrient cycling and have the potential to decrease productivity and increase or decrease herbivory.

7.1. Introduction

The Arctic is generally recognized as a treeless wilderness with cold winters and cool summers. However, definitions of the southern boundary vary according to environmental, geographic, or political biases. This chapter focuses on biota (plants, animals, and microorganisms) and processes in the region north of the northern limit of the closed forest (the taiga), but also includes processes occurring south of this boundary that affect arctic ecosystems. Examples include animals that migrate south for the winter and the regulation of the latitudinal treeline. The geographic area defined in this chapter as the present-day Arctic is the area used for developing scenarios of future impacts: the geographic area of interest will not decrease under a scenario of replacement of current arctic tundra by boreal forests.

7.1.1. Characteristics of arctic tundra and polar desert ecosystems

The southern boundary of the circumpolar Arctic as defined in this chapter is the northern extent of the closed boreal forests (section 14.2.3). This is not a clear boundary but a transition from south to north consisting of the sequence: closed forest, forest with patches of tundra, tundra with patches of forest, and tundra. The transition zone is relatively narrow (30 to 150 km) when compared to the width of the forest and tundra zones in many, but not all areas. Superimposed on the latitudinal zonation of forest and tundra is an altitudinal zonation from forest to treeless areas to barren ground in some mountainous regions of the northern taiga. The transition zone from taiga to tundra stretches for more than 13400 km around the lands of the Northern Hemisphere and is one of the most important environmental transition zones on Earth (Callaghan et al., 2002a,b) as it represents a strong temperature threshold close to an area of low temperatures. The transition zone has been called forest tundra, subarctic, and the tundra–taiga boundary or ecotone.
The vegetation of the transition zone is characterized by an open landscape with patches of trees that have a low stature and dense thickets of shrubs that, together with the trees, totally cover the ground surface.

The environmental definition of the Arctic does not correspond with the geographic zone delimited by the Arctic Circle (66.5° N), nor with political definitions. Cold waters in ocean currents flowing southward from the Arctic depress the temperatures in Greenland and the eastern Canadian Arctic whereas the northward-flowing Gulf Stream warms the northern landmasses of Europe (section 2.3). Thus, at the extremes, polar bears and tundra are found at 51° N in eastern Canada whereas agriculture is practiced north of 69° N in Norway. Arctic lands span some 20° of latitude, reaching 84° N in Greenland and locally, in eastern Canada, an extreme southern limit of 51° N.

The climate of the Arctic is largely determined by the relatively low solar angles with respect to the earth. Differences in photoperiod between summer and winter become more extreme toward the north. Beyond the Arctic Circle, the sun remains above the horizon at midnight on midsummer's day and remains below the horizon at midday on midwinter's day.

Climatically, the Arctic is often defined as the area where the average temperature for the warmest month is lower than 10 °C (Köppen, 1931), but mean annual air temperatures vary greatly according to location, even at the same latitude (see Chapter 2). They vary from -12.2 °C at Point Barrow, Alaska (71.3° N) to -28.1 °C at the summit of the Greenland Ice Sheet (about 71° N) (Weller, 2000) and from 1.5 °C at 52° N in subarctic Canada to 8.9 °C at 52° N in temperate Europe. The summer period, or period of most biological activity, progressively decreases from about 3.5 to 1.5 months from the southern boundary of the Arctic to the north, and mean July temperature decreases from 10–12 °C to 1.5 °C. In general, annual precipitation in the Arctic is low, decreasing from about 250 mm in southern areas to as low as 45 mm in the northern polar deserts (Jonasson et al., 2000), with extreme precipitation amounts in subarctic maritime areas (e.g., 1100 mm at 68° N in Norway). However, owing to low rates of evaporation the Arctic cannot be considered arid: even in the polar deserts, air humidity is high and the soils are moist during the short growth period (Bovis and Barry, 1974). In the Arctic context, "desert" refers to extreme poverty of life.

The Arctic is characterized by the presence of continuous permafrost (section 6.6.1), although there are exceptions such as the Kola Peninsula. Continuous and deep (>200 m) permafrost also exists south of the treeline in large areas of Siberia extending south to Mongolia. The depth of the active (seasonally frozen) layer of the soil during the growing season depends on summer temperatures and varies from about 80 cm near the treeline to about 40 cm in polar deserts. However, active-layer depth varies according to local conditions within landscapes according to topography: it can reach 120 cm on south-facing slopes and be as little as 30 cm in bogs even in the southern part of the tundra zone. In many areas of the Arctic, continuous permafrost occurs at greater depths beneath the soil surface and degrades into discontinuous permafrost in the southern part of the zone. Active-layer depth, the extent of discontinuous permafrost, and coastal permafrost are very likely to be particularly sensitive to climatic warming (section 6.6). Permafrost and active-layer dynamics lead to topographic patterns such as polygons in the landscape. Topography plays an important role in defining habitats in terms of moisture and temperature as well as active-layer dynamics (Brown et al., 1980; Webber et al., 1980), such that arctic landscapes are a mosaic of microenvironments. Topographic differences of even a few tens of centimeters (e.g., polygon rims and centers) are important for determining habitats, whereas larger-scale topographic differences (meters to tens of meters) determine wind exposure and snow accumulation that in turn affect plant communities and animal distribution. Topographic differences become more important as latitude increases.

Disturbances of ecosystems are characteristic of the Arctic. Mechanical disturbances include thermokarst induced by permafrost thaw (section 6.6.1); freeze–thaw processes; wind, sand, and ice blasts; seasonal ice oscillations; slope processes; snow load; flooding during thaw; changes in river volume; and coastal erosion and flooding. Biological disturbances include insect pest outbreaks, peaks of grazing animals that have cyclic populations, and fire. These disturbances operate at various spatial and temporal scales (Fig. 7.1) and affect the colonization and survival of organisms and thus ecosystem development.

Arctic lands are extensive beyond the northern limit of the tundra–taiga ecotone, encompassing an area of approximately 7 567 000 km^2, including about

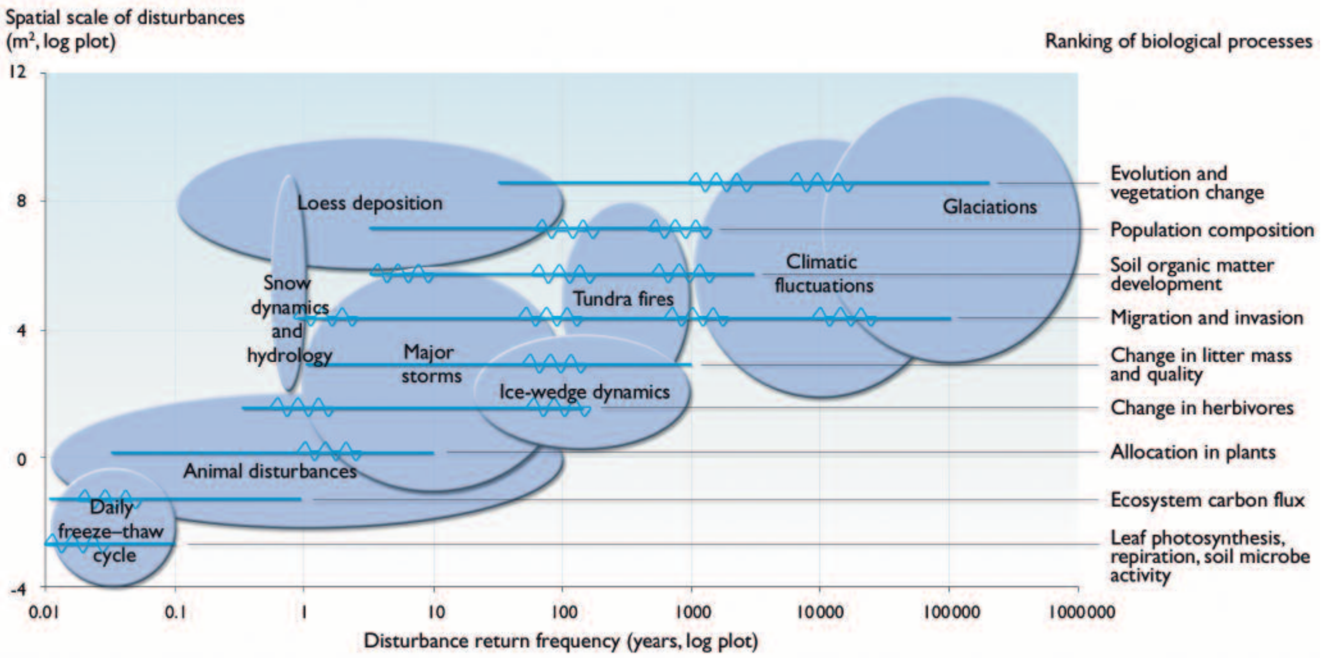


Fig. 7.1. Timescale of ecological processes in relation to disturbances (shown as breaks in horizontal lines) in the Arctic. The schematic does not show responses projected as a result of anthropogenic climate change (based on Oechel and Billings, 1992; Shaver et al., 2000; Walker D. and Walker, 1991).

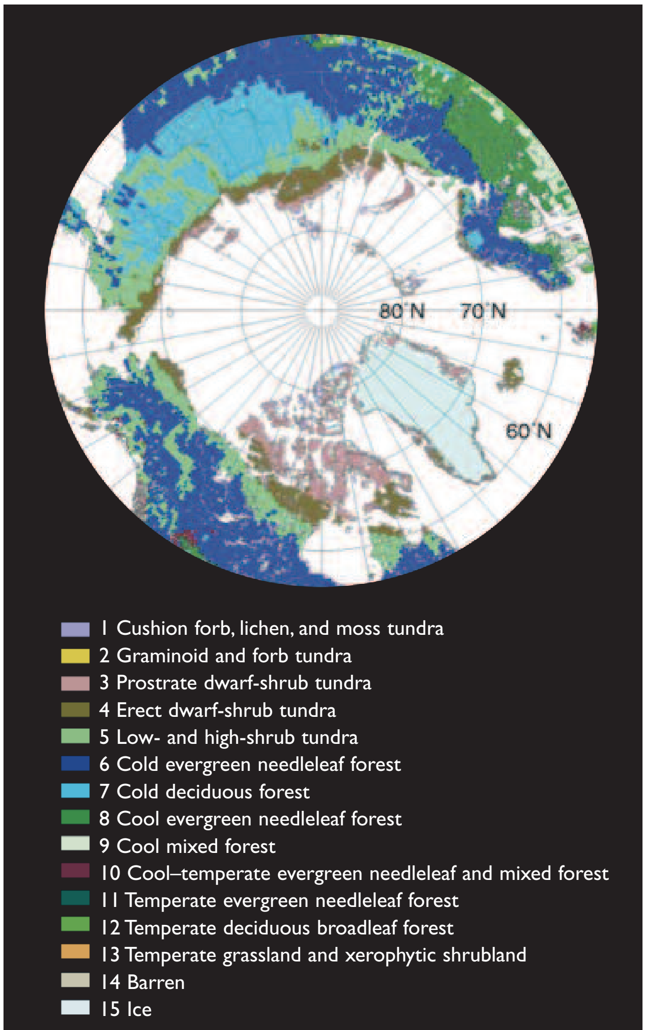


Fig. 7.2. Present-day natural vegetation of the Arctic and neighboring regions from floristic surveys. Vegetation types 1 to 5 are classified as arctic, whereas types 6 to 8 are classified as boreal forest (Kaplan et al., 2003).

2 560 000 km^2 in the former Soviet Union and Scandinavia, 2 480 000 km^2 in Canada, 2 167 000 km^2 in Greenland and Iceland, and 360 000 km^2 in Alaska (Bliss and Matveyeva, 1992). Figure 7.2 shows the distribution of arctic and other vegetation types based on a classification by Walker D. (2000) and mapped by Kaplan et al. (2003). The distribution of arctic landmasses is often fragmented: seas separate large arctic islands (e.g., Svalbard, Novaya Zemlya, Severnaya Zemlya, New Siberian Islands, and Wrangel Island) and the landmasses of the Canadian Archipelago and Greenland. Similarly, the Bering Strait separates the arctic lands of Eurasia and North America. Large mountains such as the east–west running Brooks Range in Alaska and the Putorana Plateau in Siberia separate tundra and taiga. Such areas of relief contain outposts of boreal species on their southern major slopes that are likely to expand northward and higher-elevation areas that are likely to act as refuges for arctic-alpine species. The Taymir Peninsula is the only continuous landmass that stretches 900 km from the northern tundra limit to taiga without geographic barriers to the dispersal of animals and plants (Matveyeva and Chernov, 2000). The width of the tundra zone varies greatly in different parts of its circumpolar distribution. On average, it does not exceed 300 km, and in some regions (e.g., the lower reaches of the Kolyma River), the tundra zone extends only 60 km from the treeline to the coast. In such areas, the tundra zone is very likely to be highly vulnerable to climate warming.

The vegetation of the Arctic varies from forest tundra in the south, where plant communities have all the plant life forms known in the Arctic and have continuous canopies in several layers extending to more than 3 m high, to polar deserts in the north, where vegetation colonizes 5% or less of the ground surface, is less than 10 cm high, and is dominated by herbs, lichens (symbionts of algae and fungi), and mosses (Fig. 7.3). Species richness in the Arctic is low and decreases toward the north: there are about 1800 species of vascular plants, 4000 species of cryptogams, 75 species of terrestrial mammals, 240 species of terrestrial birds, 3000 species of fungi, 3300 species of insects (Chernov, 2002; Matveyeva and Chernov, 2000), and thousands of prokaryotic species (bacteria and Archaea) whose diversity in the tundra has only recently started to be estimated. However, the Arctic is an important global pool of some groups such as mosses, lichens, springtails (and insect parasitoids: Hawkins, 1990; Kouki et al., 1994, Price et al., 1995) because their abundance in the Arctic is higher than in other biomes. Net primary production (NPP), net ecosystem production (NEP), and decomposition rates are low. Food chains are often short and typically there are few representatives at each level of the chain. Arctic soils are generally shallow and underdeveloped with low productivity and immature moor-type humus (Brown et al., 1980). Substantial heterogeneity of the soil cover, owing to numerous spatial gradients, has an important influence on the microtopographical distribution of the soil biota (invertebrates, fungi, and bacteria) that will possibly amplify any negative effects of climate change.

The Arctic has a long history of human settlement and exploitation, based initially on its rich aquatic biological resources and more recently on its minerals and fossil hydrocarbons. At the end of the last glacial stage, humans migrated from Eurasia to North America across the ice-free Bering land bridge and along the southern coast of Beringia (ca. 14 000–13 500 years BP; Dixon, 2001). As early as about 12 200 years BP, areas north of the Fennoscandian Ice Sheet in northernmost Finnmark (Norway) had been settled (Thommessen, 1996). Even earlier Paleolithic settlements (ca. 40 000 years BP) have been recorded in the eastern European Arctic (Pavlov et al., 2001). The impacts of these peoples on terrestrial ecosystems are difficult to assess but were probably small given their small populations and "hunter-gatherer" way of life. The prey species hunted by these peoples included the megafauna, such as the woolly mammoth, which became extinct. The extent to which hunting may have been principally responsible for these extinctions is a matter of continuing debate (Stuart et al., 2002) but this possibility cannot be excluded (Alroy, 2001). It is also uncertain to what extent the extinction of the megafauna may have contributed to, or been at least partly a result

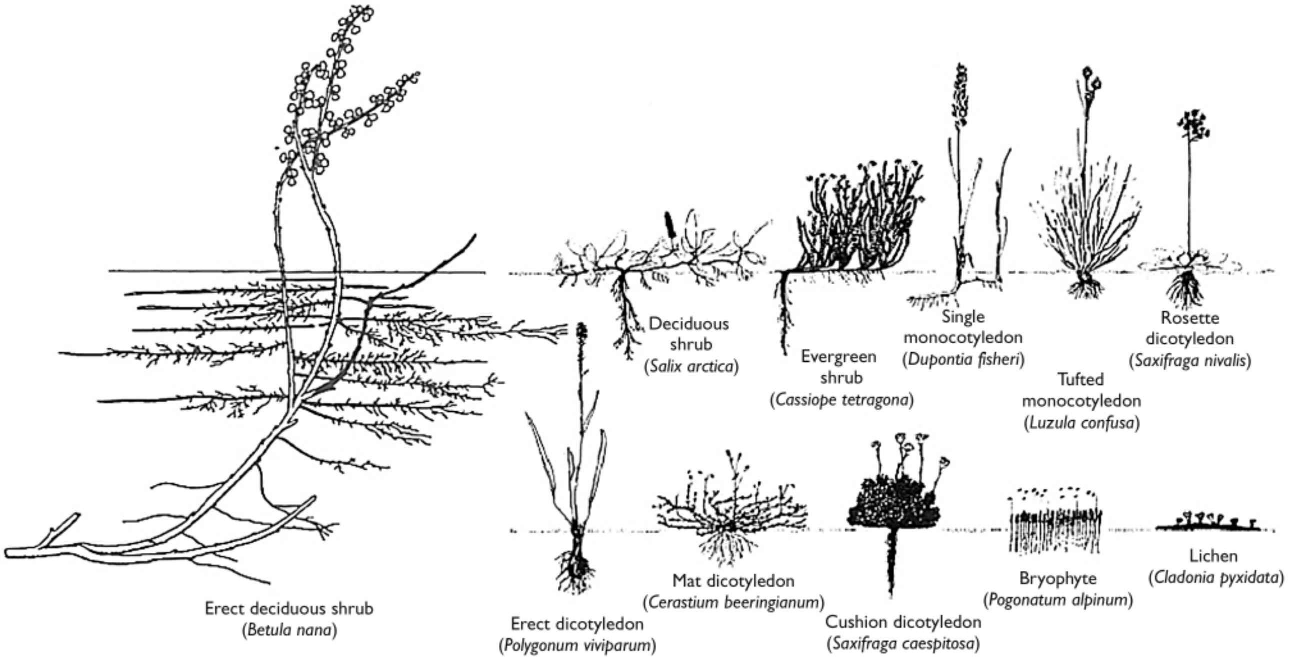


Fig. 7.3. Growth forms of arctic plants (modified from Webber et al., 1980 and T. Polozova, pers. comm., 2005).

of, the accelerated northward movement of trees and shrubs and consequent changes in vegetation structure (section 7.2). Although estimates of the population density of megafaunal species have large uncertainties, it seems unlikely that megafaunal populations were sufficient to constrain the spread of woody taxa in response to favorable environmental change.

During the last 1000 years, resources from terrestrial ecosystems have been central to the mixed economies of the Arctic: many inland indigenous communities still derive most of their protein from subsistence activities such as caribou/reindeer hunting (Berkes and Fast, 1996). During this period, increasing trade between peoples of temperate latitudes and arctic indigenous peoples is likely to have affected a few target animal species, such as the reindeer that was domesticated in Fennoscandia and Russia, ermine hunted for fur, and birds of prey used for hunting as far away as the eastern Mediterranean. However, the most dramatic impacts occurred after World War II as a result of the exploitation of minerals and oil and fragmentation of the arctic landscape by infrastructure (Nellemann et al., 2001). Vlassova (2002) suggested that industrial activities and forestry have displaced the Russian forest tundra southward by deforesting 470 000 to 500 000 km^2 of land that now superficially resembles tundra. Although this estimate has been challenged as greatly exaggerated (because northern taiga areas have been included in that estimate's definition of forest tundra), such effects have occurred locally in the Yamal Peninsula and the estimate highlights a need for reappraisal. Knowledge of possible past interactions between humans and the environment that may have shaped present-day arctic ecosystems is limited, but shows that any future increases in population density and human activity are likely to modify the projected responses of arctic ecosystems to changes in climate and ultraviolet (UV) radiation levels.

7.1.2. Raison d'être for the chapter

The Arctic is experiencing dramatic environmental changes that are likely to have profound impacts on arctic ecosystems. The Arctic is outstanding among global biomes in that climate change dominates the major factors affecting biodiversity (Sala and Chapin, 2000). Present-day arctic biota are also relatively restricted in range and population size compared with their Quaternary situation. For example, when the treeline advanced northward during the early Holocene warming, a lowered sea level allowed a belt of tundra to persist around the Arctic Basin, whereas any future northward migration of the treeline is very likely to further restrict tundra areas because sea level is projected to rise. Arctic ecosystems are known to be vulnerable to disturbances (Crawford, 1997b; Forbes et al., 2001; Walker D. and Walker, 1991) and to have long recovery times: subarctic birch forest defoliated by insects can take 70 years to recover (Tenow and Bylund, 2000). Current and projected environmental changes are likely to create additional stresses and decrease the potential for ecosystem recovery from natural disturbances, while providing thresholds for shifts to new states (e.g., disturbance opening gaps for invasion of species new to the Arctic).

Changes in arctic ecosystems and their biota are important to arctic residents in terms of food, fuel, and culture (Chapter 12) and are likely to have global impacts because of the many linkages between the Arctic and more southerly regions. Several hundreds of millions of birds migrate to the Arctic each year and their success in the Arctic determines their success and impacts at lower latitudes (section 7.3.1.2). Physical and biogeochemical processes in the Arctic affect atmospheric circulation and the climate of regions outside of the Arctic (section 7.5). It is known that ecosystems have responded to past environmental changes (section 7.2) and that environmental changes are presently occurring in the Arctic (Chapman and Walsh, 1993 as quoted in Weller, 2000; Dye, 2002; Fioletov et al., 1997; Chapters 2, 5, and 6). This understanding indicates that there are very likely to be responses of arctic ecosystems to projected future and ongoing climate change. It is also known that current levels of ultraviolet-B (UV-B) radiation, as well as higher levels, can affect subarctic plants (Gwynn-Jones et al., 1997; Johanson et al., 1995; Phoenix et al., 2000). Arctic plants may be particularly sensitive to increases in UV-B irradiance because UV-B radiation damage is not dependent on temperature whereas enzyme-mediated repair of DNA damage could be constrained by low temperatures (Björn, 2002; Li et al., 2002a,b; Paulsson, 2003).

For all of these reasons, understanding the relationships between ecosystems and the arctic environment is important. Although many aspects of its environment are changing concurrently (e.g., climate, pollution, atmospheric nitrogen deposition, atmospheric concentrations of carbon dioxide (CO_2), UV-B radiation levels, and land use), the specific mission of this chapter is to focus on the impacts of changes in climate and UV-B radiation levels on arctic terrestrial ecosystems and their species and processes.

7.1.3. Rationale for the structure of the chapter

The effects of climate are specific to species, the age and developmental stages of individuals, and processes from metabolism to evolution (Fig. 7.1). Although there are many ways in which to organize an assessment of climate and UV-B radiation impacts, this chapter follows a logical hierarchy of increasing organizational biological complexity to assess impacts on species, the structure of ecosystems, the function of ecosystems, and landscape and regional processes. A basic understanding of biological processes related to climate and UV-B radiation is required before the impacts of changes in these factors on terrestrial ecosystems can be assessed (Smaglik, 2002). Consequently, this chapter progresses from a review of climate and UV radiation controls on biological processes to an assessment of the potential impacts of changes in climate and UV-B radiation levels on processes at the species and regional levels. Some effects of climate change on ecosystems may be beneficial to humans, while others may be harmful.

The changes in climate and UV-B radiation levels that are used in this chapter to assess biological impacts are of two types: those already documented (section 2.6) and those projected by scenarios of future change in UV-B radiation levels (section 5.7) and climate (section 4.4) derived from models. Mean annual and seasonal temperatures have varied considerably in the Arctic since 1965 (Chapman and Walsh, 1993 as quoted in Weller, 2000; section 2.6.2.1). Mean annual temperatures in western parts of North America and central Siberia have increased by about 1 ºC (up to 2 ºC in winter) per decade between 1966 and 1995 while temperatures in West Greenland and the eastern Canadian Arctic have decreased by 0.25 to 1 ºC per decade (Chapman and Walsh, 1993, quoted in Weller, 2000). Over a longer period, from 1954 to 2003, the annual increase and decrease in temperatures have been slightly less: about 2 to 3 ºC for the whole period (Chapter 1, Fig. 1.3). Temperature increases in Fennoscandia over the past century have been small, ranging from about 1 ºC in the west to near 0 ºC in the east (Lee et al., 2000).

Precipitation has also changed. The duration of the snow-free period at high northern latitudes increased by 5 to 6 days per decade and the week of the last observed snow cover in spring advanced by 3 to 5 days per decade between 1972 and 2000 (Dye, 2002). Stratospheric ozone has been depleted over recent decades (e.g., by a maximum of 45% below normal over the high Arctic in spring; Fioletov et al., 1997). This has probably led to an increase in surface UV-B radiation levels in the Arctic, although the measurement period is short (section 5.5). Scenarios of future change project that mean annual temperatures in the Arctic will increase by nearly 4 ºC by 2080 (section 4.4.2) and that spring (April) UV-B radiation levels will increase by 20 to 90% in much of the Arctic by 2010–2020 (Taalas et al., 2000).

The assessment of impacts on terrestrial ecosystems presented in this chapter is based on existing literature rather than new research or ACIA modeling activities. Existing long-term experimental manipulations of temperature and/or UV-B radiation relied on earlier scenarios of climate and UV-B radiation change (IPCC, 1990). However, the most recent scenarios (Chapters 4, 5, and 6) are used to provide a context for the assessment in this chapter, and to modify projections of ecosystem responses based on earlier scenarios where appropriate. The ACIA climate scenarios (section 4.4) are also used directly to illustrate the responses of some species to projected climate changes.

7.1.4. Approaches used for the assessment: strengths, limitations, and uncertainties

This chapter assesses information on interactions between climate, UV-B radiation levels, and ecosystems from a wide range of sources including experimental manipulations of ecosystems and environments in the field; laboratory experiments; monitoring and observation of biological processes in the field; conceptual modeling using past relationships between climate and biota (paleo-analogues) and current relationships between climate and biota in different geographic areas (geographic analogues) to infer future relationships; and process-based mathematical modeling. Where possible, indigenous knowledge (limited to published sources) is included as an additional source of observational evidence. Relevant information from indigenous peoples on arctic tundra and polar desert ecosystems is given in Chapter 3.

Each method has uncertainties and strengths and these are discussed in section 7.7. By considering and comparing different types of information, it is hoped that a more robust assessment has been achieved. However, the only certainties in this assessment are that there are various levels of uncertainty in the projections and that even if an attempt is made to estimate the magnitude of these uncertainties, surprise responses of ecosystems and their species to changes in climate and UV-B radiation levels are certain to occur.

7.2. Late-Quaternary changes in arctic terrestrial ecosystems, climate, and ultraviolet radiation levels

In order to understand the present biota and ecosystems of the Arctic, and to project the nature of their responses to potentially rapid future climate change, it is necessary to examine at least the last 21 000 years of their history. This period, which is part of the late Quaternary Period, extends from the present back to the last glacial maximum (LGM), encompassing the Holocene, or postglacial period, that spans approximately the last 11 400 years. A review of this period of the history of the biota and ecosystems found in the Arctic today also must examine a spatial domain that is not restricted to the present arctic regions. At the LGM, many of these regions were submerged beneath vast ice sheets, whereas many of the biota comprising present arctic ecosystems were found at lower latitudes.

7.2.1. Environmental history

At the LGM, vast ice sheets accumulated not only on many high-latitude continental areas but also across some relatively shallow marine basins. The beds of relatively shallow seas such as the North Sea and Bering Sea were exposed as a result of a global sea-level fall of approximately 120 m, resulting in a broad land connection between eastern Siberia and Alaska and closure of the connection between the Pacific and Arctic Oceans. The reduction in sea level also exposed a broad strip of land extending northward from the present coast of Siberia. Most, if not all, of the Arctic Ocean basin may have been covered by permanent sea ice.

Although details of the extent of some of the ice sheets continue to be a controversial matter (see e.g., Astakhov, 1998; Grosswald, 1988, 1998; Lambeck, 1995; Siegert et al., 1999), it is certain that the majority of land areas north of 60º N were ice-covered. The principal exceptions were in eastern Siberia, Beringia, and Alaska, although there is some geological evidence to suggest that smaller ice-free areas also persisted in the high Arctic, for example in the northernmost parts of the Canadian Archipelago (Andrews, 1987) and perhaps even in northern and northeastern Greenland (Funder et al., 1998). This evidence is supported by recent molecular genetic studies of arctic species; for example, a study of the dwarf shrub *Dryas integrifolia* indicates glacial occurrences in the high Arctic (Tremblay and Schoen, 1999) as well as in Beringia, and a study of the collared lemming *Dicrostonyx groenlandicus* indicates separate glacial populations east and west of the Mackenzie River (Ehrich et al., 2000; Fedorov and Goropashnaya, 1999), the latter most probably in the Canadian Archipelago. The latter conclusion is supported by the phylogeography (relationship between genetic identity and geographic distribution) of the *Paranoplocephala arctica* species complex, a cestode parasite of *Dicrostonyx* spp., indicating that two subclades probably survived the LGM with their host in the Canadian High Arctic (Wickström et al., 2003). More controversial are suggestions that elements of the arctic flora and fauna may have survived the LGM on nunataks (hills or mountains extending above the surface of a glacier) in glaciated areas of high relief such as parts of Greenland, Svalbard, and Iceland (Rundgren and Ingolfsson, 1999). Although a recent molecular genetic study of the alpine cushion plant *Eritrichium nanum* (Stehlik et al., 2001) provides strong evidence for survival of that species on nunataks within the heart of the European Alps, similar studies of arctic species have so far not supported the hypothesis of survival on nunataks in areas such as Svalbard (Abbott et al., 2000) that experienced extreme climatic severity as ice sheets extended to margins beyond the current coast during the LGM.

Direct evidence of the severity of the full glacial climate in the Arctic comes from studies of ice cores from the Greenland Ice Sheet and other arctic ice sheets (section 2.7) that indicate full glacial conditions with mean annual temperatures 10 to 13 ºC colder than during the Holocene (Grootes et al., 1993). Paleotemperature reconstructions based upon dinoflagellate cyst assemblages indicate strong seasonal temperature fluctuations, with markedly cold winter temperatures (de Vernal and Hillaire-Marcel, 2000; de Vernal et al., 2000).

The LGM was, however, relatively short-lived; within a few millennia of reaching their maximum extent many of the ice sheets were decaying rapidly and seasonal temperatures had increased in many parts of the Arctic. Deglaciation was not, however, a simple unidirectional change; instead a series of climatic fluctuations occurred during the period between about 18 000 and 11 400 years BP that varied in intensity, duration, and perhaps also in geographic extent. The most marked and persistent of these fluctuations, the Younger Dryas event (Alley, 2000; Peteet, 1993, 1995), was at least hemispheric in its extent, and was marked by the reglaciation of some regions and readvances of ice-sheet margins in others. Mean annual temperatures during this event fell substantially; although not as low as during the glacial maximum, they were nonetheless 4 to 6 ºC cooler than at present over most of Europe (Walker M.J., 1995), and as much as 10 to 12 ºC colder than at present in the northern North Atlantic and the Norwegian Sea (Koç et al., 1996), as well as in much of northern Eurasia (Velichko, 1995). The end of the Younger Dryas was marked by a very rapid rise in temperatures. At some locations, mean annual temperature rose by more than 5 ºC in less than 100 years (Dansgaard et al., 1989). The most rapid changes probably were spatially and temporally transgressive, with the global mean change thus occurring much less rapidly. Nonetheless, in many areas summer temperatures during the early Holocene rose to values higher than those at present. Winter conditions remained more severe than today in many higher-latitude areas, however, because the influence of the decaying ice sheets persisted into the early millennia of the Holocene.

Despite higher summer temperatures in the early to mid-Holocene in most of the Arctic, Holocene climate has not differed qualitatively from that at present. Following the general thermal maximum there has been a modest overall cooling trend throughout the second half of the Holocene. However, a series of millennial and centennial fluctuations in climate have been superimposed upon these general longer-term patterns (Huntley et al., 2002). The most marked of these occurred about 8200 years BP and appears to have been triggered by the catastrophic discharge of freshwater into the northern North Atlantic from proglacial lakes in North America (Barber et al., 1999; Renssen et al., 2001). A reduction in strength, if not a partial shutdown, of the thermohaline circulation in the northern North Atlantic and Norwegian Sea was also associated with this event, as well as with the series of less severe climatic fluctuations that continued throughout the Holocene (Bianchi and McCave, 1999).

The most recent of these climatic fluctuations was that of the "Little Ice Age" (LIA), a generally cool interval spanning approximately the late 13th to early 19th centuries (section 2.7.5). At its most extreme, mean annual temperatures in some arctic areas fell by several degrees. Sea ice extended around Greenland and in some years filled the Denmark Strait between Greenland and Iceland (Lamb H.H., 1982; Ogilvie, 1984; Ogilvie and Jonsdottir, 2000; Ogilvie and Jonsson, 2001), the Norse settlement of Greenland died out (Barlow et al., 1997; Buckland et al., 1996), and the population of Iceland was greatly reduced (Ogilvie, 1991; Sveinbjarnardóttir, 1992). Although there was great temporal climate variability (on decadal to centennial timescales) within the LIA, and spatial variability in the magnitude of the impacts, it was apparently a period of generally more severe conditions in arctic and boreal latitudes; the marked impacts upon farming and fisheries (Lamb H.H., 1982) imply similar impacts on other components of the arctic ecosystem. Since the early 19th century, however, there has been an overall warming trend (Overpeck et al., 1997), although with clear evidence of both spatial variability and shorter-term temporal variability (Maxwell, 1997). The magnitude of this recent warming is comparable to that of the warmest part of the Holocene, at least in those parts of the Arctic that have experienced the most rapid warming during the last 30 years or so.

The solar variability thought to be responsible for the LIA, and for other similar centennial to millennial climatic fluctuations, probably also affected the ozone layer and UV-B radiation levels. Ultraviolet-B irradiance at ground level absorbed by DNA could have been between 9 and 27% higher during periods of low solar output (cool periods) than during periods of high solar output (Rozema et al., 2002; see also section 5.4.1).

7.2.2. History of arctic biota

During the LGM, when most land areas in the Arctic were ice-covered, biomes able to support the elements of the arctic biota, including some species that are now extinct, were extensive south of the Fennoscandian Ice Sheet in Europe (Huntley et al., 2003). Similar biomes apparently were extensive south of the Eurasian ice sheets of northern Russia, eastward across Siberia and the exposed seabed to the north, and via Beringia into Alaska and the northern Yukon (Ritchie, 1987), although they were much more restricted south of the Laurentide Ice Sheet in central and eastern North America (Lister and Bahn, 1995). The most extensive and important of these glacial biomes, the steppe–tundra, has been interpreted and referred to by various authors as "tundra–steppe" or "Mammoth steppe" (Guthrie, 2001; Walker D. et al., 2001; Yurtsev, 2001). The vegetation of this biome comprised a no-analogue combination of light-demanding herbaceous and dwarf-shrub taxa that are found today either in arctic tundra regions or in the steppe regions that characterize central parts of both North America and Eurasia (Yurtsev, 2001). Evidence of an abundance of grazing herbivores of large body mass, some extant (e.g., reindeer/caribou – *Rangifer tarandus*; muskox – *Ovibos moschatus*) and others extinct (e.g., giant deer or "Irish elk" – *Megaloceros giganteus*; woolly mammoth – *Mammuthus primigenius*; woolly rhinoceros – *Coelodonta antiquitatis*), associated with this biome suggests that it was much more productive than is the contemporary tundra biome. This productive biome, dominated by non-tree taxa, corresponded to a no-analogue environment that was relatively cold throughout the year, with a growing season short enough to exclude even cold-tolerant boreal trees from at least the majority of the landscape. The "light climate", however, was that of the relatively lower latitudes (as low as 45º N in Europe) at which this biome occurred, rather than that of the present arctic latitudes; the greater solar angle and consequent higher insolation intensities during the summer months probably made an important contribution to the productivity of the biome.

The productive steppe–tundra and related biomes were much more spatially extensive during the last glacial stage than is the tundra biome today (Fig. 7.4). The last glacial stage was thus a time when many elements of the present arctic biota thrived, almost certainly in greater numbers than today. Fossil remains of both arctic plants (see e.g., West, 2000) and mammals (see e.g., FAUNMAP Working Group, 1996; Lundelius et al., 1983; Stuart, 1982) found at numerous locations attest to their widespread distribution and abundance. Similar conclusions have been reached on the basis of phylogeographic studies of arctic-breeding waders (Kraaijeveld and Nieboer, 2000). Species such as red knot (*Calidris canutus*) and ruddy turnstone (*Arenaria interpres*) are

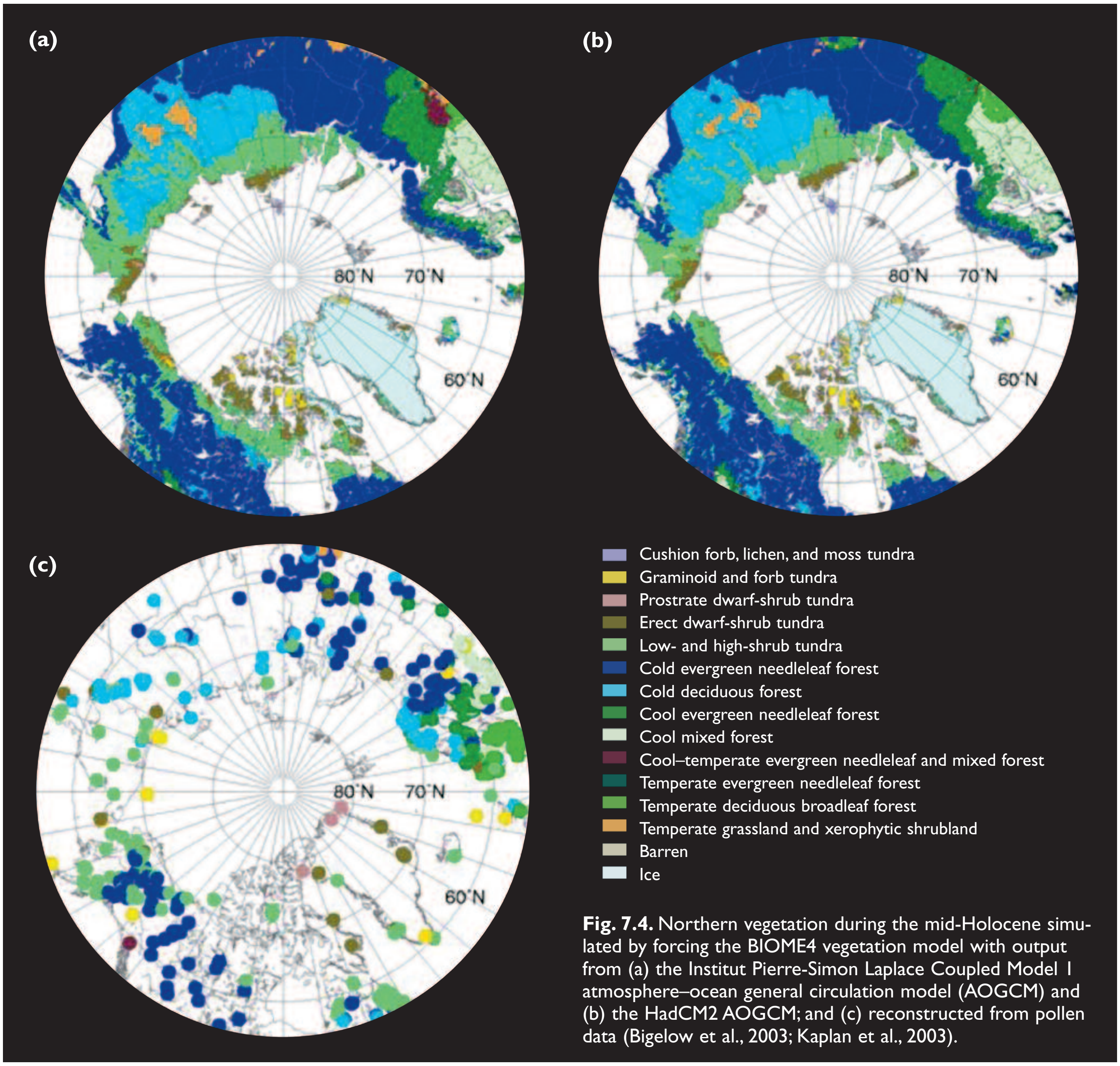


Fig. 7.4. Northern vegetation during the mid-Holocene simulated by forcing the BIOME4 vegetation model with output from (a) the Institut Pierre-Simon Laplace Coupled Model I atmosphere–ocean general circulation model (AOGCM) and (b) the HadCM2 AOGCM; and (c) reconstructed from pollen data (Bigelow et al., 2003; Kaplan et al., 2003).

inferred to have had much larger populations and more extensive breeding areas during glacial stages, although others, such as dunlin (*C. alpina*), exhibit evidence of range fragmentation during glacial stages leading to the evolution of distinct geographically restricted infraspecific taxa. Phylogeographic studies of other arctic taxa show individualistic responses (see Weider and Hobaek, 2000 for a recent review). Some species, such as Arctic char (*Salvelinus alpinus*; Brunner et al., 2001), and genera, such as whitefish (*Coregonus* spp.; Bernatchez et al., 1999), exhibit evidence of sub-taxa whose origins are apparently related to recurrent isolation of populations throughout the alternating glacial and interglacial stages of the Pleistocene. Collared lemmings (*Dicrostonyx* spp.), however, apparently parallel *C. alpina* in exhibiting genetic differentiation principally as a consequence of the relatively recent geographic isolation of populations during the last glacial stage (Fedorov and Goropashnaya, 1999; Fedorov et al., 1999b). Other species, such as the polar bear (*Ursus maritimus*; Paetkau et al., 1999), exhibit little or no evidence of genetic differentiation that might indicate past population fragmentation, and Fedorov et al. (1999a) inferred that Eurasian true lemmings (*Lemmus* spp.) experienced no effective reduction in population size during recent glacial–interglacial cycles.

In the context of their late-Quaternary history, the arctic biota at present are relatively restricted in range and population size. Although tundra areas were of even smaller extent during the early part of the Holocene than at present, as a result of greater northward extension of the treeline (Huntley, 1997; Huntley and Bradshaw, 1999; MacDonald et al., 2000), that reduction in extent was small in magnitude compared to that experienced at the end of the last glacial stage, during which they were much more extensive than at any time since. Similarly, while extant arctic taxa at the lower taxonomic levels often exhibit considerable diversity that can be related to their late-Quaternary history, the biota as a whole has suffered a recent reduction in overall diversity owing to the extinctions of many species, and some genera, that did not survive into the Holocene. Of at least 12 large herbivores and six large carnivores present in steppe–tundra areas at the LGM (Lister and Bahn, 1995; Stuart, 1982), only four and three, respectively, survive today. Of the surviving species, only two herbivores (reindeer/caribou and muskox) and two carnivores (brown bear – *Ursus arctos* and wolf – *Canis lupus*) occur today in the arctic tundra biome. Present arctic geography also imposes extreme migratory distances upon many tundra-breeding birds owing to the wide separation between their breeding and wintering areas (Davidson N. et al., 1986; Wennerberg, 2001), rendering many of them, in common with much of the arctic biota, extremely vulnerable to any further climatic warming (Evans, 1997).

7.2.3. Ecological history

Although relatively few in overall number, paleoecological studies of the late Quaternary Period have been conducted in many parts of the Arctic (see e.g., Anderson and Brubaker, 1993, 1994; Lamb H.F. and Edwards, 1988; MacDonald et al., 2000; Ritchie, 1987). In areas that were by then ice free, the transition to the Holocene was marked by evidence of rapid ecological response. Elsewhere, in proximity to the decaying ice sheets, there was a lag between the global changes and the ecological changes because of the regional influence of the ice sheets. Although the precise nature of the ecological changes depended upon location, the overall picture was one of widespread rapid replacement of the open, discontinuously vegetated tundra and polar desert that characterized most ice-free areas during the late-glacial period by closed tundra. This was in turn replaced by shrub tundra and subsequently by arctic woodlands or northern boreal forest in southern areas of the Arctic. In areas that were unglaciated at the LGM (e.g., Alaska), the ecological transition began earlier, coinciding with the first rapid climatic warming recorded in Greenland about 14 700 years BP (Björck et al., 1998; Stuiver et al., 1995). In Alaska, tundra was replaced by shrub tundra during the late-glacial stage, and the first forest stands (of balsam poplar – *Populus balsamifera*) were already present before the transition to the Holocene (Anderson and Brubaker, 1994). South of the Arctic, the extensive areas of steppe–tundra that were present at the LGM were rapidly replaced by expanding forests. Only in parts of northernmost Siberia may fragments of the steppe–tundra biome have persisted into the Holocene, supporting the last population of woolly mammoths that persisted as recently as 4000 years BP (Vartanyan et al., 1993).

The early Holocene was characterized by higher summer insolation intensities at northern latitudes than at present. The warmer summer months enabled trees to extend their ranges further northward than at present; positive feedback resulting from the contrasting albedo of forest compared to tundra (sections 7.4.2.4 and 7.5.4.2) probably enhanced this extension of the forest (Foley et al., 1994). Boreal forest trees expanded their ranges at rates of between 0.2 and 2 km/yr (Huntley and Birks, 1983; Ritchie and McDonald, 1986). They exhibited individualistic responses with respect to their distributions and abundance patterns in response to climatic patterns that differed from those of today. Milder winters and more winter precipitation in western Siberia during the early Holocene, for example, allowed Norway spruce (*Picea abies*) to dominate in areas where Siberian fir (*Abies sibirica*) and Siberian stone pine (*Pinus sibirica*) have become important forest components during the later Holocene (Huntley, 1988, 1997; Huntley and Birks, 1983). Throughout northern Russia, the arctic treeline had advanced more or less to the position of the present arctic coastline by about 10 200 years BP, although the lower sea level at that time meant that a narrow strip of tundra, up to 150 km wide at most, persisted north of the treeline (MacDonald et al., 2000). Subsequently, as sea level continued to rise during the early Holocene, tundra extent reached a minimum that persisted for several millennia. For tundra species, including tundra-breeding birds, the early Holocene thus seems likely to have been a time of particular stress. This stress may, however, have been in part relieved by enhanced productivity in these areas, compared to modern tundra ecosystems, as a consequence of the warmer summers and higher insolation intensity.

In glaciated areas of the Arctic, such as northern Fennoscandia and much of arctic Canada, peatlands became extensive only after the mid-Holocene (see e.g., Lamb H.F., 1980; Vardy et al., 1997) in response to the general pattern of climatic change toward cooler and regionally moister summer conditions. The same cooling trend led to the southward retreat of the arctic treeline, which reached more or less its present location in most regions by about 4500 years BP (MacDonald et al., 2000). The consequent increase in tundra extent probably relieved the stress experienced by tundra organisms during the early Holocene, although the cooler, less productive conditions, and the increasing extent of seasonally waterlogged tundra peatlands, may have offset this at least in part. While the early Holocene was a time of permafrost decay and thermokarst development, at least in some regions (Burn, 1997), the extent of permafrost has increased in many areas during the later Holocene (see e.g., Kienel et al., 1999; Vardy et al., 1997).

7.2.4. Human history related to ecosystems

Recently discovered evidence (Pavlov et al., 2001) shows that Paleolithic "hunter-gatherers" were present about 40 000 years BP (long before the LGM) as far north as 66°34' N in Russia, east of the Fennoscandian Ice Sheet. Although it seems likely that humans did not range as far north during the glacial maximum, it is clear that they expanded rapidly into the Arctic during the deglaciation.

Humans entered North America via the Bering "land bridge" and along the southern coast of Beringia about 14 000 to 13 500 years BP (Dixon, 2001). These so-called Clovis hunters were hunter-gatherers who had developed sophisticated ways of working stone to produce very fine spear- and arrowheads. Over the next few millennia, they expanded their range and population rapidly, occupying most of the North American continent. Their prey apparently included many of the large vertebrate species that soon became extinct. The extent to which human hunting may have been principally responsible for these extinctions is a matter of continuing debate, but recent simulations for North America indicate that this possibility cannot be excluded (Alroy, 2001). However, these extinctions also coincide with an environmental change that caused the area of the biome with which the large arctic vertebrates were associated to be reduced to an extent that was apparently unprecedented during previous glacial–interglacial cycles (Sher, 1997). It thus is more probable that the hunting pressure exerted by humans was at most an additional contributory factor leading to the extinctions, rather than their primary cause.

In Eurasia, Paleolithic hunter-gatherers shifted their range northward into the Arctic at the end of the last glacial stage, as did their large vertebrate prey. To the south, they were replaced by Mesolithic peoples who occupied the expanding forests. By the early Holocene these Mesolithic peoples had expanded well into the Arctic (Thommessen, 1996), where they probably gave rise to the indigenous peoples that in many cases continued to practice a nomadic hunter-gatherer way of life until the recent past or even up to the present day in some regions. The arrival of later immigrants has had major impacts upon indigenous peoples and their way of life (Chapters 3, 11, and 12). In turn, land use and natural resource exploitation by the immigrants, as well as the changes that they have brought about in the way of life of indigenous peoples, have had negative impacts on many arctic ecosystems. These impacts in some cases have possibly increased the vulnerability of these ecosystems to the pressures that they now face from climate change and increased exposure to UV-B radiation.

7.2.5. Future change in the context of late-Quaternary changes

The potential changes for the next century can be put into context by comparing their rates and magnitudes to those estimated for the changes documented by paleoecological and other evidence from the late Quaternary Period (Table 7.1).

It is apparent from Table 7.1 that projected future changes have several characteristics that pose a particular threat to the biota and ecosystems of the Arctic. First, climatic changes over the next century are likely to be comparable in magnitude to the changes that occurred between full glacial conditions and present conditions, and greater than the maximum changes that occurred during the Holocene. Second, the global increase in mean annual temperature is projected to occur at rates that are

Table 7.1. Comparison of key aspects of projected future environmental changes with late-Quaternary changes.

	Late Quaternary	Projected Future
Sea level	ca. 120 m lower at LGM; increased at a maximum rate of ca. 24 mm/yr (Fairbanks, 1989)	0.09–0.88 m higher by 2100; 3–10 m higher in 1000 years increasing at a rate of 1–9 mm/yr (IPCC, 2001)
Climate		
Mean annual temperature	full glacial: global mean ca. 5 °C lower; regionally in the Arctic 10–13 °C lower Holocene: global mean <1 °C higher at maximum; regionally in the Arctic similar to present	2100: global mean 1.5–5.8 °C higher; regionally in the Arctic 2.1–8.1 °C higher (IPCC, 2001)
Winter temperature	full glacial: >15 °C cooler regionally in the Arctic Holocene: ca. 2–4 °C warmer regionally in the Arctic at maximum	2100: 4–10 °C higher regionally in the Arctic (IPCC, 2001)
Rate of increase in mean annual temperature	global: ≤1°C per millennium; regionally in the Arctic: >5 °C in a century	global: 1.5–5.8 °C per century; regionally in the Arctic: 2.1–8.1 °C in a century (IPCC, 2001)
Ecosystem responses		
Treeline displacement	full glacial: >1000 km southward; Holocene: 50–200 km northward at maximum (Kaplan, 2001)	2100: >500 km northward. It is possible that anthropogenic disturbance might result in an opposite response (see section 7.5.3.2)
Range margin displacement rates	early Holocene: rates of 0.2–2 km/yr estimated for trees from pollen data (Huntley, 1988)	21st century: potential rates of 5–10 km/yr estimated from species–climate response models (Huntley et al., 1995)
Area of tundra	full glacial: 197% (ranging from 168 to 237%) of present; Holocene: 81% (ranging from 76 to 84%) of present at minimum	2100: 51% of present (J. Kaplan, pers. comm., 2002; see Kaplan et al., 2003)
UV-B radiation levels	No long-term trend known. Due to solar variability, levels of DNA-active UV-B wavelengths may have varied by up to 27% within a period of ca. 150 years (Rozema et al., 2002)	In addition to natural solar cycles, it is very likely that anthropogenic cooling of the stratosphere will delay recovery of the ozone layer

higher than the rate of global temperature increase during the last deglaciation; in parts of the Arctic the rate of warming is likely to match the most rapid regional warming of the late Quaternary Period. Third, as a consequence of this temperature increase, and the accompanying rise in sea level, tundra extent is likely to be less than at any time during the late Quaternary Period. Fourth, global mean temperatures and mean annual temperatures in the Arctic are very likely to reach levels unprecedented in the late Quaternary Period; this is very likely to result in a rapid reduction in the extent of permafrost, with associated thermokarst development in areas of permafrost decay leading to potentially severe erosion and degradation of many arctic peatlands (section 7.5.3.1). The combination of projected future climate change with other anthropogenic effects (including enhanced levels of UV-B radiation, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, and increased habitat fragmentation) suggests that the future is very likely to be without a past analogue and will pose unprecedented challenges to arctic ecosystems and biota that evolved in response to global cooling throughout the last five million years or so (the late Tertiary and Quaternary Periods), during which our own species also evolved.

7.2.6. Summary

At the LGM, vast ice sheets covered many continental areas. The beds of some shallow seas were exposed, connecting previously separated landmasses. Although some areas were ice-free and supported a flora and fauna, mean annual temperatures were 10 to 13 ºC colder than during the Holocene. Within a few millennia of the glacial maximum, deglaciation started but was not a simple unidirectional change: a series of climatic fluctuations occurred between about 18 000 and 11 400 years BP. During the Younger Dryas event, mean annual temperatures fell substantially in some areas and reglaciation occurred. At the end of the event, mean annual temperatures rose by more than 5 ºC in less than 100 years in at least some parts of the Arctic. Following the general thermal maximum in the Holocene, there has been a modest overall cooling trend. However, superimposed upon the general longer-term patterns have been a series of millennial and centennial fluctuations in climate, the most marked of which occurred about 8200 years BP. The most recent of these climatic fluctuations was that of the LIA, a generally cool interval spanning approximately the late 13th to early 19th centuries. At its most extreme, mean annual temperatures in some arctic areas fell by several degrees, with impacts on human settlements in the north.

In the context of at least the last 150 000 years, arctic ecosystems and biota have been close to their minimum extent within the last 10 000 years. They suffered loss of diversity as a result of extinctions during the rapid, large-magnitude global warming at the end of the last glacial stage. Consequently, arctic ecosystems and biota are already stressed; some are extremely vulnerable to current and projected future climate change. For example, migratory arctic-breeding birds today face maximal migration distances between their wintering and breeding areas.

Evidence from the past indicates that arctic species, especially larger vertebrates, are very likely to be vulnerable to extinction if climate warms. The treeline is very likely to advance, perhaps rapidly, into tundra areas of northern Eurasia, Canada, and Alaska, as it did during the early Holocene, reducing the extent of tundra and contributing to the pressure upon species that makes their extinction possible. Species that today have more southerly distributions are very likely to extend their ranges north, displacing arctic species. Permafrost is very likely to decay and thermokarst develop, leading to erosion and degradation of arctic peatlands. Unlike the early Holocene, when lower relative sea level allowed a belt of tundra to persist around at least some parts of the Arctic Basin when treelines advanced to the present coast, sea level is very likely to rise in the future, further restricting the area of tundra and other treeless arctic ecosystems.

The negative response of arctic ecosystems in the face of a shift to global climatic conditions that are apparently without precedent during the Pleistocene is likely to be considerable, particularly as their exposure to co-occurring environmental changes (i.e., enhanced levels of UV-B radiation, deposition of nitrogen compounds from the atmosphere, heavy metal and acidic pollution, radioactive contamination, increased habitat fragmentation) is also without precedent.

7.3. Species responses to changes in climate and ultraviolet-B radiation in the Arctic

The individual of a species is the basic unit of ecosystems that responds to changes in climate and UV-B radiation levels. Individuals respond to environmental changes over a wide range of timescales: from biochemical, physiological, and behavioral processes occurring in less than a minute to the integrative responses of reproduction and death (Fig. 7.1). Reproduction and death drive the dynamics of populations while mutation and environmental selection of particular traits in individuals within the population lead to changes in the genetic composition of the population and adaptation.

Current arctic species have characteristics that have enabled them to pass various environmental filters associated with the arctic environment (Körner, 1995; Walker M.D., 1995), whereas species of more southerly latitudes either cannot pass these filters or have not yet arrived in the Arctic. Changes in arctic landscape processes and ecosystems in a future climatic and UV-B radiation regime will depend upon the ability of arctic species to withstand or adapt to new environments and upon their interactions with immigrant species that can pass through less severe environmental filters. This section focuses on the attributes of current arctic species that constrain or facilitate their responses to a changing climate and UV-B radiation regime.

Soil characteristics will determine to some extent the responses of vegetation to climate change. Arctic soils (and particularly moisture content) vary from the forest tundra to the polar deserts and within each of these vegetation zones.

In the high-arctic polar deserts, skeletal soils and stony ground predominate (Aleksandrova, 1988). Materials range from boulders to gravel and the dominant erosion process is physical weathering (e.g., freeze–thaw cracking) rather than chemical and biochemical weathering, which are strongly suppressed by lack of heat. Freeze–thaw cycles lead to a sorting of stones by size and formation of patterned ground consisting, for example, of stone nets. An organic layer is missing from the soil profile and organic material is restricted to small pockets under sparse plant cover or in cracks. The soils are neutral or only weakly acidic and the soil complexes are almost completely saturated with moisture although this differs between the polar deserts of Canada, Greenland, and the Russian Arctic. Gleys are almost absent and the active-layer depth is about 30 cm.

In the tundra biome, soil profiles are characterized by an organic layer that is often less than 10 cm deep on dry ridges, is deeper in moist and mesic habitats, and extends to deep deposits of peat in wet areas (Nadelhoffer et al., 1992). Below the organic layer is a mineral layer. The active layer is deepest in the dry areas (~1 m) owing to the lack of summer insulation, and is shallowest in wet areas (~20 cm) due to efficient insulation by continuous vegetation cover and organic soil. The pH of tundra soils is generally acidic. Chemical and biochemical processes are important but sorting of materials and patterned ground are still evident, leading to landscapes with larger polygons than those found in the polar deserts. In both polar-desert and tundra soils, the permafrost is generally continuous. In contrast, in soils of the forest tundra, the permafrost generally becomes discontinuous and the depth of the organic layer decreases except for water-logged depressions where peat bogs are found.

Soil formation processes in the Arctic are slow and the type of soil is very likely to constrain potential rates of colonization by southern species.

7.3.1. Implications of current species distributions for future biotic change

7.3.1.1. Plants

Species diversity

About 3% (~5900 species) of the global flora occurs in the Arctic as defined in this chapter (0.7% of the angiosperms (flowering plants), 1.6% of the gymnosperms (cone-bearing plants), 6.6% of the bryophytes, and 11% of the lichens) (Table 7.2). There are more species of primitive taxa (cryptogams), that is, mosses, liverworts, lichens, and algae, in the Arctic than of vascular plants (Matveyeva and Chernov, 2000). Less than half (about 1800) of arctic plant species are vascular plants. There are about 1500 species of vascular plants common to both Eurasia (Matveyeva and Chernov, 2000; Sekretareva, 1999) and North America (Murray, 1995). Similar numbers of non-vascular plants probably occur in the Arctic on both continents, although their diversity has been less

Table 7.2. Biodiversity estimates in terms of species richness (number of species) for the Arctic north of the latitudinal treeline and percentage of world biota (Chernov, 2002; Matveyeva and Chernov, 2000).

Animals			Plants			Fungi		
Group	Number of species	% of world biota	Group	Number of species	% of world biota	Group	Number of species	% of world biota
Mammals	75	1.7	Angiosperms	1735	0.7	Fungi	2500	2.3
Birds	240	2.9	monocotyledons	399	0.6			
Insects	3300	0.4	dicotyledons	1336	0.7			
Diptera	1600	0.9	Gymnosperms	12	1.6			
Beetles	450	0.1	Pteridophytes	62	0.6			
Butterflies	400	0.3	Mosses	600	4.1			
Hymenoptera	450	0.2	Liverworts	250	2.5			
Others	400		Lichens	2000	11.0			
Springtails	400	6.0	Algae	1200	3.3			
Spiders	300	1.7						
Mites	700	1.9						
Other groups[a]	600	--						
Total estimate	6000	--		5859	3.0			

[a] Amphibians and reptiles (7 species), centipedes (10 species), terrestrial mollusks (3 species), oligochaetes (earthworms and enchytraeids) (70 species), and nematodes (~500 species).

thoroughly documented. In the Russian Arctic, for example, 735 bryophyte species (530 mosses and 205 liverworts) and 1078 lichen species have been recorded (Afonina and Czernyadjeva, 1995; Andreev et al., 1996; Konstantinova and Potemkin, 1996). In general, the North American and Eurasian Arctic are similar to one another in their numbers of vascular and non-vascular plant species, of which a large proportion (about 80%) of vascular plant species occurs on at least two continents. An even larger proportion (90%) of bryophyte species occurs in both the North American and Eurasian Arctic.

About 40% of arctic vascular plants (and a much higher percentage of mosses and lichens) are basically boreal species that now barely penetrate the Arctic (Table 7.3). They currently occur close to the treeline or along large rivers that connect the subarctic with the Arctic. These boreal species within the Arctic will probably be the primary boreal colonizers of the Arctic in the event of continued warming. Polyzonal (distributed in several zones), arctoboreal (in taiga and tundra zones), and hypoarctic (in the northern taiga and southern part of the tundra zone) species have even greater potential to widen their distribution and increase their abundance in a changing climate. The majority of cryptogams have wide distributions throughout the Arctic. Such species are likely to survive a changing climate, although their abundance is likely to be reduced (sections 7.3.3.1 and 7.4.1.2).

In contrast to the low diversity of the arctic flora at the continental and regional scales, individual communities (100 m^2 plots) within the Arctic have a diversity similar to or higher than those of boreal and temperate zones. These diversities are highest in continental parts of the Arctic such as the Taymir Peninsula of Russia, where there are about 150 species of plants (vascular plants, lichens, and mosses) per 100 m^2 plot, 40 to 50 species per square meter, and up to 25 species per square decimeter (Matveyeva, 1998).

Latitudinal gradients of species diversity

Latitudinal gradients suggest that arctic plant diversity is sensitive to climate. The number of vascular plant species declines five-fold from south to north on the Taymir Peninsula (Matveyeva, 1998). Summer temperature is the environmental variable that best predicts plant diversity in the Arctic (Young, 1971). Other factors are also important, however: regions at different latitudes that have a similar maximum monthly temperature often differ in diversity. Taymir biodiversity values are intermediate between the higher values in Chukotka and Alaska, which have a more complicated relief, geology, and floristic history, and the lower values in the eastern Canadian Arctic with its impoverished flora resulting from relatively recent glaciation. All diversity values on the Yamal Peninsula are even lower than in Canada because of a wide distribution of sandy soils and perhaps its young age. Similar patterns are observed with butterflies (Fig. 7.5c) and spiders (Chernov, 1989, 1995). Therefore, latitudinal gradients of species diversity are best described as several parallel gradients, each of which depends on summer heat, but which may differ from one geographic region to another. This must be taken into consideration when projecting future changes in biodiversity. Figure 7.5b illustrates how current bioclimatic distributions are related to climate change scenarios by plotting the likely changes in the number of ground beetles for three time slices of mean July tem-

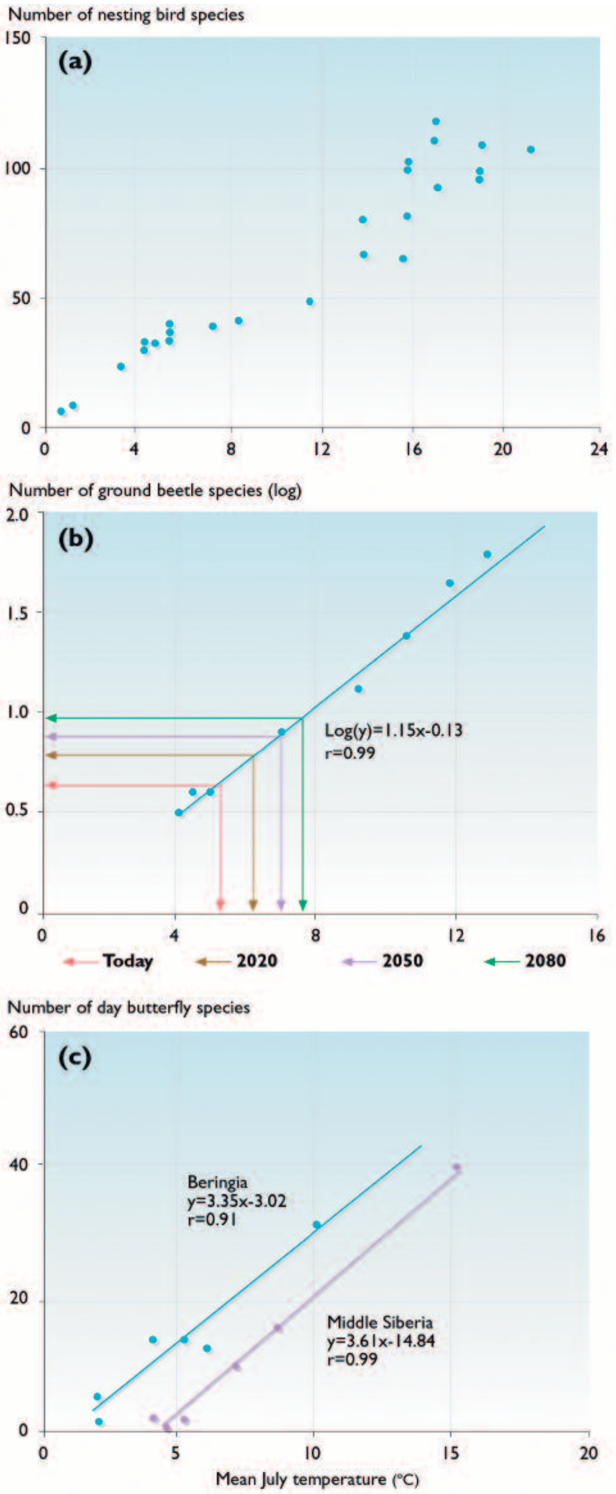


Fig. 7.5. Relationship between mean July temperature and (a) the number of nesting bird species in western and middle Siberia; (b) the number of ground beetle species in local faunas of the Taymir Peninsula; and (c) the number of day butterfly species in the middle Siberian and Beringian areas of the Arctic (Chernov, 1989, 1995; Matveyeva and Chernov, 2000).

perature derived from the mean of the scenarios generated by the five ACIA-designated models.

At the level of the local flora (the number of species present in a landscape of about 100 km^2), there is either a linear or an "S"-shaped relationship between summer temperature and the number of species (Fig. 7.6). The number of species is least sensitive to temperature near the southern margin of the tundra and most sensitive to temperatures between 3 and 8 °C. This suggests that the primary changes in species composition are very likely to occur in the northern part of the tundra zone and in the polar desert, where species are now most restricted in their distribution by summer warmth and growing-season length. July temperature, for example, accounts for 95% of the variance in number of vascular plant species in the Canadian Arctic (Rannie, 1986), although extreme winter temperatures are also important (section 7.3.3.1). Summer warmth, growing-season length, and winter temperatures all affect the growth, reproduction, and survival of arctic plants. The relative importance of each varies from species to species, site to site, and year to year.

The steep temperature gradient that has such a strong influence on species diversity occurs over much shorter distances in the Arctic than in other biomes. North of the treeline in Siberia, mean July temperature decreases from 12 to 2 °C over 900 km, whereas mean July temperature decreases by 10 °C over 2000 km in the boreal zone, and decreases by less than 10 °C from the southern boreal zone to the equator (Chernov, 1995).

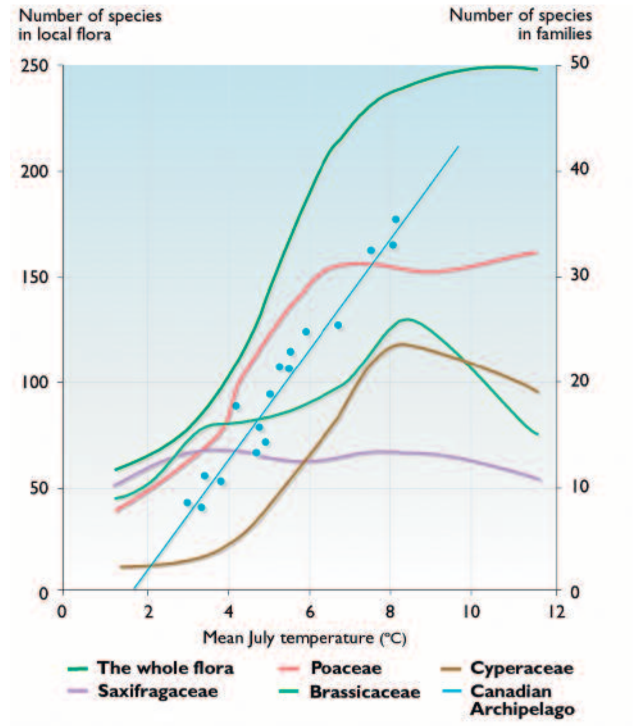


Fig. 7.6. Relationship between mean July temperature and the number of vascular plant species in local floras of the Taymir Peninsula (Matveyeva and Chernov, 2000) and the number of vascular species in the local flora of the Canadian Archipelago (Rannie, 1986).

Comparing the temperature decrease of 10 °C with the projected 2.5 °C increase in mean July temperature in the Arctic by 2080 (mean of the two extremes – 1.1 and 4.2 °C – projected by the five ACIA-designated models) suggests that much of the Arctic is very likely to remain within the arctic summer climate envelope (although the increase in winter temperature is projected to be higher).

Because of the steep latitudinal temperature gradients in the Arctic, the distance that plants must migrate in response to a change in temperature is much less in the Arctic than in other biomes, particularly where topographic variations in microclimate enable plants to grow far north of their climatic optima. The low solar angle and presence of permafrost make topographic variations in microclimate and associated plant community composition particularly pronounced in the Arctic. Thus, both the sensitivity of arctic species diversity to temperature and the short distance over which this temperature gradient occurs suggest that arctic diversity is very likely to respond strongly and rapidly to high-latitude temperature change.

Latitudinal patterns of diversity differ strikingly among different groups of plants (Table 7.3). Many polyzonal, boreal, and hypoarctic species have ranges that extend into the Arctic. Some of these (e.g., the moss *Hylocomium splendens* and the sedges *Eriophorum angustifolium* and *E. vaginatum*) are important dominants within the Arctic. Tussocks of *E. vaginatum* structure the microtopography of broad areas of tussock tundra (Bliss and Matveyeva, 1992), and *H. splendens* exerts a control over nutrient cycling (Hobbie, 1996). Tall willow (*Salix* spp.) and alder (*Alnus fruticosa*) shrubs as well as dwarf birch (*Betula exilis* and *B. nana*) form dense thickets in the southern part of the tundra zone and often have outlier populations that extend far to the north in favorable habitats (Matveyeva and Chernov, 2000).

Species that are important community dominants are likely to have a particularly rapid and strong effect on ecosystem processes where regional warming occurs. Hemiarctic species are those that occur throughout the Arctic. Many of these species are common community dominants, including *Carex bigelowii/arctisibirica*, *C. stans*, *Dryas octopetala/punctata, Cassiope tetragona*, and the moss *Tomentypnum nitens*. Due to their current widespread distribution, their initial responses to climatic warming are likely to be increased productivity and abundance, probably followed by northward extension of their ranges. The species most vulnerable to climate change are likely to be euarctic (polar willow – *Salix polaris*) and hyperarctic species that now have the greatest abundance and widest ecological amplitude in the northernmost part of the tundra zone and in polar deserts, respectively. These groups of species are best adapted to the climate conditions of the high Arctic where they are distributed in a wide range of habitats where more competitive southern species are absent. In the more southerly regions of the tundra zone, they

Table 7.3. Current diversity changes with latitude in the Arctic, excluding limnic and marine animals (compiled and modified from Matveyeva and Chernov, 2000). General information about how species within the various categories are likely to respond to changes in climate and UV radiation levels is presented in the text, but insufficient information is available for most of the species in the table.

Category	Optimum of distribution	Examples		
		Plants	Birds	Mammals and invertebrates
Polyzonal	Different zones in the Holarctic; within the tundra zone usually in local habitats and wet depressions	Soil algae; the mosses *Hylocomium splendens* sensu lato, *Aulacomnium turgidum*, and *Racomitrium lanuginosum*; the liverwort *Ptilidium ciliare*; the lichens *Cetraria islandica*, *Psora decipiens*, and *Cladina rangiferina*; the vascular species *Cardamine pratensis*, *Chrysosplenium alternifolium*, and *Eriophorum angustifolium*; the sedge *Carex duriuscula*[a]; the herb *Helictotrichon krylovii*[a]; and the moss *Tortula ruralis*[a]	Common raven (*Corvus corax*), peregrine falcon (*Falco peregrinus*), white wagtail (*Motacilla alba*), northern wheatear (*Oenanthe oenanthe*)	Wolf (*Canis lupus*), ermine (*Mustela erminea*), weasel (*M. nivalis*), voles (*Microtus gregalis* and *M. oeconomus*), and the mite *Chiloxanthus pilosus*[b]
Zonal boreal	Not abundant and constrained to the southern Arctic in benign habitats such as river valleys, south-facing slopes, and wet areas	Tree species of *Larix*; the orchid *Corallorrhiza*; the shrub *Salix myrtilloides*; the sedge *Carex chordorrhiza*; the herbs *Allium schoenoprasum*, *Cortusa matthioli, Galium densiflorum,* and *Sanguisorba officianalis*; and the forest mosses *Climacium dendroides, Pleurozium shreberi*, and *Rhytidiadelphus triquetrus*	The forest birds *Turdus iliacus* and *T. pilaris* (thrushes); the leaf warblers Arctic warbler (*Phylloscopus borealis*) and yellow-browed warbler (*P. inornatus*); and the "river" ducks *Anas acuta, A. penelope*, and *A. crecca*	Reindeer/caribou (*Rangifer tarandus*), wolverine (*Gulo gulo*), and brown bear (*Ursus arctos*)
Zonal Arctic				
Hypoarctic	Optima in the southern tundra subzone	The shrubs *Betula nana* and *B. exilis* and the sedge *Eriophorum vaginatum*[c]	Ptarmigan (*Lagopus lagopus*), spotted redshank (*Tringa erythropus*), little bunting (*Emberiza pusilla*), bar-tailed godwit (*Limosa lapponica*)	The vole *Microtus middendorffi*, the ground beetle *Carabus truncaticollis*, the bumblebee *Bombus cingulatus*, and the spider *Alopecosa hirtipes*
Hemiarctic	Throughout the tundra zone but most frequent in the middle	Most of the dominant species, including the grasses *Arctophila fulva* and *Dupontia fisheri*; the sedges *Carex bigelowii/arctisibirica* and *C. stans*; the shrub willow *Salix reptans*; the dwarf shrubs *Dryas punctata/octopetala* and *Cassiope tetragona*; the mosses *Tomentypnum nitens*, *Drepanocladus intermedius*, and *Cinclidium arcticum*; the herbs *Lagotis minor* and *Pedicularis hirsuta*; and the moss *Polytrichum juniperinum*	Lapland longspur (*Calcarius lapponicus*), lesser golden plover (*Pluvialis dominica*), Pacific golden plover (*P. fulva*), and the dunlins *Calidris alpina* and *C. minuta*	The lemming *Lemmus sibiricus*, the bumblebee *Bombus balteatus*, the ground beetles *Curtonotus alpinus* and *Pterostichus costatus*, and the flower-fly *parasyrphus tarsatus*
Euarctic	Northern part of the tundra zone, rare in the southern part	The dwarf shrubs *Salix polaris* and *S. arctica*[d]	Black-bellied plover (*Pluvialis squatarola*), curlew sandpiper (*Calidris ferruginea*), snowy owl (*Nyctea scandiaca*), snow bunting (*Plectrophenax nivalis*) and several more	The lemming *Dicrostonyx torquatus*, the bumblebees *Bombus hyperboreus* and *B. polaris*, and the crane fly *Tipula carinifrons*
Hyperarctic	Polar desert and the northernmost part of the tundra zone	Almost no plants are restricted to these zones; the following have their highest frequencies there: the grasses *Phippsia algida* and *Poa abbreviata*; the herbs *Cerastium regelii, Draba oblongata, D. subcapitata, Saxifraga hyperborea*, and *S. oppositifolia*; the mosses *Dicranoweisia crispula, Bryum cyclophyllum, Orthothecium chryseon*, and *Seligeria polaris*; and the lichens *Cetrariella delisei*, *Arctocetraria nigricascens*, *Dactylina ramulosa, D. madreporiformis*, and *Thamnolia subuliformis*	The wader species *Calidris alba* and *C. canutus*	No terrestrial mammal species are restricted to this zone. The collembolan *Vertagopus brevicaudus*

[a] "steppe" species; [b] bizonal steppe and tundra species; [c] this group characterizes the southern tundra subzone; [d] this group is relatively small, but is valuable in subdividing the tundra zone into subzones.

are able to grow only (or mainly) in snow beds (depressions in the landscape where snow accumulates and plant growth and diversity is limited by particularly short snow-free periods). It is likely that their ecological amplitude will narrow and their abundance decrease during climate warming.

Thus, responses to climate change will be different in various groups of plants. Some currently rare boreal species are likely to move further north and the relative abundance and range of habitats occupied by more common species are likely to increase. When southern species with currently narrow niches penetrate into the harsher ecosystems at high latitudes, therefore, there is likely to be a broadening of their ecological niches there. In contrast, some true arctic species (endemics) that are widespread at high latitudes are likely to become more restricted in their local distribution within and among ecosystems. They could possibly disappear in the lower latitudes where the tundra biome is particularly narrow. Only few high-arctic plants in Greenland are expected to become extinct, for example, *Ranunculus sabinei*, which is limited to the narrow outer coastal zone of North Greenland (Heide-Jørgensen and Johnsen, 1998). However, temperature is not the only factor that currently prevents some species from being distributed in the Arctic. Latitude is important, as life cycles depend not only on temperature but on the light regime as well. It is very likely that arctic species will tolerate warmer summers whereas long day lengths will initially restrict the distribution of some boreal species (section 7.3.3.1). New communities with a peculiar species composition and structure are therefore very likely to arise, and will be different from those that exist at present.

7.3.1.2. Animals

Species diversity

The diversity of arctic terrestrial animals beyond the latitudinal treeline (6000 species) is nearly twice as great as that of vascular plants and bryophytes (Chernov, 1995, 2002; Table 7.2). As with plants, the arctic fauna accounts for about 2% of the global total, and, in general, primitive groups (e.g., springtails, 6% of the global total) are better represented in the Arctic than are advanced groups such as beetles (0.1% of the global total; Chernov, 1995; Matveyeva and Chernov, 2000). There are about 322 species of vertebrates in the Arctic, including approximately 75 species of mammals, 240 species of birds, 2 species of reptiles, and 5 species of amphibians. Insects are the most diverse group of arctic animals; of approximately 3300 arctic species, about 50% are Diptera, 10% are beetles (Coleoptera), 10% are butterflies (Lepidoptera), and 10% are Hymenoptera. The Arctic has about 300 species of spiders (Arachnida), 700 species of mites (Acarina), 400 species of springtails (Collembola), 500 species of nematodes, 70 species of oligochaetes (of which most are Enchytraeidae), only a few mollusks, and an unknown number of protozoan species.

In the Arctic as defined by CAFF (Conservation of Arctic Flora and Fauna) (which includes forested areas), some 450 species of birds have been recorded breeding. Some species extend their more southern breeding areas only marginally into the Arctic. Others are not migratory and stay in the Arctic throughout the year. About 280 species have their main breeding distribution in the Arctic and migrate regularly (Scott, 1998). An estimate of the total number of individuals involved is not possible, as too little is known about the population size of most species or their arctic proportion. However, a rough first approximation suggests that there are at least several hundred million birds. Population sizes of water birds are better known and the Arctic is of particular importance for most water birds, such as divers, geese, and waders. Twelve goose species breed in the Arctic, eleven almost entirely and eight exclusively. These comprise about 8.3 million birds. The total number of arctic-breeding sandpipers (24 species) exceeds 17.5 million birds (Zöckler, 1998). The total number of water birds, including other wader species, divers, swans, ducks, and gulls is estimated to be between 85 and 100 million birds.

Latitudinal gradients of species diversity

Latitudinal patterns of diversity in arctic animals are similar to those described for arctic plants. Species diversity declines in parallel with decreasing temperature in most animal groups (Fig. 7.5), including birds, ground beetles, and butterflies (Chernov, 1995). However, in some groups (e.g., peatland birds and sawflies at local sites in the European Arctic), concentrations of both species diversity and density per unit area can increase compared with more southern territories, perhaps because the habitat types appropriate to these groups are more diverse in the tundra than in the boreal forest. In general, the latitudinal decline in the number of animal species is more pronounced (frequently greater than 2.5-fold) than in vascular plants. As with plants, at a given temperature there are more animal species in Beringia, with its complicated relief, geology, and biogeographic history than in the Taymir Peninsula. Many animal species are restricted to the boreal zone because they depend on the crown, wood, roots, or litter of trees, which are absent in the tundra zone. These groups include wood-boring insects and wood-decaying fungi and their predators (Chernov and Matveyeva, 1997), as well as mammals and birds that specialize on tree seeds and leaves. Other important animals, including the raven (*Corvus corax*), wolf, red fox (*Vulpes vulpes*), and ermine (*Mustela erminea*), are primarily boreal in distribution but remain an important component of many arctic ecosystems. There are a few terrestrial animals restricted to the high Arctic such as the sanderling (*Calidris alba*) and a common Collembola, *Vertagopus brevicaudus*. Other arctic species have their centers of distribution in the northern, mid- or southern Arctic (Table 7.3). The more diverse patterns of animal distribution compared to plants make it more difficult to project how animals will respond to climatic warming. Some herbivores have distributions that are more limited than those of their host plants (Strathdee and Bale, 1998), so it is possible that warming will allow these species to extend northward relatively rapidly.

As with plants, latitudinal patterns of diversity differ strikingly among different groups of animals (Table 7.3). The common species tend to be more broadly distributed in the far north. In northern Taymir, there are only 12 species of springtails but 80% of these occur in all microsites and topographic locations investigated (Chernov and Matveyeva, 1997). Some boreal birds, such as the American robin (*Turdus migratorius*), penetrate only into the southern part of the tundra while others can occur far from the area of their continuous distribution (climatic optimum): in the vicinity of Dixon (Taymir), the forest thrushes *T. pilaris* and *T. iliacus* form populations in the northernmost part of the tundra zone, 400 km from the last outposts of the forests. At the southern limits of the tundra, there is greater specialization among microhabitats. Many more species occur in intrazonal habitats, occupying relatively small and isolated sites, than in zonal habitats that contain only a small proportion of the regional fauna. Warming is therefore likely to lead to more pronounced habitat and niche specialization.

An important consequence of the decline in numbers of species with increasing latitude is an increase in dominance. For example, one species of collembolan, *Folsomia regularis*, may constitute 60% of the total collembolan density in the polar desert (Babenko and Bulavintsev, 1997). These "super-dominant" species are generally highly plastic, occupy a wide range of habitats, and generally have large effects on ecosystem processes. Lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) are super-dominant species during peak years of their population cycles (Stenseth and Ims, 1993) and have large effects on ecosystem processes (Batzli et al., 1980; Laine and Henttonen, 1983; Stenseth and Ims, 1993).

7.3.1.3. Microorganisms

Species diversity

Microbial organisms are critically important for the functioning of ecosystems, but are difficult to study and are poorly understood compared with other species. However, the International Biological Programme (IBP; 1964–1974) significantly advanced understanding of arctic microorganisms, compared with those of other biomes, when an inventory of microbial communities was undertaken in the tundra (Heal et al., 1981). At the beginning of the 21st century, the knowledge of microbial diversity in the tundra remains little better than 30 to 40 years ago, and recent outstanding progress in molecular microbial ecology has rarely been applied to arctic terrestrial studies.

Presently there are 5000 to 6000 named bacterial species globally and about the same number of fungi (Holt et al., 1994), compared with more than one million named plant and animal species (Mayr, 1998; Wilson E., 1992). Some scientists have interpreted this difference to mean that the bacteria are not particularly diverse (Mayr, 1998). However, there are several reasons (section 7.7.1.1) to believe that the apparent limited diversity of microbes is an artifact.

Recent progress in molecular biology and genetics has revolutionized bacterial classification and the understanding of microbial phylogeny ("family trees") and biodiversity in general. The DNA sequencing technique has reorganized bacterial classification and brought order to microbial taxonomy (Wayne et al., 1987). Moreover, the microbial inventory can now be done without isolation and cultivation of the dominant microorganisms, because it is enough to extract the total community DNA from the soil and amplify, clone, and sequence the individual genes. This culture-independent approach has been applied occasionally for analysis of microbial communities in subarctic and arctic soils, most often to study relatively simple communities in hot springs, subsoils, and contaminated aquifers (section 7.3.5.2). Analysis of Siberian subsurface permafrost samples (Gilichinsky, 2002; Tsapin et al., 1999) resulted in the formation of a clone library of 150 clones which has been separated into three main groups of Eubacteria. From 150 clones so far analyzed, the authors have identified several known species (*Arthrobacter, Clostridium*, and *Pseudomonas*), while the most abundant phylotypes were represented by completely unknown species closely affiliated with iron-oxidizing bacteria.

Another area of intensive application of molecular tools was northern wetlands (cold, oligotrophic (nutrient poor), and usually acidic habitats) related to the methane cycle (sections 7.4 and 7.5). The most challenging tasks were to determine what particular microbial organisms are responsible for the generation and uptake of methane (so-called methanogens and methanotrophs) in these northern ecosystems and what their reaction might be to warming of arctic soils. It was found that most of the boreal and subarctic wetlands contain a wide diversity of methanogens (Hales et al., 1996; Galand et al., 2002) and methanotrophs (McDonald et al., 1999; Radajewsky et al., 2000), most of them distantly related to known species. Only recently, some of these obscure microbes were obtained in pure culture or stable consortia (Dedysh et al., 1998; Sizova et al., 2003). The novel microbes of methane cycles are extreme oligotrophic species that evolved to function in media with very low concentrations of mineral nutrients. Taxonomically, these methanogens form new species, genera, and even families within the Archaea domain (Sizova et al., 2003). The acidophilic methanotrophs form two new genera: *Methylocapsa* and *Methylocella* (Dedysh et al., 1998, 2000), the latter affiliating with heterotrophic *Beijerinckia indica*.

A DNA-based technique allows determination of the upper limit for variation of microbial diversity in the Arctic as compared with other natural ecosystems, that is, how many species (both cultured and unculturable) soils contain. This technique is called DNA reassociation (how quickly the hybrid double helix is formed from denatured single-stranded DNA).

Arctic polar desert and tundra contain considerable microbial diversity, comparable with boreal forest soils and much higher than arable soils. Although extreme environmental conditions restrain the metabolic activity of arctic microbes, they preserve huge potential that is likely to display the same activity as boreal analogues during climate warming.

There is a much higher degree of genomic diversity in prokaryotic communities (prokaryotes such as cyanobacteria have a simple arrangement of genetic material whereas eukaryotes such as microalgae have genetic material arranged in a more advanced way, in that the DNA is linear and forms a number of distinct chromosomes) of heterogeneous habitats (virgin soils, pristine sediments) as compared with more homogeneous samples: the DNA diversity found in 30 to 100 cc of heterogeneous samples corresponds to about 10^4 different genomes, while in pond water and arable soils the number of genomes decreases to 10^0 to 10^2. Based on extrapolation and taking into account that listings of species can significantly overlap for microbial communities of different soils, a rough estimate is that there could be from 10^4 to 10^9 prokaryotic species globally (Staley and Gosink, 1999; Torsvik et al., 2002).

The conventional inventory approach based on cultivation suggests that at present in the Arctic, it is possible to identify in any particular soil no more than 100 prokaryotic species from the potential of 1000 to 3000 "genome equivalents" (Table 7.4) and no more than 2000 species of eukaryotes. In the broadly defined Russian Arctic, 1750 named fungi species (not including yeast and soil fungi) have been identified (Karatygin et al., 1999). About 350 of these are macromycetes. However, the number of fungi species in the Arctic proper is 20 to 30% less, but these data are far from complete. The Arctic has fewer species of bacteria, fungi, and algae than other major biomes; actinomycetes are rare or absent in most tundra sites (Bunnell et al., 1980). While most major phyla of microflora are represented in tundra ecosystems, many species and genera that are common elsewhere, even in subarctic ecosystems, are rare or absent in tundra. Gram-positive bacteria, including gram-positive spore forms, are absent or rare in most tundra sites. *Arthrobacter* and *Bacillus* can rarely be isolated and then only from drier areas. *Azotobacter*, the free-living nitrogen-fixing bacterium, is extremely rare in tundra, and the moderate rate of nitrogen fixation observed *in situ* is mainly due to the activity of cyanobacteria. Sulfur-oxidizing bacteria are also reported to be rare or absent. Even using enrichment techniques, Bunnell et al. (1980) rarely found chemoautotrophic sulfur-oxidizing bacteria. Photosynthetic sulfur bacteria were not found in any IBP tundra biome sites and were reported in only one subarctic site (Bunnell et al., 1980, Dunican and Rosswall, 1974), although they are common in coastal areas of the west and south coasts of Hudson Bay. Sulfur-reducing bacteria, while not abundant in tundra sites, have been reported in sites in the Arctic and Antarctic. Iron-oxidizing bacteria are very rare in tundra sites. Despite ample iron substrate in tundra ponds and soils, chemoautotrophic ferrous iron oxidizers were not found in IBP tundra sites (Dunican and Rosswall, 1974). In contrast, methanotrophic and methanogenic bacteria appear to be widespread in tundra areas.

As with bacteria, many generally common fungi are conspicuous by their rare occurrence or absence in tundra areas. *Aspergillus*, *Alternaria*, *Botrytis*, *Fusarium*, and *Rhizopus* simply do not occur and even *Penicillium* are rare (Flanagan and Scarborough, 1974). Yeasts can be isolated readily but there is very low species diversity in culture media. Only three different species were reported for Point Barrow tundra (Bunnell et al., 1980). Aquatic fungi show high diversity, especially Chytridiales and Saprolegniales. However they may not be endemic, and reflect the annual migration into the Arctic of many avian species, especially waterfowl. The so-called higher fungi, Basidiomycetes and Ascomycetes, also have low diversity. They are reduced in the Arctic to 17 families, 30 genera, and about 100 species. In comparison, subarctic and temperate regions contain at least 50 families, not less than 300 genera, and anywhere up to 1200 species (Miller and Farr, 1975). Mycorrhizal symbionts on tundra plants are common. Arbuscular, ecto-, ericoid, arbutoid, and orchid mycorrhizal fungi are associated with plants in arctic ecosystems

Table 7.4. Microbial genome size in the Arctic as compared with other habitats (after Torsvik et al., 2002).

DNA source	Number of cells per cm³	Community genome complexity (base pairs)[a]	Genome equivalents[b]
Arctic desert (Svalbard)	7.5×10^9	$5–10 \times 10^9$	1200–2500
Tundra soil (Norway)	37×10^9	5×10^9	1200
Boreal forest soil	4.8×10^9	25×10^9	6000
Forest soil, cultivated prokaryotes	0.014×10^9	0.14×10^9	35
Pasture soil	18×10^9	$15–35 \times 10^9$	3500–8800
Arable soil	21×10^9	$0.57–1.4 \times 10^9$	140–350
Salt-crystallizing pond, 22% salinity	0.06×10^9	0.029×10^9	7

[a]the number of nucleotides in each strand in the DNA molecule; [b]measure of diversity specified at a molecular level.

(Michelsen et al., 1998). The ectomycorrhizal symbionts are important as they form mycorrhizal associations with *Betula*, *Larix*, *Pinus*, *Salix, Dryas*, *Cassiope*, *Polygonum*, and *Kobresia*. Based on fungal fruitbodies, Borgen et al. (in press) estimate that there are 238 ectomycorrhizal fungal species in Greenland, which may increase to around 250 out of a total of 855 basidiomyceteous fungi in Greenland when some large fungal genera such as *Cortinarius* and *Inocybe* have been revised. With the exception of *Eriophorum* spp., Flanagan (unpub. data, 2004) found endotrophic *Arbuscula*-like mycorrhizae on all ten graminoid plants examined. The number of fungal species involved in other mycorrhizal symbioses is not clear.

Tundra algae exhibit the same degree of reduction in species diversity seen among the fungi and bacteria (Bunnell et al., 1980; Elster, 2002; Fogg, 1998), which documents a diversity much reduced from that of the microflora of temperate regions. Cyanobacteria and microalgae are among the oldest (in evolutionary terms) and simplest forms of life on the planet that can photosynthesize. Unicellular and filamentous photosynthetic cyanobacteria and microalgae are among the main primary colonizers adapted to conditions of the arctic terrestrial environment. They are widespread in all terrestrial and shallow wetland habitats and frequently produce visible biomass. Terrestrial photosynthetic microorganisms colonize mainly the surface and subsurface of the soil and create the crust (Elster et al., 1999). Algal communities in shallow flowing or static wetlands produce mats or mucilaginous clusters that float in the water but are attached to rocks underneath (Elster et al., 1997). Terrestrial and wetland habitats represent a unique mosaic of cyanobacteria and algae communities that occur up to the highest and lowest possible latitudes and altitudes as long as water (liquid or vapor) is available for some time during the year (Elster, 2002). The arctic soil and wetland microflora is composed mainly of species from Cyanobacteria, Chrysophyceae, Xanthophyceae, Bacillariophyceae, Chlorophyceae, Charophyceae, Ulvophyceae, and Zygnemaphyceae. A wide range of species diversity (between 53 and 150 to 160 species) has been reported from various arctic sites (Elster, 2002).

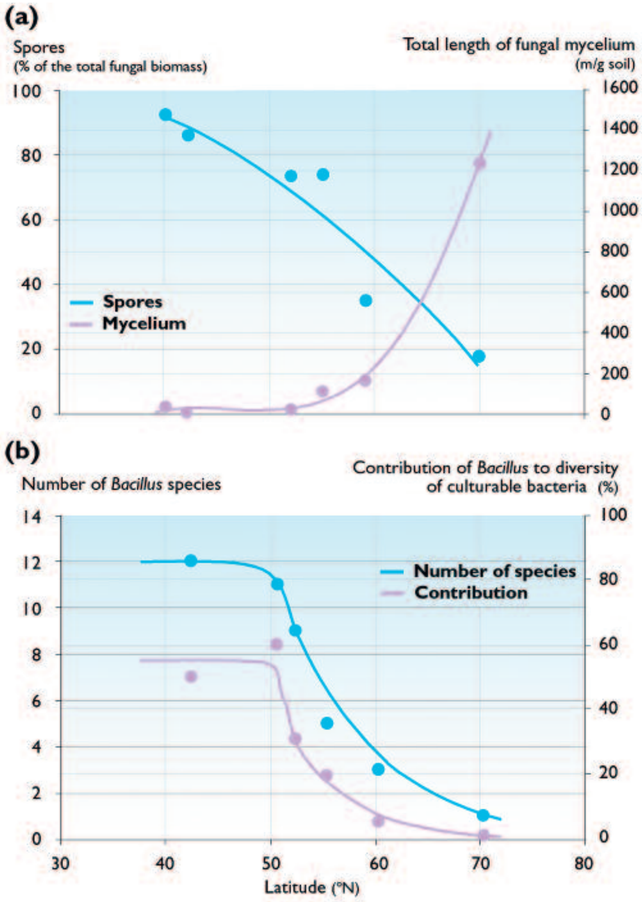


Fig. 7.7. Latitudinal distribution of (a) soil fungi and (b) bacilli; curves are hand-fitted (recalculated from data in Mirchink, 1988).

Latitudinal gradients of species diversity

Arctic soils contain large reserves (standing crops) of microbial (mainly fungal) biomass, although the rate of microbial growth is generally lower than in the boreal zone. Surprisingly, under severe arctic conditions, soil microbes fail to produce spores and other dormant structures that are adaptations to harsh environments (Fig. 7.7). The species diversity of all groups of soil microorganisms is lower in the Arctic than further south, decreasing from about 90 species in Irish grassland, through about 50 species in Alaskan birch forest, to about 30 species in Alaskan tundra (Flanagan and Scarborough, 1974). As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, although these patterns are less well documented. A correlate of the decreasing number of species with increasing latitude is increasing dominance of the species that occur, as with plants and animals. One yeast (*Cryptococcus laurentii*), for example, constitutes a large proportion of yeast biomass across a range of community types in the northern Taymir Peninsula (Chernov, 1985).

The hyphal length of fungi in the Arctic shows a latitudinal trend in which the abundance of fungi, as measured by hyphal length, decreases toward the north. Although it is not known if this trend also applies to the species diversity of fungal mycelia (the belowground network of fungal filaments or hyphae), it is clear that the amount of fungal hyphae is low in the Arctic (Robinson et al., 1996). In the high Arctic, fungal hyphal length was 23±1 m/g in a polar semi desert on Svalbard (78°56' N), 39 m/g on a beach ridge, and 2228 m/g in a mesic meadow on Devon Island (75°33' N). At Barrow, Alaska, hyphal length was 200 m/g. In a subarctic mire in Swedish Lapland, hyphal length was 3033 m/g. These values can be compared with 6050 to 9000 m/g in temperate uplands in the United Kingdom and 1900 to 4432 m/g in temperate woodland soils.

7.3.1.4. Summary

Species diversity appears to be low in the Arctic, and decreases from the boreal forests to the polar deserts of the extreme north. Only about 3% (~5900 species) of the global flora (excluding algae) occur in the Arctic north of the treeline. However, primitive plant species (mosses and lichens) are particularly abundant. Although the number of plant species in the Arctic is low in general, individual communities of small arctic plants have a diversity similar to or higher than those of boreal and temperate zones: there can be up to 25 species per square decimeter. Latitudinal gradients suggest that arctic plant diversity is sensitive to climate, and species number is least sensitive to temperature near the southern margin of the tundra. The temperature gradient that has such a strong influence on species diversity occurs over much shorter distances in the Arctic than in other biomes.

The diversity of arctic animals beyond the latitudinal treeline (~6000 species) is nearly twice as great as that of vascular plants and bryophytes. As with plants, the arctic fauna accounts for about 3% of the global total, and in general, primitive groups (e.g., springtails) are better represented in the Arctic than are advanced groups such as beetles. In general, the decline in animal species with increasing latitude is more pronounced than that of plants (frequently greater than 2.5-fold). An important consequence of the decline in numbers of species with increasing latitude is an increase in dominance. "Super-dominant" plant and animal species occupy a wide range of habitats, and generally have large effects on ecosystem processes.

Microbial organisms are more difficult to enumerate. Arctic soils contain large reserves of microbial biomass, although diversity of all groups of soil microorganisms is lower in the Arctic than further south. Many common bacteria and fungi are rare or absent in tundra areas. As with plants and animals, there are large reductions in numbers of microbial species with increasing latitude, and increasing dominance of the species that occur.

The latitudinal temperature gradient within tundra is steeper than for any other biome, and outlier populations of more southerly species frequently exist in favorable microenvironments far to the north of their centers of distribution. Consequently, migration of southerly taxa is very likely to occur more rapidly in the Arctic than in other biomes. Temperature-induced biotic change is likely to be most pronounced at the northern extreme of tundra, where species distributions are most temperature-sensitive.

The initial response of diversity to warming is likely to be an increase in the diversity of plants, animals, and microbes, and reduced dominance of species that are currently widespread. Taxa most likely to expand into tundra are boreal taxa that currently exist in river valleys and could spread into the uplands, or animal groups such as wood-boring beetles that are presently excluded due to a lack of food resources. Although current extreme environmental conditions restrain the metabolic activity of arctic microbes, they preserve huge potential that is ready to display the same activity as boreal analogues during climate warming. Warming could possibly cause the extinction of a few arctic plants that currently occur in narrow latitudinal strips of tundra adjacent to the sea. Some animals are arctic specialists and could possibly face extinction. Those plant and animal species that have their centers of distribution in the high or middle Arctic are most likely to show reduced abundance in their current locations should projected warming occur.

7.3.2. General characteristics of arctic species and their adaptations in the context of changes in climate and ultraviolet-B radiation levels

7.3.2.1. Plants

For the past 60 years, arctic plant ecologists have been concerned with the adaptations and traits of arctic plants that enable them to survive in harsh climates (e.g., Billings and Mooney, 1968; Bliss, 1971; Porsild, 1951; Russell, 1940; Savile, 1971; Sørensen, 1941). It is now important to consider how plants that are adapted to harsh environments will respond to climatic warming, and particularly how former adaptations may constrain their survival in competition with more aggressive species that are projected to immigrate from the south. Only in the past 20 years have ecologists considered arctic plant adaptations to UV-B radiation (e.g., Björn, 2002; Robberecht et al., 1980).

Plant adaptations to the arctic climate are relatively few compared with adaptations of plants to more southerly environments (Porsild, 1951; Savile, 1971) for the following reasons (Jonasson et al., 2000):

- arctic plants have inhabited the Arctic (except for ice-free refugia) for a relatively short period of time, particularly in Canada and the Yamal Peninsula;
- life spans and generation times are long, with clonal reproduction predominating;
- flowering and seed set are relatively low and insecure from year to year; and
- the complexity of the plant canopy is relatively small and the canopy is low, so that climbing plants with tendrils, thorns, etc. are not present.

Annuals and ephemeral species are very few (e.g., cold eyebright – *Euphrasia frigida* and Iceland purslane – *Koenigia islandica*). Many arctic plants are pre-adapted to arctic conditions (Crawford et al., 1994) and have migrated to the Arctic along mountain chains (Billings, 1992) or along upland mires and bogs. Although specific adaptations to arctic climate and UV-B radiation levels are absent or rare, the climate and UV-B radiation regimes of the Arctic have selected for a range of plant characteristics (Table 7.5).

The first filter for plants that can grow in the Arctic is freezing tolerance, which excludes approximately 75% of the world's vascular plants (Körner, 1995). However, many temperature effects on plants, particularly those

Table 7.5. Summary of major characteristics of current arctic plants related to climate and UV-B radiation.

Climatic factor	General effects on plants	Adaptations/characteristics of arctic plants	References
Aboveground environment			
Freezing temperatures	Plant death	Evergreen conifers tolerate temperatures between -40 and -90 °C; arctic herbaceous plants tolerate temperatures between -30 and -196 °C	Larcher, 1995
Ice encapsulation	Death through lack of oxygen	Increased anoxia tolerance	Crawford et al., 1994
Low summer temperatures	Reduced growth	Increased root growth, nutrient uptake, and respiration	Shaver and Billings, 1975; Chapin F., 1974; Mooney and Billings, 1961
		Minimized coupling between the vegetation surface and the atmosphere: cushion plants can have temperature differentials of 25 °C	Mølgaard, 1982
		Occupation of sheltered microhabitats and south-facing slopes	Bliss, 1971; Walker M.D. et al., 1991
Short, late growing seasons	Constraint on available photosynthetically active radiation and time for developmental processes	Long life cycles	Callaghan and Emanuelsson, 1985
		Slow growth and productivity	Wielgolaski et al., 1981
		Dependence on stored resources	Jonasson and Chapin, 1985
		Long flowering cycles with early flowering in some species	Sørensen, 1941
		Increased importance of vegetative reproduction	Bell and Bliss, 1980
		Clonal growth; clones surviving for thousands of years	Jónsdóttir et al., 2000
		Long-lived leaves maximizing investment of carbon	Bell and Bliss, 1977
Interannual variability	Sporadic seed set and seedling recruitment	Dependence on stored resources	Jonasson and Chapin, 1985
		Long development processes buffer effects of any one year	Sørensen, 1941
		Clonal growth	Callaghan and Emanuelsson, 1985; see also Molau and Shaver, 1997; Brooker et al., 2001; Molau and Larsson, 2000
Snow depth and duration	*Negative*: constrains length and timing of growing season	Where snow accumulates, snow beds form in which specialized plant communities occur	Gjærevoll, 1956
		Where snow is blown off exposed ridges (fellfields), plants are exposed to summer drought, winter herbivory, and extreme temperatures	Billings and Bliss, 1959; Savile, 1971
	Exerts mechanical pressure on plants	Responses and adaptations not measured	-
	Positive: Insulation in winter (it is seldom colder than -5 °C under a 0.5 m layer)	Low plant stature	Crawford, 1989
	Reduction of plant temperature extremes and freeze–thaw cycles	Low stature to remain below winter snow cover reduces the risk of premature dehardening	Ögren, 1996, 1997
	Protection from wind damage, abrasion by ice crystals, and some herbivory	Low stature to remain below winter snow cover; growth in sheltered locations	Sveinbjörnsson et al., 2002
	Protection from winter desiccation when water loss exceeds water supply from frozen ground	Low stature to remain below winter snow cover; deciduous growth	Barnes et al., 1996; Havas, 1985; Ögren, 1996; Taulavuori E. et al., 1997; Taulavuori K. et al., 1997b
	Protection from chlorophyll bleaching due to light damage in sunny habitats	Low stature to remain below winter snow cover; deciduous growth	Curl et al., 1972
	Source of water and nutrients late into the growing season	Zonation of plant species related to snow depth and duration	Fahnestock et al., 2000; Gjærevoll, 1956
Increased UV-B radiation levels	Damage to DNA that can be lethal or mutagenic	Reflective/absorptive barriers such as thick cell walls and cuticles, waxes, and hairs on leaves; physiological responses such as the induction or presence of UV-B radiation absorbing pigments (e.g., flavonoids) and an ability to repair some UV-B radiation damage to DNA	Robberecht et al., 1980; Semerdjieva et al., 2003
		Repair is mediated through the enzyme photolyase that is induced by UV-A radiation. There is so far no indication of adaptations to UV-B radiation that are specific to plants of the Arctic	Li et al., 2002a,b

Climatic factor	General effects on plants	Adaptations/characteristics of arctic plants	References
Aboveground environment			
Variable atmospheric CO_2 concentrations	Increased atmospheric CO_2 concentrations usually stimulate photosynthesis and growth if other factors are non-limiting; an increased ratio of carbon to nitrogen in plant tissues	Photosynthesis in Alaskan graminoids acclimated to high CO_2 concentrations within six weeks, with no long-term gain	Tissue and Oechel, 1987
		The dwarf willow (*Salix herbacea*) has been able to alter its carbon metabolism and morphology in relation to changing CO_2 concentrations throughout the last 9000 years	Beerling and Rundgren, 2000
		Species such as the moss *Hylocomium splendens* are already adapted to high CO_2 concentrations; frequently experiencing 400–450 ppm, and sometimes over 1100 ppm, to compensate for low light intensities under mountain birch woodland. These high CO_2 concentrations are caused by both soil and plant respiration close to the forest understory surface in still conditions and when light intensities are low	Sonesson et al., 1992
Soil environment			
Low rates of nutrient availability, particularly nitrogen	Reduced growth and reproduction	Conservation of nutrients in nutrient-poor tissues	Wielgolaski et al., 1975
		Long nitrogen retention time resulting from considerable longevity of plant organs and resorption of nutrients from senescing tissues and retention of dead leaves within plant tufts and cushions	Berendse and Jonasson, 1992
		Substantial rates of nutrient uptake at low temperatures	Chapin F. and Bloom, 1976
		Increased surface area for nutrient uptake by increased biomass of roots relative to shoots (up to 95% of plant biomass can be below ground)	Chapin F., 1974; Shaver and Cutler, 1979
		Associations with mycorrhizal fungi	Michelsen et al., 1998
		Nitrogen uptake by rhizomes	Brooker et al., 1999
		Some arctic plants can take up nutrients in organic forms, bypassing some of the slow decomposition and mineralization processes	Chapin F. et al., 1993
		Dependence on atmospheric nutrient deposition in mosses and lichens	Jónsdóttir et al. 1995
Soil movement at various spatial scales resulting from freeze–thaw cycles, permafrost dynamics, and slope processes	Freeze–thaw cycles heave ill-adapted plants from the soil and cause seedling death	Areas of active movement select for species with elastic and shallow roots or cryptogams without roots	Perfect et al., 1988; Wager, 1938; Jonasson and Callaghan, 1992; Chapter 5
Shallow active layer	Limits zone of soil biological activity and rooting depth; shallow rooting plates of trees can lead to falling	Shallow-rooting species, rhizome networks	Shaver and Cutler, 1979
Biotic environment			
Herbivory	Removal of plant tissue sometimes leading to widespread defoliation and death	Arctic plants do not have some morphological defenses (e.g., thorns) found elsewhere	Porsild, 1951
		Many plants have secondary metabolites that deter herbivores; some substances are induced by vertebrate and invertebrate herbivores	Haukioja and Neuvonen, 1987; Seldal et al. 1994
		Protected growing points; continuous leaf growth in summer; rapid modular growth in some graminoids; regeneration from torn fragments of grass leaves, mosses, and lichens	Savile, 1971; Sørensen, 1941
Competition	Suppression of some species and increased dominance of others leading to changes in community structure	Secondary metabolites in some arctic species inhibit the germination and growth of neighboring species	Michelsen et al., 1995; Zackrisson and Nilsson, 1992
Facilitation	Mutual benefits to plant species that grow together	Positive plant interactions are more important than plant competition in severe physical environments	Brooker and Callaghan, 1998; Callaway et al., 2002
		Nitrogen-fixing species in expanding glacial forefields facilitate the colonization and growth of immigrant plant species	Chapin F. et al., 1994
		Plant aggregation can confer advantages of shelter from wind	Carlsson and Callaghan, 1991
		Hemiparasites can stimulate nutrient cycling of potential benefit to the whole plant community	Quested et al., 2002

with roots and in the long term, are indirect (Chapin F., 1983). Plant nutrients in arctic soils, particularly nitrogen, are available to higher plants (with roots) at low rates (Russell R., 1940) because of slow microbial decomposition and mineralization rates of organic matter constrained by low temperatures (Heal et al., 1981). Arctic plants use different strategies for nutrient uptake (Callaghan et al., 1991), and different sources of nitrogen, which reduces competition among plants and facilitates greater plant diversity (McKane et al., 2002).

Many of the adaptations of arctic species to their current environments, such as slow and low growth, are likely to limit their responses to climate warming and other environmental changes. If changes in climate and UV radiation levels adversely affect species such as mosses that play an important role in facilitation, normal community development and recovery after disturbance are likely to be constrained. Many arctic plant characteristics are likely to enable plants to cope with abiotic selective pressures (e.g., climate) more than biotic pressures (e.g., interspecific competition). This is likely to render arctic organisms more susceptible to biological invasions at their southern distributional limits, while populations at their northern range limit (e.g., boreal species in the tundra) are likely to respond more than species at their southern limit to warming *per se*. Thus, as during past environmental changes, arctic species are very likely to change their distributions rather than evolve significantly.

Summary

Plant adaptations to the arctic climate are absent or rare: many species are pre-adapted. The first filter for arctic plants is freezing tolerance, which excludes approximately 75% of the world's vascular plants. Short growing seasons and low solar angles select for long life cycles in which slow growth often uses stored resources while development cycles are often extended over multiple growing seasons. Some plant species occupy microhabitats, or exhibit behavior or growth forms that maximize plant temperatures compared with ambient temperatures. Low soil temperatures reduce microbial activity and the rates and magnitude of nutrient availability to the roots of higher plants. Mechanisms to compensate for low nutrient availability include the conservation of nutrients in nutrient-poor tissues, resorption of nutrients from senescing tissues, enhanced rates of nutrient uptake at low temperatures, increased biomass of roots relative to shoots, associations with mycorrhizal fungi, uptake of nutrients in organic forms, and uptake of nitrogen by rhizomes. Temperature fluctuations around 0 °C cause frost-heave phenomena that can uproot ill-adapted plants.

Snow distribution determines the period over which plants can intercept solar radiation and grow. Snow cover insulates plants against low air temperatures in winter and extremes of temperature in spring, protects plants from physical damage from abrasion by ice crystals, and provides a source of water often late into the growing season. Where snow cover is thin (e.g., on exposed ridges), growing seasons are usually long but water can become limiting; where snow accumulates in sheltered depressions, snow beds form in which specialized plant communities occur.

Many arctic plants are pre-adapted to relatively high levels of UV-B radiation. They exhibit various mechanisms to protect DNA and sensitive tissues from UV-B radiation and an ability to repair some UV-B radiation damage to DNA. Thick cell walls and cuticles, waxes, and hairs on leaves, and the presence or induction of UV-B radiation absorbing chemical compounds in leaves, protect sensitive tissues. There appear to be no specific adaptations of arctic plant species to high atmospheric CO_2 concentrations.

Arctic plant species do not show the often-complex interactions with other organisms prevalent in southern latitudes. Arctic plants are adapted to grazing and browsing mainly through chemical defenses rather than the possession of spines and thorns. Facilitation increases in importance relative to competition at high latitudes and altitudes.

Thus, many of the adaptations of arctic species to their current environments are likely to limit their responses to climate warming and other environmental changes. Many characteristics are likely to enable plants to cope with abiotic selective pressures (e.g., climate) more than biotic pressures (e.g., inter-specific competition). This is likely to render arctic organisms more susceptible to biological invasions and they are very likely to change their distributions rather than evolve significantly in response to warming.

7.3.2.2. Animals

Classical arctic zoology typically focused on morphological and physiological adaptations to life under conditions of extremely low winter temperatures (Schmidt-Nielsen, 1979; Scholander et al., 1950). Physiological studies contribute to a mechanistic understanding of how arctic animals cope with extreme environmental conditions (especially low temperatures), and what makes them different from their temperate counterparts. Ecological and evolutionary studies focus on how life-history strategies of arctic animals have evolved to tolerate environmental variation in the Arctic, how flexible life histories (in terms of both phenotypic plasticity and genetic variation) are adapted to environmental variation, and how adjustments in life-history parameters such as survival and reproduction translate into population dynamics patterns.

Adaptations to low temperatures

Arctic animals have evolved a set of adaptations that enable them to conserve energy in low winter temperatures. Warm-blooded animals that persist throughout the arctic winter have thick coats of fur or feathers that often turn white (Scholander et al., 1950). The body shapes of high-arctic mammals such as reindeer/caribou, collared lemmings, Arctic hares (*Lepus arcticus*), and Arctic foxes (*Alopex lagopus*) are rounder and their extremities shorter than their temperate counterparts (Allen's rule). Body size within some vertebrate taxa increases toward the north (Bergman's rule), but there are several notable arctic exceptions to this (e.g., reindeer/caribou; Klein, 1999; muskox; Smith P. et al., 2002). There are few physiological adaptations in homeotherms (warm-blooded animals) that are unique to arctic animals. However, several adaptations may be considered to be typical of the Arctic, including fat storage (e.g., reindeer/caribou and Arctic fox; Prestrud and Nilssen, 1992) and reduced body-core temperature and basal metabolism in the winter (e.g., Arctic fox; Fuglei and Øritsland, 1999). While hibernation during the winter is found in a few arctic mammals such as the Arctic ground squirrel (*Spermophilus parryii*), most homeothermic animals are active throughout the year. Small mammals such as shrews (*Sorex* spp.), voles (*Microtus, Clethrionomys* spp.), and lemmings with relatively large heat losses due to a high surface-to-volume ratio stay in the subnivean space (a cavity below the snow) where they are protected from low temperatures during the winter. Even medium-sized birds and mammals such as ptarmigan (*Lagopus mutus*) and hares seek thermal refuges in snow caves when resting. In the high Arctic, the normal diurnal activity patterns observed at more southerly latitudes are replaced by activity patterns that are independent of the time of the day (e.g., Svalbard ptarmigan – *Lagopus mutus hyperboreus*; Reierth and Stokkan, 1998).

In heterothermic (cold-blooded) invertebrates, hairiness and melanism (dark pigmentation) enable them to warm up in the summer season. Invertebrates survive low winter temperatures in dormancy mainly due to two cold-hardiness strategies: freeze tolerance and freeze avoidance (Strathdee and Bale, 1998). Typically, supercooling points are lower in arctic than in temperate invertebrates. Freeze tolerance, which appears to be an energetically less costly strategy than extended supercooling, is a common strategy in very cold regions. Wingless morphs occur frequently among arctic insects, probably because limited energy during the short growth season is allocated to development and reproduction, rather than in an energetically costly flight apparatus. A short growth season also constrains insect body size and number of generations per year. Life cycles are often extended in time and/or simplified because invertebrates may need several seasons to complete their life cycles. Small body size in arctic insects seems to be a strategy to shorten generation time (Strathdee and Bale, 1998). Moreover, individuals from arctic populations are able to grow faster at a given temperature than southern conspecifics (e.g., Birkemoe and Leinaas, 2000). Thus, arctic invertebrates may be particularly efficient in utilizing relatively short warm periods to complete life-cycle stages.

A short breeding season also underlies several life-history adaptations in birds and mammals, such as synchronized breeding, shortened breeding season, specific molting patterns, and mating systems (Mehlum, 1999). Although adjustments to low temperatures and short growth seasons are widespread in arctic animals, successful species cannot be generalized with respect to particular life-history traits (Convey, 2000). Both flexible and programmed life cycles are common in polar arthropods (Danks, 1999).

While there are many examples that show that winter temperatures lower than species-specific tolerance limits set the northern borders of the geographic distribution of animals, there are hardly any examples that demonstrate that high temperatures alone determine how far south terrestrial arctic animals are found. Southern range borders are typically set by a combination of abiotic factors (e.g., temperature and moisture in soil invertebrates) or, probably most often, by biotic factors such as food resources, competitors, and natural enemies.

Migration and habitat selection

Many vertebrates escape unfavorable conditions through movement (either long-distance migration or more short-range seasonal movement) between different habitats in the same landscape. Seasonal migration to southern overwintering areas is almost the rule in arctic birds. Climate may interfere in several ways with migrating birds, such as mismatched migration timing, habitat loss at stopover sites, and weather en route (Lindström and Agrell, 1999), and a mismatch in the timing of migration and the development of invertebrate food in arctic ponds (section 8.5.6). Many boreal forest insects invade the low-arctic tundra in quite large quantities every summer (Chernov and Matveyeva, 1997), but few of these are likely to return in the autumn. Birds residing in the tundra throughout the year are very few and include species such as Arctic redpoll (*Carduelis hornemanni*), willow grouse (*Lagopus lagopus*), ptarmigan, raven, gyrfalcon (*Falco rusticolus*), and snowy owl (*Nyctea scandiaca*). Like several other arctic predators that specialize in feeding on lemmings and Arctic voles, the snowy owl emigrates when cyclic lemming populations crash to seek high-density prey populations elsewhere in the Arctic and subarctic. A similar nomadic lifestyle is found in small passerine seed-eating birds such as redpolls and crossbills (*Loxia* spp.) in the forest tundra. These birds move between areas with asynchronous mast years (years with exceptionally abundant seed production) in birch and conifers. A substantial fraction of the Arctic fox population migrates after lemming peaks and sometimes these migrations may extend far into the taiga zone (Hersteinsson and Macdonald, 1992). Most reindeer and caribou populations perform seasonal migrations from coastal tundra in summer to continental areas of forest tundra and taiga in the winter. Inuit ecological knowledge explains caribou migrations as triggered by seasonal "cues", such as day length, temperature, or ice thickness (Thorpe et al., 2001). Reindeer on isolated arctic islands are more sedentary without pronounced seasonal migrations (Tyler and Øritsland, 1989). Lemmings and ptarmigans shift habitat seasonally within the same landscapes (Kalela, 1961). In peak population years, the seasonal habitat shifts of the Norway lemming (*Lemmus lemmus*) may become more long-distance mass movements (Henttonen and Kaikusalo, 1993). For small mobile animals (e.g., wingless soil invertebrates such as Collembola and mites), habitat selection on a very small spatial scale (microhabitat selection) enables individuals to find spatial refuges with temperature and moisture regimes adequate for survival (Hodkinson et al., 1994; Ims et al., 2004). The variability in microclimatic conditions may be extremely large in the high Arctic (Coulson et al., 1995).

Adaptations to the biotic environment

Generalists in terms of food and habitat selection seem to be more common among arctic animals than in communities further south (e.g., Strathdee and Bale, 1998). This may be either due to fewer competitors and a less tightly packed niche space in arctic animal communities and/or because food resource availability is less predictable and the appropriate strategy is to opt for more flexible diets. Notable exceptions to food resource generalism are lemming predators (e.g., least weasels – *Mustela nivalis*, and several owls – *Asio*, *Nyctea* spp., raptors – *Buteo* spp., and skuas – *Stercorarius* spp.) and a number of host-specific phytophagous insects (e.g., aphids – *Acyrthosiphon* spp. and sawflies – Symphyta). Many water birds, such as geese and sandpipers (*Calidris* spp.) with 75 and 90%, respectively, of species breeding in the Arctic, are habitat specialists. Some species exhibit a large flexibility in their reproductive strategy based on food resources. Coastal populations of Arctic foxes with a relatively predictable food supply from the marine ecosystem (e.g., seabird colonies) have smaller litter sizes than inland "lemming foxes" that rely on a highly variable food supply (Tannerfeldt and Angerbjörn, 1998). Specialists on highly fluctuating food resources such as seeds from birch and conifers, as well as lemmings and voles, respond to temporary superabundant food supplies by having extraordinarily high clutch or litter sizes.

High Arctic environments contain fewer natural enemy species (e.g., predators and parasites) and some animals seem to be less agile (e.g., Svalbard reindeer; Tyler and Øritsland, 1989) and are possibly less resistant to disease (Piersma, 1997).

Ultraviolet-B radiation

Little is known about animal adaptations to UV-B radiation. Non-migrant species, such as reindeer/caribou, Arctic foxes, hares, and many birds, have white fur or feathers that presumably reflect some UV-B radiation. There is some evidence, however, that feathers can be affected by high UV-B radiation levels (Bergman, 1982), although this early research needs to be repeated. There is also a possibility that fur absorbs UV-B radiation. Eyes of arctic vertebrates experience extremes of UV-B radiation, from dark winter conditions to high UV-B radiation environments in spring. However, mechanisms of tolerance are unknown. Invertebrates in general have DNA that is robust to UV-B radiation damage (Koval, 1988) and various adaptations to reduce the absorption of UV-B radiation. Some subarctic caterpillars possess pigmented cuticles that absorb in the UV-B wavelengths, while pre-exposure to UV-B radiation can induce pigmentation (Buck and Callaghan, 1999). Collembolans and possibly other invertebrates have dark pigmentation that plays a role in both thermoregulation and UV-B radiation protection (Leinaas, 2002).

Patterns of population dynamics

In tundra habitats, population cycles in small- to medium-sized birds and mammals are the rule, with few exceptions. The period of the population cycle in lemmings and voles varies geographically, and is between three and five years. Cyclicity (e.g., spatial synchronicity and period between peak population years) seems to be associated with spatial climate gradients (coast to inland and south to north) in Fennoscandia (Hansson and Henttonen, 1988; Strann et al., 2002), although the biotic mechanisms involved are still much debated (Hanski et al., 2001). Some lemming populations show geographic variation in the cycle period within arctic Siberia; and also (for example) exhibit a long period (5 years on Wrangel Island) and a relatively short period (3 years in Taymir) between peak population years (Chernov and Matveyeva, 1997). Within regions (e.g., northern Fennoscandia), small rodent cycles may show distinct interspecific synchrony over large spatial scales (Myrberget, 1973). However, recent spatially extensive surveys in northern Canada (Predavec et al., 2001) and Siberia (Erlinge et al., 1999) have indicated that the spatial synchrony of lemming populations is not as large-scale as the snowshoe hare (*Lepus americanus*) cycles in boreal North America (Elton and Nicholson, 1942). This is at least partly due to the geographically variable cycle period.

Populations of small- and medium-sized bird and mammal predators follow the dynamics of their lemming and vole prey species (Wiklund et al., 1999). The signature of lemming and vole population dynamics can also be found in the reproductive success and demography of mammals and birds, for example, waders and geese (e.g., Bety et al., 2002), that serve as alternative prey for lemming predators. Among northern insects, population cycles are best known in geometrid moths, particularly the autumnal moth (*Epirrita autumnata*), which exhibits massive population outbreaks with approximately 10-year intervals that extend into the forest tundra (Tenow, 1972, 1996). In the tundra biome, no herbivorous insects are known to have population cycles (Chernov and Matveyeva, 1997). However, the population dynamics of tundra invertebrates is poorly known due to the lack of long-term data. Soil invertebrates such as Collembola (Birkemoe and Sømme, 1998; Hertzberg et al., 2000) sometimes exhibit large interannual fluctuations in population density. Large fluctuations in numbers have also been observed in arctic ungulate populations (reindeer/caribou and muskox), and seem to be the result of several biotic factors in combination with climatic variation (Klein, 1996, 1999; Morneau and Payette, 2000).

Summary: Implications for animal responses to climate change

Terrestrial arctic animals possess many adaptations that enable them to persist in the arctic climate. Physiological and morphological traits in warm-blooded vertebrates (mammals and birds) include thick fur and feather plumages, short extremities, extensive fat storage before winter, and metabolic seasonal adjustments, while cold-blooded invertebrates have developed strategies of cold hardiness, high body growth rates, and pigmented and hairy bodies. Arctic animals can survive under an amazingly wide range of temperatures, including high temperatures. The short growing season represents a challenge for most arctic animals and life-history strategies have evolved to enable individuals to fulfill their life cycles under time constraints and high environmental unpredictability. The biotic environment (e.g., the ecosystem context) of arctic species is relatively simple with few enemies, competitors, and available food resources. For those reasons, arctic animals have evolved fewer traits related to competition for resources, predator avoidance, and resistance to diseases and parasites than have their southern counterparts. Life cycles that are specifically adjusted to seasonal and multi-annual fluctuations in resources are particularly important because such fluctuations are very pronounced in terrestrial arctic environments. Many arctic animals possess adaptations for escaping unfavorable weather, resource shortages, or other unfavorable conditions through either winter dormancy or by selection of refuges at a wide range of spatial scales, including microhabitat selection at any given site, seasonal habitat shifts within landscapes, and long-distance seasonal migrations within or across geographic regions.

Based on the above general characteristics, if climate changes, terrestrial arctic animals are likely to be most vulnerable to the following conditions: higher summer temperatures that induce desiccation in invertebrates; climatic changes that interfere with migration routes and staging sites for long-distance migrants; climatic events that alter winter snow conditions and freeze–thaw cycles resulting in unfavorable temperature, oxygen, and CO_2 conditions for animals below the snow and limited resource availability (e.g., vegetation or animal prey) for animals above the snow; climatic changes that disrupt behavior and life-history adjustments to the timing of reproduction and development that are currently linked to seasonal and multi-annual peaks in food resource availability; and the influx of new competitors, predators, parasites, and diseases.

7.3.2.3. Microorganisms

As a group, microorganisms are highly mobile, can tolerate most environmental conditions, and have short generation times that can facilitate rapid adaptation to new environments associated with changes in climate and UV-B radiation levels.

Adaptations to cold

The ability to resist freezing (and to restore activity after thawing) and the ability to metabolize below the freezing point are fundamental microbial adaptations to cold climates prevailing at high latitudes.

Cell viability depends dramatically on the freezing rate, which defines the formation of intracellular water crystals (Kushner, 1981; Mazur, 1980). Cold-adapted microbial species are characterized by remarkably high resistance to freezing due to the presence of specific intracellular compounds (metabolic antifreeze), stable and flexible membranes, and other adaptations. Lichens are extreme examples (Kappen, 1993): the moist thalli of such species as *Xanthoria candelaria* and *Rhizoplaca melanophthalma* fully tolerated gradual or rapid freezing to -196 ºC, and even after being stored for up to several years, almost immediately resumed normal photosynthetic rates when warmed and wetted. For five to seven months of cold and continuous darkness, they remain green with intact photosynthetic pigments. However, freeze resistance is not a unique feature of arctic organisms.

The ability of microorganisms to grow and metabolize in frozen soils, subsoils, or water is generally thought to be insignificant. However, microbial growth and activity below the freezing point has been recorded in refrigerated food (Larkin and Stokes, 1968) as well as in arctic and antarctic habitats such as sea ice, frozen soil, and permafrost (Kappen et al., 1996; Schroeter et al., 1994). Such activity has important implications for ecosystem function. Field measurements of gas fluxes in Alaska and northern Eurasia revealed that winter CO_2 emissions can account for up to half of annual CO_2 emissions (Oechel et al., 1997; Panikov and Dedysh, 2000; Sommerfeld et al., 1993; Zimov et al., 1993), implying significant cold-season activity in psychrophilic ("cold-loving") soil microbes. Soil fungi (including mycobionts, the symbiotic fungal component of lichens) have been considered as the most probable candidates for the majority of the tundra soil respiration occurring at temperatures below 0 ºC (Flanagan and Bunnell, 1980) because their live biomass was estimated to be ten times larger than that of cohabiting bacteria.

Winter CO_2 emissions have been also explained by other mechanisms (e.g., the physical release of summer-accumulated gases or abiotic CO_2 formation due to cryoturbation; Coyne and Kelley, 1971). Most recent studies (Finegold, 1996; Geiges, 1996; Mazur, 1980; Rivkina et al., 2000; Russell N., 1990) agree that microbial growth is limited at about -12 ºC and that occasional reports of microbial activity below -12 ºC (e.g., continuous photosynthesis in arctic and antarctic lichens down to -17 ºC; Kappen et al., 1996; Schroeter et al., 1994, and photosynthetic CO_2 fixation at -24 ºC; Lange and Metzner, 1965) were not carefully recorded and confirmed. Under laboratory conditions, Rivkina et al. (2000) quantified microbial growth in permafrost samples at temperatures down to -20 ºC. However, the data points below -12 ºC turned out to be close to the detection limits of the highly sensitive technique that they employed. The authors concluded that nutrient uptake at -20 ºC could be measured, but only transiently, "whereas in nature (i.e., under stable permafrost conditions)... the level of activity, if any, is not measurable ..." (Rivkina et al., 2000).

Recently, a new precise technique was applied to frozen soil samples collected from Barrow, Alaska, and incubated at a wide range of subzero temperatures under laboratory conditions (Panikov et al., 2001). The rate of CO_2 production declined exponentially with temperature and unfrozen water content when the soil was cooled below 0 ºC, but it remained surprisingly positive and measurable (e.g., 8 ng C/d/kg) at -39 ºC. A range of experimental results and treatments confirmed that this CO_2 production at very low temperatures was due to microbial respiration, rather than to abiotic processes. The demonstration that microorganisms can survive low temperatures suggests the possibility that ancient bacteria of distinctive genotypes trapped in permafrost will be released and become active during permafrost thawing (Gilichinsky, 1994). However, the period over which ancient permafrost is likely to thaw will be significantly longer than the next 100 years (section 6.6.1.3).

Dark pigmentation causes higher heat absorption in lichens, which is especially favorable in the cold polar environment (Kershaw, 1983; Lange, 1954).

Adaptations to drought

Freezing is always associated with a deficiency of available water. Thus, true psychrophilic organisms must also be "xerotolerant" (adapted to extremely dry environments). A number of plants and microorganisms in polar deserts, such as lichens, are termed "poikilohydrous", meaning that they tend to be in moisture equilibrium with their surroundings (Blum, 1974). They have high desiccation tolerance and are able to survive water loss of more than 95% and long periods of drought. Rapid water loss inactivates the thallus, and in the inactive state the lichen is safe from heat-induced respiratory loss and heat stress (Kappen, 1974; Lange, 1953). In unicellular microorganisms, drought resistance can also be significant, although mycelial forms of microbial life (fungi and actinomycetes) seem to have a much higher resistance to drought due to their more efficient cytoplasm compartmentalization and spore formation.

Adaptations to mechanical disturbance

Wind, sand, and ice blasts, and seasonal ice oscillations, are characteristic features of arctic environments that affect the colonization and survival of organisms. Most lichens are adapted to such effects by forming a mechanically solid thallus firmly attached to the substrate. Windswept habitats such as hillsides can be favorable if they provide a suitably rough substrate and receive sufficient moisture from the air. In contrast, shallow depressions or small valleys, although more sheltered, are bare of lichens because snow recedes from them only for very brief periods each season or persists over several years. This phenomenon is one reason for the so-called trimline effect (a sharp delineation on rocks between zones with and without lichens: Corner and Smith, 1973; Koerner, 1980; Smith R., 1972). The abrasive forces of the ice at the bottoms of glaciers may destroy all epilithic (rock-attached) lichen vegetation, but lichens once established are able to survive long periods of snow cover, and even glacial periods (Kappen, 1993).

Adaptations to irradiance

Strong pigmentation is typical for numerous microorganisms inhabiting tundra and polar deserts, especially for those that are frequently or permanently exposed to sunlight at the soil surface (lichens and epiphytic bacteria). Pigments (melanin, melanoids, carotenoids, etc.) are usually interpreted as a protection against strong irradiation. Pigmentation may be constitutive for particular species or appear as a plastic response to irradiance, for example, originally colorless *Cladonia* and *Cladina* lichens quickly develop dark-pigmented thalli after exposure to higher levels of solar radiation (Ahmadjian, 1970). Buffoni Hall et al. (2002) demonstrated that in *Cladonia arbuscula* ssp. *mitis* an increase in phenolic substances is specifically induced by UV-B radiation, and that this increase leads to attenuation of the UV-B radiation penetrating into the thallus. The accumulation of the protective pigment parietin in *Xanthoria parietina* is induced specifically by UV-B radiation (Gauslaa and Ustvedt, 2003), while in *Cladonia uncialis* and *Cladina rangiferina* only UV-A radiation had a stimulating effect on the accumulation of usnic acid and atranorin, respectively. Photorepair of radiation-damaged DNA in *Cladonia* requires not only light, but also high temperature and a hydrated thallus (Buffoni Hall et al., 2003). As in higher plants, carotenoids protect algae, fungi, and lichens from excessive photosynthetically active radiation (MacKenzie et al., 2002) and perhaps also have a role in protecting them from ultraviolet radiation. In contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.

Braga et al. (2001a,b) surveyed the UV radiation sensitivity of conidia (spore-forming bodies) of 30 strains belonging to four species of the fungus *Metarhizium*, an important biological insecticide. Exposing the fungus to UV-B radiation levels within an ecologically relevant range revealed great differences between the strains, with strains from low latitudes generally more tolerant of UV-B radiation than strains from high latitudes.

Algae

Seven inter-related stress factors (temperature, water, nutrient status, light availability and/or UV radiation, freeze–thaw events, and growing-season length and unpredictability) are important for life in arctic terrestrial and shallow wetlands (Convey, 2000). Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid or at least minimize injury. Three main strategies for coping with life in arctic terrestrial and wetland habitats are avoidance, protection, and the formation of partnerships with other organisms (Elster and Benson, 2004). Poikilohydricity (tolerance of desiccation) and shelter strategies are frequently interconnected, and when combined with cell mobility and the development of complex life cycles, afford considerable potential for avoidance. The production of intracellular protective compounds, which control the cell solute composition and viscosity (changes in the carbohydrate and polyols composition of the cell), together with changes in cell wall structures (production of multi-layered cell walls and mucilage sheets) are very common phenomena. The association of cyanobacteria and algae with fungi in lichens provides the benefit of physical protection.

Summary

Arctic microorganisms are not only resistant to freezing, but some can metabolize at temperatures down to -39 °C. During winter, this process could be responsible for up to 50% of annual CO_2 emissions from tundra soils. Cold-tolerant microorganisms are usually also drought-tolerant. Microorganisms are tolerant of mechanical disturbance and high irradiance. Pigmentation protects organisms such as lichens from high irradiance, including UV radiation, and pigments can be present in considerable concentrations. Cyanobacteria and algae have developed a wide range of adaptive strategies that allow them to avoid, or at least minimize, UV injury. However, in contrast to higher plants, flavonoids do not act as screening compounds in algae, fungi, and lichens.

As a group, microorganisms are highly adaptive, can tolerate most environmental conditions, and have short generation times that can facilitate rapid adaptation to new environments associated with changes in climate and UV-B radiation levels.

7.3.3. Phenotypic responses of arctic species to changes in climate and ultraviolet-B radiation

Species responses to climate change are complex. They respond individualistically to environmental variables such as temperature (Chapin F. and Shaver, 1985a), and various processes within a given species (e.g., reproductive development, photosynthesis, respiration, leaf phenology in plants) respond individualistically to a given environmental change. Knowledge of species responses to changes in temperature comes from many sources including indigenous knowledge, current species distributions related to climate, and experimental manipulations of temperature in the laboratory and field.

7.3.3.1. Plants

The information presented in this section relates to individual plant species and how they have responded to changes in various aspects of climate and UV radiation. The information is taken mainly from experiments in which climate variables or UV radiation levels were modified and the responses of the individual species determined while they were growing in natural communities. Indigenous knowledge is also included.

Responses to current changes in climate

Indigenous knowledge studies in Canada describe poor vegetation growth in eastern regions associated with warmer summers and less rain (Fox, 2002), but describe increased plant biomass and growth in western regions, particularly in riparian areas and of moisture-tolerant species such as shrubs (Riedlinger, 2001; Thorpe et al., 2001), due to lengthening of the growing season, marked spring warming, and increased rainfall.

Inuit participating in the Tuktu and Nogak Project in the Kitikmeot region of Nunavut (Thorpe, 2000; Thorpe et al., 2001) observed that vegetation was more lush, plentiful, and diverse in the 1990s compared to earlier decades. Willows and alders were described as taller, with thicker stem diameters and producing more branches, particularly along shorelines. Other indigenous communities have also reported increases in vegetation, particularly grasses and shrubs – stating that there is grass growing in places where there used to be only gravel. On Banks Island, in the western Canadian Arctic, Inuvialuit point to observations that the *umingmak* (muskox) are staying in one place for longer periods of time as additional evidence that vegetation is richer (Riedlinger, 2001). In addition, Riedlinger (2001) has documented Inuvialuit observations of an increase in forbs such as *qungalik* (Arctic sorrel – *Oxyria digyna*), which is described as coming out earlier in the spring, and noticeably "bigger, fresher, and greener".

The Arctic Borderlands Ecological Knowledge Co-op monitors the annual quality and quantity of salmonberries locally called *akpiks* (cloudberry – *Rubus chamaemorus*), and has documented recent observations of high temperatures early in the year that "burn" berry plant flowers, early spring melt that results in inadequate moisture for the plants later in the year, and intense summer sun that "cooks" the berries before they can be picked (Kofinas et al., 2002). On Banks Island, local residents report years where the grass remained green into the autumn, leaving it vulnerable to freezing (Riedlinger, 2001). This corresponds to experiments that show a similar effect on Svalbard (Robinson et al., 1998).

In northern Finland, marshy areas are said to be drying up. Sami reindeer herders from Kaldoaivi in Utsjoki have observed that berries such as bog whortleberry (*Vaccinium uliginosum*) have almost disappeared in some areas. Other berries such as cloudberry and lingonberry

(*V. vitis-idaea*) are said to have declined in the last 30 years (Helander, 2002). Indigenous peoples' observations of declining cloudberry production are supported by experiments that postulate declines in growth in warm winters (Marks and Taylor, 1978) and provide detailed mechanisms of fruit production (Jean and Lapointe, 2001; Korpelainen, 1994; Wallenius, 1999).

Indigenous knowledge also records changes in species distribution: some existing species have become more widespread and new species have been seen. In addition to increased shrub abundance, Thorpe et al. (2001, 2002) documented reports of new types of lichens and flowering plants on Victoria Island in Nunavut and more individual plants of the same species (Thorpe, 2000). The increases in shrubs in this area correspond to aerial photographic evidence of increases in shrub abundance in Alaska (Sturm et al., 2001b). However, the reports of new types of plants, and lichens in particular, contrast with experimental evidence that shows a decrease in lichens and some mosses when flowering plant biomass increases (Cornelissen et al., 2001; Potter et al., 1995). A possible reason for this is that results from warming experiments cannot be extrapolated throughout the Arctic because of variations in recent and projected climate owing to both cooling and warming (sections 2.6.2.1 and 4.4.2): warming experiments in continuous vegetation show declines of lichens, whereas lichens may expand their distribution during warming in the high Arctic where vascular plant competitors are sparse (Heide-Jørgensen and Johnsen, 1998).

In contrast to observed responses of plants to recent warming, remote sensing by satellites has shown that the start dates of birch pollen seasons have been delayed at high altitudes and in the northern boreal regions of Fennoscandia (Høgda et al., 2002). In the Faroe Islands, there has been a lowering of the alpine zone in response to a 0.25 ºC cooling over the past 50 years (Fossa, 2003).

Projected responses to future temperature changes

Warming *per se* is very likely to be favorable to the growth, development, and reproduction of most arctic plant species, particularly those with high phenotypic plasticity (flexible/responsive growth and development). However, other limiting factors such as nutrients and moisture or competition from immigrant species are likely to modify plant responses to warming. In some cases, the direct and indirect effects of warming are projected to generate negative responses:

- Increased respiration relative to photosynthesis can result in negative carbon balances, particularly in clonal plants that accumulate old tissues, for example, the cushion form ecotype (Fig. 7.3) of purple saxifrage (*Saxifraga oppositifolia*; Crawford, 1997a) and some species of the herb *Ranunculus* (Cooper, 1996).
- It is possible that cushion forms of arctic plants, including mosses, that have low atmospheric coupling and experience high temperatures will experience thermal death during warming, particularly when combined with reduced cooling by evapotranspiration under drought conditions.
- Exposure to high levels of solar radiation and increases in temperature could possibly cause damage and death to some species, particularly those occupying shady and wet habitats, that have low thermal tolerances (as low as 42 ºC in Arctic sorrel; Gauslaa, 1984).
- During warming, arctic species with conservative nutrient-use strategies, slow growth, and particularly inflexible morphologies such as those of cushion and mat plants, are likely to be at a competitive disadvantage to more responsive, faster growing, taller species immigrating from southern latitudes. After six years of shading (simulating competition), increasing temperatures, and fertilizing a heath and a fellfield community in Swedish Lapland, shading was found to have the greatest effect on aboveground growth (Graglia et al., 1997). In another experiment, flowering of the dwarf heather-like shrub *Cassiope tetragona* stopped when it was shaded (Havström et al., 1995a). In contrast, a meta-analysis by Dormann and Woodin (2002) found no significant effect of shading on biomass.

Populations at the most environmentally extreme boundary of their distributions (in terms of latitude, altitude, and habitat mosaics within landscapes) tend to be responsive to amelioration of physical environmental factors such as temperature that limit their distributions; these populations have the potential to expand their distribution. In contrast, populations at the most environmentally benign boundary of their distribution tend to be constrained by competition with more responsive species of more benign environments (Wijk, 1986) and tend to be displaced by environmental amelioration.

An International Tundra Experiment (ITEX; Henry and Molau, 1997) meta-analysis of arctic vascular plant species responses to simulated summer warming (1.2 to 1.8 ºC mean daily near-surface and soil temperature increase) using standard open-top chambers compared key species from 13 sites over a period of one to four years (Arft et al., 1999). The simulated temperature increase is comparable to the projected increase in mean arctic summer air temperature of 1.8 ºC by 2050 (mean of the five ACIA-designated model scenarios). In ITEX and earlier experiments, phenology (bud burst and flowering) was advanced in warming treatments at some sites (Wookey et al., 1993, 1995). In Swedish Lapland, growth accelerated and the period between thawing and anther appearance advanced by two weeks (Welker et al., 1997). In contrast, there was little change in growth cessation at the end of the season in response to higher temperatures. However, nutrient addition prolonged the growth period of polar semi-desert species on Svalbard in autumn but reduced frost hardening, leading to dramatic loss of aboveground biomass during November 1993, which was extremely warm and wet (Robinson et al., 1998). This corresponds with the indigenous observations noted above.

Experiments conducted by ITEX showed that initial increases in vegetative growth were generally, but not always, reduced in later years, probably because temperature increases stimulated the use of stored resources more than the uptake of new resources. Similarly, growth responses of subarctic dwarf shrubs to soil warming increased initially but soon returned to former levels. This response followed an initial increase in nitrogen mineralization as a result of soil warming, but increases in mineralization did not persist (Hartley et al., 1999). In contrast, reproductive success improved in later years in the ITEX experiments (Arft et al., 1999) due to the extended period between flower bud initiation and seed set in arctic flowering plants. Similarly, over an 18-year period, flowering of the widespread sedge *Carex bigelowii* was strongly correlated with July temperature of the previous year (Brooker et al., 2001). *Eriophorum* species exhibited even more dramatic interannual variation in flowering than *Carex* species, but there was no simple correlation with weather in the flowering year or the previous year (Shaver et al., 1986).

The ITEX experiments showed that responses of growth and reproduction to temperature increases varied among vascular plant life forms. Herbaceous species responded more strongly and consistently to warming than did woody forms over a four-year period (Arft et al., 1999). Over longer time periods, the growth form, number, and position of meristems in some woody plants such as *Betula nana* (Fig. 7.3) allowed a much greater response that completely changed the height and structure of the whole canopy (Bret-Harte et al., 2001; but see Graglia et al., 2001a for a different response). In the subarctic, Graglia et al. (2001a) showed that initial plant responses (abundance) to temperature increases and other treatments persisted throughout a ten-year period. Graminoids were particularly responsive to fertilizer additions in the subarctic and their increased growth and litter production suppressed the growth of mosses and lichens (Cornelissen et al., 2001; Graglia et al., 2001a; Molau and Alatalo, 1998; Potter et al., 1995). Evergreens were more responsive to nutrient addition and temperature increases than deciduous species (Arft et al., 1999).

Mosses and lichens appear to be particularly vulnerable to climate warming, at least in areas of continuous vegetation cover. A meta-analysis of lichen responses to warming experiments across the Arctic showed that lichen biomass decreased as vascular plant biomass increased following warming (Cornelissen et al., 2001). This group of plants is particularly important because a large proportion of global lichen diversity is found in the Arctic, some species are important winter forage for reindeer/caribou, and some are important nitrogen fixers in strongly nitrogen-limited systems. A 22-year study of the lichen flora of the Netherlands showed changes that researchers suggest are related to an increase in temperature, although the subtropical species might be more sensitive to nitrogen (Palmqvist et al., 2002). Fifty percent of the arctic–alpine/boreal–montane lichen species were declining while subtropical species were invading (van Herk et al., 2002). The widespread moss *Hylocomium splendens* shows a complex response to warming (Callaghan et al., 1999): in warming experiments growth is reduced (Graglia et al., 2001a; Potter et al., 1995), whereas growth increases in relation to increases in mean annual temperature throughout its arctic distribution range (section 7.3.5.2, Fig. 7.15; Callaghan et al., 1997). This suggests some limitation in the experimental simulation of natural/anthropogenic warming. If, however, moss growth and abundance are reduced by higher temperatures, soil thermal regimes, biogeochemical cycling, and energy and heat exchange between the biosphere and atmosphere will be significantly affected (Hobbie, 1996).

Plant species respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations, and interactions among species. Phenological responses to warming are greatest at cold sites in the high Arctic (Arft et al., 1999; Wookey et al., 1993), whereas growth responses to warming are greatest at sites in the low Arctic. Growth responses of *Cassiope tetragona* to warming were greatest at a site in the high Arctic and a high-altitude site in the low Arctic when compared with the warmest low-altitude site in the low Arctic (Havström et al., 1993). Over a period of five years, shoot elongation responses to warming were greatest in cold summers (Molau, 2001; Richardson, 2000). Laine (1988) showed that the reproduction of bilberry (*Vaccinium myrtillus*) depended to some extent on the climate in the previous years (see section 14.7.3 for examples of this in trees), whereas Shevtsova et al. (1995, 1997) showed no such response for co-occurring lingonberry and crowberry (*Empetrum nigrum*).

Most information on plant responses to climate warming is limited to the short term and small plot – even if the short term is two decades. Because of the great longevity and clonal growth of arctic plants, it is difficult to extrapolate plant responses from an individual plant to the population. However, the impacts of climate change (temperature, nutrients, CO_2) on demographic parameters and population growth statistics were determined for the sedge *Carex bigelowii* by Carlsson and Callaghan (1994) and Callaghan and Carlsson (1997), who showed that climate change increased tiller size, vegetative production of young tiller generations, survival of young tillers, and flowering, and reduced the age of a tiller at flowering and tiller life span. Two mathematical models showed that the changes in demographic parameters led to an increase in the population growth rate, with young tillers dominating this increase. The rate of vegetative spread more than doubled, while cyclical trends in flowering and population growth decreased substantially.

Responses to precipitation changes

Precipitation in the Arctic is extremely variable between seasons and from place to place, but the amount of snow is difficult to measure (section 2.4). Precipitation varies from over 1000 mm in coastal areas (e.g., Norway and Iceland) to less than 45 mm in the polar deserts, where most of the annual precipitation occurs as snow. The interaction between precipitation and temperature is extremely important for plant growth and ecosystem processes and it is difficult to separate their effects.

Observations show that precipitation has increased by up to 20% in northern latitudes within the last 40 years (section 2.6.2.2), although there has been a 10% decrease in snow-cover extent in the Northern Hemisphere in the last 20 years (section 2.4.1). The most recent climate scenarios for the North Atlantic region suggest increased mean annual temperatures and precipitation for the entire region over the next 100 years (IPCC, 2001; section 4.4).

Effects of changes in snow depth, duration, and timing of the snow-free period

The interaction between snow amount and temperature determines the start and duration of the snow-free period. The duration of the snow-free period at high northern latitudes has increased by five to six days per decade and the week of the last observed snow cover in spring has advanced by three to five days per decade between 1972 and 2000 (Dye, 2002). Even if precipitation increases, therefore, temperature increases may still result in shorter duration of snow and less snow cover (sections 2.6 and 4.4.3). In contrast, the start of the growing season has been delayed by up to one week over the last 20 years in the high-altitude and northern boreal regions of Fennoscandia (Høgda et al., 2001). Hydrological models applied to the Tana River Basin of northernmost Finland project increases in growing-season length, from 30 days in the mountains to 70 days near the coast of the Barents Sea, by 2100 (Dankers, 2002). This change is associated with an earlier start to the growing season of about three weeks and a delayed end of two to three weeks.

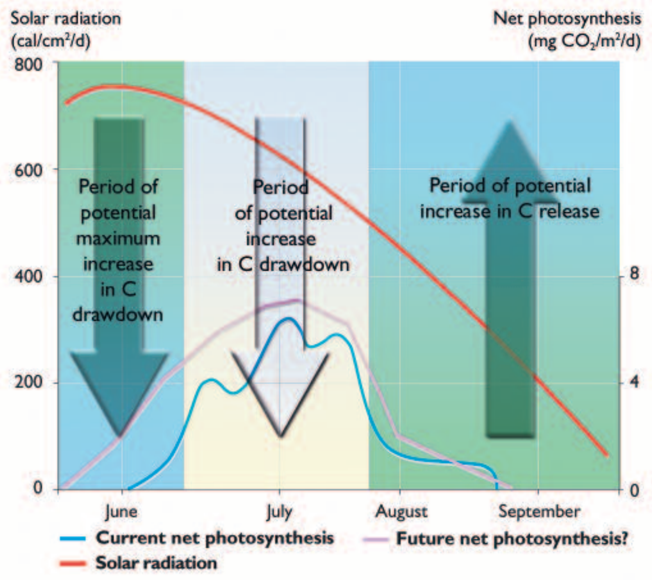


Fig. 7.8. Relationship between timing of the growing season and the seasonal pattern of irradiance together with an indication of where transient switches from carbon (C) sink to carbon source could occur (modified from Chapin F. and Shaver, 1985b).

The timing of the start of the snow-free period is of critical importance, and more important than the timing of autumn snowfall, because solar angles are already high when plants start growth and each extra snow-free day at the beginning of the growing season will enable plants to access high levels of photosynthetically active radiation (Fig. 7.8; see also section 7.5). In an alpine area, productivity decreased by about 3% per day that the snow release date was delayed (Ostler et al., 1982). The timing of snowmelt has also been found to have considerable effects on plant phenology (more so than temperature in some cases: Hollister and Webber, 2000), with a contracting of development time that is associated with a decrease in productivity and reproductive output (Callaghan, 1974). Some plant species, such as the deciduous shrub species *Salix pulchra* and *Betula nana*, can respond to changes in growing-season timing (Pop et al., 2000), but others, particularly evergreen and early-flowering species appear to be particularly vulnerable (Kudo, 1991, 1993).

An experiment that manipulated snow conditions by using snow fences at Toolik Lake, Alaska, showed that drifts increased winter temperatures and CO_2 flux (Jones et al., 1998, Walker M.D. et al., 1999; Welker et al., 2000). Under the drifts, temperatures were more constant than in control plots. Plant growth increased despite a shorter growing season, although this was thought to be a transitory response and contrasts with the reduced growth of plants associated with late snow beds (Fig. 7.9).

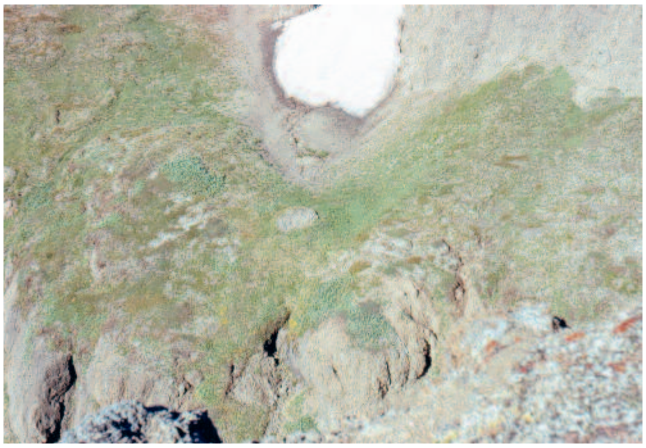


Fig. 7.9. Snow bank vegetation showing increasing vegetation development with increasing growing-season length represented as distance from the snow patch, Disko Island, West Greenland (photo: T.V. Callaghan).

Frost resistance and avoidance

Changes in snow depth and duration are likely to negatively affect the frost resistance and avoidance of many plants at high latitudes. Damage to foliage and apical meristems occurs when they are "triggered" to premature bud burst and development by an earlier onset of the growing season (resulting from early snowmelt) when the annual hardening/dehardening process is at its most sensitive phase, and when there is a risk of short periods of cold weather. Bilberry is a species whose requirement for cool temperatures to enable it to break dormancy (i.e., chilling requirement) is fulfilled early (Havas, 1971). Accelerated dehardening of bilberry was found as consequence of a minor (2 to 3 ºC) increase in temperature (Taulavuori K. et al., 1997b), suggesting that climatic warming is very likely to entail a real risk of early dehardening and subsequent frost damage of shoots. The explanation for this may be the higher but fluctuating temperatures, which increase the cryoprotectant-consuming freeze–thaw cycles (Ögren, 1996, 1997; Ögren et al., 1997). In addition to frost resistance, frost avoidance is likely to be disturbed by a thin or lacking snow cover. The risk is likely to be highest at high latitudes, where plants that are genetically adapted to the presence of snow may have lost some potential for frost resistance during their evolution. Subarctic provenances of bilberry, for example, have shown reduced frost resistance compared to provenances from southern Finland (Havas, 1971).

Other global change factors might affect frost resistance, but few, sometimes conflicting, reports have been published of studies performed at high latitudes. Nitrogen pollutant (or fertilizer) can impair the frost resistance of plants. Such an effect was demonstrated for mountain avens (*Dryas octopetala*) on Svalbard during a warm period in early winter (Robinson et al., 1998; see previous subsection on projected temperature responses). However, recent studies with the heather *Calluna vulgaris* (Caporn et al., 1994), bilberry (Taulavuori E. et al., 1997), and lingonberry (Taulavuori K. et al., 2001) have demonstrated improved frost resistance caused by extra nitrogen, probably because these ericaceous species are plants adapted to low-nutrient habitats, such as those at high latitudes.

Snow depth and duration vary greatly with topography at the landscape level. High summer temperatures are very likely to decrease the abundance and size of snow beds. Changes in snow patches observed by indigenous peoples are already causing concern in Baker Lake, Clyde River, and Iqualuit; Fox (2002) describes *aniuvak* (permanent snow patches) that are melting in the hills around those communities. *Aniuvak* are good areas for caching meat and provide a sanctuary for caribou to evade flying insects. Indigenous peoples' explanations for the melting snow patches relate more to changes in precipitation and mean relative humidity than to temperature increases. The specialized plants characteristic of late snow beds (Gjærevoll, 1956) are very likely to be at particular risk as temperatures increase.

Summer precipitation

Altered timing and rate of snowmelt are very likely to differentially alter the availability of water in different facies of the tundra landscape mosaic, which are very likely to in turn significantly affect the predominant vegetation type and its growth dynamic through the active season (Molau, 1996). Artificial increases in summer precipitation produced few responses in arctic plants compared with manipulations of other environmental variables (Dormann and Woodin, 2002). However, mosses benefited from moderate summer watering (Phoenix et al., 2001; Potter et al., 1995; Sonesson et al., 2002) and nitrogen fixation rates by blue-green algae associated with the moss *Hylocomium splendens* increased (Solheim et al., 2002). Addition of water to a polar semi-desert community in summer produced surprisingly few responses (Press et al., 1998a). Also in the high Arctic, comparisons were made between sites with high and low plant densities. Although there was little difference in soil moisture and plant water relations, and water availability did not constrain the adult vascular plants, surface water flow in snow-flush areas (accumulations of snow that provide water during summer) allowed greater development of cyanobacterial soil crusts, prolonged their nitrogen fixing activity, and resulted in greater soil nitrogen concentrations (Gold and Bliss, 1995). Because of their importance in facilitating vascular plant community development, Gold and Bliss (1995) projected that the effects of climate change on non-vascular species are very likely to be of great consequence for high-arctic ecosystems.

Responses to increased atmospheric carbon dioxide concentrations

There are very few arctic experiments that have manipulated atmospheric CO_2 concentrations in the field (Gwynn-Jones et al., 1996, 1999; Tissue and Oechel, 1987), but more laboratory experiments have been conducted on arctic vascular plants (Oberbauer et al., 1986), mosses, and lichens (Schipperges and Gehrke, 1996; Sonesson et al., 1992, 1995, 1996).

The first experiment that manipulated CO_2 in the Arctic concluded that elevated CO_2 concentrations had no long-term effects because photosynthetic acclimation (i.e., down-regulation, the physiological adjustment of photosynthetic rate so that no differences are found between plants grown at ambient and elevated CO_2 levels) in cottongrass (*Eriophorum vaginatum*) was apparent within three weeks and biomass did not increase. However, there was prolonged photosynthetic activity in autumn and more biomass was allocated to roots (Tissue and Oechel, 1987). The lack of response and enhanced root biomass were attributed to nutrient limitation (Oechel et al., 1997). Although increases in tiller production of cottongrass were not considered to be an important response, this can lead to long-term increases in population growth (Carlsson and Callaghan, 1994).

Longer-term CO_2 enrichment experiments in the subarctic also show that growth responses are dominated by early, transient responses (Gwynn-Jones et al., 1997). Four dwarf shrubs were studied over the first three years of the experiment; one, the deciduous bilberry, showed increased annual stem growth (length) in the first year whereas two other evergreen dwarf shrubs (mountain crowberry – *Empetrum hermaphroditum* and lingonberry) showed reduced growth. In the seventh year, increased CO_2 concentrations significantly increased the leaf ice nucleation temperature (i.e., reduced frost resistance, which can be harmful during the growing season) in three of the four species tested (Beerling et al., 2001). Bog whortleberry (or bog bilberry – *Vaccinium uliginosum*), lingonberry, and mountain crowberry showed increases in leaf ice nucleation temperature exceeding 2.5 ºC whereas bilberry showed no significant effect, as in another study (Taulavuori E. et al., 1997). Increased CO_2 concentrations interacted with high UV-B radiation levels to increase leaf ice nucleation temperature by 5 ºC in bog whortleberry. This effect coincides with indigenous knowledge and other experiments that show increased frost sensitivity of some arctic plants to changes in climate and UV-B radiation levels (see responses to cloudiness and photoperiod in this section).

An expected (and subsequently observed) response to increased atmospheric CO_2 concentrations was a change in leaf chemistry (e.g., an increase in the carbon to nitrogen ratio) that was expected to affect herbivory (Fajer et al., 1989) and decomposition (Robinson et al., 1997). Surprisingly, herbivory was not affected. However, increased CO_2 concentrations were found to play a role in nutrient cycling by altering the composition of microbial communities after five years (Johnson et al., 2002; section 7.3.3.3), suggesting that chemical changes are occurring in plants exposed to high CO_2 concentrations but the changes have not yet been identified.

In laboratory studies, the moss *Hylocomium splendens* that naturally experiences high CO_2 levels in the birch woodlands of the Swedish subarctic was shown to have photosynthetic rates that were limited by light, temperature, and water for most of the growing season (Sonesson et al., 1992). Enhanced CO_2 concentrations for five months decreased photosynthetic efficiency, light compensation point, maximum net photosynthesis, and surprisingly, growth (Sonesson et al., 1996). Similar experiments with three lichen species, *Cladonia arbuscula*, *Cetraria islandica*, and *Stereocaulon paschale*, failed to show any response of fluorescence yield to enhanced CO_2 concentration (1000 ppm), although there was an interaction between CO_2 and UV-B radiation levels (Sonesson et al., 1995). Perhaps the lack of response in moss and lichens reflects their adaptation to the currently high levels of CO_2 that they experience close to the ground surface (Sonesson et al., 1992) via the process of down-regulation.

In contrast to some views that responses of plants (mainly growth) to increased CO_2 concentrations are relatively small and by inference insignificant (Dormann and Woodin, 2002), recent results show that in the long term, increased CO_2 concentrations can have the wide-ranging and important effects discussed previously (Beerling et al., 2001; Johnson et al., 2002).

Responses to increased ultraviolet-B radiation levels

One common method for simulating the effects of ozone depletion has been to irradiate organisms and ecosystems with artificial UV-B radiation. Results are often reported in relation to the equivalent percentage of ozone depletion. It should be noted, however, that the radiation spectrum from the lamps used in experiments differs from the spectrum of the radiation increase that would ensue from real ozone depletion. Therefore, the degree of simulated ozone depletion depends on the "weighting func-

Table 7.6. Summary of UV-B radiation effects on subarctic dwarf shrubs (based on Phoenix, 2000 and other sources referred to in the text).

	Bilberry (*Vaccinium myrtillus*)	Bog whortleberry (*Vaccinium uliginosum*)		Lingonberry (*Vaccinium vitis-idaea*)		Mountain crowberry (*Empetrum hermaphroditum*)	
	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B	Zero to ambient UV	Ambient to enhanced UV-B
Stem length	-	0	0	0	0	0	0
Branching	0	0	0	0	0	0	0
Leaf thickness	+	0	0	0	0		
Flowering	+	+		0	0		
Berry production	+	0		0	0	0	0
Phenology	0	0	0	0	0	0	0
Total UV-B radiation-absorbing compounds	-	-	-	-	0	0	0
Leaf ice nucleation temperature	0		+		+	0	+

+ indicates an increase; - indicates a decrease; 0 indicates no effect compared to control; blank indicates no information

tion" applied in the calculations, and the knowledge of the appropriate weighting function is very incomplete. Weighting functions are also species-specific: a certain amount of applied artificial radiation does not correspond to the same degree of ozone depletion for a plant and a tadpole, for example. The information in the following sections should be read with this in mind.

Relatively little is known about plant responses to changes in UV-B radiation levels. Field experiments on subarctic (Table 7.6) and high-arctic ecosystems show species-specific responses to ambient UV-B radiation levels and to enhanced UV-B radiation levels equivalent to a 15% decrease in stratospheric ozone from 1990 levels. (The 15% decrease is equivalent to losses of ozone projected to occur throughout much of the Arctic by 2015. However, the values do not apply to Beringia for April and October 2015; Taalas et al., 2000.) On the whole, the effects of increased UV-B radiation levels are relatively few compared with effects of increased temperature and nitrogen (Dormann and Woodin, 2002).

A global meta-analysis of plant responses to increased UV-B radiation levels showed that there was a small but significant reduction in biomass and plant height (Searles et al., 2001). In the subarctic, measurements of stem length, branching, leaf thickness, flowering, berry production, phenology, and total UV-B radiation absorbing compounds were affected significantly by ambient UV-B radiation levels in only two of three dwarf shrubs (i.e., bog whortleberry and lingonberry; Phoenix, 2000). Mountain crowberry and lingonberry showed no responses to enhanced UV-B radiation levels after seven years of exposure whereas bog whortleberry and bilberry showed few responses (Table 7.6). Enhanced UV-B radiation levels have been shown to reduce the height growth, but not biomass, of the mosses *Sphagnum fuscum* and *Hylocomium splendens* in the subarctic (Gehrke et al., 1995).

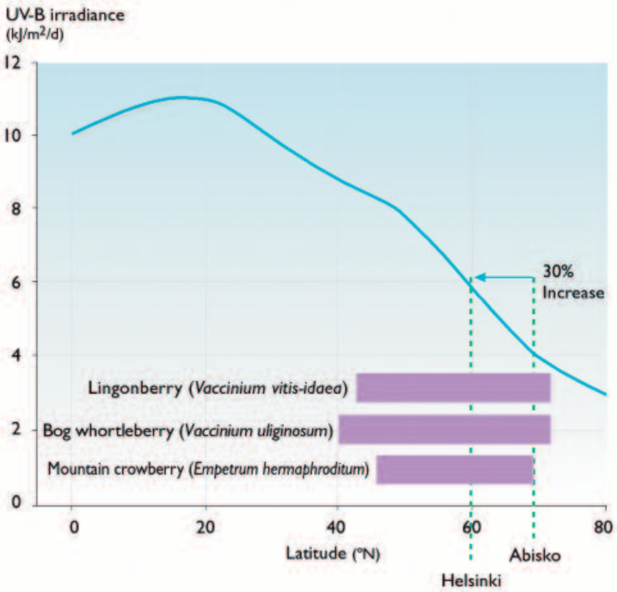


Fig. 7.10. Dwarf shrub distributions in relation to latitude and solar UV-B radiation incident at the surface of the earth (Gwynn-Jones et al., 1999; Hultén, 1964; Phoenix, 2000).

The UV-B radiation studies (Table 7.6) showed that arctic species were more tolerant of enhanced UV-B radiation levels than previously thought, and that the production of UV-B radiation absorbing compounds did not show the simple relationship with UV-B radiation dose expected from laboratory studies. Another surprise effect was the responsiveness of frost hardiness in some arctic dwarf shrubs to increased UV-B radiation levels. Dunning et al. (1994) pioneered investigation of the relationship between UV-B radiation levels and frost resistance in a *Rhododendron* species and concluded that increased exposure to UV-B radiation increases (although only marginally) cold resistance. In contrast, K. Taulavuori et al., (unpubl. data, 2004) found decreased frost resistance in bilberry in response to elevated UV-B radiation levels and Beerling et al. (2001) showed decreased frost resistance in bog whortleberry, lingonberry, and mountain crowberry. A combination of elevated CO_2 and UV-B radiation levels increased late-season frost sensitivity of leaves of bog whortleberry from -11.5 to -6 °C. Increased frost sensitivity at the beginning and/or end of the short arctic growing season is likely to curtail the season even further. As some models of vegetation redistribution related to temperature change use the critical freezing temperatures for leaf damage in temperate trees and shrubs (Prentice et al., 1992), modeled past and future northward migration of temperate vegetation should be reconsidered in relation to changing CO_2 and UV-B radiation levels.

The resilience of the subarctic dwarf shrubs to enhanced UV-B radiation levels probably reflects pre-adaptation to higher levels than are currently experienced in the Arctic (Phoenix, 2000). These species currently extend southward to about 40° N and they probably existed even further south in a higher UV-B radiation regime during the early Holocene. The increased UV-B radiation levels currently applied in experiments are equivalent to the difference in ambient UV-B radiation levels between the site of the experiment (68° N) and Helsinki (59° N) (Fig. 7.10). In addition, many arctic plants have thick leaves that might attenuate UV-B radiation entering leaf tissues. However, one particular climate–UV radiation interaction that could possibly increase the damage experienced by plants is the combination of possible earlier snow-free periods (Dankers, 2002) with higher spring UV-B radiation levels at the surface of the earth (Taalas et al., 2000). Such a combination of effects would expose young, potentially sensitive plant shoots and flower buds to particularly high UV irradiation (Zepp et al., 2003).

Responses to changes in cloudiness and photoperiod

An important characteristic of the arctic environment is the daily and seasonal patterns of the light period or photoperiod. At midwinter, intermediate latitudes (40°

to 50º N) have about an eight-hour day length, whereas a polar night without sunrise prevails north of the Arctic Circle (66.5º N). Consequently, day-length change during spring and autumn occurs much faster at high latitudes.

Frost-resistance patterns change seasonally and are environmentally controlled, mainly by temperature and day length; which of these factors predominate depends on the seasonal growth cycle (Fuchigami et al., 1982). The development of frost resistance by almost all woody plants at high latitudes is characterized by strong dependency on the photoperiod for growth cessation and cold hardening. Scots pine (*Pinus sylvestris*) seedlings from the northern boreal forest develop a high degree of frost resistance during the late summer as a consequence of the shortening days (Taulavuori K. et al., 1997a). The frost-hardening process is initiated even at high temperatures (20 ºC) in experimental conditions that mimic the ambient photoperiod (Taulavuori K. et al., 2000). Given the marked photoperiodic control of the frost-hardening process in woody species at high latitudes, it is understandable that they harden more extensively compared to populations at lower latitudes under similar temperatures. For example, the lowest survival temperature of bilberry in the central Alps (~50º N) at midwinter is around -35 ºC (Sakai and Larcher, 1987 and references therein), while the same level of frost resistance is already achieved at the end of September in northern Finland (65º N) (Taulavuori E. et al., 1997).

In a changing climate, photoperiod will not change, but species that are migrating will experience changes in photoperiod. It is unlikely however, that this will constrain species initially. Many northern boreal species, for example, experienced arctic photoperiods earlier in the Holocene before they were displaced southward by climate cooling (section 7.2). If and when species with a more southerly distribution migrate into the Arctic, photoperiod constraints could possibly affect growth and flowering but this is largely unknown. However, experiments with transplanting herbs between the Austrian Alps, Abisko, and Svalbard showed that allocation of biomass in some species such as glacier buttercup (*Ranunculus glacialis*) was affected by photoperiod and this constrained any potential increases of vigor that might have occurred due to climate warming (Prock and Körner, 1996). In contrast, herbs such as *Geum* (Prock and Körner, 1996) and some grasses (Heide et al., 1995) that are not sensitive to photoperiod could possibly benefit from climate warming.

It has been suggested that increased UV-B radiation effects might be small in the future because of increased cloudiness (section 4.4.4) that is likely to counteract to some extent the effect of decreasing ozone levels (Dormann and Woodin, 2002). However, projections of increased cloudiness, and particularly future cloud types, are uncertain. It is more likely that UV-B radiation effects will be reduced by decreases in albedo as snow and ice distribution and seasonal duration decline, and as the boreal forest displaces part of the current tundra.

Arctic plants differ in the degree to which they gain or lose carbon in photosynthesis at "night" (22:00 to 04:00 hours when light intensity is low but it is not necessarily dark). Under conditions of cloudy nights, those species that gain carbon at night, for example, Arctic dryad (*Dryas integrifolia*), alpine foxtail (*Alopecurus alpinus*), glaucous willow (*Salix glauca*), and arctic willow (*Salix arctica*) (25–30% of diurnal carbon gain; Semikhatova et al., 1992), are likely to have reduced competitive ability compared with species that do not. In contrast, increased cloudiness during the day probably favors those species that gain carbon at night. Those species that lose carbon at night (e.g., *Eriophorum angustifolium*; Semikhatova et al., 1992) are likely to be disadvantaged by warming.

Responses to potential changes in pollinator abundance and activity

The rapid phenological changes that have been observed in response to simulated climate change have the potential to disrupt the relationships that plants have with animal, fungal, and bacterial species that act as pollinators, seed dispersers, herbivores, seed predators, and pathogens (Dunne et al., 2003). These disruptions are likely to have the strongest impact if the interacting species are influenced by different abiotic factors or if their relative responses to the same factors (e.g., elevated temperatures) are different. However, wind and self-pollination are more widespread among arctic flowering plants, so any mismatch between pollinator activity and flowering phenology is likely to be of greater significance to any plants immigrating to the Arctic as temperatures increase. Little appears to be known about these processes.

Summary

Species responses to changes in temperature and other environmental variables are complex. Species respond individualistically to each environmental variable. Plant species also respond differently to warming according to previous temperature history related to latitude, altitude, interannual temperature variations, and interactions among species. Some species are already responding to recent environmental changes. Indigenous knowledge, aerial photographs, and satellite images show that some arctic vegetation is becoming more shrubby and productive.

Summer warming experiments showed that initial increases in the growth of vascular species were generally reduced with time, whereas reproductive success improved in later years. Over short periods (four years), herbaceous plants responded more than woody plants, but over longer periods, woody plant responses were dominant and could change the canopy height and structure. Mosses and lichens were generally disadvantaged by higher-plant responses to warming.

Responses to warming are critically controlled by moisture availability and snow cover. Already, indigenous observations from North America and Lapland show a drying trend with reduced growth of economically important berries. However, experimental increases in summer precipitation produced few responses in arctic plants, except for mosses, which showed increased growth. An experiment that manipulated snow conditions showed that drifts increased winter temperatures and CO_2 flux and, surprisingly, that plant growth increased despite a shorter growing season. In general, however, any earlier onset of the snow-free period is likely to stimulate increased plant growth because of high solar angles, whereas an increase in the snow-free period in autumn, when solar angles are low, will probably have little impact.

Carbon dioxide enrichment experiments show that plant growth responses are dominated by early, transient responses. Surprisingly, enhanced CO_2 did not affect levels of herbivory, but significantly increased the leaf ice-nucleation temperature (i.e., increased frost sensitivity) of three of four dwarf shrub species, and altered the composition of microbial communities after five years. A general lack of responses of mosses and lichens reflects their adaptation to the currently high levels of CO_2 that they experience close to the ground surface.

Ambient and supplemental UV-B radiation levels produced complex, individualistic, and somewhat small responses in species. Overall, arctic species were far more tolerant of enhanced UV-B radiation levels than previously thought, and the production of UV-B absorbing compounds did not show the simple relationship with UV-B radiation dose expected from laboratory studies. Some arctic dwarf shrubs exhibited increased frost sensitivity under increased UV-B radiation levels. The arctic photoperiod is unlikely to be a general constraint to species migrations from the south, as trees and southern species previously occurred further north than at present.

7.3.3.2. Animals

In contrast to plants, there are relatively few experiments that have addressed how animal populations respond to simulated climate change and UV-B radiation levels in the Arctic. The few experiments have focused on invertebrates (e.g., insects and soil animals) for which the microclimate can be manipulated on small experimental plots. Experiments on free-ranging vertebrate populations may not be feasible for logistical reasons. On the other hand, more time series of population data are available for conspicuous vertebrates such as reindeer/caribou and lemmings than, for example, soil invertebrates. Time series can be analyzed with respect to the influence of current climate variability (including recent changes).

Responses to current changes in climate and ultraviolet radiation levels

Ice-crust formation on the tundra as a result of freeze–thaw events during the winter affects most terrestrial arctic animals. Dense snow and ice severely limit forage availability for large ungulates such as reindeer/caribou and muskox (Klein, 1999). Dramatic reindeer population crashes resulting from periodic ice crusting have been reported from the western coastal part of the Russian Arctic, Svalbard, and Fennoscandia (Aanes et al., 2000; Putkonen and Roe, 2003; Reimers, 1982; Syroechovski and Kuprionov, 1995). Similar events have been reported for muskox in the southern parts of their range in Greenland (Forchhammer and Boertmann, 1993). Inuit in Nunavut report that caribou numbers decrease in years when there are many freeze–thaw cycles (Thorpe et al., 2001) and the probability of such freeze–thaw events is said to have increased as a result of more short-term fluctuations in temperature. In central Siberia, where winter climate is colder and more stable, reindeer population dynamics are less climate-driven (Syroechovski and Kuprionov, 1995). Swedish Saami note that over the last decade, autumn snow lies on unfrozen ground rather than on frozen ground in the summer grazing areas and this results in poor-quality spring vegetation that has rotted (Nutti, pers. comm., 2004); certain microfungi seem to be responsible for this (Kumpula et al., 2000).

Long and accurate time series data on Svalbard reindeer populations (Aanes et al., 2000; Solberg et al., 2001) show that the amount of precipitation during the winter, which is highly variable and is well described by the Arctic Oscillation index (Aanes et al., 2002), provides the most important check on the reindeer population growth rate in concert with population density. Winters with freezing rain were associated with severe population crashes both in one reindeer population (although the natural dynamics of an introduced herd may have contributed to this) and in an introduced population of sibling voles (*Microtus rossiaemeridionalis*; Fig. 7.11).

Episodes of mild weather and wet snow lead to a collapse of the subnivean space and subsequent frost encapsulates food plants in ice, making them unavailable to small mammal herbivores, and even killing plants in some cases (Callaghan et al., 1999; Robinson et al., 1998). Accordingly, the survival rate of tundra voles (*Microtus oeconomus*) decreases dramatically in winters with many freeze–thaw cycles (Aars and Ims, 2002; Fig. 7.12). For example, the lemming increases observed at Kilpisjärvi (northwest Finnish Lapland) in 1997 and 2001 were probably curtailed by warm spells and rain in January that resulted in freezing of the ground layer (Henttonen, unpubl. data, 2004). Inuit residents of the western Canadian Arctic are also concerned with the impacts of thaw slumping on lemming populations and their predators (owls). Thaw slumps at lake edges have been occurring more extensively and at a faster rate in recent years, linked to warmer temperatures and an increase in wind activity and rain; thawing of ice-bound soil destroys lemming burrows (IISD and the community of Sachs Harbour, 2000).

There has been speculation about whether the recent dampened amplitude of population cycles and more spatially asynchronous dynamics of voles and lemmings in northern Fennoscandia may be the result of occasionally unfavorable winters disrupting the normal population dynamics (Yoccoz and Ims, 1999). Figure 7.13 illustrates changes since the beginning of the 1990s in populations of the formerly cyclic and numerically dominant grey-sided vole (*Clethrionomys rufocanus*) and other vole species. In long qualitative time series (up to 100 years), periods with loss of cyclicity and synchrony are evident (Angerbjörn et al., 2001; Steen et al., 1990; Stenseth and Ims, 1993), but it is unclear whether this is related to fluctuations in climate. There is a correlation between sunspot activity and snowshoe hare cycles in North America (Sinclair et al., 1993), but no such relationship has been found for the mountain hare (*Lepus timidus*) in northern Finland (Ranta et al., 1997). There are no relationships between sunspot activity and outbreak years in the autumnal moth in Fennoscandia (Ruohomäki et al., 2000), although there are few studies of the role of climatic variability in arctic insect and soil arthropod populations because of the lack of long quantitative time series.

Arctic indigenous peoples are rich sources of information about recent changes in animal health and behavior, in particular reindeer/caribou. Increases in vegetation (longer grass, riparian areas with denser vegetation) are linked to increased forage availability and more mosquitoes and flies, resulting in increased insect harassment of reindeer/caribou (Riedlinger, 2001). Changes in "the warmth of the sun", day length, and the timing of the growing season may trigger reindeer/caribou to cross a frozen lake or river when the ice is no longer thick enough to support their weight (Thorpe et al., 2001). However, some of the environmental changes may be beneficial. Stronger and more frequent winds are said to provide reindeer/caribou with relief from insect harassment, meaning they can spend more time inland and not in coastal areas (Riedlinger, 2001). Qitirmiut in Nunavut know that caribou adapt to the heat by staying near coastal areas and shorelines, lying on patches of snow, drinking water, standing in the water, eating moist plants, and sucking mushrooms (Thorpe et al., 2001). However, increases in the number of extremely hot days, combined with changing water levels and vegetation patterns, are likely to affect the ability of reindeer/caribou to respond in these ways.

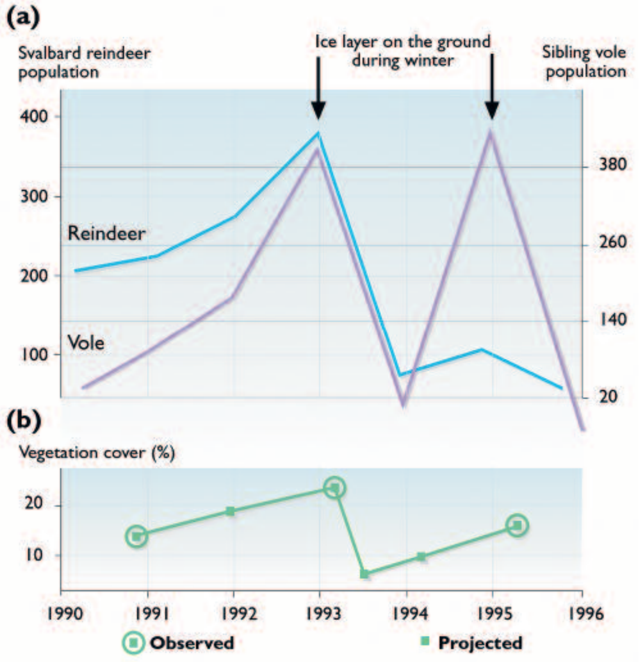


Fig. 7.11. (a) Population dynamics of Svalbard reindeer at Brøggerhalvøya and sibling voles at Fuglefjella on Svalbard (Aanes et al., 2000; Yoccoz and Ims, 1999); (b) observed and projected changes in vegetation (Robinson et al., 1998; Callaghan et al., 1999).

Climatic cooling has to some extent caused habitat degradation in some coastal areas as a result of grubbing by snow geese on their staging ground. The lesser snow goose (*Anser caerulescens caerulescens*) breeds in coastal areas of the Hudson Bay region, which has experienced climatic cooling since the mid-1970s. This has delayed migration of the breeding populations (Hansell et al., 1998). Huge aggregations of staging and local geese in the coastal marshes have led to intense grubbing and degradation of salt-marsh sward (Srivastava and Jefferies, 1996). Long-term observations and modeling have shown that goose reproductive variables are directly and indirectly dependent on selected climatic variables, particularly those relating to spring (Skinner W. et al., 1998). Nest initiation date, hatching date, and clutch size were associated with the date of the last snow on the ground and mean daily temperature between 6 and 20 May. Early snowmelt allows geese to forage and females to build up nutrient stores before nest initiation. Goslings that hatch earlier in the spring have a higher probability of survival than those hatching later. Inclement weather, such as cumulative snowfall, freezing rain, and northerly and easterly winds can result in nest abandonment by females and even adult starvation while incubating eggs.

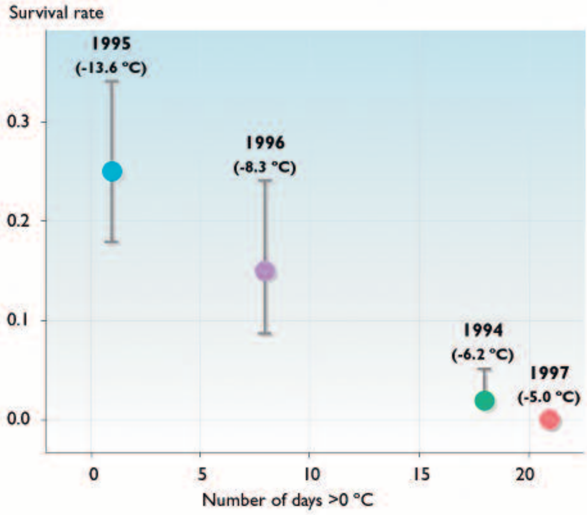


Fig. 7.12. Yearly winter survival rate (with 95% confidence intervals) of experimental tundra vole populations plotted against the number of days with temperatures above 0 °C during December through February. Mean winter temperature and the year are denoted above the survival rate estimates (Aars and Ims, 2002).

Responses to projected changes in climate

Despite adaptations to low temperatures, warming experiments have shown that temperatures higher than normal do not present any physiological problem for arctic arthropods provided that water is available (Hodkinson et al., 1998). Arctic aphids were more successful in terms of the number of completed generations through the summer when temperature was experimentally elevated (Strathdee et al., 1993). The effects of experimental warming were more pronounced in the high Arctic at Svalbard than in subarctic Abisko (Strathdee et al., 1995). The combination of high temperatures and drought seem to be very problematic for terrestrial invertebrates (Strathdee and Bale, 1998), but the hydrological aspect of climate change in tundra habitats is an important issue that has rarely been addressed in studies of arctic animals (Hodkinson et al., 1999).

Some of the most important effects of higher summer temperatures on arctic terrestrial animals are likely to be mediated through intensified interspecific interactions (parasitism, predation, and competition). Higher temperatures in the Arctic are very likely to lead to invasions of species with more southerly distributions. Such range expansions are projected to be particularly rapid in those species for which food resources (e.g., host plants) are already present (Hodkinson and Bird, 1998). For example, the mountain birch *Betula pubescens* ssp. *czerepanovii*, the main food plant of the autumnal moth, occurs in the continental parts of the Fennoscandian forest tundra where winter temperatures are occasionally lower than the tolerance limit for over-wintering eggs (Tenow, 1972); however, warmer winters are likely to lead to the exploitation of this existing food source. Many insects belonging to the boreal forest already invade the low-arctic tundra in quite large quantities every summer (Chernov and Matveyeva, 1997) and the Arctic is subject to a "steady rain" of wind-dispersed small invertebrates (Elton, 1925) that are likely to rapidly become established when environmental conditions are adequate. Due to the lack of long-term monitoring programs, there are presently no arctic equivalents of the detailed and quantitative documentation of the northward spread of insects in Europe (e.g., Parmesan et al., 1999). Several generalist predators not yet present in the Arctic are likely to spread northward with increased ecosystem productivity due to warming. The red fox has already expanded into the Arctic, probably at the expense of the Arctic fox (Hersteinsson and MacDonald, 1992).

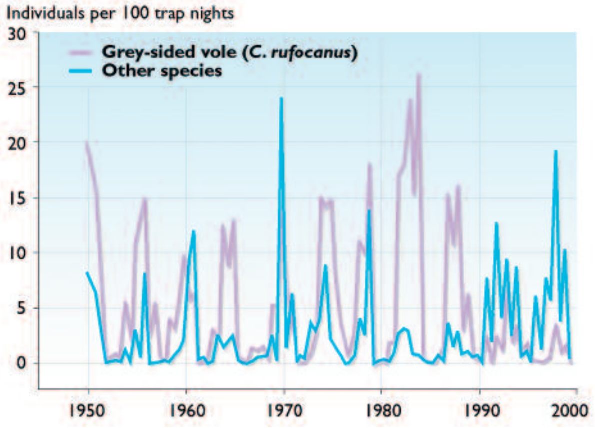


Fig. 7.13. Population dynamics of the grey-sided vole and other vole species (combined) at Kilpisjärvi, northern Finland between 1950 and 2000 (Henttonen and Wallgren, 2001).

Winter warming will alter snow cover, texture, and thickness. A deeper snow cover is likely to restrict reindeer/caribou access to winter pastures, their ability to flee from predators, and energy expenditure traveling across snow. Changes in snow depth and texture are very likely to also determine whether warm-blooded small vertebrates will find thermal refuges for resting in snow dens (ptarmigan and hares) or for being active in the subnivean space (Pruitt, 1957). Ice-crust formation reduces the insulating properties of the snowpack (Aitchinson, 2001) and makes vegetation inaccessible to herbivores. There is ample observational evidence that the current incidence and degree of winter ice crusting clearly affects the population dynamics patterns of both large and small mammal herbivore species (see previous subsection). Moreover, there is experimental evidence that population densities of numerically dominant tundra Collembola (springtail) species such as *Folsomia quadrioculata* and *Hypogastrura tullbergi* can be halved following an episode of freezing rain on Spitzbergen (Coulson et al., 2000). The projected winter temperature increase of 6.3 °C by 2080 (mean of the five ACIA-designated model scenarios) is very likely to result in an increase of alternating periods of melting and freezing (section 6.4.4). Putkonen and Roe (2003) found that episodes with rain-on-snow in the winter presently occur over an area of 8.4×10^6 km^2 in the Arctic and they projected that this area would increase 40% by 2080–2089. The projected increase in the frequency of winter warming is very likely to severely suppress population densities; distort the cyclic dynamics and degree of geographic synchrony in lemmings, voles, and geometrid moths; and in some cases even lead to population extinctions.

Responses to projected increases in ultraviolet-B radiation levels

The extent to which animals are adapted to incident UV-B radiation levels must be inferred in most cases. Hairs and feathers necessary for insulation against low temperatures also presumably protect the skins of mammals and birds from UV-B radiation, while white winter hair and feathers reflect UV-B radiation to some extent. The eyes of non-migratory animals must be extremely well adapted to UV-B radiation in order to be effective in the dark arctic winter yet also cope with high UV-B radiation levels in the bright, snowy spring. Invertebrates have coloring that may serve many functions. Melanic forms of invertebrates might have advantages in thermoregulation and UV-B radiation protection (Leinaas, 2002). If white coloration, insulation, and melanistic thermal regulation decrease due to reduced snow cover and higher temperatures, sensitivity to increased UV-B radiation levels is likely to increase.

Four species of Collembola on Svalbard were investigated by Leinaas (2002) with respect to UV-B radiation tolerance: *Hypogastrura viatica*, *Folsomia sexoculata*, *Onychiurus groenlandicus*, and *O. arcticus*. The first three species coexist in wet shore habitats, with the very heavily pigmented *H. viatica* on the surface and *F. sexoculata*, which as an adult is also very heavily pigmented, lower down. *O. groenlandicus* is a soil-dwelling, unpigmented species. Although *O. arcticus* is most commonly found under small stones and in rock crevices, and is thus rather unexposed, it has some pigmentation. In an experiment with enhanced UV-B radiation levels (0.5 W/m^2 in the 300 to 320 nm band for 12 to 14 hours per day, approximately equivalent to clear sky summer conditions in southern Norway) the unpigmented *O. groenlandicus* experienced 100% mortality within one week, while the heavily pigmented *H. viatica* was not affected.

Caterpillars of subarctic moths have skins that absorb UV-B radiation to varying extents and the degree of absorption may depend on previous exposure to high UV-B radiation levels (Buck and Callaghan, 1999). However, UV-B radiation levels affect animals indirectly via the quality and quantity of food that is available to them as a result of UV-B radiation impacts on plant growth and secondary metabolite production (section 7.4.1.4).

It is possible to infer some responses of animals to future increases in UV-B radiation levels by comparing them to the effects of natural UV-B radiation levels on animals along latitudinal gradients. Along a south-to-north gradient starting at 55.7° N, ambient UV-B radiation levels reduced hatchling size in frogs at sites up to 66° N, with no latitudinal gradient in UV-B radiation tolerance (Pahkala et al., 2002). Surprisingly, for a given time of the year, although UV-B radiation levels decrease with increasing latitudes, the frogs were exposed to higher UV-B radiation levels during the sensitive stages of their life cycles (egg and tadpole) at high latitudes than at low latitudes (Merilä et al., 2000). These studies suggest that an increase in UV-B radiation levels due to anthropogenic ozone depletion is likely to reduce the populations of those amphibians that have distribution ranges extending into the Arctic.

Enhanced UV-B radiation levels are thought to improve the immune system of the autumnal moth in the subarctic and to destroy the polyhedrosis virus. As this virus and the parasitoid wasp *Cotesia jucunda* are both important controllers of the survival of moth caterpillars, increased UV-B radiation levels could possibly lead to increased moth populations and birch forest defoliation. However, no direct effects of enhanced UV-B radiation levels on moth fecundity or survival have been detected (Buck and Callaghan, 1999).

Summary

Evidence for animal responses to climate change is scarcer than for plants because field experiments are less feasible for mobile animals, especially vertebrates. In many cases inferences are made based on time-series analyses of population abundance data for a few conspicuous species such as ungulates and lemmings.

Winter climate impacts, especially those events that affect properties of snow and ice, are particularly important. Freeze–thaw cycles leading to ice-crust formation have been shown to severely reduce the winter survival rate of a variety of species, ranging from soil-dwelling springtails (Collembola) to small mammals (lemmings and voles) to ungulates (in particular reindeer/caribou). Such icing induces conditions of anoxia that affect invertebrates, creates unfavorable thermal conditions for animals under the snow, and renders vegetation unavailable for herbivores. A deeper snow cover is likely to restrict reindeer/caribou access to winter pastures and their ability to flee from predators. The projected increase in the frequency of freeze–thaw cycles is very likely to disrupt the population dynamics of many terrestrial animals, and indications that this is already happening to some extent are apparent in the recent loss of the typical three-to-four year population cycles of voles and lemmings in subarctic Europe.

Experimental elevation of summer temperature has shown that many invertebrates respond positively to higher temperatures in terms of population growth, as long as desiccation is not induced. Many invertebrates, such as insects, are very likely to rapidly expand their ranges northward into the Arctic if climate warming occurs, because they have vast capacities to become passively or actively dispersed and host species (both plants and animals) are already present north of their present range borders.

Little is known about the responses in arctic animals to expected increases in UV-B radiation levels. However, there are some indications that arctic animals are likely to be more exposed and susceptible to such changes than their southern counterparts. The effects of increased UV-B radiation levels on animals are likely to be subtle and indirect, such as reduced food quality for herbivores and increased disease resistance in insect pest species.

7.3.3.3. Microorganisms

Recent experiments that manipulate the environment (e.g., soil heating, changing the water table, atmospheric CO_2 enrichment, and UV-B radiation supplementation and attenuation) have added new information about the effects of environmental change on the soil microbial community at the species level. In general, climate change is likely to alter microbial community composition and substrate utilization (Lipson et al., 1999). Tundra soil heating, atmospheric CO_2 enrichment, and amendment with mineral nutrients generally accelerate microbial activity (leading to a higher growth rate). Higher CO_2 concentrations tend to intensify root exudation, which is the main source of available carbon for soil and rhizosphere bacteria. Much less is known about the transient changes in the species composition of soil microorganisms induced by manipulation of UV radiation levels, although supplementation of UV-B radiation in the field resulted in changes in the composition of microbial communities (Johnson et al., 2002). Laboratory incubation of tundra soils from Barrow, Alaska, at different temperatures had strong effects on community composition assessed from a molecular biology approach, but only after a temperature shift of more than 10 °C (Panikov, 1999).

A mathematical simulation of the changes in tundra microbial community structure (Panikov, 1994, 1997) showed, surprisingly, that the effects of temperature on the soil microbial community were less significant compared with effects on the plant community. Probable reasons for this include strong metabolic interactions between individual populations within the microbial community (in which the product of one organism is used as a nutrient substrate by other organisms) that stabilize community structure in a wide range of environmental conditions; the wide temperature tolerance of microbial species; and the lower resolution power of microbial taxonomy as compared with plant taxonomy.

The model (Panikov, 1994, 1997) generated realistic patterns of mass and energy flow (primary productivity, decomposition rates, and soil respiration) under present-day conditions and in response to warming, pollution, fertilization, drying/rewetting of soil, etc. (Fig. 7.14). Figure 7.14a shows that L-selected species (*Bacillus*) display only sporadic occurrence under normal cold tundra conditions, in agreement with observations, and attain high population density after soil warming. Simulated soil warming accelerated both primary productivity and organic matter decomposition, but the latter was more affected. Soil warming also led to a negative carbon balance in the soil, as respiration exceeded photosynthesis leading to a decline in accumulated organic carbon (Fig. 7.14b; sections 7.4.2.1, 7.4.2.2, 7.5.1.1, and 7.5.4).

Conidia (spores) of the fungus *Metarhizium* are sensitive to UV-B radiation. There are great differences between strains, but strains from high latitudes are less tolerant than those from lower latitudes (Braga et al., 2001a,b). In one species (*M. anisopliae*) it was shown that UV-A also had a negative effect and, when comparing strains, the sensitivity to UV-A radiation did not correlate with the sensitivity to UV-B radiation (Braga et al., 2001c). Several groups have studied the effects of UV-B radiation on phylloplane (leaf surface-dwelling) fungi and litter-decomposing fungi. Moody et al. (1999) found that five of the investigated species were sensitive and seven relatively insensitive to UV-B radiation. The spore production in the litter decomposers was generally inhibited by UV-B radiation (except for one species), while that in phylloplane species was unaffected. However, the sensitivity of spores is not equivalent to the sensitivity of the metabolic machinery of the vegetative body of a fungus (i.e., the thallus or mycelium) that produces the spores.

In the subarctic (Abisko), a study of the decomposition rates of a standard litter type showed that there was a change in the composition of fungal species resulting from elevated UV-B radiation levels (Moody et al., 2001). These results to some extent resemble those from an earlier experiment studying the decomposition of dwarf-shrub litter at the same site (Gehrke et al., 1995).

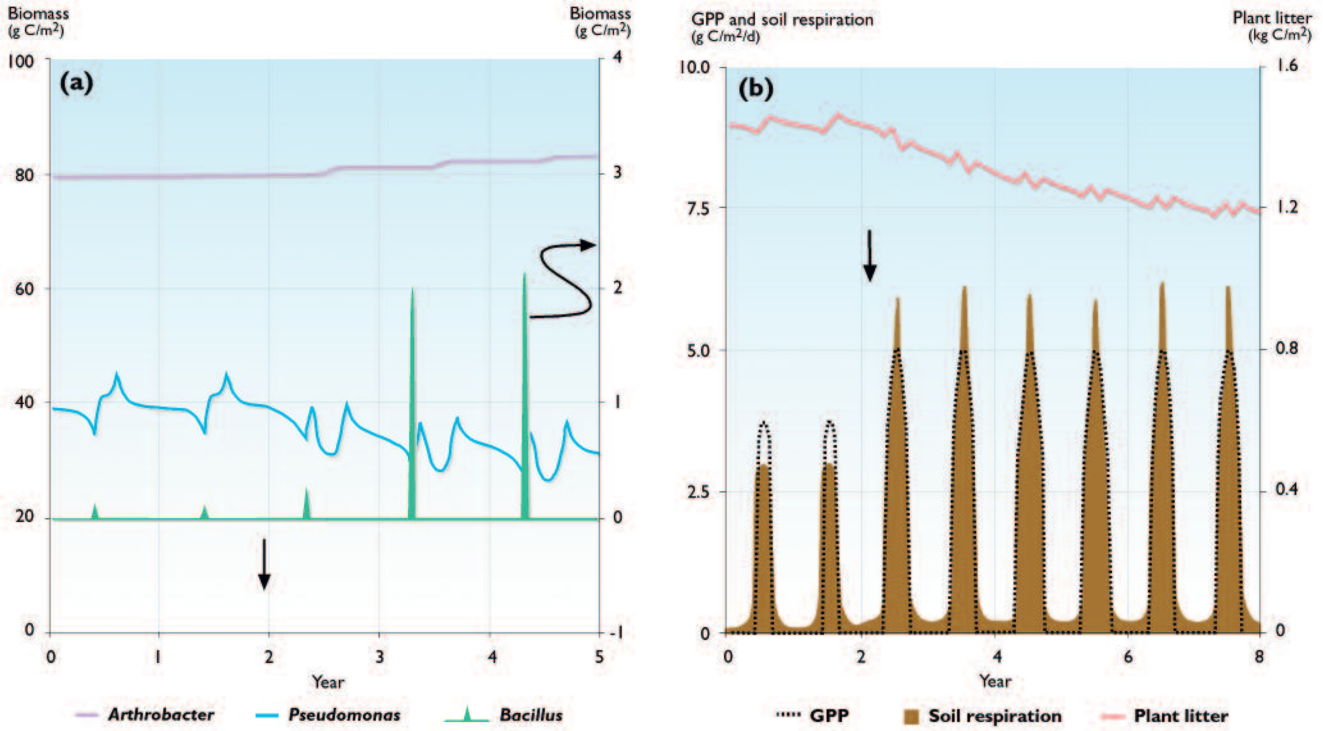


Fig. 7.14. Simulation of changes in a tundra microbial community (Barrow, Alaska) induced by climate warming: (a) population dynamics of dominant soil bacteria (right axis applies to *Bacillus*); (b) carbon budget including gross primary production (GPP), soil respiration, and litter dynamics. The simulation assumed that average air temperature instantly increased by 10 °C in year two of the simulation, indicated by the vertical arrows in each panel (Panikov, 1994).

The arctic periglacial environment represents a unique mosaic of unstable habitats (gradation between terrestrial and shallow wetland environments) where large variations in cyanobacterial and algal diversity, productivity, and life strategy exist (Elster and Svoboda, 1995, 1996; Elster et al., 1997, 2002; Kubeckova et al., 2001). Prokaryotic cyanobacteria and eukaryotic algae have different life strategies with respect to their susceptibility to severe and unstable conditions (Elster, 2002). Cyanobacteria are well adapted to changeable conditions involving low and high radiation levels (including UV-B radiation), and cycles of desiccation and rehydration, increasing and decreasing salinity, and freezing and thawing. This gives them a great ecological advantage and allows them to be perennial. In contrast, eukaryotic algae have higher rates of photosynthesis and lower resistance to changes in irradiation, desiccation, rehydration, and freeze–thaw cycles. These features predetermine their annual character. If the arctic terrestrial environment becomes colder, the cyanobacteria are very likely to become the dominant community. In contrast, if temperatures become warmer, the eukaryotic algae are very likely to start to predominate. In addition, the ongoing temperature increase in the Arctic is very likely to influence cyanobacteria and algal production, as well as the balance between cyanobacteria and algae and invertebrate herbivore activity. Invertebrate grazing pressure is likely to increase and much of the visible cyanobacteria and algae biomass could possibly disappear from arctic locales (Elster et al., 2001).

Summary

Tundra soil heating, CO_2 enrichment, and amendment with mineral nutrients generally accelerate microbial activity. Higher CO_2 concentrations tend to intensify root exudation, which is the main source of available carbon for soil and rhizosphere bacteria. Supplementation of UV-B radiation in the field resulted in changes in the composition of microbial communities. Laboratory incubation of tundra soils had strong effects on community composition after a temperature shift of more than 10 °C. Surprisingly, the effects of many factors on the soil microbial community were less significant compared with effects on the plant community. However, a mathematical simulation of the changes in microbial community structure in the tundra showed that soil warming resulted in stimulation of bacterial growth.

The effects of increased UV-B radiation levels on microorganisms include damage to high-latitude strains of fungal spores, and damage to some species of leaf-dwelling fungi and soil-dwelling decomposer fungi that resulted in a change in the composition of the fungal communities.

Cyanobacteria are better adapted to changeable and harsh conditions than algae, and in milder climates are likely to be dominated by algae. However, herbivory of both cyanobacteria and algal biomass is likely to increase in a warmer climate.

7.3.4. Genetic responses of species to changes in climate and ultraviolet-B radiation levels

Many widely distributed arctic species show large ecological amplitude (broad niches) and are taxonomically complex, often with many subspecies, while species with a narrower distribution range often show a more restricted ecological amplitude. It is necessary to know the extent of genetic variation in arctic species and the underlying causes of differentiation or homogenization (biogeography, historical bottlenecks, reproductive biology, and demography) in order to assess responses of species to climate change.

7.3.4.1. Plants

In spite of rapid development in recent years of different molecular techniques suited for population genetic studies, there are still few studies of arctic plants, most of which have focused on biogeographical and phylogeographical questions related to vascular plant species. Such studies may reveal the migratory potential of the species in response to climate change. During the Pleistocene glaciations, arctic plants were restricted to refugia within or south of the present-day Arctic, from which they could re-colonize areas as conditions improved during interglacial periods (Abbott et al., 2000; Tremblay and Schoen, 1999). The rate of colonization by different species during the Holocene probably depended on the location of their closest refugia, their dispersal biology, and their genetic makeup. Genetic phylogeographical studies provide evidence for relatively fast migration rates in most vascular species (Abbott and Brochmann, 2003; Bennike, 1999; Brochmann et al., 2003) and possibly bryophytes as well (Derda and Wyatt, 1999). However, in the modern context of rapid climate change, migration rates need to be considered on somewhat shorter timescales than thousands of years.

The level of genetic variation within and between populations indicates the potential for local adaptation to environmental change and hence population resilience to environmental change. Based on the relatively young age of populations and low recruitment of sexually reproduced offspring, it was long believed that genetic variation in arctic plants would be low. However, the number of genetic studies is limited and no such general pattern of genetic variation has been identified. Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels (Bauert, 1996; Gabrielsen and Brochmann, 1998; Jefferies and Gottlieb, 1983; Jonsson et al., 1996; Philipp, 1997; Stenström et al., 2001) to very low levels (Bayer, 1991; Max et al., 1999; Odasz and Savolainen, 1996; Philipp, 1998; Stenström et al., 2001) of variation. However, genetic variation among arctic plants may be of greater value in terms of biodiversity than in other biomes due to much lower species diversity. Furthermore, high levels of polyploidy in many arctic vascular plant species may promote the proportion of the genetic variation partitioned within individuals, which may be important when passing through evolutionary bottlenecks (Brochmann and Steen, 1999).

By comparing 19 different populations of three rhizomatous *Carex* taxa, distributed among 16 sites within arctic Eurasia, ranging from northern Scandinavia in the west to Wrangel Island in the east, Stenström et al. (2001) showed that the levels of genetic variation were not related to climate, but were to a large extent explained by differences in glaciation history at the sampling sites. Populations in areas deglaciated about 10 000 years BP had significantly lower genetic variation than populations in areas deglaciated 60 000 years BP or those in areas not glaciated at all during the Weichselian. Relatively young population age may also be responsible for a low genetic variation in some other populations (e.g., Bayer, 1991; Max et al., 1999), while in yet others, breeding systems apparently play a large role (e.g., Odasz and Savolainen, 1996; Philipp, 1998). In general, populations of insect- or self-pollinated plant species have lower genetic variation than populations of wind-pollinated species (Hamrick and Godt, 1990), and this seems to apply to arctic plants as well.

Those plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution, for example purple saxifrage (Abbott et al., 1995), nodding saxifrage (*Saxifraga cernua*; Gabrielsen and Brochmann, 1998), moss campion (*Silene acaulis*; Abbott et al., 1995; Philipp, 1997), *Carex bigelowii* sensu lato (Jonsson et al., 1996; Stenström et al., 2001), and *C. stans* (Stenström et al., 2001). In these species, the genetic variation among populations (G_{ST}) is a relatively small proportion of the total genetic variation (i.e., they show low degrees of population differentiation). Large variation within populations, however, increases possibilities for ecotypic differentiation. In the Arctic, extremely steep environmental gradients are frequent on a microtopographical scale and ecotypic differentiation has been demonstrated over such short distances for alpine timothy (*Phleum alpinum*; Callaghan, 1974), *Carex aquatilis* (Shaver et al., 1979), mountain avens (McGraw and Antonovics, 1983), and purple saxifrage (Crawford and Smith, 1997), all widely distributed plant species in the Arctic. Ecotypic differentiation in response to this small-scale heterogeneity may preserve genetic variation and in that way contribute to resilience to change at the species rather than the population level. Thus, an initial response to climate change in such species is likely to be a change in the distribution and abundance of ecotypes within a species distribution (Crawford and Smith, 1997). In addition, many arctic plants show large phenotypic plasticity, which is likely to further increase their resilience (Stenström et al., 2002; Table 7.5).

If the degree of genetic variation can be used as an indication of resilience of populations to change, it is likely that this resilience will be greatest among plants in old populations of widely distributed, wind-pollinated vascular species (e.g., rhizomatous *Carex* populations in eastern Siberia). However, generation time and seedling recruitment may affect the adaptation rate. Many of the dominant arctic plants such as the rhizomatous *Carex* species are clonal, that is, they do not rely on seed production through sexual reproduction for short-term population maintenance. Genetic individuals of these plant species may live to be thousands of years old (Jónsdóttir et al., 2000), which may decrease the adaptation rate. However, experiments with plants from outside of the Arctic have shown that UV-B radiation may increase the rate of genetic change. Exposure to high UV-B radiation levels can activate mutator transposons that amplify the mutation effect beyond the immediate UV-B radiation damage (Walbot, 1999), and increased levels of UV-B radiation may lead to an increased tendency to mutations in future generations (Ries et al., 2000).

For plants with long-lived seed, further genetic variation is preserved in the seed banks. Dormant seed populations may be genetically different from the aboveground populations (McGraw, 1995) and potentially able to better exploit a new climate.

Genetic variation has been studied in fewer moss and lichen species than in vascular plants. Boreal and antarctic bryophytes usually show high levels of variation (Cronberg et al., 1997; Derda and Wyatt, 1999; Skotnicki et al., 1998, 1999), but the partitioning of genetic variation among and within populations depends on species. Scandinavian populations of the widely distributed moss *Hylocomium splendens*, including two subarctic alpine populations, showed high genetic variation within populations and low G_{ST}, a pattern similar to widely distributed, wind-pollinated vascular species (Cronberg et al., 1997). In contrast, North American and European populations of *Polytrichum commune* have low within-population variation and high G_{ST} (Derda and Wyatt, 1999).

7.3.4.2. Animals

The genetics of arctic terrestrial animals have been thoroughly studied mainly for a few well-known mammal species such as reindeer/caribou (Flagstad and Røed, 2003), lemmings (Ehrich et al., 2000; Fedorov et al., 1999a,b), and Arctic fox (Dalén et al., 2005). These studies have focused on phylogeographical patterns and the relative roles of present gene flow and historic processes (especially glacial–interglacial cycles; see section 7.2) based on neutral genetic markers (especially mitochondrial DNA). The present genetic differentiation reflects to a large extent historic processes and the presence of current migration barriers. For mammals with relatively restricted mobility such as lemmings, even small-scale barriers (e.g., large rivers) can form the borders between subspecies (Fedorov et al., 1999a,b), while a very mobile animal such as the Arctic fox, which readily moves between continents and islands on sea ice, appears to be relatively panmictic (i.e., shows little genetic structuring) at the circumpolar scale (Dalén et al., 2005).

Current gene flow (an indication of mobility) and population history (origin and differentiation) indicate the ability of a species to track the location of its habitats through time (i.e., a species is able to relocate its distributional range according to any changes in the distribution of its habitat through the process of dispersal). A mobile species will have better prospects for survival than a relatively sedentary species. Moreover, a species with high genetic/racial diversity has proved an ability to adapt to different environmental conditions in the past and is likely to do the same in the future. It should be noted, however, that markers of genetic variation/differentiation currently used (e.g., mitochondrial DNA) may have little bearing on the genetic variation in morphology and life-history traits (see Flagstad and Røed, 2003). It is these latter traits that decide whether a species or a morph will be able to adapt to future changes. Currently, there are few studies of arctic animals using a quantitative genetics approach (Roff, 1997) that address the potential for rapid adaptations to climatic change. Elsewhere, using a quantitative genetic research protocol, Réale et al. (2003) showed that northern boreal red squirrels (*Tamiasciurus hudsonicus*) were able to respond genetically within a decade to increased spring temperatures.

7.3.4.3. Microorganisms

Assessment of genetic responses of microorganisms to climate change is based on laboratory models, as observations made within arctic terrestrial ecosystems are absent. Short generation times and the impressive genetic plasticity of bacteria make them a favorite topic in theoretical studies of general population genetics. Because most mutations are deleterious, mutation rates are generally thought to be low and, consequently, mutator alleles should be selected against. However, up to 1% of natural bacterial isolates have been found to be mutators. A mutator can be viewed as behaving altruistically because, although it reduces individual fitness, it increases the probability of an adaptive mutation appearing. These results may help to explain observations that associate high mutation rates with emerging pathogens that cause spontaneous epidemic outbreaks (Sniegowski et al., 1997; Wilke et al., 2001).

In the arctic environment, intensive mutagenic effects are likely to result from increased UV radiation levels and also from aerosols and volatile chemical mutagens transported to the cool polar atmosphere from the mid- and low latitudes. The direct mutagenic effects are very likely to be weak, especially if the protective shielding effects of soil particles and impressive genetic plasticity of bacteria are taken into account. However, it is possible that mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the whole ecosystem.

7.3.4.4. Summary

Arctic plants show the same range of genetic variation as temperate plants, ranging from comparatively high levels to very low levels. In widespread *Carex* taxa, levels of genetic variation were not related to climate, but were to a large extent explained by differences in glaciation history at the sampling sites: populations in areas deglaciated approximately 10000 years BP had significantly lower genetic variation than populations in areas deglaciated 60000 years BP.

Plant species representing populations with relatively high levels of genetic variation usually have a large geographic distribution. On a microtopographical scale, extremely steep environmental gradients are frequent and ecotypic differentiation has been demonstrated over short distances for several widespread species. This heterogeneity, together with large phenotypic plasticity, is likely to contribute to resilience to change at the population and species levels. For plants with long-lived seed, further genetic variation related to former environments is preserved in the seed banks. Thus, there are several mechanisms for widespread arctic plant species to respond to environmental change.

Experiments with plants from outside the Arctic have shown that increased levels of UV-B radiation can speed up genetic change and may lead to an increased tendency for mutations in future generations.

The present genetic differentiation of arctic terrestrial animals that have been studied thoroughly (e.g., reindeer/caribou, lemmings, Arctic fox) to a large extent reflects historic processes and the presence of current migration barriers. For mammals with relatively restricted mobility such as lemmings, even small-scale barriers (e.g., large rivers) can form the borders between subspecies, while a very mobile animal such as the Arctic fox shows little genetic structuring at the circumpolar scale. A species with high genetic/racial diversity has proved an ability to adapt to different environmental conditions in the past and is likely to do the same in the future.

There is a paucity of studies of arctic animals that have addressed the potential for rapid adaptations to climatic change. Elsewhere, it was shown that northern boreal red squirrels were able to respond genetically within a decade to increased spring temperatures.

Up to 1% of natural bacterial isolates have been found to be mutators, and high mutation rates are associated with emerging pathogens causing spontaneous epidemic outbreaks. In the Arctic, intensive mutagenic effects are likely to result from increased UV radiation levels and also from aerosols and volatile chemical mutagens. Although the effects are very likely to be weak, it is possible that mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the whole ecosystem.

7.3.5. Recent and projected changes in species distributions and potential ranges

Paleoecological research (section 7.2) and observations over many decades demonstrate that the geographic ranges of terrestrial species in general are well correlated with bioclimatic variables. Furthermore, the strength of these relationships is independent of trophic level (Huntley et al., 2003). Major climate-related species distributions at the large scale include the limit of trees, which is associated with the isoline for mean July air temperatures of about 10 ºC (Brockmann-Jerosch, 1919 as discussed in Körner, 1999) and soil temperature of 7 ºC (Körner, 1998), and the limit of woody plants such as dwarf shrubs that are one indicator of the boundary of the polar desert biome (Edlund and Alt, 1989). Such relationships suggest that species distributions at the macrogeographical and landscape scale are very likely to change as temperature changes. This section assesses the effects of climate change on recent changes in species distributions and those projected to occur in the future.

7.3.5.1. Recent changes

Indigenous knowledge projects have documented recent changes in the ranges of caribou in relation to changes in weather, based on hunters' understanding of how environmental conditions affect seasonal caribou distribution patterns (Kofinas et al., 2002). Hunters' explanations of caribou distributions may provide indications of potential range changes given projected climate change. For example, in the El Niño year of 1997–1998, several thousand Porcupine Caribou overwintered on the Yukon Coast in arctic Canada. Hunters in Aklavik, Northwest Territories, explained this phenomenon in terms of the Beaufort Sea ice pack, which was farther from the Yukon North Slope than in most years, resulting in warmer coastal temperatures and thus more abundant forage for caribou. In July 1997, as the caribou moved into Canada from their Alaskan calving grounds, several large groups remained on the coast, taking advantage of the rich forage opportunities. A mild autumn and the lack of icing events that push the caribou south for the winter kept the caribou in the area into October, as the animals could continue to access summer forage. The herd that remained on the coast for the winter was reported to be in better condition than the herd wintering in the usual locations.

Indigenous knowledge has also documented recent changes in the ranges of other animals in relation to changes in the weather. In the Canadian Arctic, Inuit in communities such as Baker Lake have reported insects previously associated with areas south of the treeline (Fox, 2002). In more western regions, there have been more frequent sightings of "mainland ducks" such as pintail ducks (*Anas acuta*) and mallard (*A. platyrhynchos*; Riedlinger, 2001).

Working in the Canadian Arctic using a conventional scientific approach, Morrison et al. (2001) summarized the trends in population data for breeding waders, and found that almost all arctic-breeding species were declining. The reasons for the trends were not always clear and were probably of multiple origins. Long-term monitoring in Finland has shown a substantial decline in the populations of many arctic and subarctic bird species over the past 20 years (Väisänen et al., 1998), but the trend in bird populations is not always negative. Zöckler et al. (2003) found that almost half of the arctic-breeding, long-distance migrants studied are presently in decline. For many species there are still insufficient data available, and only a few species (8%) show an increasing trend. In most cases, it is not easy to correlate trends with climate change. As the trends in some species are different outside and inside the Arctic, there is an indication that factors of a more global nature are involved. An example is the drastic decline of the ruff (*Philomachus pugnax*) in almost all breeding sites outside the Arctic in contrast to their stable or even increasing populations in some (but not all) northern arctic areas (Zöckler, 2002). This coincides with the recent northern expansion of other wet-grassland waders, such as the common snipe (*Gallinago gallinago*) in the Bolshemelzkaya tundra (Morozov, 1998), the black-tailed godwit (*Limosa limosa*), and the northern lapwing (*Vanellus vanellus*) in northern Russia concomitant with a northward expansion of agriculture including sown meadows (Lebedeva, 1998). Several other bird species have recently been recorded in more northerly locations in the Arctic (Zöckler et al., 1997), suggesting that some species are shifting their distribution in response to alteration of habitats by climate change. The emerging picture is that the ruff is being forced to retreat to its core arctic habitats owing to the effects of global climate change in combination with increasing nutrient enrichment on the quality of wet grassland habitats (Zöckler, 2002).

A recent global meta-analysis of plants claims that a climate change signal has been identified across natural ecosystems (Parmesan and Yohe, 2003). Range shifts of plants averaging 6.1 km per decade toward the poles and 6.1 m per decade in altitude have been identified in response to a mean advancement of spring (initiation of greening) by 2 to 3 days per decade. Although some northern treeline data were included in the analysis, little information was available for arctic ecosystems.

7.3.5.2. Projected future changes in species distributions

Models of species–climate response surfaces based upon correlations between species ranges and bioclimatic variables are able to simulate the recently observed range changes of at least some species of birds (Zöckler and Lysenko, 2000) and butterflies (Hill et al., 1999; 2003; Virtanen and Neuvonen, 1999). Related studies have shown that, at least in the case of butterflies, the extent to which species have realized their projected range changes over the last 30 to 50 years is strongly related to their degree of habitat restriction: generalist species are much more able to achieve the projected range expansions than are specialist species (Warren et al., 2001).

Such models (Hill et al., 2003; Huntley et al., 1995) project future ranges of arctic species that are often markedly reduced in spatial extent compared to the species' present ranges. The range limits of boreal and temperate species shift poleward in response to the same future climate scenarios. However, the large magnitude of the shifts in projected range margins results in potential reductions in the ranges of many boreal species because they are limited to the north by the Arctic Ocean.

The extent to which arctic plant species experience the rapid range reductions simulated by such models will depend principally upon two factors. First, such reductions are likely to happen most rapidly in species that experience some physiological constraint at their southern range margin, for example, the winter thermal constraint postulated for cloudberry (Marks, 1978; Marks and Taylor, 1978) or the summer thermal constraints postulated for the great skua (*Catharacta skua*; Furness, 1990). Species whose southern range margin is determined by biotic interactions are likely to experience less rapid range reductions. Second, such reductions are very likely to happen more rapidly where the northward migration of boreal or temperate species is not limited either by habitat availability or propagule (dispersal stage of a plant or animal, such as fertilized eggs, larvae, or seeds) dispersal. "Fugitive" species of the early successional communities that characteristically follow disturbance of the boreal forests have the required dispersal ability to achieve rapid poleward range expansions. Unless other factors (e.g., herbivore pressure or a lack of microsites for successful seedling establishment) exclude them, these species are likely to extend into the Arctic rapidly, forming transient ecosystems that will persist until the arrival of the more slowly expanding late-successional boreal species.

Loss of habitat is a particularly important possibility that would constrain species ranges. The most dramatic change in habitat for many water birds is the projected loss of tundra habitat, which varies between 39 and 57% by the end of the 21st century (Harding et al., 2002; Haxeltine and Prentice, 1996). Vegetation models (Neilson and Drapek, 1998) combined with maps of water-bird distributions show a large variation in the impact of projected vegetation changes on 25 selected

Table 7.7. Loss of breeding area habitat projected by two different general circulation models for arctic water-bird species, and their globally threatened status (based on Zöckler and Lysenko, 2000).

		Loss of habitat (%)[a]		
		HadCM2GSa1[b]	UKMO[c]	Red List[d]
Tundra bean goose	*Anser fabalis rossicus/serrirostris*	76	93	
Red-breasted goose	*Branta ruficollis*	67	85	VU
Spoon-billed sandpiper	*Eurynorhynchus pygmaeus*	57	57	VU/EN
Emperor goose	*Anser canagicus*	54	54	!
Ross's gull	*Rhodostethia rosea*	51	73	
Red-necked stint	*Calidris ruficollis*	48	68	
Sharp-tailed sandpiper	*Calidris acuminata*	46	74	
Little stint	*Calidris minuta*	45	65	
Curlew sandpiper	*Calidris ferruginea*	41	70	
Pectoral sandpiper	*Calidris melanotos*	38	60	
Dunlin	*Calidris alpina*	36	58	
White-fronted goose	*Anser albifrons*	36	57	
Long-billed dowitcher	*Limnodromus scolopaceus*	31	54	
Great knot	*Calidris tenuirostris*	31	42	
Lesser white-fronted goose	*Anser erythropus*	28	29	VU
Barnacle goose	*Branta leucopsis*	21	27	
Western sandpiper	*Calidris mauri*	19	21	
Brent goose	*Branta bernicla*	16	44	
Red knot	*Calidris canutus*	16	33	
Greater snow goose	*Anser caerulescens*	14	46	
Canada goose	*Branta canadensis*	13	22	
Pink-footed goose	*Anser brachyrhynchus*	10	10	
Sanderling	*Calidris alba*	5	25	

[a]Value could be substantially higher as unclassified areas in these analyses may contain different tundra types; [b]moderate warming; [c]extreme warming; [d]VU=vulnerable as a globally threatened species (BirdLife International, 2001), EN=suggested for upgrading to endangered as a globally threatened species, !=suggested for inclusion in the Red List.

species (Zöckler and Lysenko, 2000). Vegetation scenarios derived from the HadCM2GSa1 model project that 76% of tundra bean goose (*Anser fabalis rossicus/serrirostris*) habitat will be affected by the alteration of tundra vegetation, while only 5% of sanderling habitat will be affected (Neilson and Drapek, 1998). However, the sanderling, similar to many other high-arctic breeders, might be affected even more strongly, as southern tundra habitat types are projected to replace their specific high-arctic habitats. Whereas the more southerly breeding species can shift northwards, it is likely to be increasingly difficult for high-arctic breeders to compete. For two of the three water-bird species that are considered globally threatened, namely the red-breasted goose (*Branta ruficollis*) and the spoon-billed sandpiper (*Eurynorhynchus pygmaeus*), 67 and 57% of their current breeding range is projected to change from tundra to forest, respectively (Table 7.7). This additional loss of habitat is likely to place these two species at a higher risk of extinction. The emperor goose (*Anser canagicus*), already in decline and with 54% of its small range projected to be affected, is highlighted as needing further conservation attention.

Geographic ranges of plants

Strong relationships between growth and temperature in the circumpolar ericaceous dwarf shrub *Cassiope tetragona* and the feather moss *Hylocomium splendens* can be used to model range changes. The growth of *C. tetragona* is strongly related to mean July temperature (Havström et al., 1995b) and that of *H. splendens* is related to mean annual temperature (Callaghan et al., 1997) throughout their northern ranges (Fig. 7.15a). Mean July and mean annual temperatures are to some extent representative of latitude, as they decrease toward the north. The natural climatic warming from the beginning of the Little Ice Age to the present is the equivalent of only a minor shift in latitude for *C. tetragona*. On the other hand, projected future warming is likely to produce a greater latitudinal displacement that, at the northern limit of the current ranges of the two species, is very likely to result in a northern range extension (Fig. 7.15a). In contrast, at the southern edge of the ranges, future warming is very unlikely to increase growth beyond the genetic capabilities of the species, and the dynamics of the species in this part of their ranges are very likely to be determined by the responses of competi-

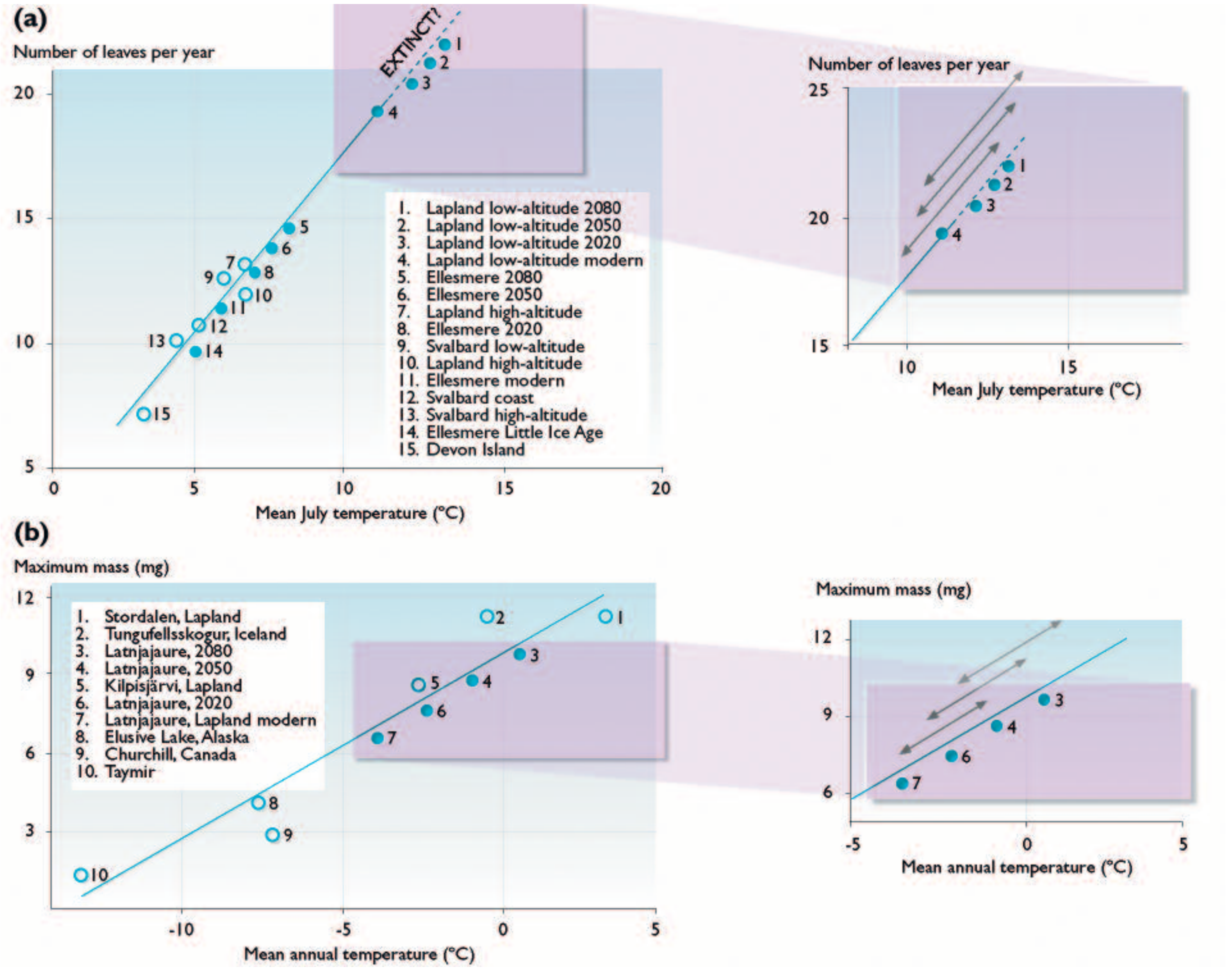


Fig. 7.15. (a) Number of leaves produced per year in shoots of *Cassiope tetragona* as a function of mean July temperature and (b) correlation between a growth parameter in *Hylocomium splendens* and mean annual temperature at seven arctic and subarctic sites. The boxes on the regression lines contain scenarios of growth in ACIA time slices resulting from temperature increases projected by the five ACIA-designated models. The hatched line in (a) depicts projected growth that is probably outside the capability of the species. The expanded boxes to the right of each panel depict uncertainty ranges associated with each of the projections (doubled-ended arrows). Open circles represent sequences of present-day relationships between climate and growth, while filled circles represent present-day and projected growth at three sites (based on Callaghan et al., 1997 and Havström et al., 1995b).

tors to warming. A similar analysis for *H. splendens* shows how a current alpine population is very likely to resemble a population from a lowland forested area under projected future climate conditions (Fig. 7.15b).

At the landscape scale, plants are distributed in mosaics associated with microhabitats, and the larger-scale latitudinal range changes are very likely to be associated with initial changes in landscape mosaics. Cushion plants and other species characteristic of wind-exposed patches are likely to become restricted in distribution by increased snow cover. In contrast, plants of snow beds might become more restricted if snow duration decreases. Wetland species will become restricted by drying and species in drier areas will become more restricted by increased soil moisture. Plants currently restricted to south-facing slopes and warm springs (to some extent analogues of future warmer habitats and hot spots of biodiversity) north of their main distribution areas are likely to provide an "inoculum" for rapid colonization of surrounding habitats when climate becomes warmer, although they themselves are likely to be displaced from their current niches by less diverse shrub–thicket communities. Examples include orchids, ferns, and herbs in warm springs on West Greenland (although orchids and ferns are unlikely to become widely distributed), ericaceous dwarf shrubs in some inner fjords of Svalbard, and the large shrubs/small trees of the North Slope of Alaska.

Geographic ranges of animals

Often, causes of observed trends in migrant bird population numbers cannot easily be attributed to local, site-related factors within and outside the Arctic, such as drainage, land use change, hunting and persecution by humans, and predation. Even among global factors, climate change is one of an array of drivers, such as eutrophication, often working in synergy with climate change and reinforcing the effect. In addition, migratory birds are also strongly affected by climate change outside of their arctic breeding grounds. Desertification, droughts, and wetland loss; eutrophication of staging and wintering wetlands; changes in land use; and application of chemicals and nutrients on wintering grounds lead to changes in vegetation and biomass on coastal staging and wintering grounds. The effects of sea-level rise on the extent of coastal staging and wintering grounds are very likely to be particularly harmful, and the hunting pressure on wintering waders in certain areas will also reduce bird populations.

There are few studies of the impacts of climate change on migratory species, although recent trends in some species (e.g., arctic geese) are well known (Madsen et al., 1999). Very little can be concluded from the observed impacts of current climate variability on migratory birds, as existing monitoring programs are few (e.g., Soloviev et al., 1998) and often began only recently.

An analysis of Hadley Centre spring and summer temperature and precipitation data over the last 50 years, interpolated over the currently known arctic distribution areas of the white-fronted goose (*Anser albifrons*) and the Taymir population of the red knot (*Calidris canutus canutus*), demonstrates a significant correlation between the mean June temperature and the percentage of juveniles in the population as a measure of breeding success. The Nearctic population of the red knot (*C. c. islandica*) and the curlew sandpiper (*Calidris ferruginea*) breeding on the Taymir Peninsula do not show such a correlation (Zöckler and Lysenko, 2000). The HadCM2GSa1 model, forced with a 1% per year increase in atmospheric CO_2 concentrations, projects a moderate increase in mean June temperature (by the time CO_2 concentrations double) in the Taymir breeding area of the white-fronted goose, which is likely to favor the goose population. The conditions for the Taymir population are projected to be particularly favorable in the period around 2020. However, a considerable initial cooling and lack of warming over present-day values by 2080 in the breeding grounds of the West Greenland goose population is likely to lead to a drop in the size of the fragile Greenland population. Although the ACIA-designated model projections differ from those used in Zöckler and Lysenko (2000), possible decreases in temperature in ACIA Region 1 (section 18.3.1) are within the range of the projections (section 7.6, Table 7.14). The Zöckler and Lysenko (2000) study must be interpreted in relation to other factors, such as other weather parameters and natural predation that often fluctuates in three- to four-year cycles according to the abundance of the main prey (i.e., the lemming; see section 7.4.1.4). Furthermore, hunting by humans, mainly outside of the Arctic, and the effects of climate change outside of the Arctic, in particular sea-level rise, need to be taken into account.

Investigations of the breeding wader population in northeast Greenland for over 30 years showed that spring snow cover is the main factor governing initiation of egg laying in high-arctic waders, such as the red knot and other sandpipers, while June temperature does not appear to be important (Meltofte, 1985, 2000; pers. comm., 2004). In fact, waders breed earlier in the arid but cool far north of Greenland than they do in the "mild", humid southern areas of the high Arctic, where snow cover is much deeper and more extensive. Projections of future climate for northeast Greenland include cooler summers, later snowmelt, and less snow-free space for the arriving waders to feed, which are likely to lead to later breeding and smaller populations. Snow cover must still be considered the prime regulating factor for initiation of egg laying, but temperature – so important for determining invertebrate food availability (section 8.5.6) – is important as well when sufficient snow-free habitat is already present.

Although global climate change in synergy with global eutrophication is likely to lead to an increase in biomass in the Arctic, a change in vegetation height and density, and a general change in vegetation structure with shifts in species distribution that are very likely to have an enormous impact on water birds (which are highly dependent on open landscapes and lightly vegetated breeding sites), global climate change and eutrophication are very likely to provide opportunities for other birds with more southerly distributions, such as owls and woodpeckers. Some birds, including most goose species and a few waders, have demonstrated a certain ability to adjust to new and changing habitats (Lugert and Zöckler, 2001), but the majority of birds breeding in the high Arctic are likely to be to be pushed to the edge of survival with little habitat left.

Geographic ranges of microorganisms

Studies of geographic ranges of microbes related to extremely cold environments such as the Arctic, and also to climate change, are in their infancy. Unlike plant and animal ecology, soil microbiology still does not have a solution to the central biogeographical problem of whether soil microorganisms are cosmopolitan (widely distributed) or endemic (restricted to one location) species. Until the ranges of species are known, the bacteria that might be threatened by climate change cannot be identified (Staley, 1997).

The prevailing hypothesis for bacterial biogeography is based on the axiom of the Dutch microbiologists Baas-Becking and Beijerinck, who stated, "Everything is everywhere, but the environment selects" (Beijerinck, 1913). This hypothesis assumes that free-living bacteria are cosmopolitan in their geographic distribution; they are readily disseminated from one location on earth to another by water and air currents or by animal vectors such as birds that migrate between regions. Only recently has it been possible to rigorously test the cosmopolitan distribution of bacteria with unbiased molecular biology approaches. Studies outside of the Arctic demonstrate that the cyanobacterium *Microcoleus chthonoplastes* is a cosmopolitan species (Garcia-Pichel et al., 1996). Using different molecular biology techniques, Stetter et al. (1993) discovered that hyperthermophilic (heat-loving) Archaea isolated from Alaskan oil reservoirs showed a high degree of DNA–DNA reassociation with selected *Archaeoglobus*, *Thermococcus*, and *Pyrococcus* species, and concluded that the species were the same as those from European thermal marine sources. In a separate study, DNA–DNA reassociation of a strain of *Archaeoglobus fulgidus* isolated from North Sea crude oil fields showed 100% relatedness to an *Archaeoglobus fulgidus* strain from Italian hydrothermal systems (Beeder et al., 1994). These two studies comprise some of the best evidence to date supporting the cosmopolitan hypothesis of Baas-Becking.

However, 3-chlorobenzoate-degrading bacteria isolated from soils in six regions on five continents (Fulthorpe et al., 1998) were found to have restricted or unique ranges. Also, plant species have been reported to harbor their own unique symbiotic species of fungi associated with leaves, bark, roots, etc (Hawksworth, 1991), so, by definition, the existence of endemic plants should imply the existence of respective microbial symbionts. Therefore, arctic microbial communities may consist of a mixture of species: some that are endemic and some that are cosmopolitan.

7.3.5.3. Summary

Monitoring of distribution ranges with a spatial representation as good as for temperate latitudes is not available for the terrestrial Arctic. Indigenous knowledge projects have documented recent changes in caribou ranges in relation to changes in weather. Hunters' explanations of caribou distributions may provide indications of potential range changes under scenarios of warming temperatures, such as overwintering of caribou in coastal areas during warm winters. Other arctic indigenous observations include insects previously associated with areas south of the treeline and more frequent sightings of "mainland ducks". In contrast, almost all arctic-breeding species are declining. The reasons for the trends are not always clear and probably of multiple origins, although there are suggestions that some species are shifting their distribution in response to alteration of habitats by climate change.

Quantitative monitoring of conspicuous and popular species such as birds and butterflies has demonstrated that many formerly southern species are rapidly approaching arctic regions and some have already entered. Arctic birds, especially arctic-breeding water birds and waders that can be counted on staging and wintering grounds, show mostly declining population trends; some species have declined dramatically. It is likely that these changes result from the combined action of eutrophication and habitat loss on wintering and staging sites as well as concurrent climate change, although separating the relative contributions of these factors is difficult. Based on climate models, dramatic reductions in the populations of tundra birds are projected as a generally warmer climate is likely to increase vegetation height and decrease the Arctic's landmass.

Species–climate response-surface models are able to simulate the recently observed range changes of at least some species of both birds and butterflies. At least in the case of butterflies, the extent to which species have realized their projected range changes over the last 30 to 50 years is strongly related to their degree of habitat restriction: generalist species are much more able to achieve the projected range expansions than are specialist species. Simulated potential future ranges are often markedly reduced in spatial extent compared to present ranges. The range limits of boreal and temperate species shift poleward but the large magnitude of the shifts in projected range margins results in potential reductions in the ranges of many boreal species because they are limited to the north by the Arctic Ocean. Species that experience some physiological constraint at their southern range margin are likely to be affected sooner than those that are affected by biotic relationships such as competition from immigrant species. Loss of habitat, such as tundra ponds for many arctic birds, is a particularly important possibility that would constrain species ranges.

In contrast, plant populations that are outliers of more southerly regions and restricted to particularly favorable habitats in the Arctic, are likely to spread rapidly during

Fig. 7.16. Forest tundra vegetation represented by the Fennoscandian mountain birch forest, Abisko, northern Sweden (photo: T.V. Callaghan).

Fig. 7.17. Zonal tussock tundra near Toolik Lake, Alaska, with large shrubs/small trees of *Salix* in moist sheltered depressions (photo: T.V. Callaghan).

warming. Models of moss and dwarf-shrub growth along latitudinal gradients show considerable potential for range expansion in the north, but considerable uncertainty, in relation to ACIA scenarios of warming.

Most microorganisms detected in northern ecosystems, such as free-living bacteria, are probably cosmopolitan in their geographic distribution and readily disseminated from one location to another, and the environment selects those that can proliferate. However, some species, particularly symbionts with endemic plants, can themselves be candidates for endemic status.

7.4. Effects of changes in climate and UV radiation levels on structure and function of arctic ecosystems in the short and long term

Section 7.3 assessed the responses of individual species to changes in climate and UV-B radiation levels. The present section assesses the responses of species aggregated into communities and ecosystems. The two main attributes of ecosystems that respond to environmental change are structure and function: each is assessed separately although the two attributes strongly interact.

In this section, ecosystem structure is defined in terms of spatial structure (e.g., canopy structure and habitat), trophic interactions, and community composition in terms of biodiversity; while ecosystem function is defined in terms of carbon and nutrient cycling including dissolved organic carbon export, soil processes, controls on trace gas exchange processes, primary and secondary productivity, and water and energy balance.

Although ecosystem structure and function are closely interconnected, this section focuses on the two aspects separately for clarity, and limits the discussion here to plot (single square meter) scales: processes at the landscape and regional scales are covered in sections 7.5 and 7.6. Community responses to climate and UV radiation change presented in this section include effects on the diversity of plant growth forms in terms of biomass contribution, but the details of impacts on biodiversity in terms of organism survival and population dynamics are included in section 7.3.

7.4.1. Ecosystem structure

7.4.1.1. Local and latitudinal variation

The Arctic is characterized by ecosystems that lack trees. There is a broad diversity in ecosystem structure among these northern treeless ecosystems that follows a latitudinal gradient from the treeline to the polar deserts. Typical communities for a particular latitude are called "zonal", but local variation at the landscape level occurs and these "intrazonal communities" are frequently associated with variations in soil moisture and snow accumulation (Chernov and Matveyeva, 1997; Walker M.D. et al., 1989).

According to Bliss and Matveyeva (1992), zonal communities south of the arctic boundary near the mean July isotherms of 10 to 12 ºC consist of taiga (i.e., the northern edge of the boreal forest). This is characterized by a closed-canopy forest of northern coniferous trees with mires in poorly drained areas. To the north of this transition zone is the forest tundra. It is characterized by white spruce (*Picea glauca*) in Alaska, mountain birch (*Betula pubescens* ssp. *czerepanovii*) in Fennoscandia (Fig. 7.16), by birch and Norway spruce in the European Russian Arctic (Kola Peninsula and the Pechora lowlands), by Dahurian larch (*Larix dahurica*) in central and eastern Siberia, and by evergreen coniferous trees in Canada (Hustich, 1983). The vegetation of the forest tundra is characterized by sparse, low-growing trees with thickets of shrubs. North of this zone is the low Arctic, which is characterized by tundra vegetation in the strict sense (Fig. 7.17), consisting of communities of low, thicket-forming shrubs with sedges, tussock-forming sedges with dwarf shrubs, and mires in poorly drained areas. To the north of this zone is the high Arctic, which consists of polar semi-desert communities (Fig. 7.18) in the south, characterized by

Fig. 7.18. Polar semi-desert dominated by mountain avens (*Dryas octopetala*), Ny Ålesund, Svalbard (photo: T.V. Callaghan).

Fig. 7.19. Polar desert, Cornwallis Island, Northwest Territories, Canada (photo: J. Svoboda).

cryptogam–herb, cushion plant–cryptogam, and, to a limited extent, mire communities. To the extreme north is the polar desert where only about 5% of the ground surface is covered by herb–cryptogam communities (Fig. 7.19). In this zone, the mean July temperature is below 2 °C and precipitation, which falls mainly as snow, is about 50 mm per year.

The tundra zone can be further subdivided into three subzones: the southern tundra with shrub–sedge, tussock–dwarf shrub, and mire communities; the typical tundra with sedge–dwarf shrub and polygonal mire communities (Fig. 7.20); and the northern arctic tundra that consists of dwarf shrub–herb communities. The northern end of the latitudinal gradient, occurring primarily on islands and on the mainland only at Cape Chelyuskin (Taymir Peninsula), is occupied by polar deserts where woody plants are absent, and forbs and grasses with mosses and lichens are the main components of plant communities (Matveyeva and Chernov, 2000).

This vegetation classification has geographic connotations and cannot be applied easily to reconstructions of past vegetation throughout the circumpolar Arctic (Kaplan et al., 2003). A recent classification of tundra vegetation at the biome level (Walker D., 2000) has been proposed by Kaplan et al. (2003; Table 7.8, Fig. 7.2).

Within the biomes or zonal vegetation types, there are intrazonal habitats that are frequently associated with variations in soil moisture and snow accumulation, and that have a microclimate that deviates from the general macroclimate associated with flat surfaces. The intrazonal habitats form a mosaic of communities. Each of these tend to have fewer species than the "plakor," or zonal, communities. For example, poorly drained areas are often dominated by sedges with an understory of mosses and liverworts, but lack fruticose lichens (Matveyeva and Chernov, 2000). Although each intrazonal community has relatively few species, together they are more differentiated and diverse than zonal ones, and are responsible for about 80% of total species diversity in the regional flora and fauna. Disturbances, particularly freeze–thaw cycles and thermokarst (Fig. 7.21) that form patterned ground, also create landscape mosaics (Fig. 7.20). Diversity "focal points/hot spots" (Walker M.D., 1995) and "oases" (Edlund and Alt, 1989; Svoboda and Freedman, 1994) enrich landscapes by possessing a larger number of species, including those of more southerly distribution. Examples include dense willow thickets

Table 7.8. Circumpolar tundra biome classification (Walker D., 2000; Kaplan et al., 2003).

Biome	Definition	Typical taxa
Low- and high-shrub tundra	Continuous shrubland, 50 cm to 2 m tall, deciduous or evergreen, sometimes with tussock-forming graminoids and true mosses[a], bog mosses, and lichens	*Alnus, Betula, Salix, Pinus pumila* (in eastern Siberia), *Eriophorum, Sphagnum*
Erect dwarf-shrub tundra	Continuous shrubland 2 to 50 cm tall, deciduous or evergreen, with graminoids, true mosses[a], and lichens	*Betula, Cassiope, Empetrum, Salix, Vaccinium,* Poaceae, Cyperaceae
Prostrate dwarf-shrub tundra	Discontinuous "shrubland" of prostrate deciduous dwarf-shrubs 0 to 2 cm tall, true mosses[a], and lichens	*Salix, Dryas, Pedicularis,* Asteraceae, Caryophyllaceae, Poaceae, true mosses[a]
Cushion forb, lichen, and moss tundra	Discontinuous cover of rosette plants or cushion forbs with lichens and true mosses[a]	Saxifragaceae, Caryophyllaceae, *Papaver, Draba,* lichens, true mosses[a]
Graminoid and forb tundra	Predominantly herbaceous vegetation dominated by forbs, graminoids, true mosses[a], and lichens	*Artemisia, Kobresia,* Brassicaceae, Asteraceae, Caryophyllaceae, Poaceae, true mosses[a]

[a] "true" mosses exclude the genus *Sphagnum*

Fig. 7.20. Polygonal wet tundra near Prudhoe Bay, Alaska (photo: T.V. Callaghan).

Fig. 7.21. Thermokarst in the Russian tundra, New Siberian Islands (photo: T.V. Callaghan).

two meters in height in sheltered valleys at 75° N in Taymir and stands of balsam poplar north of the treeline in the northern foothills of the Brooks Range, Alaska, that are likely to respond rapidly to warming. There are numerous other types of plant communities, such as the moss-dominated tundra of Iceland (Fig. 7.22).

The vertical structure of arctic ecosystems is as important as horizontal structure in explaining their current and future functioning. This structure is most pronounced in low-arctic shrub communities, where there is a well-developed shrub canopy and an understory of mosses, similar to the vertical structure of boreal forests. Vertical structure is also pronounced below ground, with mosses and lichens lacking roots, some species rooted in the moss layer, others rooted just beneath the mosses, and a few species rooted more deeply.

The most striking latitudinal trend in plant functional types is the decrease in height of woody plants (from trees to tall shrubs, to low and prostrate shrubs, to dwarf shrubs, and eventually the loss of woody plants with increasing latitude). These functional types often occur in low abundance in zones north of their main areas of dominance, suggesting that they are likely to expand rapidly in response to warming through vegetative reproduction (Bret-Harte et al., 2001; Chapin F. et al., 1995) and sexual reproduction (Molau and Larsson, 2000), although range expansion will depend on geographic barriers such as mountains and seas (section 7.6, Table 7.14). Recent warming in Alaska has caused a substantial increase in shrub density and size in the moist tundra of northern Alaska (Sturm et al., 2001b). In areas where shrubs are absent, shrubs are likely to exhibit time lags in migrating to new habitats (Chapin F. and Starfield, 1997). Shrubs colonize most effectively in association with disturbances such as flooding in riparian zones, thermokarst, and frost boils (patterned ground formation caused by soil heave) throughout their latitudinal range, so migration may be strongly influenced by climate- or human-induced changes in the disturbance regime. Woody species affect ecosystem structure and function because of their potential to dominate the canopy and reduce light availability to understory species (Bret-Harte et al., 2001; Chapin F. et al., 1996) and to reduce overall litter quality (Hobbie, 1996) and rates of nutrient cycling.

A similar latitudinal decline in abundance occurs with sedges, which are absent from polar deserts, suggesting that this group is also likely to expand northward with warming (Matveyeva and Chernov, 2000). *Carex stans* and *C. bigelowii* now mark the northernmost boundary of the tundra zone and might be a sensitive indicator of species responses to warming. Sedges have important effects on many ecosystem processes, including methane flux, because of their transport of oxygen to soils, transport of methane to the atmosphere, and inputs of labile carbon to the rhizosphere (Joabsson and Christensen, 2001; Torn and Chapin, 1993). Prostrate and dwarf shrubs such as *Dryas* spp., arctic willow, and polar willow are likely to decline in abundance with warming in the

Fig. 7.22. *Racomitrium/Empetrum* heath in Iceland showing erosion (photo: T.V. Callaghan).

low Arctic, due to competition with taller plants, but are likely to increase in abundance in the current polar deserts. These changes in distribution are very likely to substantially reduce the extent of polar desert ecosystems (section 7.5.3.2), which are characterized by the absence of woody plants.

7.4.1.2. Response to experimental manipulations

Experimental manipulation of environmental factors projected to change at high latitudes (temperature, snow, nutrients, solar radiation, atmospheric CO_2 concentrations, and UV-B radiation levels) has substantial effects on the structure of arctic ecosystems, but the effects are regionally variable. The effects of these variables on individual species are discussed in section 7.3; while this section focuses on overall community structure and species interactions.

Plant communities

Nutrient addition is the environmental manipulation that has the greatest effect on the productivity, canopy height, and community composition of arctic plant communities (Jonasson et al., 2001; Press et al., 1998a; van Wijk et al., 2004; Fig. 7.23). Fertilization also increases biomass turnover rate, so eventual biomass may or may not change in response to nutrient addition. In northern Sweden, for example, nutrient addition to a mountain birch (*Betula pubescens* ssp. *czerepanovii*) site (cf. a Swedish treeline heath and fellfield) caused an initial biomass increase. This biomass increase was not maintained over the long term, however, because expansion of the grass *Calamagrostis lapponica* negatively affected the growth of mosses and evergreen shrubs, leading to a negligible change in community biomass (Parsons et al., 1994; Press et al., 1998b). Similarly, addition of nitrogen and phosphorus at a site in northern Alaska increased productivity and turnover within three years (Chapin F. et al., 1995). There was, however, little change in biomass because the rapidly growing sedges, forbs, and deciduous shrubs responded most strongly, whereas evergreen shrubs and mosses declined in abundance (Fig. 7.24). After 9 and 15 years, competitive interactions altered the relative abundance of plant functional types, with the tallest species (the deciduous shrub *Betula nana;* Fig. 7.3) responding most strongly (Bret-Harte et al., 2001; Chapin F. et al., 1995; Shaver et al., 2001). Litter and/or shade from this species reduced the growth of lichens, mosses, and evergreen shrubs. In vegetation types without any pronounced change in relative proportions of dominant species or life forms following fertilizer addition, as in Swedish treeline and high-altitude heaths and in Alaskan wet-sedge tundra, the biomass of most dominant life forms increased. This resulted in up to a doubling of biomass after five to nine years of treatment

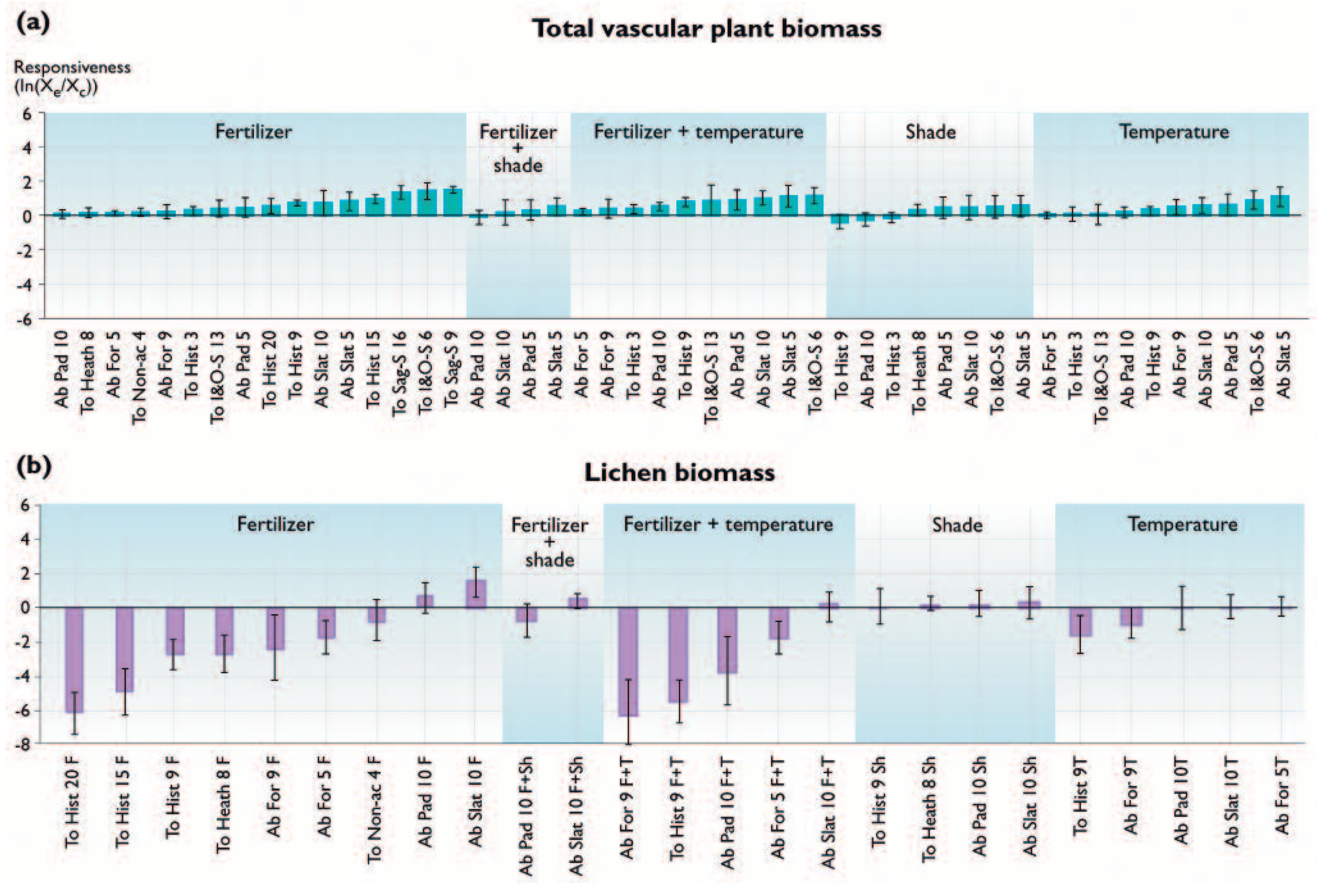
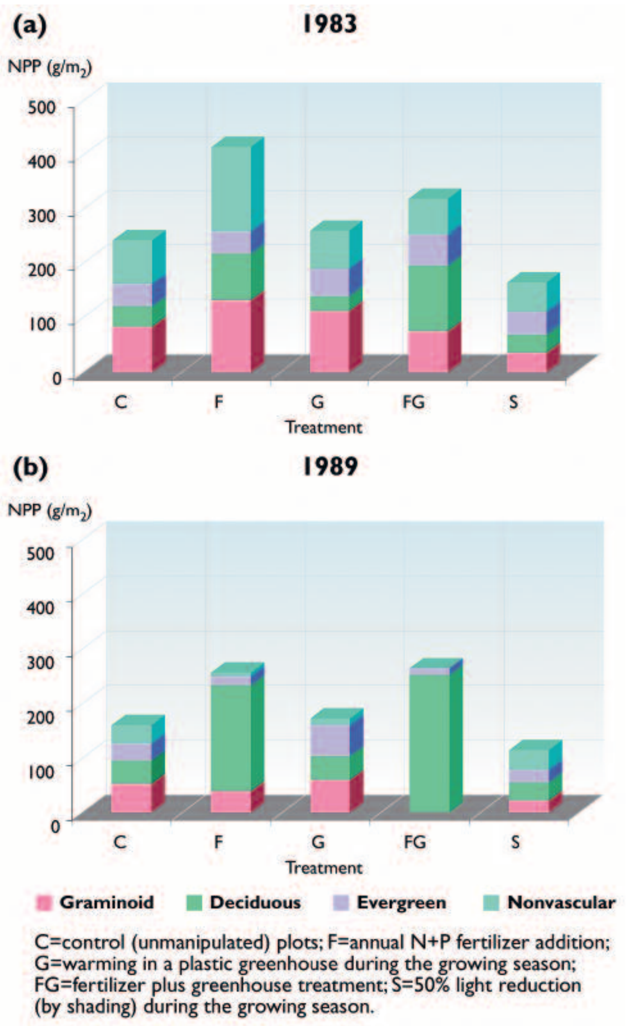


Fig. 7.23. Results of long-term (generally 10 years or more) experiments in a range of habitats at Toolik Lake, Alaska, and Abisko, Sweden, showing the responsiveness of aboveground biomass ordered by treatment and degree of responsiveness (X is the mean value of the analyzed characteristic for the experimental (X_e) and control (X_c) groups). Data are given for (a) total vascular plant biomass and (b) lichen biomass. Codes relate to the geographical region (To=Toolik, Ab=Abisko), the site name, and the duration of the experiment (van Wijk et al., 2004).



C=control (unmanipulated) plots; F=annual N+P fertilizer addition; G=warming in a plastic greenhouse during the growing season; FG=fertilizer plus greenhouse treatment; S=50% light reduction (by shading) during the growing season.

Fig. 7.24. Effects of long-term fertilizer addition and experimental warming and shading during the growing season on above-ground net primary production (NPP) of different plant functional types at Toolik Lake, Alaska, showing NPP by functional type and treatment (a) in 1983, after three years of treatment, and (b) in 1989, after nine years of treatment (Chapin F. et al., 1995).

(Jonasson et al., 1999b; Shaver et al., 1998). In polar semi-deserts, nutrient addition generally had a negative effect on vascular plants, due to enhanced winterkill, but stimulated the growth of mosses (Robinson et al., 1998), an effect opposite to that in low-arctic tundra. This difference is probably due to the immigration of nitrogen-demanding mosses from nearby bird-cliff communities in the high Arctic compared with loss of existing moss species in the low Arctic.

Water additions to simulate increased precipitation have generally had only minor effects on total biomass and production (Press et al., 1998a).

Experimental summer warming of tundra vegetation within the range of projected temperature increases (2 to 4 °C over the next 100 years) has generally led to smaller changes than fertilizer addition (Arft et al., 1999; Jonasson et al., 2001; Shaver and Jonasson, 2000; van Wijk et al., 2004; Fig. 7.23). For example, temperature enhancement in the high-arctic semi-desert increased plant cover within growing seasons but the effect did not persist from year to year (Arft et al., 1999; Robinson et al., 1998). In the low Arctic, community biomass and nutrient mass changed little in response to warming of two Alaskan tussock sites (Chapin F. et al., 1995; Hobbie and Chapin, 1998) and two wet-sedge tundra sites (Shaver et al., 1998), coincident with relatively low changes in soil nutrient pools and net mineralization. Tussock tundra showed little response to warming, as some species increased in abundance and others decreased (Chapin F. and Shaver, 1985a,b; Chapin F. et al., 1995), similar to a pattern observed in subarctic Swedish forest floor vegetation (Press et al., 1998b). The responses to warming were much greater in Swedish treeline heath and in fellfield (Jonasson et al., 1999b). Biomass in the low-altitude heath increased by about 60% after air temperatures were increased by about 2.5 °C, but there was little additional effect when temperatures were further increased by about 2 °C. In contrast, biomass approximately doubled after the first temperature increase (2.5 °C) and tripled after the higher temperature increase (an additional 2 °C) in the colder fellfield. Hence, the growth response increased from the climatically relatively mild forest understory through the treeline heath to the cold, high-altitude fellfield where the response to warming was of the same magnitude as the response to fertilizer addition (Jonasson et al., 2001). A general long-term (10 years or more) response to environmental manipulations at sites in subarctic Sweden and in Alaska was a decrease in total nonvascular plant biomass and particularly the biomass of lichens (van Wijk et al., 2004: Fig. 7.23).

Animal communities

Air-warming experiments at Svalbard (79° N) had greater effects on the fauna above ground than below ground, probably because the soil is more buffered against fluctuations in temperature and moisture than the surface (Hodkinson et al., 1998). Species with rapid life cycles (aphids and Collembola) responded demographically more quickly than species (e.g., mites) with slow life cycles (Coulson et al., 1996). Responses to warming differed among sites. The abundance of Collembola declined at barren sites where higher temperatures also caused drought and mortality due to desiccation, whereas the abundance of Collembola increased at moister sites. In summer, water availability is probably much more important to many invertebrates than is temperature. Mites are more resistant than Collembola to summer desiccation (Hodkinson et al., 1998) and to anoxic conditions in winter due to ice-crust formation following episodes of mild weather (Coulson et al., 2000). Ice-crust formation during the winter may increase winter mortality by 50% in Collembola (Coulson et al., 2000). Freeze–thaw events in spring may also cause differential mortality among species, thus altering community composition (Coulson et al., 1995). In experiments conducted simultaneously at several sites and over several years, the natural spatial and temporal variability in community structure and population density of soil invertebrates was larger than the effects of the experimental manipulation within years and sites. This demonstrates that there is a large variability in the structure and function of high-arctic invertebrate communities due to current variation in abiotic conditions. It also indicates that arctic invertebrate communities can respond rapidly to change.

Compared to the high Arctic, subarctic invertebrate communities at Abisko responded less to experimental temperature increases (Hodkinson et al., 1998). However, nematode population density increased substantially, and the dominance changed in favor of plant- and fungal-feeding species with elevated summer temperatures and nitrogen (N), phosphorus (P), and potassium (K) fertilization, indicating a shift in the decomposition pathway (Ruess et al., 1999a,b).

Microbial communities

Although the biomass of microorganisms is a poor predictor of the productivity and turnover of microorganisms and their carbon, alternative methods focusing on population dynamics of microbial species within communities are extremely difficult to employ in the field. Microbial biomass has therefore been used to quantify microbial processes within ecosystems. The sensitivity of microbial biomass, generally measured as biomass carbon (C), and nutrient content to changed environmental conditions in the Arctic has not been well studied. Long-term addition of easily processed C generally increases the microbial biomass; and addition of inorganic nutrients generally, but not always, increases microbial nutrient content without appreciable effect on the biomass (Jonasson et al., 1996, 1999b; Michelsen et al., 1999; Schmidt et al., 2000). In some cases, however, a combination of C and nutrient addition has led to a pronounced increase in both microbial biomass and nutrient content (Schmidt et al., 2000). This suggests a general C limitation of microbial biomass production, and increased sink strength for soil nutrients (i.e., increased sequestration of nutrients) if the amounts of both labile C and nutrients increase, but relatively weak effects from increased nutrient availability alone. In the widespread drier ecosystem types in the Arctic, the soil microbial biomass is likely to be further limited by low water supply. Water addition to a high-arctic semi-desert led to a substantial increase in microbial biomass C and microbial activity (Illeris et al., 2003).

Data on the effects on ecosystems of growing-season temperature increases of 2 to 4 ºC over five (Jonasson et al., 1999b; Ruess et al., 1999a,b) and ten (Jonasson and Michelsen, unpub. data, 2005) years have not shown appreciable long-term changes in microbial biomass and nutrient stocks. This suggests that an increase in growing-season temperature alone is unlikely to have any strong impact on microbial C and nutrient sequestration, and that changes in soil nutrient availability are likely to lead to greater changes than the direct effects of increased temperature. Temperature effects on ecosystem processes are likely, however, to be different from the observed relatively small effects on microbial biomass and nutrient stocks, because temperature changes are likely to affect rates of decomposition and nutrient mineralization, rather than pool sizes, resulting in altered C balance and rates of nutrient supply to the plants (section 7.4.2.1).

Appreciable seasonality in microbial biomass and nutrient mass have been reported, however, that seemingly are independent of ambient temperature. In general, the masses change little, or fluctuate, during summer (Giblin et al., 1991; Jonasson et al., 1999b; Schmidt et al., 1999, 2002). In contrast, pronounced increases in both biomass and nutrient mass have been reported in autumn (Bardgett et al., 2002; Jaeger et al., 1999; Lipson et al., 1999), probably as a function of increased input of labile C and nutrients from plants as they senesce, although these data are from mountain and alpine, rather than from arctic soils. The increase seems to continue through winter, although at a slower rate (Grogan and Jonasson, 2003; Schmidt et al., 1999), despite soil temperatures below 0 ºC (Clein and Schimel, 1995; see section 7.3.2.3). It is followed by a sharp biomass decline in the transition between winter and spring (Bardgett et al., 2002; Brooks et al., 1998; Grogan and Jonasson, 2003), which may (Brooks et al., 1998) or may not (Grogan and Jonasson, 2003; Larsen et al., 2002) coincide with a decrease in microbial N and an increase in mineralized N, indicating a pronounced transformation of microbial N to soil inorganic N (Giblin et al., 1991; Schmidt et al., 1999). Indeed, this seasonal pattern suggests a temporal partitioning of resource uptake with low competition between plants and microbes for nutrients, as microbes absorb most nutrients in autumn and plants in spring, coincident with the nutrient release from declining microbial populations. However, it may also be an indication that plants compete well for nutrients during the growing season (Schimel and Chapin, 1996), and microbes access nutrients efficiently only when the sink strength for nutrients in plants is low (Jonasson et al., 1999b).

Laboratory experiments have shown that the spring decline of microbial mass is likely to be an effect of repeated freeze–thaw cycles (Schimel and Clein, 1996). Indeed, Larsen et al. (2002) reported a microbial decline in soils subjected to repeated freezing and thawing but not in the same soils kept constantly frozen before thawing. The seasonal dynamics of microbial biomass and microbial and inorganic soil nutrients therefore suggests that "off growing-season" changes in climate during the transition between winter and spring (e.g., changed frequency of freeze–thaw events and warmer winters) are likely to have greater impacts on nutrient transformations between microbes, soils, and plants than changes during the growing season.

Manipulations simulating enhanced UV-B radiation levels (equivalent to a 15% reduction in stratospheric ozone levels) and a doubling of atmospheric CO_2 concentrations for seven years altered the use of labile C sub-

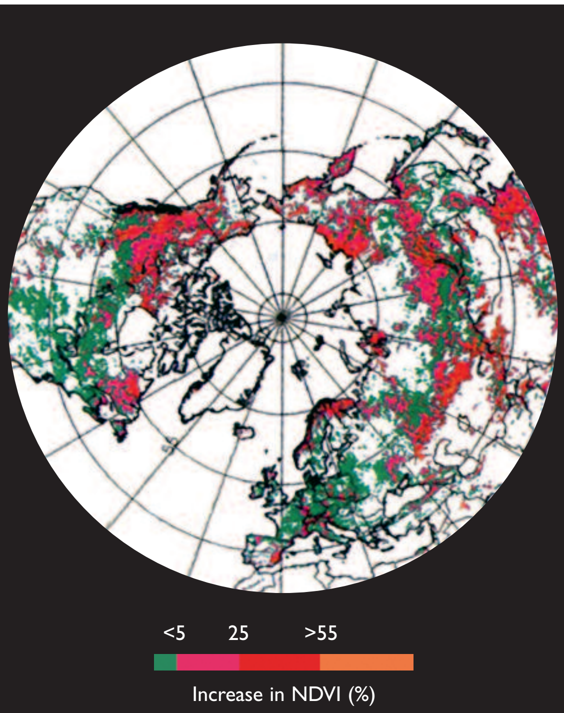


Fig. 7.25. Changes in greenness of northern vegetation (depicted by NDVI) between 1981 and 1991 as measured by satellite instruments (Myneni et al., 1997).

strates by gram-negative bacteria (Johnson et al., 2002). Although these rhizosphere bacteria are a relatively small component of the belowground microbial biomass, they are likely to be particularly responsive to environmentally induced changes in belowground plant C flow.

Ultraviolet-B radiation also affects the structure of fungal communities. Microcosms of subarctic birch forest floor litter exposed to enhanced UV-B radiation levels showed a reduction in fungal colonization of leaf veins and lamina (Gehrke et al., 1995). Fungal composition was also altered in the UV-B radiation treatments, with a reduction in *Mucor hiemalis* and a loss of *Truncatella truncata*. Similar findings of fungal community change were obtained in subarctic Abisko, in an ecosystem that was the source of the litter used by Gehrke et al. (1995). In this field study of the decomposition rates of a standard litter type, there was also a change in the composition of the fungal community associated with litter resulting from elevated UV-B radiation levels (Moody et al., 2001). So far, no change in plant community structure has been found in the Arctic in response to artificially enhanced or reduced UV-B radiation levels and CO_2 concentrations.

7.4.1.3. Recent decadal changes within permanent plots

Satellite measurements suggest a widespread increase in indices of vegetation greenness (e.g., the normalized difference vegetation index – NDVI) and biomass at high latitudes (Myneni et al., 1997, 2001; Fig. 7.25), although changes in satellites and sensor degradation may have contributed to this trend (Fung, 1997). Aerial photographs show a general increase in shrubbiness in arctic Alaska (Sturm et al., 2001b) and indigenous knowledge also reports an increase in shrubbiness in some areas. These observations are consistent with the satellite observations. However, it has been difficult to corroborate these with studies of permanent plots, because of the paucity of long-term vegetation studies in the Arctic. In arctic Alaska, for example, a trend toward reduced abundance of graminoids and deciduous shrubs during the 1980s was reversed in the 1990s (Shaver et al., 2001). In Scandinavia, decadal changes in vegetation were affected more strongly by the cyclic abundance of lemmings than by climatic trends (Laine and Henttonen, 1983).

7.4.1.4. Trophic interactions

Trophic-level structure is simpler in the Arctic than further south. In all taxonomic groups, the Arctic has an unusually high proportion of carnivorous species and a low proportion of herbivores (Chernov, 1995). As herbivores are strongly dependent on responses of vegetation to climate variability, warming is very likely to substantially alter the trophic structure and dynamics of arctic ecosystems. The herbivore-based trophic system in most tundra habitats is dominated by one or two lemming species (Batzli et al., 1980; Oksanen et al., 1997; Wiklund et al., 1999) while the abundance of phytophagous (plant-eating) insects relative to plant biomass is low in arctic tundra (Strathdee and Bale, 1998). Large predators such as wolves, wolverines, and bears are less numerous in the tundra than in the boreal forest (Chernov and Matveyeva, 1997) and predation impacts on tundra ungulates are usually low. Thus, the dynamics and assemblages of vertebrate predators in arctic tundra are almost entirely based on lemmings and other small rodent species (*Microtus* spp. and *Clethrionomys* spp.; Batzli, 1975; Wiklund et al., 1999), while lemmings and small rodents consume more plant biomass than other herbivores. Climate has direct and indirect impacts on the interactions among trophic levels, but there is greater uncertainty about the responses to climate change of animals at the higher trophic levels.

Plant-herbivore interactions

Plant tissue chemistry and herbivory

Arctic and boreal plant species often contain significant concentrations of secondary metabolites that are important to the regulation of herbivory and herbivore abundance (Haukioja, 1980; Jefferies et al., 1994). Secondary compounds also retard decomposition of leaves after litter fall (Cornelissen et al., 1999). These secondary metabolites are highly variable in their chemical composition and in their antiherbivore effects, both within and among species. One hypothesis about the regulation of these compounds that has received widespread discussion is the carbon–nutrient balance hypothesis of Bryant et al. (1983; Coley et al., 1985), which attempts to explain this variation in part on the basis of C versus nutrient limitation of plant growth. Although many other factors in addition to carbon–nutrient balance are probably important to the regulation of plant–herbivore interactions in the Arctic (e.g., Iason and Hester, 1993; Jefferies et al., 1994; Jonasson et al., 1986), the abundance of secondary chemicals is often strongly responsive to changes in the environment including temperature, light, and nutrient availability (e.g., Graglia et al., 2001b; Haukioja et al., 1998; Laine and Henttonen, 1987). In a widespread arctic shrub species, *Betula nana* (Fig. 7.3), Graglia et al. (2001b) found that fertilization and shading generally led to decreased condensed and hydrolyzable tannin concentrations in leaves, whereas warming in small field greenhouses increased condensed tannins and decreased hydrolyzable tannins. There was also a large difference in both the average concentrations and the responsiveness of the concentrations of phenolics in plants from northern Alaska versus northern Sweden, with the plants from Sweden having generally higher concentrations but being less responsive to environmental changes. Such data suggest that the effects of climate change on plant–herbivore interactions are likely to be highly variable, species-specific, and also dependent on the nature of the change and on ecotypic or subspecific differences, perhaps related to local evolution in the presence or absence of herbivores.

Plant exposure to UV-B radiation has the ability to change the chemistry of leaf tissues, which has the potential to affect the odor that herbivores such as reindeer/caribou use to detect food, and the quality of food in terms of palatability and digestibility (Gwynn-Jones, 1999). In general, enhanced UV-B radiation levels can reduce soluble carbohydrates and increase phenolic compounds and flavonoids. Such changes are expected to reduce forage quality.

Plant exposure to increased CO_2 concentrations can also affect plant tissue quality and consequently herbivory (Agrell et al., 1999). Enriched CO_2 concentrations may lead to the accumulation of carbohydrates and phenolic compounds while reducing N concentrations in leaves. However, these phytochemical responses can be significantly modified by the availability of other resources such as nutrients, water, and light. Unfortunately, little information about the impacts of increased CO_2 concentrations on herbivory is available for the Arctic.

Herbivore abundance and vegetation production

Invertebrates

Insect population outbreaks seldom extend into the tundra. However, in the forest near the treeline, insect defoliators can have devastating impacts on the ecosystem. Climate change is very likely to modify the population dynamics of such insects in several ways (Bylund, 1999; Neuvonen et al., 1999). In the autumnal moth, eggs laid on birch twigs in autumn cannot tolerate winter temperatures lower than -36 ºC. For this reason, the moth is destroyed in parts of the terrain (e.g., depressions) where winter temperatures drop below this critical minimum (Tenow and Nilssen, 1990; Virtanen and Neuvonen, 1999). Warmer winters are very likely to reduce winter mortality and possibly increase outbreak intensity. Moreover, lower minimum temperatures are likely to allow the autumnal moth and the related, less cold-tolerant winter moth (*Operophtera brumata*) to extend their geographic distributions into continental areas with cold winters (Tenow, 1996). However, predicting the effect of a changing climate is not straightforward because moth responses are season-specific. For instance, increasing spring temperatures are likely to cause a mismatch between the phenology of birch leaves and hatching of larvae that are currently synchronized (Bale et al., 2002). Moreover, natural enemies such as parasitoid wasps and ants are likely to increase their abundances and activity rates if summer temperature rises. Currently, there is cyclicity in the populations of the autumnal moth and outbreak proportions occur approximately every 10 to 11 years (Tenow, 1972, 1996). The defoliated forests require about 70 years to attain their former leaf area, although insect outbreaks in subarctic Finland followed by heavy reindeer browsing of regenerating birch shoots have led to more or less permanent tundra (Kallio and Lehtonen, 1973; Lehtonen and Heikkinen, 1995). There are no population outbreaks in the autumnal moth further south in Fennoscandia, most likely due to the high abundance of generalist parasitoids that keep moth populations below outbreak levels (Tanhuanpää et al., 2001). However, the border between outbreaking and non-outbreaking populations of geometrid moths is likely to move northward if climate changes.

Enhanced UV-B radiation levels applied to birch leaves alters the chemistry or structure of the leaves such that caterpillars eat three times as much leaf biomass to maintain body development (Buck and Callaghan, 1999; Lavola et al., 1997, 1998). There is also a tendency for enhanced UV-B radiation levels to increase the immunocompetence of the caterpillars, which could possibly make them more tolerant to the wasp parasitoid (Buck, 1999). Although the effects of winter warming on eggs, increased UV-B radiation levels on leaves, and immunocompetence on caterpillars are likely to increase future damage to subarctic birch forests, it is not known to what extent other processes susceptible to spring and summer climate variability may alleviate these effects.

Vertebrates

The herbivore-based trophic system in most tundra habitats is dominated by one or two lemming species (Batzli et al., 1980; Oksanen et al., 1997; Wiklund et al., 1999). Lemming abundance is the highest in coastal tundra, especially in moist sedge meadows that are the optimum habitat for *Lemmus*. Collared lemmings (*Dicrostonyx*) usually do not reach as high densities in their preferred habitats on drier ridges where herbs and dwarf shrubs dominate. Voles (*Microtus* and *Clethrionomys* spp.) are likely to become more abundant than lemmings in some low-arctic tundra habitats and forest tundra (Chernov and Matveyeva, 1997). At the landscape scale, lemmings and voles are very patchily distributed according to the abundance of their preferred food plants, as well as the distribution of snow (Batzli, 1975; section 7.3.2.2). Lemming peak densities exceed 200 individuals per hectare in the most productive *Lemmus* habitats in both Siberia and North America (Batzli, 1981) and the standing crop of lemmings may approach 2.6 kg dry weight per hectare. The population builds up during the winter (due to winter breeding) and peak densities may be reached in late winter/early spring when the standing crop of food plants is minimal. The diet of *Lemmus* consists mainly of mosses and graminoids, while *Dicrostonyx* prefers herbs and dwarf shrubs (Batzli, 1993). Lemmings have a high metabolic rate, and *Lemmus* in particular has a low digestive efficiency (about 30%, compared to 50% in other small rodents). Consequently, their consumption rate and impact on the vegetation exceeds that of all other herbivores combined (with the exception of local effects of geese near breeding colonies). Moreover, lemmings destroy much more vegetation than they ingest and after population peaks typically 50% of the aboveground biomass has been removed by the time the snow melts (Turchin and Batzli, 2001). In unproductive snow beds, which are favored winter habitats of the Norway lemming (Kalela, 1961), up to 90–100% of the mosses and graminoids present during the winter may be removed (Koskina, 1961). If winters become so unfavorable for lemmings that they are unable to build up cyclic peak densities, the species-rich predator community relying on lemmings is likely to collapse (see next subsection). Moreover, their important, pulsed impact on vegetation as a result of grazing and nutrient recycling is likely to cease. Changes in snow conditions, relative abundances of preferred food plants, and climate impacts on primary production are all very likely to affect lemming populations, and are likely to result in a northward displacement of the climatically determined geographic borders between cyclic and non-cyclic populations of small herbivores (small rodents and moths), as well as the species distributions *per se*.

Wild populations of other herbivorous mammal species in the tundra, such as hares, squirrels, muskox, and reindeer/caribou, never reach population densities or biomass levels that can compare with peak lemming populations (Chernov and Matveyeva, 1997). Moving herds of reindeer/caribou represent only patchy and temporary excursions in numbers, biomass, and impacts on vegetation; averaged over space and time some of the largest herds approach only 0.01 individuals and 0.5 kg of dry weight per hectare (Batzli, 1981) on their summer pastures and usually take less than 10% of the vegetation (Jefferies et al., 1994). The only cases where reindeer/caribou have been shown to have large impacts on vegetation seem to be in unusual circumstances (stranding on islands; Klein, 1968) or under human intervention (e.g., removing top predators or introductions to islands) where overshooting reindeer/caribou populations have led to vegetation destruction, habitat degradation, and subsequent population crashes.

Although the cooling since the mid-1970s in the Hudson Bay region has affected the reproduction of snow geese (*Anser caerulescens*), the mid-continental population is currently growing by 5% per year (Skinner W. et al., 1998). This, in combination with the staging of snow geese in La Pérouse Bay, Manitoba, because of bad weather further north, leads to increasing foraging for roots and rhizomes of the graminoids *Puccinellia phryganodes* and *Carex subspathacea* (Jefferies et al., 1995). The rate of removal of belowground organs in the salt marshes combined with intense grazing of sward during summer exceeds the rate of recovery of the vegetation. It is estimated that geese have destroyed 50% of the salt marsh graminoid sward of La Pérouse Bay since 1985. This loss of vegetation cover exposes the sediments of the salt marshes, which have become hypersaline (salinities exceeding 3.2) as a result of increased evapotranspiration. This further reduces plant growth and forage availability to the geese. In turn, this is reducing goose size, survivorship, and fecundity. Other factors that are affected by the trophic cascades initiated by the geese include reduced N mineralization rates and declines in the populations of soil invertebrates, waders, and some species of duck such as the widgeon (*Anas americana*).

Cyclic populations

Herbivore–plant interactions have been proposed to produce population cycles in arctic herbivores through several mechanisms including nutrient recycling (Schultz, 1969), production cycles inherent in food plants (Tast and Kalela, 1971), induced chemical defense in plants (Haukioja, 1991), and recurrent overgrazing (Oksanen et al., 1981). The empirical evidence is mixed. There is at least partly supporting evidence for induced chemical defense in the *Epirrita*–birch system (Ruohomäki et al., 2000) and for overgrazing in the *Lemmus*–plant system in unproductive tundra habitats (Turchin et al., 2000). There is little evidence, however, for mechanisms involving nutrient cycling and chemical defense in the case of lemmings and voles (Andersson and Jonasson, 1986; Jonasson et al., 1986). Climate is somehow involved in all the hypotheses of population cycles related to plant–herbivore interactions. For example, allocation strategies in plants and the amount of secondary compounds (induced chemical defense hypothesis) depend on temperature and growing-season length (see plant tissue chemistry subsection). Plant production and biomass are also controlled by temperature (overgrazing hypothesis). Climate change is thus likely to modify the population dynamics patterns and roles of key herbivores such as lemmings and moths because the dynamics of herbivore-plant interactions are likely to change. As early as 1924, Charles Elton pointed out the potentially decisive role of climate in determining the generation of cycles in northern animal populations (Elton, 1924).

Mathematical modeling shows that specialist resident predators such as small mustelids and the Arctic fox can also impose prey population cycles due to sufficiently strong numerical and adequate functional responses (Gilg et al., 2003; Turchin and Hanski, 1997). Moreover, nomadic specialists such as birds of prey can dampen lemming cycles and decrease the degree of regional asynchrony if their predation rates are sufficiently high (Ims and Andreassen, 2000; Ims and Steen, 1990). The impacts of bird predators have a strong seasonal component since most migrate south for the winter (Ims and Steen, 1990). Reliable estimates of predation rates on cyclic lemming populations are rare. Indirect estimates based on the energy requirements of predators at Point Barrow, Alaska, indicated that avian predators could account for 88% of the early summer mortality, but it was concluded that neither this nor winter predation by weasels could stop lemming population growth under otherwise favorable winter conditions (Batzli, 1981). In the Karup Valley, Greenland, the combined impact of different predators both limited population growth and caused population crashes in collared lemmings (Gilg et al., 2003). In a declining lemming population in an alpine area in Norway, almost 50% predation was demonstrated by following the fates of radio-tagged individuals (Heske et al., 1993). Using the same methodology, Reid et al. (1995), Wilson D. et al. (1999), and Gilg (2002) showed that predation was the predominant mortality factor in populations of collared lemmings at various locations in northern Canada and eastern Greenland.

Predator–prey interactions

The dynamics and assemblages of vertebrate predators in arctic tundra are almost entirely based on lemmings and other small rodent species (*Microtus* spp. and *Clethrionomys* spp.; Batzli, 1975; Wiklund et al., 1999). Birds of prey such as snowy owls, short-eared owls (*Asio flammeus*), jaegers (skuas – *Stercorarius* spp.), and rough-legged buzzards (*Buteo lagopus*) are lemming and vole specialists that are only able to breed at peak lemming densities and which aggregate in areas with high lemming densities. Since lemming cycles are not synchronized over large distances (Erlinge et al., 1999; Predavec et al., 2001), the highly mobile avian predators can track lemming population peaks in space. Mammal lemming and vole specialists in the Arctic, such as the least weasel (*Mustela nivalis*) and the ermine, are less mobile than birds but both have high pregnancy rates and produce large litters in lemming peak years (MacLean et al., 1974). In lemming low years, weasel and ermine reproduction frequently fails and mortality rates increase (Gilg et al., 2003; Hanski et al., 2001). In coastal and inland tundra habitats where bird colonies are lacking, the Arctic fox also exhibits the population dynamics typical of a lemming specialist (Angerbjörn et al., 1999). The lemming cycles also impose cyclic dynamics in other animals such as geese and waders because they serve as alternative prey for predators in lemming crash years (Bety et al., 2002; Sutherland, 1988). Recently observed increased predation pressure on water birds in various arctic regions might reflect a change of the lemming cycle in response to climate change, with secondary effects on predators and water birds as an alternative prey (Soloviev et al., 1998; Summers and Underhill, 1987). Thus, a large part of the tundra vertebrate community cycle is in a rhythm dictated by the lemming populations (Chernov and Matveyeva, 1997; Stenseth and Ims, 1993).

This rhythm is likely to be disrupted by projected future variations in snow properties (e.g., snow-season length, snow density, and snow-cover thickness; Yoccoz and Ims, 1999). For small mammals living in the subnivean space, snow provides insulation from low temperatures as well as protection from most predators such as foxes and raptors (Hansson and Henttonen, 1988) and increases in snow are likely to be beneficial. The effect on large mammal prey species (ungulates) is likely to be the opposite, as deeper snow makes reindeer/caribou and moose (*Alces alces*) more vulnerable to predators such as wolves (Post et al., 1999), but more extensive snow patches provide relief from insect pests (section 7.3.3.2). If climate change results in more frequent freeze-thaw events leading to a more shallow and icy snowpack (section 6.4.4), this is likely to expose small mammals to predators, disrupt population increases, and thereby prevent cyclic peak abundances of lemmings and voles. For nomadic predators whose life-history tactic is based on asynchronous lemming populations at the continental scale, an increased frequency of large-scale climatic anomalies that induces continent-wide synchrony (the "Moran effect"; Moran, 1953) is very likely to have devastating effects.

Long-term monitoring (>50 years) of small rodents near the treeline at Kilpisjärvi in subarctic Finland has shown a pronounced shift in small rodent community structure and dynamics since the early 1990s (Henttonen and Wallgren, 2001; see Fig. 7.13). In particular, the previously numerically dominant and cyclically fluctuating grey-sided vole has become both less abundant and less variable in abundance. The Norway lemming and *Microtus* voles also have lower peak abundances, and the small rodent community is currently dominated by the relatively more stable red-backed vole (*Clethrionomys rutilus*). Similar changes took place in the mid-1980s in the northern taiga (Hanski and Henttonen, 1996; Henttonen, 2000; Henttonen et al., 1987) and are still prevailing. For predators that specialize in feeding on small rodents, the lack of cyclic peak abundances of small rodents, especially in the spring (Oksanen et al., 1997), is likely to have detrimental consequences, as they need to breed successfully at least every three to four years to sustain viable populations. At Kilpisjärvi, the least weasel has become rare. Moreover, the severe decline of the Arctic fox and the snowy owl in Fennoscandia, both of which prey on *Microtus* voles and lemmings in mountain and tundra habitats, may be due to lower peak abundances of small mammal prey species in their habitats (Angerbjörn et al., 2001). In Alaska, a similar decrease in lemming cyclicity occurred in the 1970s (Batzli et al., 1980).

Large predators such as wolves, wolverines, and bears are less numerous in the tundra than in the boreal forest (Chernov and Matveyeva, 1997). Consequently, predation impacts on tundra ungulates are usually low. While 79% of the production in small herbivores (voles, lemmings, ptarmigan, and Arctic hares) was consumed by predators averaged across a number of sites in arctic Canada, the corresponding number was only 9% for large herbivores (caribou and muskox; Krebs et al., 2003).

Insect pests, parasites, and pathogens

Plants

Disease in plants is likely to increase in those parts of species distribution ranges where a mismatch between the rate of relocation of the species and the northward/upward shift of climatic zones results in populations remaining in supra-optimal temperature conditions. Under these conditions, species can experience thermal injury (particularly plants of wet and shady habitats; Gauslaa, 1984), drought, and other stresses that make plants more susceptible to disease.

Very little is known about the incidence and impacts of plant diseases in arctic ecosystems. However, recent work has shown that a fungal pathogen (*Exobasidium*) of *Cassiope tetragona* and *Andromeda polifolia* reduces host plant growth, reproductive investment, and survival (Skinner L., 2002). As the incidence of disease increases with an increase in temperature downward along an altitudinal gradient, climate warming is likely to increase the incidence of at least this naturally occurring disease in the Arctic. The incidence of new diseases from increasing mobility of pathogens with a southern distribution is a possibility.

Animals

Ultraviolet-B radiation can reduce the impact of viral and fungal pathogens on insects. The nuclear polyhedrosis virus is a major cause of death of the defoliating autumnal moth. However, this virus is killed by UV-B radiation (Killick and Warden, 1991). Species and strains of the fungus *Metarhizium* are important agents of insect disease, but some, particularly high-latitude strains, are sensitive to UV-B radiation (Braga et al., 2001a,b).

Parasitism is perhaps the most successful form of life, but until recently has been underestimated, especially in the Arctic (Henttonen and Burek, 2001; Hoberg et al., 2003). Parasitism in the Arctic has been poorly studied with respect to both taxonomy and biodiversity as well as the ecological impact parasites may have on animal species and communities.

Recent research on the evolution and phylogeography of typical arctic animals like lemmings has revealed how greatly the alternating glacial and interglacial periods have influenced their distribution and genetic diversity (Fedorov et al., 1999a,b). The impact seems to be at least as profound on the helminth parasites of arctic rodents (Haukisalmi et al., 2004; Hoberg et al., 2003). Such impacts of past climatic fluctuations can be used to project some possible consequences of the present warming. If the arctic host populations become fragmented due to the northward expansion of southern biogeographic elements, extinction of parasites in small host populations and/or cryptic speciation (isolation events seen in parasites, often only by using molecular methods, that are not evident in host populations) in refugia are likely to follow. Phylogeographic structure (often cryptic speciation) can be seen in rodent cestodes in the Arctic even if there is no such structure in the host. This is true also for ruminant parasites.

Phylogenetic studies have shown that host switches have occurred in many clades of rodent cestodes (Wickström et al., in press). It seems plausible that host switches have been promoted by climatic events that force host assemblages, earlier separated by geography or habitat, to overlap in their distribution.

Macroparasites, such as intestinal worms, often have complicated life cycles. In the main host, in which the parasite reproduces, parasites are controlled by host immunity. On the other hand, the free-living intermediate stages (eggs and larvae), and those in intermediate hosts, are subject to extrinsic environmental conditions like temperature and humidity. Temperature strongly affects the development rate of parasite larvae. For example, a small increase in temperature has a clear effect on the development of the muskox lungworm *Umingmakstrongylus pallikuukensis* in its gastropod intermediate hosts (Kutz et al., 2002). Therefore, a slight increase in temperature and in growing-season length is very likely to profoundly affect the abundance and geographic distribution of potentially harmful parasites such as lungworms. Lungworm infections have become conspicuous in recent years as summer temperatures in the Arctic have increased.

The free-living stages of parasites are prone to desiccation. In addition to temperature effects on their development, the survival and abundance of free-living intermediate stages depend greatly on humidity. In addition, the same factors affect drastically the abundance, survival, and distribution of the intermediate hosts of parasites, like insects, gastropods, and soil mites. Haukisalmi and Henttonen (1990) found that precipitation in early summer was the most important factor affecting the prevalence of common nematodes and cestodes in *Clethrionomys* voles in Finnish Lapland. Temperature and humidity also affect the primary production and development of the free-living stages of abomasal nematodes of reindeer/caribou (Irvine et al., 2000). Recently, Albon et al. (2002) showed that abomasal nematodes affect the dynamics of Svalbard reindeer through fecundity. Consequently, even slight climatic changes are likely to have surprising effects on the large ungulates, and possibly on humans exploiting them, through enhanced parasite development (Chapter 15).

The complicated life cycles of parasites cause intrinsic lags in their capacity to track the changes in the population density of their hosts, and these lags are further retarded by unfavorable arctic conditions. Any climatic factor promoting the development of a parasite, so that it can respond in a density-dependent way to host dynamics, is likely to alter the interaction between parasite and host, and the dynamics of both.

There is considerable uncertainty about the possibilities for invasion of pathogens and parasites into the Arctic as a result of climate warming (but see section 15.4.1.2). However, increased tourism combined with a warmer climate could possibly increase the risk of such invasions.

Climate change is likely to affect the important interaction between parasitic insects and reindeer/caribou. Insect harassment is already a significant factor affecting the condition of reindeer/caribou in the summer (section 7.3.3.2). These insects are likely to become more widespread, abundant, and active during warmer summers while many refuges for reindeer/caribou on glaciers and late snow patches are likely to disappear.

Microbe–plant and microbe–microbivore interactions

Although data on the dynamics and processes in arctic microbial communities and on processes in the soil–microbial–plant interface are accumulating rapidly, it is not yet possible to reach firm conclusions about how the dynamics and processes will change in a changing climate. However, the following can be stated. First, short-term (seasonal) changes in microbial processes may not necessarily have major influences on longer-term (annual to multi-annual) processes. Second, microbes and plants share common nutrient resources, although they may not be limited by the same resource. For example, while nutrient supply rates generally control plant productivity, microbial productivity may be constantly or periodically controlled by the abundance of labile C. Third, the nutrient supply rate to the pool available to plants may not be controlled principally by continuous nutrient mineralization, but rather by pulses of supply and sequestration of nutrients linked to microbial population dynamics and abiotic change, such as freeze–thaw cycles.

Jonasson et al. (1999b) showed that despite no appreciable effect on the microbial biomass and nutrient mass, warming increased plant productivity. Because plant productivity was limited principally by a low rate of N supply, it appears that the mineralization of litter or soil organic matter, or microbial solubilization of organic N, increased, and that the plants rather than the microbes sequestered the "extra" N in inorganic or organic form. However, microbes increased their nutrient content in cases when the sink strength for nutrients in the plants decreased (e.g., after shading) at the same time as soil inorganic N also increased. This suggests either that plants compete successfully with microbes for nutrients, or that the microbial requirement for nutrients was satisfied, and the microbes absorbed a "surplus" of nutrients, which is likely if they were limited by C rather than nutrients. This does not fully preclude nutrient competition, however, because it is possible that the plants accessed the nutrients from pulse releases from microbes during periods of population dieback. If so, seasonal changes in the frequency of such pulses are of importance for projecting changes in ecosystem function and need further investigation.
This is particularly obvious, considering that the microbial N and P content typically exceeds the amounts annually sequestered by plants several-fold, and should constitute an important plant nutrient source (Jonasson et al., 1999a, 2001).

The plant–microbe interaction may also be mutualistic through the mycorrhiza by which the fungal partner supplies nutrients to the plant in exchange for C supplied by the plant. A large proportion of the plant species in shrubby vegetation, common in the Arctic, associate with ecto- or ericaceous mycorrhizal fungi. These mycorrhiza types have enzyme systems able to break down complex organic molecules and thereby supply the plant partner with N (Read et al., 1989), the most common production-limiting element for plants. Changes in plant species composition as a consequence of climatic changes are very likely to substantially affect microbial community composition, including that of mycorrhizal fungi. Unfortunately, studies of the effects of projected climate change on mycorrhizal associations in the Arctic are virtually nonexistent. However, a decade of warming of a fellfield led to a substantial increase in willow (*Salix*) biomass, but few changes in the community of associated ecto-mycorrhizal fungi (Clemmensen and Michelsen, unpub. data, 2004).

The effects of microbivores on the microbial community are yet poorly explored and can only be listed as potentially important for projecting effects of global change. It appears, however, that populations of nematodes increase strongly with warming. Because nematodes are the main predators of fungi and bacteria, it may be that increased biomass production of microbes is masked in a warmer environment because of predation by strongly responding microbivores (Ruess et al., 1999a,b). If so, the release rate of plant-available nutrients is likely to increase (e.g., Ingham et al., 1985), which may explain the enhanced nutrient sequestration by plants in warmer soils (rather than pulse sequestration after microbial dieback).

7.4.1.5. Summary

Changes in climate and UV radiation levels are very likely to affect three important attributes of ecosystem structure: spatial structure (e.g., canopy structure and habitat), trophic interactions, and community composition in terms of biodiversity. Ecosystem structure varies along a latitudinal gradient from the treeline to the polar deserts of the high Arctic. Along this gradient there is a decreasing complexity of vertical canopy structure and ground cover ranging from the continuous and high canopies (>2 m) of the forest tundra in the south to the low canopies (~5 cm) that occupy less than 5% of the ground surface in the polar deserts. Within each arctic vegetation zone, there are often outliers of more southerly zones. Changes in vegetation distribution in relation to climate warming are likely to occur by local expansion of these intrazonal communities and northward movement of zones. Satellite measurements, aerial photographs, and indigenous knowledge show a recent increase in shrubbiness in parts of the Arctic.

Experimental manipulations of environmental factors projected to change at high latitudes show that some of these factors have strong effects on the structure of arctic ecosystems, but the effects are regionally variable. Nutrient addition has the greatest effect on the productivity, canopy height, and community composition of arctic plant communities. Nutrients also increase biomass turnover, so biomass may or may not respond to nutrient addition. Summer warming of tundra vegetation within the range of projected temperature increases (2 to 4 ºC over the next 100 years) has generally led to smaller changes compared with fertilization and always to greater responses compared with irrigation. Plant growth response increased from a climatically relatively mild forest understory through a treeline heath to a cold, high-altitude fellfield. Total nonvascular plant biomass and particularly the biomass of lichens decreased in response to 10 years or more of environmental manipulations at sites in subarctic Sweden and in Alaska. Warming experiments in the high Arctic had a greater effect on the fauna above ground compared with fauna below ground and in the subarctic. Spring freeze–thaw events are important, and will probably cause differential mortality among species, thus altering community composition. In general, arctic invertebrate communities are very likely to respond rapidly to change. In contrast, long-term data on the effects of summer warming (2–4 ºC) of ecosystems have not shown appreciable changes in microbial biomass and nutrient stocks. This suggests that a temperature increase alone is unlikely to have any strong impact on microbial carbon and nutrient sequestration. Manipulations simulating enhanced UV-B radiation levels and a doubling of atmospheric CO_2 concentration for seven years altered the use of labile carbon substrates by gram-negative bacteria, suggesting a change in community composition. UV-B radiation also affects the structure of fungal communities. So far, no change in plant community structure has been found in the Arctic in response to manipulations of UV-B radiation levels and CO_2 concentration.

Trophic interactions of tundra and subarctic forest plant-based food webs are centered on a few dominant animal species, which often have cyclic population fluctuations that lead to extremely high peak abundances in some years. Small herbivorous rodents of the tundra (mainly lemmings) are the main trophic link between plants and carnivores. Small-rodent population cycles with peak densities every three to five years induce strong pulses of disturbance, energy, and nutrient flows, and a host of indirect interactions throughout the food web. Lemming population cycles are crucial for nutrient cycling, structure and diversity of vegetation, and for the viability of a number of predators and parasites that are specialists on rodent prey/hosts. Trophic interactions are likely to be affected by climate change. Ice crusting in winter is likely to render vegetation inaccessible for lemmings, deep snow is likely to render rodent prey less accessible to predators, and increased plant productivity due to warmer summers is likely to dominate food-web dynamics. Long-term monitoring of small rodents at the border of arctic Fennoscandia provides evidence of pronounced shifts in small rodent community structure and dynamics that have resulted in a decline in predators (including Arctic fox, snowy owls, buzzards, and skuas) that specialize in feeding on small rodents.

In subarctic forests, a few insect defoliators such as the autumnal moth that exhibit cyclic peak densities at approximately 10-year intervals are dominant actors in the forest food web. At outbreak densities, insects can devastate large tracts of birch forest and play a crucial role in forest structure and dynamics. Trophic interactions with either the mountain birch host or its insect parasitoids are the most plausible mechanisms generating cyclic outbreaks in *Epirrita*. Climate is likely to alter the role of *Epirrita* and other insect pests in the birch forest system in several ways. Warmer winters are likely to increase egg survival and expand the range of the insects into areas outside their present outbreak ranges. However, the distribution range and activity of natural enemies are likely to keep the insect herbivore populations below outbreak densities in some areas.

Climate change is likely to also affect the important interaction between parasitic insects and reindeer/caribou. Insect harassment is already a significant factor affecting the condition of reindeer in the summer. These insects are likely to become more widespread, abundant, and active during warmer summers while refuges for reindeer/caribou on glaciers and late snow patches are likely to disappear. There are large uncertainties about the outcome of the potential spread of new trophic interactants, especially pests and pathogens, into the Arctic.

Disease in plants is likely to increase in those parts of species distribution ranges where a mismatch between the rate of relocation of the species and the northward/upward shift of climatic zones results in populations remaining in supra-optimal temperature conditions. The incidence of new diseases from increasing mobility of pathogens with a southern distribution is a possibility, but increases in UV-B radiation levels could possibly reduce the impact of viral and fungal pathogens.

Microbe–plant interactions can be competitive for nutrients and also mutualistic through mycorrhizal associations. Warming will probably affect both types of relationship, but information is scarce.

7.4.2. Ecosystem function

7.4.2.1. Biogeochemical cycling: dynamics of carbon and nutrients

Arctic ecosystems are characterized by low primary productivity, low element inputs, and slow element cycling, yet they tend to accumulate organic matter, C, and other elements because decomposition and mineralization processes are even more strongly limited than productivity by the arctic environment, particularly the cold, wet soil environment (Jonasson et al., 2001). Because of this slow decomposition, the total C and element stocks of wet and moist arctic tundra frequently equal and may exceed the stocks of the same elements in the much more productive systems of temperate and even tropical latitudes (Table 7.9).

Low-arctic sites with warmer and dryer soils, and extremely unproductive high-arctic polar deserts and semi-deserts, have smaller accumulations of organic matter (Table 7.10). Most of the organic matter and element accumulation occurs in soils, while large accumulations of biomass are limited by a lack of tall woody plant forms such as trees; by selection for slow-growing, low, compact plant forms; and by low productivity and low availability of soil-available elements such as N or P. Typically, the majority of the biomass consists of roots and belowground stems, with aboveground plant mass accounting for less than one-third, and sometimes only 5 to 10%, of the total.

In addition to the large C stocks within the seasonally thawed active layer of the soil (Table 7.10), an equally large pool of organic C may be held in the upper permafrost, within 1 to 2 m of the surface (Michaelson et al., 1996). While these frozen C stocks are not actively involved in C cycling on a seasonal or yearly basis, in the long term, they represent an important C sink, and they are likely to be of particular importance if climate change leads to greater soil thawing or to loss of permafrost (section 6.6.1.3).

The largest body of information on organic matter, C, and nutrient budgets of a wide range of arctic ecosystems comes from the IBP Tundra Biome program, which took place during the late 1960s and early 1970s (Bliss et al., 1981). Since then, research on arctic element cycling has tended to focus on controls over individual biogeochemical processes rather than on comparisons of overall budgets and element stocks. The recent surge of interest in climate change and feedbacks from the Arctic to the globe has highlighted the relevance and utility of those earlier studies, particularly as currently only a few sites are being studied at the whole-system level.

Microbes in arctic soils contain only one or a few percent of the ecosystem C pool. However, the proportions of ecosystem N and P are appreciably higher due to high concentrations of N and P in the microbial tissue compared to the concentrations in plants and soil organic matter (Jonasson et al., 1999a). As a proportion of the total soil organic matter, microbial biomass and nutrient content are similar to ecosystems outside the Arctic, but as a proportion of the total organic matter in the ecosystem (soil plus vegetation) microbial biomass and nutrient content are high in comparison with other systems due to the relatively small vegetation component in the Arctic. Data from various arctic and subarctic sites have shown that microbes commonly contain appreciably less C, slightly less or comparable amounts of N, and much higher amounts of P than the entire plant biomass (Cheng and Virginia, 1993; Hobbie and Chapin, 1996; Jonasson et al., 1996, 1999a; Schmidt et al., 2002).

Nutrient mineralization rates are low, however: typically ten-fold lower than in the boreal region. The low rate is mainly due to low soil temperatures, and it leads to low supply rates of nutrients to the plant-available pool and nutrient-constrained plant productivity in most arctic ecosystems (Nadelhoffer et al., 1992). The combination of low mineralization rates and high proportions of nutrients in microbes compared to plants leads to possible competition for nutrients between microbes and plants during periods of rapid microbial growth (Kaye and Hart, 1997). However, microbes are likely to also release a pulse of nutrients during periods of population decline when the cells are lysed and nutrients are leached (Giblin et al., 1991; Jonasson et al., 2001).
To project microbial effects on nutrient-constrained plant productivity as a result of environmental changes, it is essential to understand not only how the microbial processing rate of organic matter will change, but also the controls on microbial population sizes and how

Table 7.9. Average carbon (C) pools and total C in arctic and alpine tundra, the neighboring boreal zone, and all terrestrial ecosystems. The soil pools do not include organic C in permafrost beneath the seasonally thawed active layer (from Jonasson et al., 2001, after data in McGuire et al., 1997).

	Area (10^6 km^2)	Soil (g C/m^2)	Vegetation (g C/m^2)	Soil: Vegetation ratio	Total C (10^{12} kg)		
					Soil	Vegetation	Soil and vegetation
Arctic and alpine tundra	10.5	9200	550	17	96	5.7	102
Boreal woodlands[a]	6.5	11750	4150	2.8	76	27	103
Boreal forest	12.5	11000	9450	1.2	138	118	256
Global terrestrial	130.3	5900	7150	0.8	772	930	1702

[a]comparable to forest tundra

Table 7.10. Soil organic matter, plant biomass, and net primary production (NPP) in the primary arctic ecosystem types (after Jonasson et al., 2001; based on data from Bliss and Matveyeva, 1992 and Oechel and Billings, 1992).

	Soil organic matter (g/m^2)	Vegetation biomass (g/m^2)	NPP (g/m^2/yr)	Soil: Vegetation Ratio	Soil: NPP Ratio (yr)	Vegetation: NPP Ratio (yr)	Percentage of total area
High Arctic							
Polar desert	20	2	1	10	20	2.0	15
Semi-desert	1030	250	35	4.1	29	7.1	8
Wet sedge/mire	21000	750	140	28	150	5.4	2
Low Arctic							
Semi-desert	9200	290	45	32	204	6.4	6
Low shrub	3800	770	375	4.9	10	2.1	23
Wet sedge/mire	38750	959	220	40	176	4.3	16
Tall shrub	400	2600	1000	0.2[a]	0.4	2.6	3
Tussock/sedge dwarf shrub	29000	3330	225	8.7	129	16	17

[a] source data for this value, which is surprisingly low, have not been found

changes in the populations affect nutrient cycling and interact with plant processes (see also section 7.4.1.4).

Spatial variability

Although the productivity of the most productive tundra may rival that of highly productive shrub and marsh systems at lower latitudes, most arctic systems lie at the low end of the global productivity range. What is striking is the wide range of variation (about three orders of magnitude) in NPP and standing stocks of organic matter in soils and vegetation within the Arctic (Table 7.10). In general, productivity and organic matter stocks decrease with temperature and precipitation from south to north, but local variation in productivity in relation to topography is dramatic (often 10- to 100-fold). Among the most important correlates of topographic variation in productivity are the duration and depth of winter snow cover and degree of protection from winter wind damage, as well as variation in soil moisture, soil thaw, and soil temperature. Local variation in these factors can be nearly as great as that across a wide range of latitudes (Billings, 1973; Jonasson et al., 2001; Shaver et al., 1996). Local variation in productivity is also associated with dramatic shifts in the relative abundance of plant functional types including both vascular and nonvascular plants (sections 7.3 and 7.4.1). Because of this dramatic local variability, primary production and organic matter accumulation are distributed in a mosaic fashion across the Arctic, with a higher frequency of more productive sites (usually wet or moist lowlands) at lower latitudes.

The spatial distribution of productivity and organic matter in the Arctic is broadly predictable in relation to temperature, soil moisture, and other soil factors such as pH, topography, and snow cover (Walker D. et al., 1998, 2002; Walker M.D. et al., 1989, 1994). The proximate controls on C cycling in these ecosystems, however, are much more closely tied to the inputs and turnover of other elements, especially N and P (Shaver et al., 1992). Because N and P inputs (by deposition, fixation, or weathering) are low, even where rapid photosynthesis is possible C cannot be stored in organic matter any faster than the rate of N or P accumulation. Thus, for example, in the Canadian High Arctic where a large portion of the surface is bare ground, C fixation and accumulation is closely tied to low, wet areas where anaerobic soil conditions favor N fixation (Gold and Bliss, 1995). In other arctic systems, such as Alaskan wet and moist tundras, the total amounts of N and P in soil organic matter may be very high but, due to slow rates of decomposition, the availability of these elements to plants is low, leading to low productivity despite high element and soil organic matter stocks (Giblin et al., 1991).

Temporal variability

Interannual variation in biogeochemical cycles has received little attention in the Arctic, although a few multi-year records of ecosystem C exchange, N deposition, and C and N losses at the watershed or catchment level do exist (Hershey et al., 1997; Kling et al., 2000; Oechel et al., 2000a; Steiglitz et al., 2000). Clearly, the trend over the Holocene, at least, has been one of overall accumulation of elements in organic matter since the loss of the glacial ice cover, but the variation in rates of accumulation (or loss) at the scale of years to decades is particularly poorly understood.

The net C balance of arctic ecosystems, as in any terrestrial ecosystem, may be positive or negative depending on the timescale over which it is measured and the environmental conditions during the measurement period. This dynamic balance is called net ecosystem production (NEP[3]) and is defined as the difference between two large, opposing fluxes: gross ecosystem production

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[3] The biological definition of NEP results in positive values when carbon accumulates in the biosphere, whereas measurements of carbon fluxes and the concept of carbon sinks and sources use a convention of negative fluxes when carbon accumulates in the biosphere.

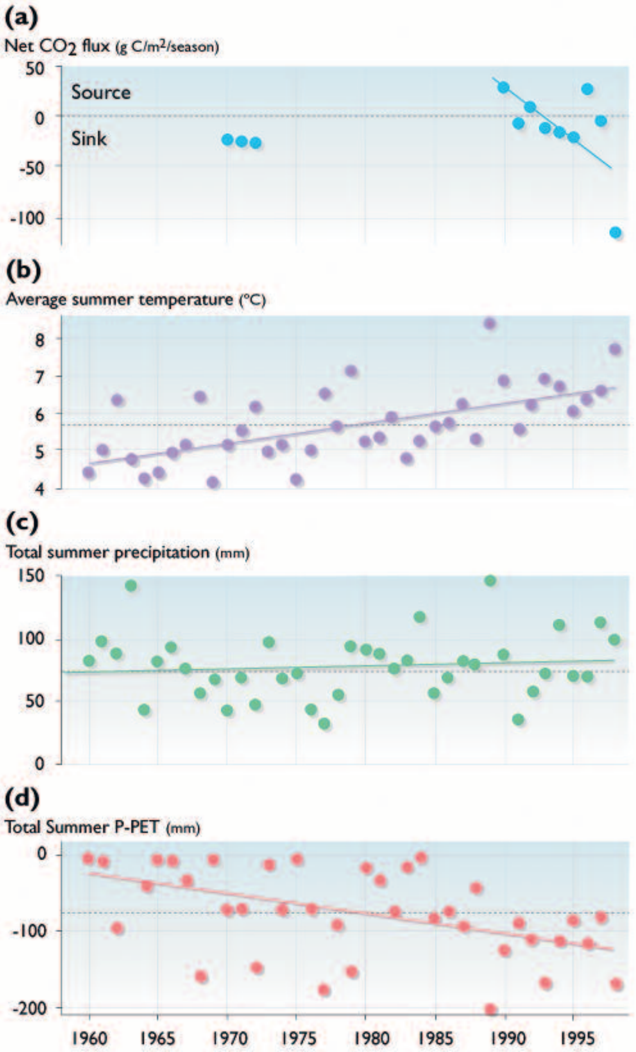

Fig. 7.26. Long-term trends in (a) summer net CO_2 flux, (b) average summer temperature, (c) total summer precipitation, and (d) summer precipitation (P) less potential evapotranspiration (PET) for Alaskan coastal wet-sedge tundra (Oechel et al., 1993, 2000b).

(GEP, or gross ecosystem photosynthesis) and ecosystem respiration (R_E), both measured in units of C (mass or moles) per unit area and time. Ecosystem respiration has two major components, R_A (autotrophic or plant respiration) and R_H (heterotrophic or animal plus microbial respiration). Each of these components of NEP has different relationships to current temperature, moisture, and light conditions. Because they are measured at the whole-system level, all three components are also a function of the current functional mass or surface area of the organisms as well as their current nutritional status. Thus, for example, even though long-term NEP must be positive for the large C accumulations in tundra ecosystems to occur, on a daily or seasonal basis NEP swings from strongly negative (at "night", even under the midnight sun, or in winter) to strongly positive (at midday in midsummer). These daily and seasonal fluctuations have been measured at an increasing number of arctic sites in recent years (Nordström et al., 2001; Oechel et al., 2000a; Søgaard et al., 2000; Vourlitis and Oechel, 1997, 1999).

Carbon balance may also vary sharply among years, and may be either positive or negative on an annual basis. Recent work in Alaska (Oechel et al., 2000a) indicates that although C was accumulating in wet and moist tundras in the 1960s and 1970s (i.e., "negative" C balance), during much of the 1980s and 1990s there was a net loss of C from these ecosystems in both winter *and* summer (i.e., "positive" C balance). In the late 1990s, the summer C balances changed again so that the ecosystems were net sinks, but it is not yet clear whether the C balances for the full year have returned to net C accumulation (Fig. 7.26; see also section 7.5.1.1). It is also unclear whether the shifts in NEP (from C sink to C source) that have occurred over the past 40 years are related in any direct way to weather, because the entire period has been one of general warming in northern Alaska (section 7.5). Modeling studies (e.g., Clein et al., 2000; McGuire et al., 2000; McKane et al., 1997) suggest that in the short term (within one or a few years) the response of R_E (both R_A and R_H) to temperature is more rapid than the response of GEP, leading to a short-term loss of C with warming. In the long term, however, the interaction between temperature and soil nutrient availability might increase GEP sufficiently to cause an eventual return to net C accumulation. There is also evidence from manipulation experiments (Shaver and Chapin, 1991; Shaver et al., 1998) and latitudinal gradients (Callaghan and Jonasson, 1995) that increases in air temperature can result in soil cooling after long periods, as higher air temperatures lead to increased leaf area indices that intercept a greater proportion of incoming radiation before it reaches the soil surface, thereby leading to soil cooling.

Species and functional type composition of the vegetation are keys to long-term change in productivity, because of differences in nutrient use and allocation, canopy structure, phenology, and relative growth rates among plants (Chapin F. et al., 1993; Hobbie, 1995). Large differences exist, for example, in the *rate* at which tundra plants can respond to changes in weather and climate, due to differences in allocation to stems versus leaves or to secondary chemistry versus new growth (Shaver et al., 2001), in the ability to add new meristems (Bret-Harte et al., 2001), and in the constraints on the amount of growth that can be achieved by a single meristem within a single year (i.e., determinate versus indeterminate growth). Species and functional types also differ in their growth phenology and thus in their ability to take advantage of a change in the timing and duration of the growing season. For example, moss-dominated ecosystems in Iceland have limited ability to respond to climate change without a complete change to a vascular plant-dominated community (Jónsdóttir et al., 1995), whereas shrubs and small trees already present in sheltered, moist depressions on the North Slope of Alaska seem to be already expanding their distribution (Sturm et al., 2001b) and therefore productivity.

The chemical composition of primary productivity (leaves versus wood, secondary chemistry, species composition) is important as a long-term feedback to productivity and its responsiveness to climate change. It is also important in terms of both animal community composition and secondary (herbivore) productivity. Carbon to nitrogen ratios; lignin and protein content; and tannin, resin, and phenolic content are all important in determining forage quality (section 7.4.1.4) and the susceptibility of plant litter to decomposition, and thus the remineralization of essential limiting nutrients like N and P (Hobbie, 1996).

Despite the critical importance of NPP together with NEP and the considerable research already conducted on these parameters, additional field measurements and focused process studies are needed to resolve issues relating to the different methodologies used for measuring NPP and NEP (Hobbie et al., 2000; Williams et al., 2000). Results from different methodologies also need to be reconciled (section 7.7.1.1).

Budgets of N and P were developed for several arctic sites during the IBP studies 30 years ago (Chapin F. et al., 1980) but complete documentation of inputs and outputs of any element other than C has not been attempted since then for any arctic site. Part of the problem is that individual N and P inputs and outputs in arctic ecosystems, such as N fixation, N deposition, denitrification, rock weathering, or losses in streamflow (see next subsection), are even smaller than the amounts annually recycled by mineralization of organic matter (Fig. 7.27; Nadelhoffer et al., 1991; Peterson et al., 1992; Shaver et al., 1992), except perhaps in the high Arctic (Gold and Bliss, 1995). Thus, very long-term records are needed to evaluate the significance of interannual variation in N and P budgets, while most studies of the component processes last only one to three years.

Inputs/outputs, primary production, and net ecosystem production

The dominant C input to arctic ecosystems is from photosynthesis in vascular and nonvascular plants, which in total comprises GEP. The relative (apparent) importance of various controls on primary production differs depending on the level (leaf, canopy, or whole vegetation) and timescale (daily, seasonal, or decadal) of examination (Williams et al., 2001). Carbon inputs at the leaf level are clearly limited in the short term by generally low irradiance and consequent low temperatures during usually short, and late, growing seasons (Fig. 7.8), despite a wide range of specific photosynthesis-related adaptations to the arctic environment (section 7.3). Photosynthesis in arctic plants is also often sensitive to changes in CO_2 concentrations (in the short term), moisture conditions, and snow (UV radiation effects are variable and comparatively small). Although arctic plants in general are well adapted to the arctic climate, there is considerable variation in the responses of photosynthesis to microclimate among plant functional types. In the longer term and at the level of whole vegetation canopies, however, C inputs are limited by generally low canopy leaf areas, leaf phenology and duration, and light interception (Williams et al., 2001). Canopy leaf area is low because low soil nutrient availability, particularly N, limits the ability of the vegetation to develop a large, photosynthetically efficient leaf area (Williams and Rastetter, 1999), and it also limits the ability of the vegetation to use newly fixed C for new growth, because growth requires adequate supplies of multiple elements in addition to C (Jonasson et al., 2001; Shaver et al., 1992). It is also low because of the low stature of the vegetation, which prevents development of a multilayered canopy. Other environmental factors such as wind and soil disturbance also limit C gain. Storage of photosynthate and nutrients acquired in previous years plays a key role in determining the current year's productivity (Chapin F. and Shaver, 1985b).

Carbon outputs from arctic ecosystems occur via a wider array of processes and are regulated very differently from C inputs (section 7.4.2.2). The dominant form of C loss is as CO_2, produced by both plants and soil biota. Autotrophic or plant respiration (R_A) typically accounts for about half of GEP on an annual basis (Williams et al., 2000, 2001) but follows a very different seasonal and daily pattern (discussed previously).

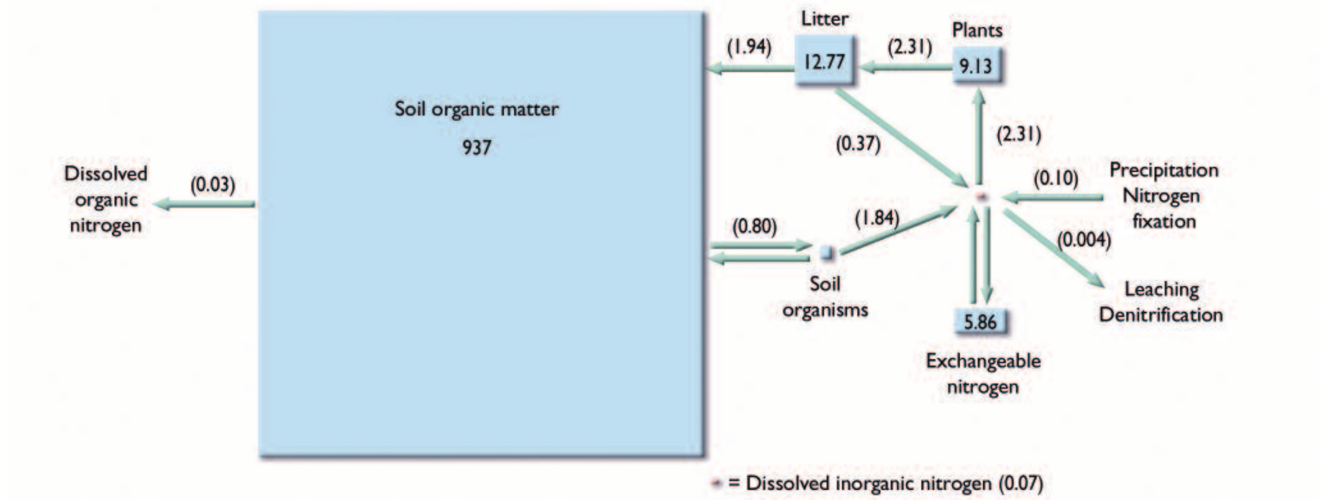

Fig. 7.27. Nitrogen budget for wet-sedge tundra at Barrow, Alaska. Numbers in boxes are N stocks in g/m^2; numbers in parentheses are N fluxes in $g/m^2/yr$ (Shaver et al., 1992; adapted from Chapin F. et al., 1980).

Heterotrophic respiration (R_H), mostly by soil organisms, accounts for most of the other half of GEP, although in the long term the sum of R_A and R_H must be slightly less than GEP if C is to accumulate in soil organic matter. Heterotrophic respiration produces both CO_2 and methane (CH_4), the latter produced anaerobically in wet soils (section 7.4.2.2). Much of the CH_4 produced in arctic soils is oxidized to CO_2 before it reaches the atmosphere; net CH_4 emissions thus are normally only a fraction of CO_2 emissions from arctic soils (less than 5%), but CH_4 is a much more powerful greenhouse gas than CO_2. Other aspects of C balance are important yet difficult to quantify. Examples are plant root respiration, the sloughing of dead material from roots, root exudation, and the growth and respiration of microorganisms intimately associated with plant roots.

Most of the respiratory CO_2 and CH_4 losses from arctic systems move directly to the atmosphere. Significant fractions of these gases, however, travel in dissolved forms in soil water, eventually reaching streams and lakes where they are released to the atmosphere (Kling et al., 1991, 1992). In addition, soil and surface waters contain significant amounts of dissolved organic forms of C, much of which is eventually consumed by aquatic microbes, producing more CO_2 (Chapter 8). Together, these losses to aquatic systems may add up to a significant component of the net C balance of arctic systems. Synoptic, simultaneous analysis of aquatic C losses at the same time, place, and scale as direct atmospheric exchanges has not been completed, but estimates of aquatic C losses suggest that these may equal as much as 20 to 30% of GEP.

Winter CO_2 losses are a second major gap in the understanding of C losses from arctic ecosystems. Although winter CO_2 losses have long been recognized (Coyne and Kelley, 1971), more recent research indicates that these losses are greater than was previously thought and may be the product of significant respiratory activity during the winter (Fahnestock et al., 1999; Hobbie et al., 2000; Oechel et al., 1997; Welker et al., 2000; section 7.3.2.3), when recently fixed C is respired (Grogan et al., 2001).

There are few studies of inputs and outputs of N in the Arctic, largely because early work suggested that they were small relative to standing N stocks and internal recycling, and thus were less important, at least on a short-term basis (Shaver et al., 1992). In the long term (several decades or more), however, understanding of N inputs and outputs is essential to understanding how the total pool sizes of N change over time. Changes in standing stocks of N are closely tied to the accumulation or loss of organic matter and C in the Arctic (Gold and Bliss, 1995).

Nitrogen enters arctic ecosystems through atmospheric deposition and microbially mediated N fixation (Fig. 7.27). Nitrogen deposition rates are low in the Arctic relative to other parts of the world, mostly because the atmosphere is cold enough that it cannot hold the high concentrations of N species such as nitrate (NO_3) that are deposited at lower latitudes. Thus, N deposition can account for only about 5% or less of the annual plant N uptake requirement in Alaskan wet-sedge tundra (Chapin F. et al., 1980), although this might increase with increased industrial activity at lower latitudes. In regions such as northern Scandinavia that are subject to N deposition from lower-latitude anthropogenic sources, however, N deposition may be greater than 0.1 $g/m^2/yr$, which if continued for many years is sufficient to affect plant growth and productivity (Back et al., 1994). Nitrogen fixation rates are usually assumed to be of similar magnitude, although the only relatively recent studies (Chapin D. and Bledsoe, 1992; Lennihan et al., 1994) indicate that, at least in the high Arctic, N fixation might account for more than 10% of plant requirements with the remaining 90% supplied by recycling from the soils.

Nitrogen losses are also poorly understood. There have been no recent, published studies of denitrification in the Arctic; although anaerobic soils might be expected to have high potential for denitrification, the generally low rates of NO_3 production in tundra soils suggest that this is also a small component of the annual N budget. Possible spring losses of N in the form of nitrous oxide (N_2O) have been suggested (Christensen T. et al., 1999a) but not yet verified in the Arctic. Nitrogen losses in streams have been monitored at several locations, and are of roughly the same magnitude as N deposition (Hershey et al., 1997).

Responses to climate change

Responses of element cycles in arctic ecosystems to climate change factors have been studied in multi-year manipulation experiments in several contrasting ecosystem types (Dormann and Woodin, 2002; Shaver and Jonasson, 2000; Fig. 7.28). These experiments include manipulations of air temperature, CO_2 concentration, light, water (both excess and deficit), nutrients, and UV-B radiation levels. One common observation from these experiments is that although short-term responses to single factors like changing CO_2 concentrations or temperature increases are measurable and often significant, these responses are often not sustained due to other limitations. A general conclusion is that nutrient limitation dominates the multi-year responses and is linked to changes in other factors (e.g., temperature and water) through their indirect effects on nutrient mineralization and availability to plants. In wet systems, water-table depth and soil drainage are critical variables limiting nutrient turnover in the soil; increases in C turnover in these systems are not linked to increases in C accumulation because increased C accumulation requires increased N and/or P supply (Oechel et al., 1998, 2000a; Shaver et al., 1998). A large pool of nutrients exists in organic matter, and may drive large changes in organic matter stocks if the nutrients can be mineralized and not leached from the system. Similarly, short-term increases in photosynthesis and growth in response to high CO_2 concentrations are often not sustained due to nutrient limitation (Grulke et al., 1990; Hartley et al., 1999; Oechel et al., 1994; section 7.3).

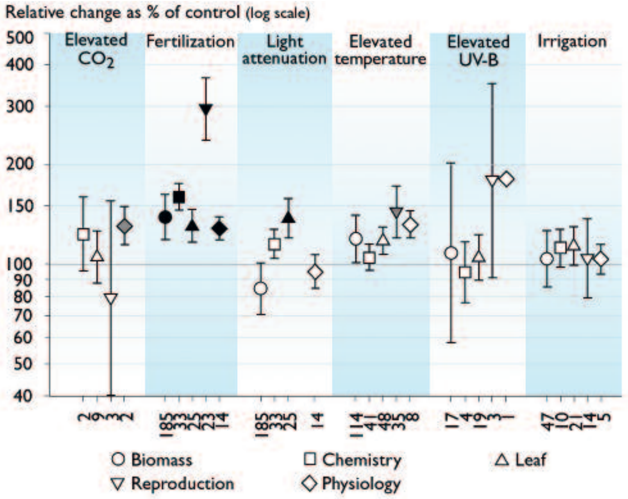

Fig. 7.28. Mean response of plants to environmental perturbations, shown as a percentage of untreated controls (vertical lines depict ±1 standard deviation). Black and grey symbols indicate that means differ significantly from 100% ($P<0.05$ and $0.1>P>0.05$, respectively; two-tailed t-test). Numbers along the horizontal axis refer to corrected sample size (df+1) (Dormann and Woodin, 2002).

The results of several manipulation experiments indicate that nutrient mineralization stimulated by increased soil temperatures is unlikely to be sustained in the long term. Soil temperature increases cause an immediate increase in soil respiration in laboratory studies, but few arctic field studies have shown increased mineralization rates in response to increased air temperatures (but see Schmidt et al., 1999) and longer-term field studies show an acclimation to increased soil temperature (Hartley et al., 1999; Luo et al., 2001). Some studies have shown soil *cooling* in response to increasing air temperatures in experiments (Shaver and Chapin, 1991) and along latitudinal gradients (Callaghan and Jonasson, 1995). Higher air temperatures stimulate leaf area development (Myneni et al., 1997) and a greater leaf area index would be expected to intercept thermal radiation before it reaches the soil, leading to soil cooling. In addition, organic matter in deeper soil profiles is less responsive to temperature increases than that in surface layers (Christensen T. et al., 1999b; Grogan et al., 2001), again suggesting that any temperature-induced mineralization is likely to be transitory.

Overall, however, multi-year experiments suggest that the arctic ecosystems most responsive to climate change are very likely to be those in which the environmental change is linked to a large change in nutrient inputs or soil nutrient turnover, and/or large changes in leaching or erosional losses of soil-available nutrients (Fig. 7.27). The effects of UV radiation on overall organic matter cycling are generally unknown, but not unimportant. Recent work by Niemi et al. (2002) showed that increased UV-B radiation decreased CH_4 emissions from a peatland in northern Finland, while three studies show UV-B radiation effects on *Sphagnum* growth (Gehrke et al., 1995; Searles et al., 1999; Sonesson et al., 2002) with potential implications for C sequestration. Long-term responses of biogeochemical cycling to increased CO_2 concentrations and UV-B radiation levels are small in magnitude but are likely to lead to longer-term changes in biogeochemical cycling and ecosystem structure (sections 7.3.3.3 and 7.4.1.2). However, most of the current understanding of UV radiation responses is based on species- and tissue-level research.

Biodiversity and species effects on biogeochemistry

It is important to determine if species or growth form composition of the vegetation have any impact on biogeochemistry of arctic ecosystems, or if biogeochemistry is largely regulated by climate and resource availability irrespective of species composition. Although only partial answers to this question are currently available, there are at least five main mechanisms by which species composition are likely to have important consequences for biogeochemistry. These are:

1. Species composition is likely to affect the rate of change in ecosystems in response to environmental change, through differences in species growth, reproduction, and dispersal rate potential (e.g., Bret-Harte et al., 2001).
2. Species are likely to affect nutrient availability and C cycling through differences in the turnover of elements in their living tissues and in the decomposability of their dead parts (Hobbie and Chapin, 1998; Quested et al., 2003).
3. Species are likely to affect element accumulations in living plants through differences in their biomass allocation patterns and in their biomass element concentrations and element ratios (Bret-Harte et al., 2002; Quested et al., 2003; Shaver et al., 2000).
4. Species are likely to differ in their effects on snow accumulation and snowmelt, surface energy balance, and soil temperature regimes, with important feedbacks to element cycles (McFadden et al., 2001; Sturm et al., 2001a).
5. Physiological mechanisms, for example, wetland species that act as conduits for CH_4 transport from the soil to the atmosphere (Fig. 7.29; Joabsson and Christensen, 2001; Niemi et al., 2002; Öquist and Svensson, 2002).

All five of these species effects have been documented in arctic systems, although it is often uncertain how to scale up from small experimental communities to larger units of the landscape.

Species richness or diversity itself is likely to also affect the biogeochemistry of arctic ecosystems, although the magnitude of the effect is hard to judge. There is a weak positive correlation between productivity and vascular species richness in arctic vegetation, but, like most vegetation, richness declines when productivity is increased artificially by fertilizer addition or other disturbance (Gough et al., 2000). Recent evidence suggests that arctic plants obtain their N from diverse sources in the soil (Michelsen et al., 1996, 1998; Nadelhoffer et al., 1996) and that the

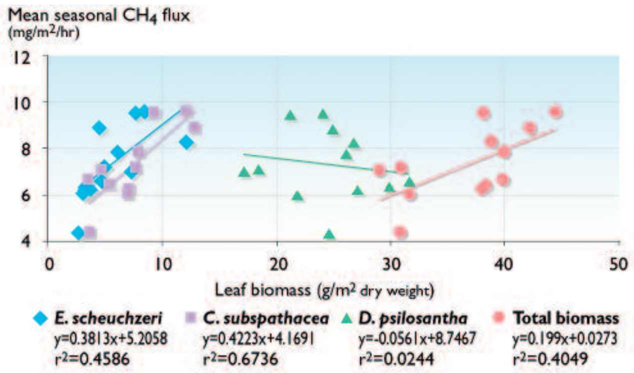

Fig. 7.29. Mean seasonal methane emissions from a high-arctic fen in Zackenberg, northeast Greenland, as a function of leaf biomass of the grasses *Eriophorum scheuchzeri*, *Dupontia psilosantha*, and *Carex subspathacea*, and total leaf biomass of the three species (Joabsson and Christensen, 2001).

relative abundance of different species reflects different abilities to acquire the different forms of N (McKane et al., 2002). These latter studies suggest that diversity will probably increase productivity in arctic vegetation by increasing total uptake of different forms of a strongly limiting element, N. Partial support for this conclusion comes from experiments involving removal of individual species from arctic vegetation, in which the remaining species failed to increase in abundance (Fetcher, 1985; Jonasson, 1992; Shevtsova et al., 1995, 1997).

Vascular plants directly affect the substrate availability for methanogens and have the capability to transport gases between the anaerobic parts of soils and the atmosphere (Bubier and Moore, 1994; Joabsson and Christensen, 2001; Joabsson et al., 1999; Niemi et al., 2002). Different vascular plant species have different effects, however, and the vascular plant species composition in wet tundra ecosystems may be a key determinant of the scale of CH_4 emissions; for example, Fig. 7.29 shows that the minor constituents of the total vascular plant biomass (*Carex* and *Eriophorum*) seem to be "driving" net CH_4 emissions from the site, suggesting that shifts in vascular plant species composition alone could lead to significant effects on trace-gas exchange (Joabsson and Christensen, 2001; Ström et al., 2003). Changes in species composition *per se* caused by climate warming and increased UV-B radiation levels are likely to cause a change in CH_4 emissions, adding to the direct effect of a changing soil climate on these emissions (Niemi et al., 2002; see section 7.4.2.2).

Role of disturbance

Disturbances are expected to increase with climatic warming, mainly through thermokarst (section 7.5.2) and possibly also through increased fire in some northern ecosystems and insect pest outbreaks in subarctic forests (section 7.4.1.4). In general, physical disturbance of arctic ecosystems results in greater soil warming and permafrost thawing, which tend to increase soil organic matter and nutrient turnover. Typically, vegetation productivity increases dramatically although soil respiration also increases. It is not yet clear whether the increased plant growth is sufficient to compensate for losses of soil organic matter. In the long term, however, arctic landscapes should gain organic matter in both soils and vegetation on disturbed sites. The timing and trajectory of these changes are key unknowns requiring further research.

7.4.2.2. Soil processes and controls over trace-gas exchanges

During the last decade, trace-gas production, emissions, and assimilation have attracted considerable attention from the scientific community, for the following reasons:

- most of these gases are "radiatively active" (i.e., they affect the heat balance and contribute to the "greenhouse effect" responsible for climate instability and change);
- the atmospheric concentration (mixing ratios) of these gases underwent remarkably rapid changes after the industrial revolution (e.g., the concentration of atmospheric CH_4 has been growing at an annual rate of 0.8 to 1%, which can have a significant impact on the biosphere apart from the greenhouse effect); and
- most trace gases are intermediate or end products/ substrates of key biogeochemical processes, such that monitoring these gas species can be used for early detection of any anomaly in ecosystem functioning.

Table 7.11 lists the major trace gases and their potential impacts on ecosystems, although not all of the listed gases are of primary importance for arctic terrestrial ecosystems. This review is restricted to CO_2 (section 7.4.2.1), CH_4, and N_2O.

Soil and ecosystem processes responsible for trace-gas emissions

Trace-gas exchange with the atmosphere occurs through a set of coupled soil/ecosystem processes, including:

- production of substrate(s) for processing by trace gas-producing organisms;
- conversion of substrate(s) to respective gaseous species in parallel with gas consumption (Table 7.12); and
- mass transfer of produced gas to the free atmosphere, which includes three main mechanisms: molecular diffusion, vascular gas transfer (i.e., through plant "conduits"), and ebullition (i.e., bubble formation).

Substrates are formed by one of three processes: decomposition (hydrolytic breakdown of plant litter, oxidation, fermentation); N mineralization, and photosynthesis and photorespiration. However, the starting point for almost all substrates is the primary production of organic matter by plant photosynthesis or (occasionally) bacterial chemosynthesis. There are two main flows of C substrates from plants: plant litter formation with lignocellulose as a main component resistant to microbial breakdown; and the continuous supply of readily available C monomers (root and foliage exudation). The chain of events leading to the formation of immediate precursors of trace gases can be long and intricate (Panikov, 1999). It is worthwhile to note that the most successful model simulations of trace gas emissions include vegetation or primary productivity modules.

Trace-gas transport

There are three main transport mechanisms: molecular diffusion, vascular transport of gas through plant roots, and ebullition. Vascular transport can be described as a diffusion process through plant root aerochyma (parenchyma containing large air spaces typical of emergent and marginal wetland species), which is a continuous network of gas-filled channels. Vascular transport is two or three orders of magnitude more rapid than diffusion in water. Ebullition is probably the most difficult process to simulate and describe mathematically due to its stochastic nature. In northern soils, ebullition and vascular transport were shown to be the major transport mechanisms, accounting for up to 98% of total CH_4 emissions (Christensen T. et al., 2003a).

Environmental controls on methane fluxes

Methane is produced from anaerobic decomposition of organic material in waterlogged, anaerobic parts of the soil. Wet and moist tundra environments are known to be significant contributors to atmospheric CH_4 (Bartlett and Harriss, 1993; Fung et al., 1991). Methane is formed through the microbial process of methanogenesis, which is controlled by a range of factors: most notably temperature, the persistence of anaerobic conditions, gas transport by vascular plants, and the supply of labile organic substrates (Joabsson and Christensen, 2001; Schimel, 1995; Ström et al., 2003; Whalen and Reeburgh, 1992). Figure 7.30 shows the variety of controls on CH_4 formation rates at different spatial and

Table 7.11. Trace gases produced in tundra soils and their potential impacts on terrestrial ecosystems.

Gas species	Main soil sources	Main soil sinks	Environmental control on "source–sink" balance	Impact[a]	Reference related to the Arctic
Carbon dioxide (CO_2)	Organic matter decomposition	Photosynthetic uptake; formation of carbonates	Temperature; moisture; available nutrients	GHG; productivity of plant community (indirectly)	Nordström et al., 2001; Oechel et al, 2000b; Søgaard et al., 2000;
Methane (CH_4)	Methanogenesis (anaerobic decomposition of organic matter)	Uptake by methanotrophic bacteria	Temperature; moisture; nutrients; plant community structure	GHG; highly combustible	Christensen T. et al., 2000; Friborg et al., 2000; Whalen and Reeburgh 1990
Nitrous oxide (N_2O)	Denitrification; nitrification	Uptake by aerobic and anaerobic soil bacteria	Temperature; moisture; N fertilizers	GHG	Christensen T. et al., 1999a
Carbon monoxide (CO)	Anaerobic decomposition of organic matter; airborne pollution	Uptake by carboxydobacteria	Temperature; moisture	Atmospheric photochemical reactions; toxicity	Conrad, 1996; Whalen and Reeburgh, 2001
Molecular hydrogen (H_2)	Fermentation, Pollution	Uptake by methanogens, acetogens, sulfite reducers, and H_2-oxidizing bacteria	Temperature; moisture	Atmospheric photochemical reactions; toxicity	Conrad, 1996; no specific arctic works
non-methyl hydrocarbons (terpene and isoprene derivatives)	Plants and microorganisms (bacteria, fungi)	Photooxidation; uptake by aerobic soil bacteria	Temperature; moisture; plant phenology and physiological state	GHG; ozone and aerosol formation within plant canopy	Guenther et al., 1993; Isidorov et al., 1983; Isidorov and Jdanova, 2002
Methylated halogens (methyl bromide, methyl iodide, etc.)	Soil affected by oceanic water	Bacterial decomposition	Soil hydrology; location within landscape relative to oceanic shoreline	Ozone depletion; phytotoxicity	Dimmer et al., 2001 (data for Irish peatland ecosystems)
Dimethyl sulfide (DMS)		Hydrolysis; uptake as a sulfur source by plants	Soil hydrology and location within landscape relative to oceanic shoreline	Phytotoxicity	Legrand, 1995
Sulfur oxides (SO_2; SO)	Fuel combustion: airborne contamination of soil	Sulfate and sulfite formation; ion exchange; plant and microbial uptake	Temperature; moisture	Acid rain; phytotoxicity	Conrad, 1996
Ammonia (NH_3)	Airborne soil contamination	Conversion to ammonium (NH_4^+); ion exchange; plant and microbial uptake	Temperature; moisture	Plant productivity	Conrad, 1996

[a] GHG=greenhouse gas

temporal scales. Methane is not only produced but also consumed in the aerobic parts of the soil through the microbial process of methanotrophy, which can even take place in dry soils with the bacteria utilizing atmospheric CH_4 (Christensen T. et al., 1999a; Panikov, 1999; Sjögersten and Wookey, 2002; Whalen and Reeburgh, 1992). Methanotrophy is responsible for the oxidation of approximately 50% of the CH_4 produced at depth in the soil and therefore is as important to net CH_4 emissions as methanogenesis. The anaerobic process of methanogenesis is much more responsive to temperature than CH_4 uptake, so soil warming in the absence of any other changes is very likely to accelerate emissions (the difference between production and consumption), in spite of the simultaneous stimulation of the two opposing processes.

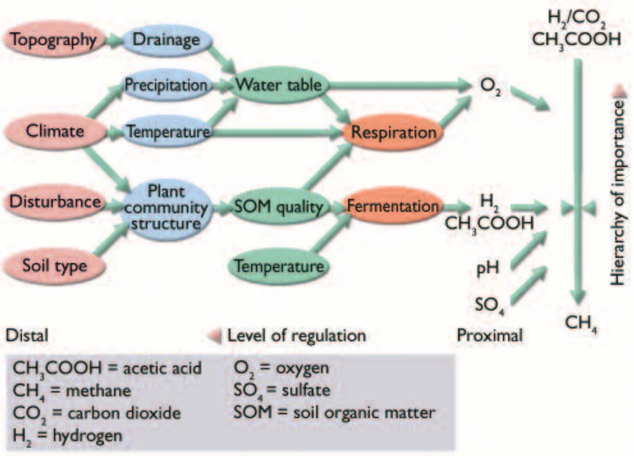

Fig. 7.30. Controls on methanogenesis (redrawn from Davidson E. and Schimel, 1995).

Apart from temperature, water regime, and plant cover, methanogenic bacteria are strongly affected by biological interactions within the soil community. Competition with acetogenic and sulfidogenic bacteria for molecular hydrogen (the outcome of which depends on the affinity to hydrogen, the temperature, and density of the various populations) determines the pattern of gas formation not only quantitatively, but also in qualitative terms. For example, ecosystems can be a source of CH_4 (if methanogenic bacteria prevail), or hydrogen sulfide and other sulfides (if sulfate-reducing bacteria dominate), or acetic acid (if a large population of acetogens is present).

Early empirical models of northern wetland/tundra CH_4 exchanges suggested sensitivity to climate change (Harriss et al., 1993; Roulet et al., 1992). A simple mechanistic model of tundra CH_4 emissions that included the combined effects of temperature, moisture, and active-layer depth also suggested significant changes in CH_4 emissions as a result of climate change (Christensen T. and Cox, 1995). More complex wetland CH_4 emission models suggest that winter processes have a strong influence on net annual CH_4 emissions (Panikov and Dedysh, 2000). Variations in CH_4 emissions at the regional and global scale are driven largely by temperature (Crill et al., 1992; Harriss et al., 1993) with the important modulating effects of vascular plant species composition superimposed (Christensen T. et al., 2003b; Ström et al., 2003). An initial warming is, hence, projected to lead to increased CH_4 emissions, the scale of which will depend on associated changes in soil moisture conditions and the secondary effects of changes in vegetation composition (section 7.5.1.2).

Table 7.12. Examples of soil processes where trace gases are formed or consumed.

Gas species	Source reaction	Sink reaction
CO_2	Oxidative decomposition of dead organic matter (OM): $OM+O_2 \rightarrow CO_2+H_2O+$"ash" Oxidation of root exudates Fermentation: $(CH_2O)_n$ [a] $\rightarrow CO_2+VOC^b+H_2$	sulfur[c] (S) oxidizing bacteria Photosynthesis (plant and green bacteria): $nCO_2+nH_2O \rightarrow nCH_2O^a +nO_2$ Soil chemosynthesis (nitrifying, hydrogen-oxidizing, iron (Fe^{2+})-oxidizing, and sulfur[c] (S) bacteria) Carbonate formation and leaching
CO	Fermentation O_2-limited oxidation reactions	Activity of carboxydobacteria: $CO + 1/2\ O_2 \rightarrow CO_2$ Spontaneous chemical oxidation
CH_4	Methanogenesis: $CO_2 + H_2 \rightarrow CH_4$ or CH_3COO^-(acetate)$\rightarrow CH_4$	Methanotrophy: $CH_4 \rightarrow CO_2 + H_2O$ Photochemical reactions with hydroxyl and chlorine radicals
N_2O	Nitrification: $NH_4^+ \rightarrow \approx 99\%\ NO_3^- + \approx 1\%\ N_2O$ Denitrification $NO_3^- \rightarrow N_2O \rightarrow N_2$ (molecular nitrogen)	The N_2O is finally converted to stable end products such as NO_3^- (nitrification, aerobic conditions) or N_2 and NH_3 (denitrification, anaerobic conditions) upon completion of the respective processes
Nitric oxide (NO)	Nitrate reduction $NO_3^- \rightarrow NO$	NO oxidation
Isoprene (C_5H_8)	Secondary metabolic reactions in plants: pyruvate → …→ isoprene Fermentation	Microbial oxidation Formation of phytogenic aerosols and sedimentation

[a] carbohydrate; [b] volatile organic carbon (acetic, propionic, or butyric acid; aldehydes; alcohols; ketones; ethers; etc.); [c] these bacteria can use several S-containing reduced compounds (S, S^{2-}, SO_3^{2-}, etc.) as an energy source.

Controls on nitrous oxide fluxes

The simulation of N_2O emissions requires consideration of the combined N and C cycles, because the substrates of denitrification include electron acceptors (NO_3) as well as oxidizable C substrates. The ecosystem–atmosphere fluxes of N_2O are associated with fundamental transformations of N in the soil, namely the processes of nitrification and denitrification. Very few field studies of N_2O fluxes are available from the Arctic (Christensen T. et al., 1999a), but very small releases of N_2O are expected from arctic soils due to their general nutrient limitation. However, one issue of potentially great importance in the Arctic is early spring fluxes of N_2O. Denitrification has been found to take place even below the freezing point (Dorland and Beauchamp, 1991; Malhi et al., 1990). During freezing and thawing, C is liberated and this may increase denitrification activity in the soil (Christensen S. and Christensen, 1991). During the spring thaw of the soil, a significant percentage of annual N_2O emissions can take place (Papen and Butterbach-Bahl, 1999). The early spring fluxes may also explain the significant N_2O production measured in fertilized plots on a subarctic heath (Christensen T. et al., 1999a) on soils that showed no emissions from control plots. Hence, as with CH_4, the winter and "shoulder" season processes are generally very important but also the least well understood.

7.4.2.3. Water and energy balance

Arctic ecosystems exhibit the greatest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation, to summer when the ecosystem absorbs most incoming radiation. About 90% of the energy absorbed during summer is transferred to the atmosphere, with the rest transferred to the soil in summer and released to the atmosphere in winter (Eugster et al., 2000). Consequently, arctic ecosystems have a strong warming effect on the atmosphere during the snow-free season.

Vegetation profoundly influences the water and energy exchange of arctic ecosystems. In general, ecosystems with high soil moisture have greater evapotranspiration than dry ecosystems, as in any climatic zone. Arctic ecosystems differ from those at lower latitudes, however, in that there is no consistent relationship between CO_2 flux and water vapor flux, because vascular plants account for most CO_2 flux, whereas mosses account for most water vapor flux (McFadden et al., 2003). This contrasts with other major biomes on Earth, where these two fluxes are strongly correlated (Kelliher et al., 1995; Schulze et al., 1994).

Within tundra, vegetation strongly influences the winter energy budget through its effects on snow depth and density. Shrubs increase snow depth by reducing the velocity of blowing snow and reducing sublimation rates; models suggest that in northern Alaska this shrub-induced reduction in sublimation can increase ecosystem-scale winter snow accumulation by 20% (Sturm et al., 2001a). By acting as a "snow fence", shrubs also cause snow to accumulate within shrub patches and to be depleted from shrub-free zones, increasing the spatial heterogeneity of snow depth. Snow within shrub canopies is deeper and less dense, which reduces heat transfer through the snowpack and increases winter soil temperatures by 2 °C relative to adjacent shrub-free tundra. Warmer soil temperatures beneath shrubs may increase winter decomposition and enhance nutrient availability, creating a positive feedback that promotes shrub growth (Sturm et al., 2001a).

Midsummer vegetation feedbacks to regional climate are determined largely by midsummer patterns of water and energy exchange (Chapin F. et al., 2000a). Midsummer albedo is greatest in sedge communities, whose standing dead leaves reflect much of the incoming radiation (Chapin F. et al., 2000a; McFadden et al., 1998). Evergreen forests and forest tundra, in contrast, have a particularly low albedo because of the dark absorptive nature of evergreen leaves and the effectiveness of complex forest canopies in capturing light (Chapin F. et al., 2000b; Eugster et al., 2000). Tundra and forest tundra canopies dominated by deciduous plants are intermediate in albedo and therefore in the quantity of energy that they absorb and transfer to the atmosphere (Baldocchi et al., 2000; Chapin F. et al., 2000b). A larger proportion of the energy transfer to the atmosphere occurs as sensible heat flux in forests, forest tundra, and shrub tundra than in wet tundra (Boudreau and Rouse, 1995; Chapin F. et al., 2000a; Eugster et al., 2000; Lafleur et al., 1992; McFadden et al., 1998).

All arctic ecosystems exhibit greater ground heat flux during summer (5 to 15% of net radiation) than do temperate ecosystems (generally close to zero), due to the strong thermal gradient between the ground surface and permafrost and the long hours of solar radiation (Chapin F. et al., 2000a). Ground heat fluxes are reduced in tundra ecosystems with a large leaf area, which shades the ground surface (McFadden et al., 1998), or where the ground cover is highly insulative, as with *Sphagnum* mosses (Beringer et al., 2001a). Grazing and other processes causing surface disturbance increase ground heat flux and thaw depth (Walker D. et al., 1998). Future changes in vegetation driven by climate change are very likely to profoundly alter regional climate.

7.4.2.4. Summary

Arctic ecosystems tend to accumulate organic matter and elements despite low inputs because organic matter decomposition is very slow. As a result, soil-available elements like N and P place key limits on increases in C fixation and further biomass and organic matter accumulation. Key issues for projecting whole-system responses to climate change include the importance of carbon–nutrient interactions; the interactions of C and nutrient cycles with temperature, water, and snow cover; the magnitude of dissolved organic and inorganic C losses in soil water; and the magnitude and role of wintertime processes. Most disturbances are expected to increase C and element turnover, particularly in soils. This is likely to lead to initial losses of elements but eventual, slow recovery. Individual species and species diversity have clear impacts on element inputs and retention in arctic ecosystems, but their magnitude relative to climate and resource supply is still uncertain. Similarly, the current information about the long-term effects of increasing CO_2 concentrations and UV-B radiation levels on whole ecosystems indicates that direct effects of these variables will probably be small relative to changes in soil resources and element turnover. Indirect effects of increasing CO_2 concentrations and UV-B radiation levels are likely to be more important at the ecosystem level (e.g., through changes in species composition).

The most important trace gases in arctic ecosystems are CO_2 and CH_4. Trace-gas exchange with the atmosphere occurs through a set of coupled soil ecosystem processes. Wet and moist tundra environments are known to be significant contributors to atmospheric CH_4. However, CH_4 is also consumed in aerobic parts of the soil. Methane emissions from the ecosystems are a balance between production and consumption, with production more responsive to warming than consumption. Soil warming in the absence of any other changes is very likely to accelerate emissions. Winter processes and vegetation type also affect CH_4 emissions. Nitrous oxide emissions are also sensitive to winter conditions and potential winter warming.

Arctic ecosystems exhibit the largest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation, to summer when the ecosystem absorbs most incoming radiation. Vegetation profoundly influences the water and energy exchange of arctic ecosystems. Vascular plants account for most CO_2 flux, whereas mosses account for most water vapor flux. Albedo during the period of snow cover declines from tundra to forest tundra to deciduous forest to evergreen forest. Shrubs and trees increase snow depth, which in turn increases ground heat fluxes; ecosystems with a large leaf area and insulating moss carpets reduce ground heat fluxes and conserve permafrost. Future changes in vegetation driven by climate change are very likely to profoundly alter regional climate.

7.5. Effects of climate change on landscape and regional processes and feedbacks to the climate system

Biological and physical processes and phenomena in the arctic system operate at various temporal and spatial scales to affect large-scale feedbacks and interactions with the earth system. Understanding these processes at multiple scales is critical because the effects of the complex interactions between physical, biological, and human dimensions on system performance cannot be projected by simply applying a different scale to existing results. Therefore, a multidisciplinary and quantitative approach is necessary to understand and project the response of the arctic system to variability in temperature and moisture. The large scale, inter-related processes described in this section include:

- ecosystem processes extrapolated to the landscape or regional scale (e.g., trace-gas exchange, water and energy exchange, and disturbance);
- changes in ecosystem distribution and abundance in the landscape;
- changes in vegetation zonation (e.g., treeline movement);
- interactions between terrestrial and freshwater ecosystems; and
- regional feedbacks.

Paleoclimate studies and studies of the contemporary Arctic together have identified four potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system; these are:

- albedo (reflectivity);
- greenhouse gas emissions and/or uptake through biological responses to warming;
- greenhouse gas emissions from methane hydrates released from thawing permafrost; and
- freshwater fluxes that affect thermohaline circulation.

In the past, three of the potential feedbacks have been generally positive and only one negative.

Some of the feedbacks such as energy and water exchange operate at local to regional scales whereas others, particularly trace-gas fluxes, have the potential to operate at regional to global scales. This section assesses the impacts of changes in climate (but not UV radiation levels, for which data are lacking) on ecosystem processes at the larger scale. The section explores the implications of these changes for feedbacks from terrestrial ecosystems to the climate system, but does not calculate changes in forcing (section 4.7.1). Nor does it consider freshwater discharge (sections 6.8.3 and 8.4.2) or methane hydrate feedbacks (section 6.6.2).

7.5.1. Impacts of recent and current climate on carbon flux

There are two complementary approaches to solve the carbon-flux inventory problem: “bottom-up” and “top-down”. The first is based on the long-term monitoring of gas emissions within networks of field stations or sites that cover the main types of habitats. At its simplest, total circumpolar emissions are estimated from the number and area of the types of northern ecosystems differentiated in terms of easily mapped features (e.g., vegetation, soil properties, relief, and geomorphology) and the characteristic annual exchange of CO_2 and CH_4 from each ecosystem. The data on CO_2 and CH_4 fluxes come from three main groups of available techniques that operate at different spatial scales: closed and open-top chambers (0.1 to 1 m^2), micrometeorological towers based on eddy covariance and gradient methods (10 to 10 000 m^2), and aircraft sensing (up to tens and hundreds of square kilometers). All three groups of techniques have their advantages and disadvantages. However, continuous measurements with towers seem to be the most appropriate for providing reliable information on the temporal variation of gas emissions at the ecosystem and landscape spatial levels.

7.5.1.1. Recent changes in carbon dioxide fluxes

Recent variations in arctic climate have had profound effects on some ecosystem- and regional-level C fluxes and, in general, these fluxes reflect the recent spatial variability in climate change. The assessment in this section is restricted to C in the active layer of soils and in plants, and does not consider C in permafrost and methane hydrates (section 6.6).

The North Slope of Alaska has experienced a rise in temperature (Fig. 7.26; Weller, 2000), an increase in growing-season length, and a decrease in available soil moisture (Oechel et al., 1993, 1995, 2000a; Serreze et al., 2000) over the last three to four decades. This has resulted in North Slope ecosystems changing from a sink for C throughout the Holocene (Marion and Oechel, 1993) to a source of C to the atmosphere beginning in the mid-1970s to early 1990s (Oechel et al., 1993, 1995, 2000a; Fig. 7.26). However, as there has been a change in climate, with progressive warming, drying, and lengthening of the growing season, there has been physiological, community, and ecosystem level adjustment that has reduced the rate of C loss from North Slope ecosystems (Fig. 7.26). In addition, wetter areas of the North Slope are not showing the same increase in CO_2 emissions (Harazono et al., 2003). The interannual variations in the C balance measured on the coastal plain of Alaska are very large, ranging from a net summer CO_2 uptake of about 25 g C/m^2/yr to a summer loss of over 225 g C/m^2/yr. If the latter fluxes held worldwide for wet coastal and moist tussock tundra, this would result in a net loss of up to 0.3 Pg C/yr from these two ecosystem types alone.

In northeast Greenland, the recent climatic history is different than that of Alaska: there has been no significant trend toward higher temperatures (Weller, 2000) and integrating over all vegetation types shows that the Zackenberg valley is a small net sink (2.3 g C/m^2/yr) with a large uncertainty range (±16.2 g C/m^2/yr). This integrated study of the valley shows that Landsat-derived C flux estimates are in good agreement with ground-based eddy correlation flux measurements covering all the dominant vegetation types in the valley. The Landsat method estimated a midday uptake rate in August 1997 of 0.77 g C/m^2/d for the valley as a whole whereas the ground-based measurements showed the uptake rate to be 0.88 g C/m^2/d (Søgaard et al., 2000). The measured annual balance in the valley varies from significant uptake in the intensively studied fen areas (on the order of 18.8±6.7 g C/m^2/yr) to net C losses in the dry heath (Christensen T. et al., 2000; Nordström et al., 2001; Søgaard et al., 2000).

Like Alaska, northern Scandinavian areas have experienced warming in recent years. The ecosystem C balance for a subarctic Swedish peatland was found to be a sink of between 15 and 25 g C/m^2/yr (Friborg, pers. comm., 2005). Similarly, in Finland, a net annual uptake of about 20 g C/m^2/yr was reported for a subarctic fen at Kaamanen (Aurela et al., 2002). Six years of continuous measurements at this fen show marked interannual variation in the CO_2 balances (sinks ranging from 4 to 52 g C/m^2/yr), which mainly reflect the variations in spring temperatures and the timing of the snow melt (Aurela et al., 2004). Studies of fluxes in high-arctic barren tundra on Svalbard show a very limited source of around 1 g C/m^2/yr (Lloyd C., 2001). Overall, the synthesis of regional C flux information from measurements at several sites in northern Europe and Greenland (the Land Arctic Physical Processes project; Laurila et al., 2001) indicates that arctic landscapes are remarkably similar in their C fluxes during midsummer, but the length of the growing season and the shoulder season fluxes are the key determinants for the net annual fluxes. This causes substantial interannual variability at the individual sites, and general uncertainty about whether the circumpolar Arctic is presently a source or a sink for C.

Recent work in East European tundra indicates a substantial current source of C in the northeastern European tundra areas (Heikkinen et al., 2004). When combined with the areas of the northern Alaska tundra mentioned above that are also a source of C, source areas (East European tundra, Svalbard, and Alaska) may exceed sink areas (northeast Greenland, northern Scandinavia). However, data are available for only a small part of the Arctic.

There may be a correlation between C balance and recent climatic history in areas that have seen a significant warming and drying: these areas experienced at least a temporary release of CO_2, while areas that have not experienced the same extent of warming and drying, or have possibly experienced a warming and wetting, remain atmospheric CO_2 sinks and could possibly even become large sinks. A complete synthesis of the available information from the circumpolar Arctic is underway but not yet available.

New models and approaches make estimation of current and future global C balances possible. The modeling approach has been used to explore potential changes in arctic terrestrial ecosystems from C sink to source status (Clein et al., 2000; McGuire et al., 2000). The Terrestrial Ecosystem Model (Marine Biological Laboratory, Woods Hole) has been used to estimate current and future C fluxes, while the model Hybrid v4.1

(Institute of Terrestrial Ecology, United Kingdom: Friend et al., 1997) has been used to simulate vegetation and carbon-pool changes at high latitudes for the period from 1860 to 2100 (White et al., 2000). For the present day, the models simulate a mix of C sinks and sources that reflect variations in current and past climate. McGuire et al. (2000) estimate that average circumpolar C fluxes presently constitute a small sink of 17 g C/m^2/yr with a standard deviation of 40 g C/m^2/yr that crosses the boundary between sink and source status. This uncertainty range is comparable to the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ) outputs (section 7.5.4.1; Sitch et al., 2003) and the calculation of current sink status corresponds to the projections by White et al. (2000).

Although it can be concluded that source areas currently exceed sink areas, there is great uncertainty about the current CO_2 balance of the Arctic, owing to geographically sparse measurements and inadequate representation of ecosystem dynamics in current models.

7.5.1.2. Current circumpolar methane fluxes

Probably the most intensive studies and the longest observations of CH_4 fluxes were performed in North America, mainly within the central Alaskan and North Slope sites at Barrow, Atqasuk, Toolik Lake, and Prudhoe Bay (Christensen T., 1993; Morrissey and Livingston, 1992; Vourlitis et al., 1993; Whalen and Reeburgh, 1990, 1992). In northern Eurasia including Russia, extensive measurements of gas emissions were initiated in the late 1980s, either as short-term measurements across geographic transects or as long time series of flux measurements at individual sites. The first approach is illustrated by chamber measurements of CH_4 (and CO_2) fluxes across the Russian Arctic (Christensen T. et al., 1995, 1998). The second approach is found at a number of field stations where gas fluxes are measured mainly during the summer season (Panikov et al., 1995, 1997; Wagner et al., 2003; Zimov et al., 1993).

The general characteristics of spatial and temporal flux variations can be formulated as follows. First, there are evident temperature-related variations: even within northern wetlands, the highest net fluxes occur in warmer soils, with maximum values attained in the boreal zone. This trend is especially evident with respect to CH_4 emissions, which increase along the latitudinal sequence Barrow–Toolik Lake–Fairbanks or Taymir–Surgut–Tomsk. Seasonal variations also follow a temperature curve, although winter, autumn, and spring emissions are often measurable (sections 7.3.2.3 and 7.4.2.1). Seasonal measurements of CH_4 emissions from five different wetland sites along a transect from northeast Greenland across Iceland and Scandinavia to Siberia also showed a clear positive relationship to the mean seasonal temperatures of the sites (Christensen T. et al., 2003b). Second, there are always enhanced emissions from wetland patches covered by vascular plants (e.g., *Eriophorum*, *Carex*, and *Menyanthes*) as compared with pure *Sphagnum* lawn (section 7.4.2.2). Third, variations in the water table affect CH_4 (and CO_2) emissions in opposite ways, with CH_4 fluxes stimulated and CO_2 suppressed by an increase in the water table. However, the range of fluxes varies so widely that uncertainty in regional and global estimates remains too large and is very dependent on the site-specific features of a particular study.
For example, extensive measurements using various techniques over the Hudson Bay Lowland (Roulet et al., 1994) led to the conclusion that northern wetlands are modest sources of atmospheric CH_4 (average July emissions as low as 10 to 20 mg CH_4/m^2/d). On the other hand, Alaskan wet meadow and shrub/tussock tundra have average summer emissions as high as 100 to 700 mg CH_4/m^2/d (Christensen T., 1993; Whalen and Reeburgh, 1992). The uncertainty in regional and global estimates that follows from these differences in measured fluxes is very frustrating and calls for alternative ways to solve the problem of scaling up fluxes.

One such alternative is the inverse modeling approach. In this top-down approach, information about the temporal and spatial variation of CH_4 and CO_2 emissions from soils is deduced from observations of gas mixing ratios in the atmosphere (obtained from a network of National Oceanic and Atmospheric Administration/Climate Monitoring and Diagnostics Laboratory field stations scattered over the globe, mainly in oceanic regions far from industrial effects). These data are fitted to a three-dimensional atmospheric transport model, which is combined with a tropospheric background chemistry module and accounts for all essential sources and sinks of gases. The model is validated against an "internal standard" such as methyl chloroform. Presently available results from inverse modeling (Hein et al., 1997) do not deviate significantly from data obtained by the bottom-up approach. The contribution of high-latitude regions (>60º N) to the global CH_4 source was less than 13% (70 Tg CH_4/yr), and northern wetlands were responsible for emissions of less than 30 Tg CH_4/yr. This estimate appears to contradict the latitudinal gradient of atmospheric CH_4 concentration that has a well-expressed maximum in the north, however, the higher concentration of CH_4 in the high-latitude atmosphere can be explained by low concentrations of the hydroxyl radical and, hence, lower rates of photochemical reactions that break down atmospheric CH_4.

7.5.1.3. Relative contributions of methane and carbon dioxide to the carbon budget

The formation of CO_2 and CH_4 is a result of aerobic and anaerobic decomposition, respectively. The ratio of respired CO_2 to CH_4 is hence an indication of how reduced the soil environment is. An increasingly reduced soil environment (i.e., higher CH_4/CO_2 ratio) also leads to slower overall decomposition rates, as anaerobic decomposition is less efficient in absolute C terms (i.e., less C is released compared to aerobic decomposition). This generally leads to a buildup of stored organic C in wet tundra soils, as net primary production is not normally limited by wet soil conditions to the same extent as respiration.

The net CH_4/CO_2 ratio of the total respiration is also a function of the amount of CH_4 that is oxidized in the aerobic soil layers above a given anaerobic zone of production and even the atmospheric CH_4 uptake that takes place in some dry tundra soil environments. The CH_4/CO_2 ratio or the percentage contribution of CH_4 to total respired C varies from <1% in dry ecosystems to >20% in extreme cases in wet tundra ecosystems. Typical annual average contributions of CH_4 to the total C flux range from 2 to 10% for wet tundra and northern wetlands (e.g., Christensen T. et al., 1996; Clymo and Reddaway, 1971; Klinger et al., 1994; Svensson, 1980; Svensson et al., 1999).

In the context of climate change, it is very important to note that the relative contribution of CH_4 to total radiative forcing is much greater on a per molecule basis than CO_2 (IPCC, 2001). The "global warming potential" (GWP) indicates how many times stronger a given greenhouse gas is compared to CO_2 on a per molecule basis, and this is dependent on the time horizon of interest. For example, over a 100-year time horizon, the GWP of CH_4 is 23 and over a 20-year horizon it is 63 (IPCC, 2001).

From the perspective of climate change, it is, hence, not very informative to look only at the C balance of an ecosystem if there are fluxes of CH_4 or other greenhouse gases such as N_2O (Christensen T. and Keller, 2003). Calculations have shown that ecosystems such as the huge western Siberian lowlands, despite being strong sinks for C, are sources of radiative forcing due to considerable CH_4 emissions (Friborg et al., 2003). Data are, however, scarce when it comes to full annual budgets of both CO_2 and CH_4 fluxes from tundra regions. Figure 7.31 shows calculations based on accumulated continuous eddy correlation measurements of CO_2 and CH_4 fluxes in the Zackenberg Valley, northeast Greenland during the summer of 1997 (Friborg et al., 2000; Søgaard et al., 2000). The figure illustrates that the effect of a net C accumulation ("minus" in the budget) during the season is completely offset if the CO_2 equivalent of CH_4 is calculated (using a 20-year time horizon) and added to the budget. Using the 100-year time horizon, the ecosystem is still a small sink of CO_2 equivalent at the end of the growing season. However, if the autumn and winter fluxes (which are entirely sources) were included, the annual total would probably add up to a source as well.

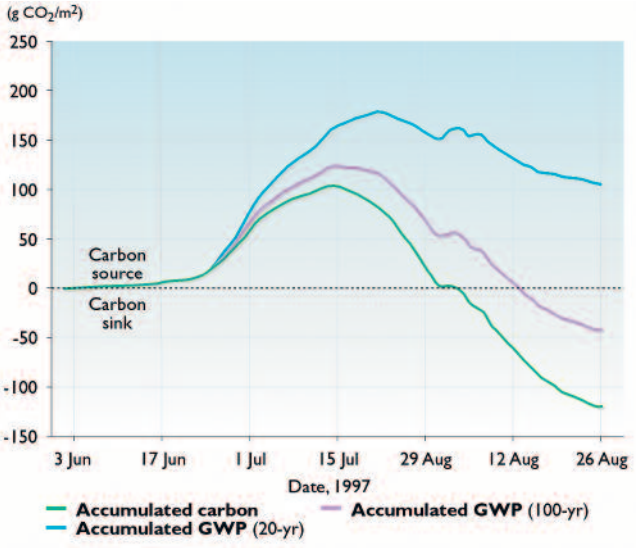

Fig. 7.31. Accumulated carbon and global warming potential (GWP, calculated as CO_2 equivalent) from CO_2 and CH_4 fluxes measured throughout the summer of 1997 at Zackenberg, northeast Greenland (data from Friborg et al., 2000; Søgaard et al., 2000).

In general, there are significant CH_4 emissions from the most productive tundra areas due to the predominantly wet soil conditions. It is very likely that, at the landscape, regional, and global scales, the tundra represents a source of radiative forcing due to emissions of CH_4, which is the most important greenhouse gas driving the ecosystem influence on atmospheric radiative forcing.

7.5.2. Current circumpolar water and energy balances

Arctic ecosystems exhibit the greatest seasonal changes in energy exchange of any terrestrial ecosystem because of the large changes in albedo from late winter, when snow reflects most incoming radiation (albedo about 0.7), to summer when the ecosystem absorbs most incoming radiation (albedo about 0.15). This change in albedo combined with greater incoming solar radiation in summer than in winter causes much greater energy absorption in summer than in winter. About 90% of the energy absorbed during summer is transferred to the atmosphere, with the rest transferred to the soil in summer and released to the atmosphere in winter (Eugster et al., 2000). Also, snow within shrub canopies is deeper and less dense, which reduces heat transfer through the snowpack and increases winter soil temperatures by 2 ºC relative to adjacent shrub-free tundra. Consequently, arctic ecosystems have a strong warming effect on the atmosphere during the snow-free season, and any increase in the duration of snow-free conditions results in a strong positive feedback to regional climate warming (Bonan et al., 1995; Foley et al., 1994).

Climate influences the partitioning of energy between sensible and latent heat fluxes. Cold moist air from coastal oceans, for example, minimizes latent heat flux (evapotranspiration), as does extremely warm dry air, which can induce stomatal closure (Eugster et al., 2000; Rouse, 2000); evapotranspiration is therefore greatest at intermediate temperatures. Conversely, sensible heat flux is a larger proportion of the energy transfer to the atmosphere when air is cold and moist or when drought limits stomatal conductance under dry conditions. Heat that is conducted into the ground during summer is released to the atmosphere in winter, with any seasonal imbalance causing changes in permafrost temperature leading to a probability of thermokarst (Osterkamp and Romanovsky, 1999).

There are large regional differences among arctic ecosystems in energy exchange and partitioning. Albedo during the period of snow cover is extremely high in tundra and declines with increasing development of a plant canopy above the snow, from tundra to shrub tundra to forest tundra to deciduous forest to evergreen forest (Betts A. and Ball, 1997). These differences in albedo are an important feedback to climate during spring, when the ground is snow-covered, and incoming radiation is high. As a result of differences in albedo and sensible heat flux, forests at the arctic treeline transfer about 5 W/m^2 more energy to the atmosphere than does adjacent tundra (Beringer et al., 2001b). This difference in energy transfer to the atmosphere depending on vegetation type is an order of magnitude less than the heating contrast that had been hypothesized to be required for treeline to regulate the position of the Arctic Front (Pielke and Vidale, 1995). Thus, the location of the Arctic Front is more likely to govern the position of the treeline than the other way around (Bryson, 1966).

7.5.3. Large-scale processes affecting future balances of carbon, water, and energy

This section assesses the effects of climate change on permafrost degradation and vegetation redistribution as a prerequisite for assessing changes in feedbacks from future terrestrial ecosystems to the climate system.

7.5.3.1. Permafrost degradation

Soil C storage is greatest where the drainage is slight and the limited precipitation is held near the surface by permafrost and modest topography. This results in ponds, wetlands, and moist tundra with a saturated seasonal active layer that limits microbial activity. Increases in active-layer depth can cause subsidence at the surface, a lowering of the soil water table (Hinzman et al., 2003), and, potentially, thermokarst erosion (Hinzman et al., 1997). This can drain surrounding areas, often increasing the decomposition rate of soil organic matter, which accelerates the loss of belowground C stores (Oberbauer et al., 1991, 1996) and results in a change in plant communities and their abilities to sequester atmospheric CO$_2$. Initially, increased soil decomposition rates can increase mineralization rates (Rastetter et al., 1997) and result in increased NPP (section 7.4.2.1). However, continued thawing of permafrost and increased drainage of surface water in areas with low precipitation are likely to lead to drier soils, a decrease in NPP, and possibly even desertification (section 7.5.3.2).

Full permafrost disintegration in subarctic discontinuous permafrost regions may in some cases show a different response. Monitoring of changes in permafrost distribution in subarctic Sweden as part of the Circumpolar Active Layer Monitoring Program (Brown et al., 2000) shows that permafrost loss causes mires to shift from ombrotrophic moss- and shrub-dominated systems to wetland systems dominated by minerotrophic vascular plants (Christensen T. et al., 2004; Svensson et al., 1999). This, in turn, leads to a significant lowering of soil redox potentials, an increase in anaerobic decomposition, and increased CH$_4$ emissions. Wet minerotrophic soils and vegetation are in general associated with the highest CH$_4$ emissions in subarctic and arctic tundra environments. Discontinuous permafrost regions are considered some of the most vulnerable to climate warming; given projected temperature increases over the next 100 years, effects such as the changes in vegetation composition discussed here are likely.

Permafrost degradation and disintegration are therefore very likely to have major effects on ecosystem C balances and CH$_4$ emissions. The rate of permafrost thawing, the amount of ground surface subsidence, and the response of the hydrological regime to permafrost degradation will depend on numerous site characteristics. Changes in the hydrological regime will also alter the soil thermal regime. In areas with significant topographic variations, flowing water can carry heat into drainage channels, causing increased soil temperatures and increased active-layer thickness (Hastings et al., 1989; Kane et al., 2001). In regions with minor topographic variations, subtle differences in elevation can create cooler, saturated wetlands (as mentioned in the previous paragraph) or markedly drier, warmer uplands (Rovansek et al., 1996).

7.5.3.2. Changes in circumpolar vegetation zones

While climate-driven changes in the structure and distribution of plant communities affect trace gas fluxes and water and energy balances at the landscape scale (section 7.4.2), changes in the location and extent of broad vegetation zones is a longer-term integrative process that is likely to lead to regional and even global impacts on feedbacks to the climate system (Betts R., 2000; Chapin F. et al., 2000a; Harding et al., 2002; McGuire et al., 2002). Such vegetation zone changes are also likely to affect permafrost dynamics (section 6.6), biodiversity (section 7.3.1), and ecosystem services (Vlassova, 2002). Past climate-driven changes in vegetation zones such as forest and tundra (section 7.2; Payette et al., 2002) lead to the expectation that future climate warming is very likely to result in vegetation and ecosystem change, but projecting future changes is complex and relies on modeling.

Dynamics of the treeline and changes in the areas of tundra and taiga vegetation

The latitudinal treeline or tundra–taiga boundary is an exceptionally important transition zone in terms of global vegetation, climate feedbacks, biodiversity, and human settlement.

The treeline stretches for more than 13 000 km around the Northern Hemisphere and through areas that are experiencing different types of environmental change, for example, cooling, warming, or marginal temperature change and increasing or decreasing land use. Climate is only one of a suite of environmental factors that are now changing, and a critically important challenge is to determine how human impacts in the ecotone will modify its projected response to climate change (Vlassova, 2002).

The lack of standardized terminology and the wide variation in methodology applied to locate, characterize, and observe changes in the boundary have resulted in a poor understanding of even the current location and characteristics of the boundary. Particular areas of uncertainty include the Lena Delta of Siberia (Callaghan et al., 2002a) and forests in Iceland that have been subjected to major environmental and land-use changes since colonization by people about 1100 years BP (section 14.3.4.4). One of the major problems with current studies of the latitudinal "treeline" is the concept of "line" inappropriately applied to the transition from forest, through an area dominated by forest in which patches of tundra occur, to tundra in which patches of forest occur, and then eventually to tundra without trees. Often there are east–west gradients related to the presence of a river valley, bogs, mires, uplands, etc. that also confound the concept of a linear boundary.

Dynamics of the boundary

Current and projected changes in the location of the tundra–taiga boundary should be seen in the context of the longer-term past cooling trend during which the treeline has been at its lowest latitudinal and altitudinal locations for several thousands of years (section 7.2.4). Examples of recent treeline advance include a 40 m increase in the elevation of the subarctic treeline in northern Sweden during the 20th century (Emanuelsson, 1987; Kullman, 1979; Rapp, 1996; Sonesson and Hoogesteger, 1983), an increase in shrub growth in Alaska (Sturm et al., 2001b), and an increase in shrubbiness and larch advance in the northeast Russian European Arctic (Katenin, unpub. data, 2004). In contrast, other studies show a surprising southward displacement of the tundra–taiga boundary (Crawford et al., 2003; Kozhevnikov, 2000; Vlassova, 2002). Part of this is a counter-intuitive response to warming in which an increasingly oceanic climate (e.g., in the western Russian Arctic: see section 8.4.1, Fig. 8.9) together with permafrost thawing have led to paludification (waterlogging and peat formation) and the death of treeline trees (Skre et al., 2002). Part is associated with human activities, including mining, farming, and forestry, that have led to ecosystem degradation in the forest tundra zone and the movement of its northern boundary southward in some locations (Vlassova, 2002). In the Archangelsk region and the Komi Republic, the southern border of the forest tundra zone now lies 40 to 100 km further south than when previously surveyed. One report claims that anthropogenic tundra now covers about 470000 to 500000 km^2 of the forest tundra stretching from Archangelsk to Chukotka (Vlassova, 2002), although it is likely that this estimate includes deforestation in some of the northern boreal forest zone.

Although records of recent changes in the location of the latitudinal treeline are surprisingly rare, there is good evidence of increased growth in current northern forests. Comparisons of the greenness index (NDVI) from satellite images show that May to September values for the Northern Hemisphere between 55º and 75º N increased by around 5 to 50% from 1982 to 1990 (Myneni et al., 1997; Fig. 7.25), with greater increases in North America than in Eurasia. The increased greenness was associated with an increase in growing-season length of between 3.8 and 4.3 days for the circumpolar area, mainly due to an earlier start of the growing season.

Projecting future changes in the tundra–taiga boundary

In order to model changes in the location of the tundra–taiga ecotone and estimate future areas of tundra to the north and taiga to the south, it is necessary to understand the causes of the treeline. Opinions on the mechanisms controlling the location of the treeline vary greatly. Some researchers see the limit of tree growth as a universal mechanism related to a specific process such as sink (C and nutrient) limitation (Körner, 1998, 1999) or C limitation (Nojd and Hari, 2001). Others see a range of possible mechanisms that operate in different places and at different times (Sveinbjörnsson et al., 2002). These mechanisms are in turn affected by environmental factors such as incident radiation, temperature, wind, moisture, and soil nutrients, which affect tree reproduction, seedling establishment, and the growth and physiology of mature trees. Extreme conditions such as ice-crystal abrasion and soil movement also directly damage tree tissues (e.g., conifer needles) and displace individuals. Diseases, pests, fires, and human activities all exert some control on the treeline at certain places and at certain times (Chapter 14).

Models of vegetation redistribution resulting from global change utilize more general driving variables, related to, for example, biogeography and biogeochemistry. Most current global vegetation models and regional models project that a major part of the tundra (between 11 and 50% according to location) will be displaced by a northward shift of the boreal forest over the period in which atmospheric CO_2 concentrations double (Harding et al., 2002; Kaplan et al., 2003; Skre et al., 2002; Table 7.13; section 7.6, Table 7.14; Fig. 7.32). The treeline is projected to move north in all sectors of the Arctic, even in Greenland and Chukotka where only fragments of forest exist today (Kaplan et al., 2003). However, to date there have been fewer observations of this type of forest response than projections suggest, even though temperature has already risen dramatically in some areas.

The observations of the latitudinal treeline that show a recent *southern* displacement suggest that there is very unlikely to be a general northward displacement of the latitudinal treeline throughout the circumpolar region as the models project. In addition to potential paludification (Crawford et al., 2003) and local human activities displacing treelines southward, permafrost thawing, surface-water drainage, and soil drying in areas of low precipitation are likely to lead to the formation of vegetation similar to the tundra–steppe (Yurtsev, 2001; section 7.2.2). Increased disturbances such as pest outbreaks, thermokarst, and fire are also likely to locally affect the direction of treeline response. In addition, some tree species show reduced responsiveness to increases in temperature with increasing continentality of their location and decreased precipitation (Linderholm et al., 2003; section 14.7). This suggests that increased temperatures with no comparable increase in precipitation are likely to lead to reduced tree growth and/or changes in species and lack of treeline advance. Even in areas projected to undergo warming with none of the moderating factors listed above, it is uncertain if the rate of tree migration can keep up with the rate of projected temperature increases. Past tree migration rates were generally of the order of 0.2 to 0.4 km/yr but sometimes reached 4.0 km/yr (section 7.2; Payette et al., 2002). These rates suggest that in those areas of the Arctic that have warmed substantially in the last 30 years, treeline should already have advanced by about 6 to 120 km. Such shifts have not been recorded in the Arctic, although Parmesan and Yohe (2003) claim to have identified a poleward displacement of species ranges of 6.1 km per decade globally.

Table 7.13. Averages and ranges of the drivers and responses of a leading dynamic global vegetation model (LPJ) driven with the outputs for the terrestrial Arctic (>60° N) from four different climate models (CGCM2, GFDL-R20_c, HadCM3, ECHAM4/OPYC3) forced with the B2 emissions scenario (Sitch et al., 2003; Sitch et al., submitted).

	Average	Range
Temperature change (°C)		
2000–2100	5.0	4.7 to 5.7
Precipitation change (mm/yr)		
2000–2100	42.9	9.0 to 78.0
NPP (Pg C/yr)		
1960s	2.83	2.77 to 2.88
2080s	4.87	4.57 to 5.19
Change (%)	72.4	60.9 to 87.4
Change in C storage 1960–2080 (Pg C)		
Vegetation	5.73	3.59 to 7.65
Soil	6.98	1.6 to 15.6
Litter	5.6	3.4 to 9.6
Total	18.3	12.2 to 31.3
Percent areal vegetation change[a]		
Increase in taiga area[b]		
1960–2020	4.4	3.1 to 5.3
1960–2050	7.4	6.4 to 8.4
1960–2080	11.3	9.8 to 14.4
Change in polar desert area[c]		
1960–2020	-7.5	-13.3 to -4.2
1960–2050	-13.2	-18.5 to -10.6
1960–2080	-17.6	-23.0 to -14.2

[a] Only a proxy as the change is derived from functional characteristics of the vegetation produced by the model rather than projections of specific vegetation composition *per se*. For a proper vegetation distribution estimate, it would be more appropriate to use a coupled biogeography and biogeochemistry model such as BIOME4; [b] based on the percentage increase in woody plants simulated by LPJ; [c] based on the percentage reduction in bare ground simulated by LPJ

Overall, it is likely that treeline will show many different responses throughout the circumpolar north according to different degrees of temperature change associated with various changes in precipitation, permafrost dynamics, land use, and tree species migration potential.

Projecting future changes in the areas of tundra and polar desert

The LPJ model was used to project vegetation changes in the northern areas of the Arctic (Sitch et al., 2003; Table 7.13; section 7.6, Table 7.14), using climate scenarios generated by four of the five ACIA-designated models (CGCM2, GFDL-R30_c, HadCM3, and ECHAM4/OPYC3; section 4.2.7) forced with the B2 emissions scenario (section 4.4.1). Although the results and interpretations are preliminary, LPJ simulations are consistent in projecting a decrease in the area of polar desert that will be replaced by northward-moving tundra (Table 7.13). The area of the Arctic covered by polar desert is projected to decrease by 17.6% (range 14 to 23%) between 1960 and 2080. In this model, the two vegetation zones were defined by plant functional types: woody species for the tundra, and absence of woody species for the polar desert. In the BIOME4 (coupled biogeography and biogeochemistry model) simulations by Kaplan et al. (2003), driven by output from the HadCM2GSa1 model forced with the IS92a emissions scenario, five tundra biomes were constructed (Table 7.8). The most significant changes appear to be a significant northward advance of the cold evergreen needleleaf forest that is particularly dramatic in the region of arctic Russia between Chukotka and the Taymir Peninsula. This greatly reduces the area of tundra. However, low- and high-shrub tundra in the Canadian Archipelago remains as a wide zone and displaces prostrate dwarf-shrub tundra (Figs. 7.2 and 7.32). Earlier modeling by White et al. (2000) projected that the area of tundra would be halved by forest expansion by 2100.

7.5.4. Projections of future balances of carbon, water, and energy exchange

Because the Arctic contains huge stores of C in the soil and permafrost (section 7.4.2), and because the Arctic has the capacity for unlimited additional storage or significant loss (Billings et al., 1982, 1984), it can be a major positive or negative feedback to increasing trace-gas concentrations in the atmosphere and to global climate change. Loss of CO_2 from arctic ecosystems could potentially lead to enormous positive feedbacks to global climate change by release to the atmosphere of the estimated 250 Pg C stored in the large arctic soil pool, although this is unlikely to happen (Billings, 1987;

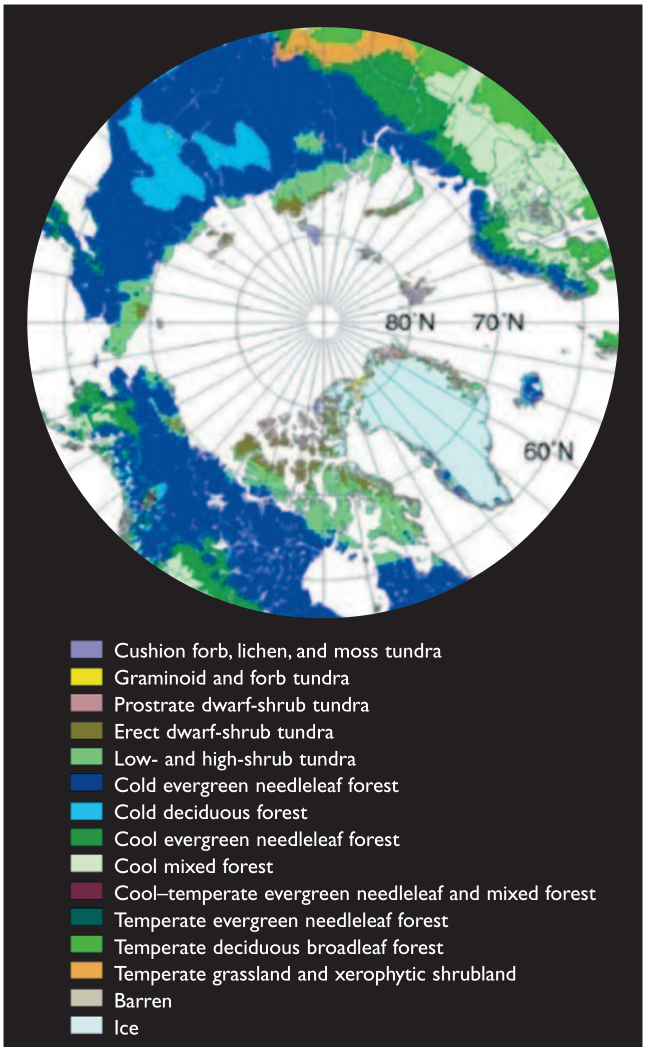

Fig. 7.32. Potential vegetation distribution in 2090–2100 as projected by the BIOME4 model driven with output from the HadCM2GSa1 model forced with the IS92a emissions scenario (Kaplan et al., 2003).

Billings et al., 1982; Lal et al., 2000; Oechel and Billings, 1992; Oechel et al., 1993, 1995, 2000a). In addition, an increasing snow-free period (Engstrom et al., 2002; Keyser et al., 2000), increasing shrub cover (Silapaswan et al., 2001; Sturm et al., 2001a,b), and the northward migration of the treeline (Lloyd A. et al., 2003) are very likely to decrease arctic albedo and further increase regional warming (Bonan et al., 1992; Chapin F. et al., 2000a,b; Foley et al., 1994; McFadden et al., 1998; Thomas and Rowntree, 1992). This section assesses likely changes in the C balance and water and energy exchange in relation to vegetation change.

7.5.4.1. Carbon balance

The vegetation distribution model BIOME3, forced with present-day and doubled atmospheric CO_2 concentrations, projected decreases in the extent of the Scandinavian, central northern Siberian, and Eurasian tundra areas ranging from 10 to 35% as a result of displacement by taiga (Harding et al., 2002). This vegetation change was projected to significantly increase CO_2 uptake and reduce CH_4 emissions, with net C sequestration in the biosphere of a magnitude (4.6 Pg C) that would alter the radiative forcing of the earth. Using another model, McGuire et al. (2000) estimated that circumpolar mean C uptake would increase from a current 12 g C/m^2/yr to 22 g C/m^2/yr by 2100, because NPP increased more than respiration throughout the period (McGuire et al., 2000). It should be noted, however, that throughout the 200-year model run, the standard deviation of C uptake always crosses the zero line (McGuire et al., 2000). White et al. (2000) obtained comparable results from their Hybrid v4.1 model, projecting that high-latitude terrestrial ecosystems would remain a sink for C.

The LPJ model (Sitch et al., 2003; Box 7.1) was used to produce estimates of future changes in arctic C storage and fluxes for this assessment, based on four different general circulation model (GCM) outputs. The results and analyses are preliminary but indicate a consistent net additional sink in the Arctic in 2080 compared to 2000, with increases in accumulated arctic C storage varying between 12 and 31 Pg C depending on the climate scenario used. Figure 7.33 shows the C storage anomalies projected by the LPJ model, and Table 7.14 (section 7.6) shows further details of the regional subdivision of these projections.

There are great uncertainties associated with these estimates due to the complex differential response of NPP and respiration to the climate drivers (temperature, precipitation), which themselves are highly spatially variable and interact. However, the general response of the model seems to be as follows. In areas with little or no vegetation (e.g., polar desert), increasing CO_2 concentrations and temperature (e.g., increasing growing-season length) lead to increased vegetation growth and northward plant migration, resulting in an increase in C stocks. This seems to be a general pattern acting through increased productivity throughout the Arctic, all else being equal (see NPP projections in Table 7.13). However, increased temperature leads also to increased heterotrophic (soil microorganism) respiration. Therefore, areas that at present contain large soil C stocks are likely to release larger amounts of C from the soil as respiration responds to a warmer climate. Whether these areas become net sources or sinks depends on the balance between temperature-enhanced respiration and increased productivity (hence increased biomass and litterfall) due to increased CO_2 concentrations and longer growing seasons. When the LPJ model was forced with the climate projections of the ECHAM4/OPYC3 model, which projects very large temperature increases, projected respiration was enhanced more than productivity. Over the entire Arctic, C storage is projected by the LPJ model to balance, due to northward migration of plants, etc., with C loss in areas that experience large temperature changes and have large stocks of soil C. On the whole, all runs of the LPJ model project that C storage will increase. The scenario with the highest projected temperature change (ECHAM4/OPYC3) results in the low-

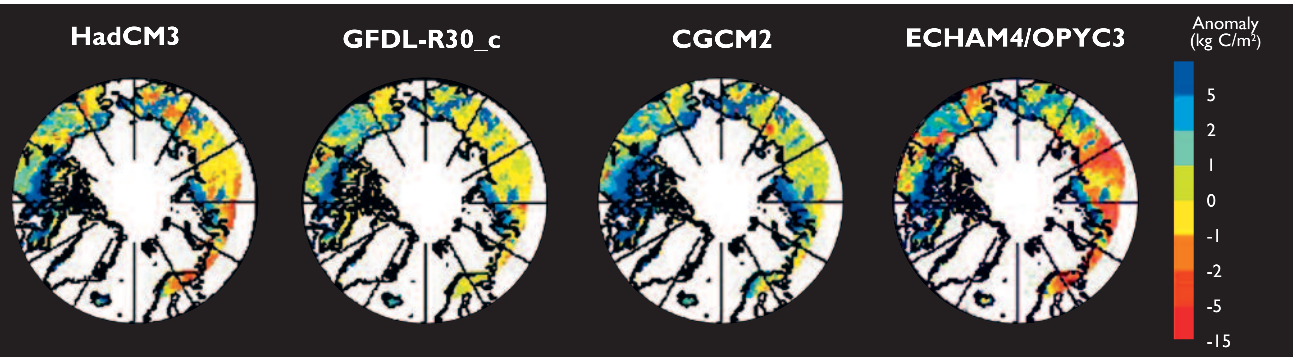

Fig. 7.33. Carbon storage anomalies between 1960 and 2080 projected by the LPJ model using climate scenarios generated by four of the five ACIA-designated models (Sitch et al., 2003).

est overall C gain, while the scenario with the lowest projected temperature change (CGCM2) results in the highest C gain.

The current estimated circumpolar emissions of CH_4 are in the range of 20 to 60 Tg CH_4/yr. These have a significant potential for feedback to a changing climate. Large-scale CH_4 flux models are currently not as advanced as general carbon-cycle models and few allow for projections of future change based on climate change scenarios. Early attempts to assess and model tundra CH_4 emissions driven by climate change all indicated a potential increase in emissions (Christensen T. and Cox, 1995; Harriss et al., 1993; Roulet et al., 1992) but more recent improved mechanistic models (Granberg et al., 2001; Walter and Heimann, 2000) have not yet been followed up by full coupling to GCM projections to assess future circumpolar CH_4 emissions. Another critical factor is the geographic extent of wetlands and how these may change in the future. There is, however, little doubt that with climate scenarios of warming and wetting of arctic soils, CH_4 emissions are very likely to increase, while with warming and drying, emissions are likely to change little or decline relative to current emissions.

Lakes and streams cover large portions of many arctic landscapes and, due to low evapotranspiration, runoff is a major component of arctic water budgets. These surface freshwaters contain large amounts of dissolved organic and inorganic C that is carried into them by soil and groundwater flow from the terrestrial portions of their watersheds (Kling et al., 1992, 2000). The inorganic C is largely CO_2 produced by soil and root respiration. Organic C concentrations in soil water, groundwater, and surface waters are typically several times greater than inorganic C concentrations and are a major source of respiratory CO_2 produced in lakes and streams, thus adding to their already high dissolved inorganic C content.

Because the dissolved CO_2 in surface waters is typically supersaturated with respect to the atmosphere, and the surface area and flow of freshwater is large, surface waters of arctic landscapes emit large amounts of CO_2 to the atmosphere (Kling et al., 1991; section 8.4.4.4). Estimates of CO_2 emissions from surface waters are as large as 20 to 25% of gross landscape CO_2 fixation and thus may be a major component of landscape C balance that is not accounted for in studies that include terrestri-

Box 7.1. The Lund-Potsdam-Jena model

The Lund-Potsdam-Jena (LPJ) dynamic global vegetation model combines process-based, large-scale representations of terrestrial vegetation dynamics and land–atmosphere carbon and water exchanges in a modular framework. Features include feedback through canopy conductance between photosynthesis and transpiration, and interactive coupling between these rapid processes and other ecosystem processes including resource competition, tissue turnover, population dynamics, soil organic matter and litter dynamics, and fire disturbance. Ten plant functional types (PFTs) are differentiated by physiological, morphological, phenological, bioclimatic, and fire-response attributes. Resource competition and differential responses to fire between PFTs influence their relative fractional cover from year to year. Photosynthesis, evapotranspiration, and soil water dynamics are modeled on a daily time step, while vegetation structure and PFT population densities are updated annually.

Within the biosphere model (Sitch et al., 2003), the raw GCM (CGCM2, GFDL-R30_c, HadCM3, and ECHAM4/OPYC3 forced with the B2 emissions scenario) climatologies for 1900 to 2100 were not used directly. The climate simulated by present-day GCMs is not spatially detailed enough to directly drive a biosphere model, therefore the anomaly approach was used. The data were downscaled from the GCM-specific grid onto a grid with 0.5° resolution. Climate anomalies projected by the GCMs were normalized to the 1961–1990 observed average monthly Climatic Research Unit climatology (CRU CL 1.0: New et al., 1999).

al CO_2 fluxes only. Similar large CO_2 losses also occur in freshwaters of boreal, temperate, and tropical landscapes (Cole et al., 1994), but they are generally not considered in landscape-level C budgets. At present, little is known about controls over these CO_2 losses or how they might change with changes in climate or water balance. Attempts to measure the losses directly have yielded inconsistent results (Eugster et al., 2003).

7.5.4.2. Energy and water exchange

Many of the likely changes in water and energy exchange that occur in response to projected future warming are likely to act as a positive feedback to warming. Earlier disappearance of snow from the tundra is very likely to lead to a decline in albedo and an increase in regional warming (Bonan et al., 1992; Thomas and Rowntree, 1992). Similarly, an expansion of forest will lead to a reduction in albedo, because trees mask a snow-covered surface. In areas where forest expansion occurs, this is very likely to lead to significant heating of the lower atmosphere (sections 7.4.2.3 and 7.5.2). Paleoclimate modeling experiments have shown that the northward movement of the treeline 6000 years BP accounted for half of the climatic warming that occurred at that time (Foley et al., 1994). Although the current arctic treeline appears relatively stable or retreating in some areas of human impact (Callaghan et al., 2002a; Vlassova, 2002; section 7.5.3.2), any future northward advance of the treeline is likely to contribute to regional warming, while treeline retreat is likely to contribute to regional cooling, particularly in late spring due to the large differences in albedo between snow-covered tundra and adjacent forest.

A positive feedback (leading to increased warming) of displacement of tundra by trees and shrubs could possibly offset the negative feedback (leading to cooling) due to increased C sequestration at the local level (Harding et al., 2002), but the climate forcing by energy and water exchange operates primarily at the regional scale, where the energy exchange occurs, whereas the negative feedback due to sequestration of atmospheric C is likely to vary between regions and contribute to warming through changes in the globally mixed pool of atmospheric CO_2. Models suggest that forests in the eastern Canadian Arctic would have a net negative feedback through sequestration of C whereas forests in arctic Russia would have a net positive feedback to climate through decreased albedo (Betts R., 2000; Betts A. and Ball, 1997). This complex balance between opposing feedbacks indicates that encouraging forest to displace tundra as an appropriate strategy to mitigate *global* climate change should take into account the local feedback.

An important contributing factor to the effect of vegetation change on albedo is the characteristics of the plant canopy in terms of canopy height relative to snow height, leaf duration, and leaf optical properties. The greatest changes in albedo are likely to occur after increases in area relative to tundra vegetation of the following vegetation types (in decreasing order of effect): dark, evergreen boreal trees such as pine and spruce, deciduous conifer trees such as larch, deciduous angiosperm trees such as birch, and low shrubs such as willows and dwarf birch.

The vegetation changes projected to occur in northern Alaska in response to climatic warming are calculated to increase summer heating of the atmosphere by 3.7 W/m^2 (Chapin F. et al., 2000a). This warming is equivalent to the unit-area effect of a doubling of atmospheric CO_2 concentrations or a 2% increase in the solar constant (i.e., the difference that caused a switch from a glacial to an interglacial climate), two forcings that are known to have large climatic effects (Kattenberg et al., 1996). Regional climate simulations suggested that a conversion from moist tussock tundra to shrub tundra would cause a 1.5 to 3.5 ºC increase in mean July temperature on the Alaskan North Slope, reflecting greater sensible heat fluxes to the atmosphere from the shrub-dominated ecosystem. Thus vegetation changes of the sort that have recently been observed (Sturm et al., 2001b) are very likely to have large positive feedbacks to regional warming if the increased shrub cover is extensive. This vegetation–climate feedback requires only modest increases in shrub density to enhance sensible heat flux (McFadden et al., 1998).

The transition from tundra to forest also affects evapotranspiration and the water storage capacity of the biosphere, such that freshwater runoff via rivers to the Arctic Ocean could possibly decrease (Harding et al., 2002).

Other human activities also have impacts on the local climate of the forest tundra. Deforestation, as a result of industrial activities or forestry, increases wind speeds; pollution leads to earlier snowmelt and increased temperatures, and the northward extension of farming and settlements in general induces permafrost thawing (Vlassova, 2002).

7.5.5. Summary

Biological and physical processes in the Arctic operate at various temporal and spatial scales to affect large-scale feedbacks and interactions with the earth system. There are four main potential feedback mechanisms between the impacts of climate change on the Arctic and the global climate system: albedo, greenhouse gas emissions or uptake by ecosystems, greenhouse gas emissions from methane hydrates, and freshwater fluxes that affect the thermohaline circulation. All of these feedbacks are controlled to some extent by changes in ecosystem distribution and character and particularly by large-scale movement of vegetation zones. However, it is difficult to assess the consequences of the interacting feedbacks or even of individual feedbacks.

There are currently too few full annual measurements available to give a solid answer to the question as to whether the circumpolar Arctic is an atmospheric source or a sink of CO_2 at the landscape scale (Box 7.2). Indications are, however, that source areas currently exceed sink areas. Measurements of CH_4 sources are also inadequate, but the available information indicates emissions at the landscape level that are of great importance to the total greenhouse gas balance of the circumpolar north. In addition to the effect of greenhouse gases, the energy and water balances of arctic landscapes encompass important feedback mechanisms in a changing climate. Increasing density and spatial expansion of the vegetation cover will reduce albedo and cause more energy to be absorbed on the ground; this effect is likely to exceed the negative feedback of increased C sequestration via greater primary productivity. The degradation of permafrost has complex consequences. In areas of discontinuous permafrost, warming is very likely to lead to a complete loss of the permafrost. Depending on local hydrological conditions, this may in turn lead to a wetting or drying of the environment with subsequent implications for greenhouse gas fluxes. Models projecting vegetation change in response to scenarios of future climate change indicate a 7 to 18% decrease in the area occupied by polar desert and a 4 to 11% increase in the area occupied by taiga over the next 80 years. This is projected to lead to increased carbon storage over this same period due to productivity being stimulated more than respiration. However, the balance depends on the degree of projected warming. With greater temperature increases, heterotrophic respiration is stimulated more and the projected carbon gain is less. Very few models are available for projections of future CH_4 emissions, but these emissions will be extremely important to the total greenhouse gas balance and functioning of the circumpolar Arctic.

Box 7.2. Will the Arctic become a source of carbon, or remain a sink?

There is not yet a definitive answer to this question, although past opinions favored the hypothesis that the tundra will switch from being a sink for carbon during recent millennia to becoming a source under future warming scenarios, based mainly on the response of increased soil respiration to warming relative to increases in photosynthesis. At a recent meeting of experts on carbon dynamics in the Arctic, the following authoritative consensus statements were made.

Consensus statements on arctic carbon source/sink functioning from the Synthesis Workshop on "Current and future status of carbon storage and ecosystem–atmosphere exchange in the circumpolar north: Processes, budgets and projections", Skogar, Iceland, 21 June 2003.

- The available carbon flux data show large interannual variability. Arctic terrestrial ecosystems are a patchwork, with some regions being sources of carbon to the atmosphere (mostly dry and mesic ecosystems) and some regions being sinks (mostly wet tundra). Current indications are that source areas exceed sink areas.
- The available data indicate that when considering both CO_2 and CH_4, the Arctic is a source of radiative forcing.
- Contrary to the data from ground-based measurements, current global carbon models indicate that the Arctic is a small carbon sink. This apparent discrepancy is, however, within the uncertainty range of the data and model outputs.
- The recent remote-sensing record indicates a greening of the Arctic, suggesting increased photosynthetic activity and net primary productivity, but does not address the belowground processes (i.e., respiration).
- Projections from global models of vegetation and soil responses to climate change suggest that enhanced vegetation production will exceed increases in decomposition, thereby resulting in net carbon sequestration. However, there are large uncertainties, including the response of heterotrophic respiration, nutrient cycling, permafrost dynamics, land-cover change, and scaling issues.
- Experimental data indicate that warming enhances carbon loss under dry soil conditions and enhances carbon sequestration under wet soil conditions. Thus, future responses to regional warming will depend substantially on changes in soil moisture.
- Recent observations indicate that cold-season greenhouse gas emissions contribute substantially to the annual budget.

The new, but uncertain, insights from these statements are that the Arctic is already a source of carbon and radiative forcing, and that it is likely to become a weak sink of carbon during future warming. Other uncertainties, not addressed in the consensus statements, include:

- potential complex flux patterns over long time periods during which acclimation of carbon fluxes to warming leads to transient trends within millennia-long smoothing of shorter-term dynamics;
- probable increased physical and biotic disturbance during warming that might increase carbon emissions, particularly if carbon storage shifts from tundra soils to invading forests; and
- various feedbacks between changing vegetation, soil temperatures, quality and quantity of litter, and biodiversity of decomposer organisms.

Many uncertainties remain, and it should be noted that the carbon considered in this discussion is that in the active layer of the soil and in vegetation, and not that trapped in permafrost and methane hydrates.

Table 7.14. Summary baseline information for the four ACIA regions.

	Region 1	Region 2	Region 3	Region 4
	Arctic Europe, East Greenland, European Russian North, and North Atlantic	Central Siberia	Chukotka, Bering Sea, Alaska, and western Arctic Canada	Northeast Canada, Labrador Sea, Davis Strait, and West Greenland
Projected environmental changes				
Mean Annual Temperature[a] (°C)				
Baseline 1981–2000	-17 to 16	-8 to 4	-8 to 12	-20 to 12
2020 (change from baseline)	-1 to 3	0 to 2.5	-0.5 to 3.0	-1 to 4
2050 (change from baseline)	-0.5 to 4.0	0.5 to 4.0	0 to 4	0 to 7
2080 (change from baseline)	1 to 7	1 to 6	0.5 to 6	0 to 8
Precipitation[a] (mm/month)				
Baseline 1981–2000	10 to 150	10 to 70	10 to 150	5 to 130
2020 (change from baseline)	-10 to 12	-8 to 5	-10 to 8	-10 to 20
2050 (change from baseline)	-20 to 20	-2 to 5	-4 to 12	-8 to 35
2080 (change from baseline)	-20 to 25	0 to 10	-3 to 12	-15 to 35
Increase in UV-B radiation levels from 1979–1992 baseline (%)[b]				
Mean for 2010–2020	0 to 10	0 to 8	0 to 2	0 to 14
Mean for 2040–2050	0 to 2	0 to 2	0 to 2	0 to 2
Change in albedo[c] (due to vegetation change)				
2050	-0.10 to 0.05	-0.050 to 0.025	-0.10 to 0.025	-0.050 to 0.025
2080	-0.10 to 0.01	-0.050 to 0.025	-0.10 to 0.025	-0.10 to 0.025
Ecosystem processes projected by the LPJ model[d]				
NPP (Pg C/yr)	See Table 7.13 for the arctic total			
1960s	1.2	4.0	4.6	1.5
2080s	1.8	6.5	7.5	3.8
Change (%)	46.3	62.3	63.8	144.4
NEP: Change in C storage 1960–2080 (Pg C)	See Table 7.13 for the arctic total			
Vegetation	0.2	1.7	2.5	1.3
Soil	-0.1	0.5	1.9	4.7
Litter	-0.02	0.5	1.8	3.4
Total	0.04 (-0.7 to 0.8)	2.8 (-0.9 to 7.1)	6.2 (4.1 to 9.5)	9.3 (6.5 to 14.0)
Landscape processes projected by the LPJ model[d]				
Increase in taiga area (%)[e,f]				
1960–2020	1.1 (-1.1 to 2.3)	6.1 (4.2 to 8.6)	4.2 (1.9 to 5.7)	3.7 (2.9 to 4.4)
1960–2050	3.2 (1.6 to 4.3)	9.4 (7.5 to 10.2)	8.2 (6.5 to 9.7)	5.0 (3.8 to 6.2)
1960–2080	5.0 (3.7 to 5.9)	13.7 (11.1 to 17.3)	11.9 (9.8 to 15.1)	9.5 (6.8 to 12.5)
Change in polar desert area (%)[e,g]				
1960–2020	-2.3 (-3.1 to -1.1)	-6.9 (-11.0 to -3.9)	-5.3 (-10.8 to -2.4)	-12.7 (-23.0 to -7.2)
1960–2050	-3.5 (-4.8 to -2.7)	-9.9 (-13.2 to -7.7)	-11.0 (-15.7 to -8.9)	-23.6 (-33.5 to -16.3)
1960–2080	-4.2 (-5.9 to -3.2)	-11.4 (-14.6 to -10)	-13.2 (-16.6 to -11.4)	-35.6 (-47.8 to -25.9)
Biodiversity				
Rare endemic vascular plant species[h]	2	18	69	8
Threatened vascular plant species (occurring at a single unprotected location in each region)[h]	1	4	11	0
Threatened animal species[i]	2	4	6	1

[a]from the ACIA-designated model simulations; [b]from Taalas et al. (2000); [c]Betts R. (2001) using IS92a emissions scenario; [d]averages and ranges (in parentheses) of the responses of the LPJ model (Sitch et al., 2003) driven with outputs from four different climate models (CGCM2, GFDL-R30_c, HadCM3, ECHAM4/OPYC3) forced with the B2 emissions scenario (section 4.4); [e]only a proxy as the change is derived from functional characteristics of the vegetation simulated by the model rather than projections of specific vegetation composition *per se*. For a proper vegetation distribution estimate, it would be more appropriate to use a coupled biogeography and biogeochemistry model such as BIOME4; [f]based on the percentage increase in woody plants simulated by LPJ; [g]based on the percentage reduction in bare ground simulated by LPJ; [h]from Talbot et al. (1999); [i]IUCN (2003).

7.6. Synthesis: Scenarios of projected changes in the four ACIA regions for 2020, 2050, and 2080

This synthesis draws on information in this chapter that can be assessed within the four ACIA regions. Most of the information is therefore based on model output. Details of the regions and the logic determining them are presented in section 18.3, while details of the models that generate the UV-B radiation and climate scenarios are presented in sections 5.6 and 4.2.7, respectively. Many of the details relating to vegetation and carbon dynamics are derived specifically for this section from the LPJ model (Sitch et al., 2003), details of which are presented in Box 7.1. Other aspects of the assessment that cannot currently be divided into the ACIA regions are summarized within and at the end of the various sections of this chapter.

7.6.1. Environmental characteristics

The four ACIA regions (section 18.3) differ greatly in their geography and climatology, which leads to variation in future possibilities for the relocation of species and ecosystems, and differences in scenarios of future changes in climate and UV-B radiation levels (Table 7.14).

Geographically, Region 4 has a far greater extent of land at high latitudes compared with the other regions. This is likely to support northward migration of arctic biota even if the Canadian Archipelago and the glacial landscape of Greenland together with lack of suitable soils will, to some extent, pose barriers to migration. Relatively narrow tundra zones in some parts of Regions 1 and 3 could possibly, with sea-level rise and northward boreal forest expansion, disappear and forest reach the shore of the Arctic Ocean (Fig. 7.32). Region 1 contains the relatively isolated high-arctic islands of Svalbard, and the islands of Iceland and the Faroe Islands, that are likely to experience delayed immigration of southern species during warming. Both Iceland and the Faroe Islands have equivocal positions within classifications of the Arctic: the northern part of Iceland and the alpine zones of the Faroe Islands (Fossa, 2003) have the strongest arctic characteristics and climate warming is likely to lead to altitudinal displacement of tundra-like vegetation in both areas, and displacement from the northern coastal area in Iceland. The imbalance of species loss and replacement by species migrating more slowly to islands is projected to lead to an initial loss in diversity (Heide-Jørgensen and Johnsen, 1998).

The scenarios of temperature change generated by the five ACIA-designated models show complex temporal patterns, in some areas shifting from initial cooling to substantial warming. The data used for the modeling of vegetation zone displacement and carbon storage used a different baseline period (1961–1990) than that used for the ACIA-designated model projections (1981–2000) and excluded output from the CSM_1.4 model. In addition, the output from the LPJ model is provided for 2100, rather than the 2071–2090 time slice used in the ACIA scenarios (section 7.5). It is therefore difficult to compare the results, even though both approaches had four GCMs in common and used the same emissions scenario.

Changes in UV-B radiation levels are projected to vary among regions, but only over the next 20 years.
By 2050, recovery of the stratospheric ozone layer is projected to reduce UV-B radiation to relatively low levels above present-day levels, with no differences among the ACIA regions. Of course, this recovery depends entirely on the success of management and regulation of ozone-depleting substances. In the near future, however, increases in UV-B radiation levels are projected to be greatest in Region 4, followed by Regions 1 and 2 (Taalas et al., 2000).

Active-layer thickness is projected to increase by 20 to 60% by 2071–2100 (compared to the IPCC baseline, 1961–1990). The greatest percentage increases are projected to occur in northern Siberia and the interior of the Alaska–Yukon area. In general, the greatest relative changes in the active layer are projected to occur in those regions where the active layer is presently shallow (section 6.6.1.3). Degradation of continuous permafrost to discontinuous permafrost and the disappearance of discontinuous permafrost are projected to occur at the southern boundaries of all of the ACIA regions.

7.6.2. Vegetation zones and carbon balance

Region 1 (Arctic Europe, East Greenland, European Russian North, and North Atlantic) includes many high-arctic areas but these are separated from terrestrial ecosystems at lower latitudes by barriers of open sea. The possibilities for future species relocation are limited, even though moderate warming is projected here (Table 7.14). In contrast, Region 2 (Central Siberia) has continuous landmasses from the tropics to the high Arctic. This region is currently warming, and scenarios project that future warming will be greater here than elsewhere. The possibilities for responses in ecosystem distribution, structure, and C balance are therefore considerable. This is illustrated by large projected increases in taiga that displaces tundra in particular, and also in projected decreases in polar desert that is displaced to some extent by northward movement of the tundra (Table 7.14). There is also a projected northward displacement and reduction in prostrate dwarf-shrub tundra, particularly in Yakutsia and the Taymir Peninsula, together with a displacement of erect dwarf-shrub tundra from much of the Russian Arctic by low- and high-shrub tundra that is projected to expand markedly there (Figs. 7.2 and 7.32). Region 3 (Chukotka, Bering Sea, Alaska, and the western Canadian Arctic) has little high-arctic area and a large maritime influence. Increases in temperature and precipitation are projected to be moderate, as are changes in vegetation (Table 7.14). Region 4 (Northeast Canada, Labrador Sea, Davis Strait, and West Greenland) is a region of fragmented landmasses that are often extensively glaciated or have recently become deglaciated. This area has experienced recent cooling, but a warming trend is projected to occur between now and 2100. Increases in temperature and precipitation are projected to lead to relatively small increases in taiga (compared with other regions) but a particularly large (~36%) loss of polar desert by 2080.

In terms of C storage, all regions are projected to accumulate C, largely because of the replacement of bare ground by tundra. Consequently, the greatest carbon gain is projected to occur in Region 4 (Table 7.14; Fig. 7.33). In contrast, the smallest gains – but still gains – are projected to occur in Region 1, which has the smallest projected increase in temperature.

7.6.3. Biodiversity

Biodiversity is affected by habitat fragmentation. Scenarios of the impacts of projected human infrastructure development on arctic flora and fauna suggest that in the Arctic, these impacts are likely to extend for 4 to 10 km away from the infrastructure (Nellemann et al., 2001). This is a much wider zone of influence than in other regions of the earth. Nellemann et al. (2001) calculated that 50 to 80% of the Arctic is likely to be affected by infrastructure development by 2050. Of course, infrastructure development varies among the ACIA regions and this remains to be characterized. However, threats to flora and fauna are likely to be increased by the additive or possibly interactive effects of infrastructure development and climate change.

The number of rare endemic vascular plant species in the Arctic varies greatly between the regions (Table 7.14). Region 1 has relatively little land mass and supports only two of the rare endemic vascular plant species. Region 4, which encompasses a significant proportion of the high Arctic, contains 8% of the species and Region 2 contains 18%. In contrast, over 70% of the rare endemic vascular plant species are found in Beringia (Region 3). Twenty-four species are found on Wrangel Island (Talbot et al., 1999). A recent modification (Talbot and Murray, 2001) of the list of threatened arctic plant species (Talbot et al., 1999) adds a further 63 plant species, but data have not yet been compiled on their distributions within the ACIA regions. Although Table 7.14 shows clear regional differences in the distribution of rare and endemic plant species, and also a surprisingly high number of these species, it should be noted that the taxonomic treatment of species is likely to vary from region to region and there is uncertainty about the taxonomic status of some of the species.

It is not clear to what extent the rarity of the species listed in Tables 7.7 and 7.14 will be affected by climate change, as many other factors determine rarity. However, species concentrated in small areas such as Wrangel Island are particularly at risk from any future climate warming and species invasion.

The likely impacts of climate change on biodiversity in terms of threatened species require new concepts of "threatened species" and "protection" of currently per-

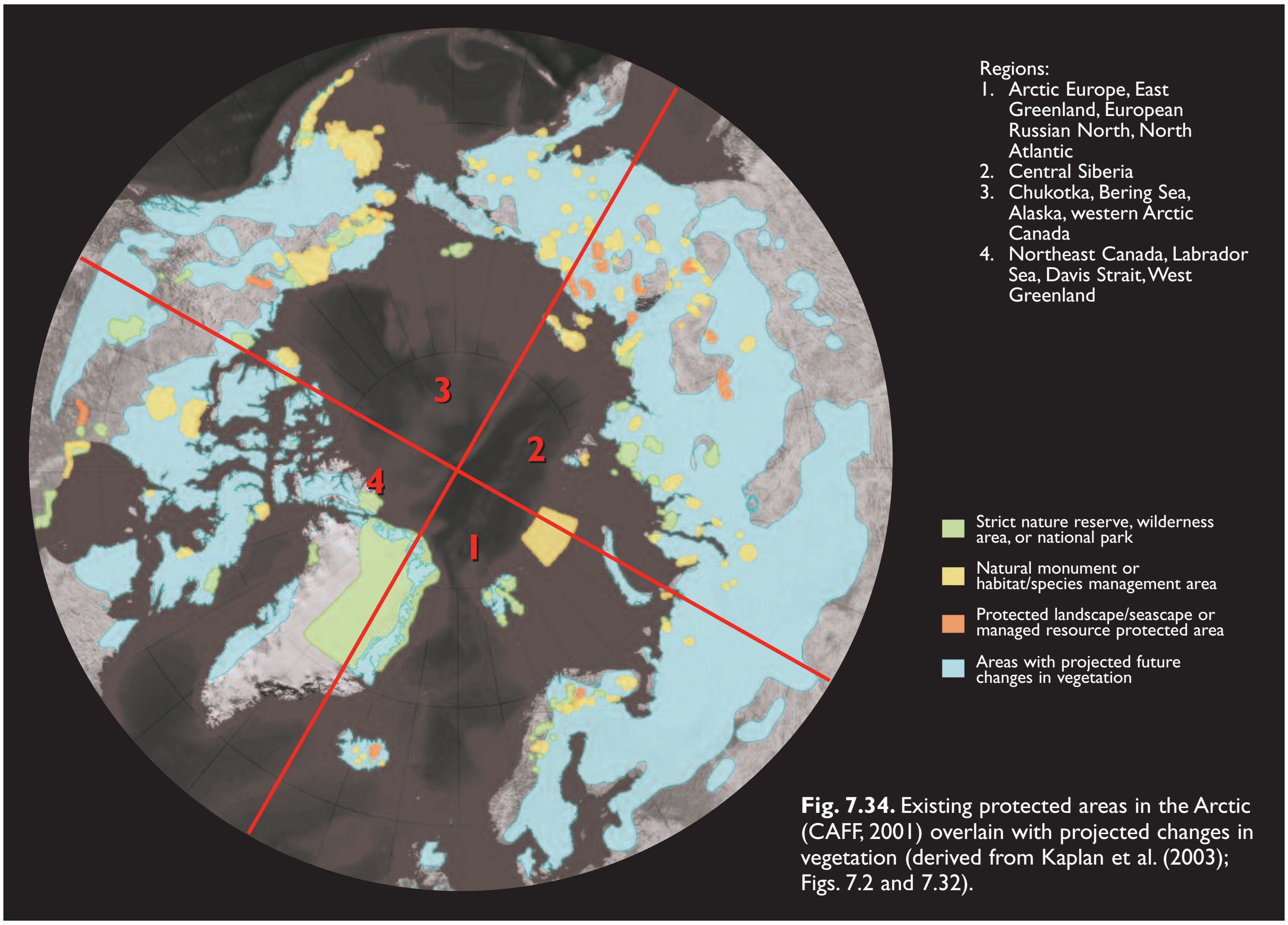

Fig. 7.34. Existing protected areas in the Arctic (CAFF, 2001) overlain with projected changes in vegetation (derived from Kaplan et al. (2003); Figs. 7.2 and 7.32).

ceived threatened species (Fig. 7.34; Chapter 11). The numbers of species currently perceived as threatened vary between regions. Region 3 contains significantly more rare plant species and threatened animal and plant species than other regions. Although temperature and precipitation changes are likely to be less in this region than in others, the vulnerability of the biodiversity of this area is likely to be considerable. Northward expansion of dwarf-shrub and tree-dominated vegetation into an area such as Wrangel Island that is rich in rare endemic species could possibly result in the loss of many plant species. Although some of these might not be considered vulnerable because they are currently in "protected" areas, this protection is against local human activities (e.g., hunting, infrastructure development, etc.) and protection cannot extend to changes in climate and UV-B radiation levels. It is possible that some plant species, particularly outliers of more southerly distributions, might experience population expansion or reproduction and recruitment to populations, leading to initial expansion in response to warming. However, displacement of herbaceous species by woody immigrants is possible in the long term in mesic areas. In contrast to the possibility that some threatened species will proliferate in a warmer climate, some currently widespread species are very likely to become less abundant and even "threatened".

The greatest long-term threat to arctic diversity is the loss of arctic habitat (section 7.2.6). In locations where the tundra zone is narrow, boreal forest moves northward, and the ocean moves southward due to sea-level rise, there is very likely to be, over a period of centuries, a loss of arctic ecosystems and the species that characterize them.

7.7. Uncertainties and recommendations

7.7.1. Uncertainties

Current understanding of ecological processes and changes driven by climate and UV-B radiation is strong in some geographic areas and in some disciplines, but is weak in others. Although the ability to make projections has recently increased dramatically with increased research effort in the Arctic and the introduction of new technologies, current understanding is constrained by various uncertainties. This section focuses on these uncertainties and recommends ways in which they can be reduced.

7.7.1.1. Uncertainties due to methodologies and conceptual frameworks

Methods of projecting impacts on species and ecosystems

Each method has advantages and strengths and has led to the important and extensive current knowledge base. However, each method also has uncertainties that need to be identified so that methods can be refined and uncertainties quantified.

The use of *paleo analogues* to infer future changes under-represents the differences between past changes and those likely to occur in the future due to differences in the starting state of the environment and biota, and the different nature of past and likely future changes. Major differences include anthropogenic effects (e.g., extent of land-use change, current and future stratospheric ozone depletion, and trans-boundary pollution) that are probably unprecedented.

Using *geographic analogues* can indicate where communities and species should be in a warmer world, but they do not indicate at what rate species can relocate or if new barriers to dispersal such as fragmented habitats will prevent potential distributions from being achieved.

Observations and monitoring provide essential data about changes as they occur, and can be used to test hypotheses and model projections, but they have little predictive power in a time of changing climate during which many biotic responses are nonlinear.

Experiments that simulate future environmental conditions (e.g., CO_2 concentrations, UV-B radiation levels, temperature, precipitation, snow depth and duration, etc.) all have artifacts, despite attempts to minimize them. It is difficult in field experiments to include simulations of all likely eventualities: in warming experiments, it is very difficult to identify separate effects of seasonal warming and extreme events because most experiments are small in spatial extent, and are short-term in the context of the life cycles of arctic plants and animals. It is also difficult to identify the complex interactions among all the co-occurring environmental change variables, and ecological processes determined from experiments in one geographic area may not relate sufficiently to other areas because of different ecological conditions and histories.

Indigenous knowledge, although a valuable contributor to current understanding of ecological changes (section 7.7.2.2), is more qualitative than quantitative, and often characterized by relatively coarse measures (i.e., monthly and seasonal change rather than daily or weekly). The information available is sometimes limited to phenomena that fall within the cycle of subsistence resource use, and is more likely to be diachronic (long time series of local information) and not synchronic (simultaneously observed). It is often difficult to assign particular environmental changes to individual changes in biota, to determine mechanisms of change, and distinguish climate-related change from other changes occurring in the environment. Indigenous knowledge is variable between and within communities, and interpretation and verification processes are as important as collection and documentation. It is a knowledge system.

Uncertainties can be reduced when information from several methods converges. This chapter accepts all methodologies, knowing their limitations, and qualifies the information presented by the methodologies used to obtain it.

Measuring primary production and controlling factors

Key unknowns about primary productivity in the Arctic include root production and turnover and belowground allocation processes in general, including allocation to mycorrhizae and exudation. Also poorly understood are long-term (multi-year to multi-decade) interactions between the carbon cycle and nutrient cycles, in which relatively slow changes in soil processes and nutrient availability interact with relatively rapid changes in photosynthesis in response to climate change. One major unknown is the control on dispersal, establishment, and rate of change in abundance of species and functional types that are more productive than current arctic species but are not now present or common in arctic vegetation (e.g., trees and tall shrubs).

There are two major approaches to assessing NEP: classic biomass weighing and year-round CO_2 flux recording, but these approaches are not always compatible. One particular gap in current estimates is the lateral transport of organic C from one ecosystem to another. The two methodologies give opposite results when accounting for the input of allochthonous (produced outside) organic matter to a particular ecosystem: CO_2 flux measurement gives negative NEP due to increased CO_2 emission from soil to atmosphere, while weighing gives a higher accumulation of organic C in the soil. In addition, current estimates of buried C released to ecosystems due to thermokarst and soil erosion (Figs. 7.21 and 7.22) are poor.

Difficulties in studying microorganisms

Understanding of microbes that are critically important in many ecosystem processes is limited. Knowledge of microbial diversity and function has been strongly constrained by lack of development in methodology and conceptual frameworks.

Bacteria and even the more advanced microscopic yeast and fungi cannot be characterized by visual observation alone due to their very simple shapes (rods, spheres, filaments). Typically, microbial strains must be cultivated in pure culture to reveal their various functional features, and an appreciable amount of laboratory work is required to differentiate a microbe from close relatives. Only a small fraction of soil microorganisms are able to grow on artificial laboratory media, and less than 1% of the cells observed with a microscope form colonies on the plate. The main reasons for this "Great Plate Count Anomaly" (Staley and Konopka, 1985) include the metabolic stress of the "famine-to-feast" transition occurring when cells are brought from soil to artificial, nutrient-rich media; inadequacy of cultivation conditions compared with the natural environment; and metabiotic interactions/cooperation in natural communities that are broken after cells have been separated by plating (Panikov, 1995). This technical problem has resulted in an underestimation of diversity in natural habitats. Fortunately, new cultivation approaches are being developed that are helping to overcome this problem (Staley and Gosink, 1999). However, it is not presently possible to make a fair comparison between the numbers of species of animals and plants versus bacteria given that these groups are defined differently (Staley, 1997).

Lack of feasible technologies to measure microbial population dynamics in the field has lead to the use of microbial biomass, which is convenient but a poor predictor of productivity and C and nutrient turnover. More sensitive measurements of microbial activity need to be developed for field application.

Incomplete databases

Length of time series of data: Although many long time series of relevant data (e.g., species performance and phenology) exist, most information relates to short time series. This is a particular problem in the Arctic where complex population dynamics (e.g., cycles) need to be understood over periods long enough to allow trends to be separated from underlying natural dynamics. Observations of trace gas emissions also require annual observations over time periods long enough to encompass significant climate variability. Experiments are usually too brief to capture stable responses to environmental manipulations and to avoid artifacts that are disturbance responses. Long time series of data are also necessary in order to identify extreme events and non-linear system changes.

Geographic coverage and spatial scaling: The ecosystems and environments in the Arctic are surprisingly variable yet generalizations to the circumpolar Arctic are often made from a few plot-level studies. Sometimes, particular experiments (e.g., CO_2 concentration and UV-B radiation manipulations) or observations are restricted to a few square meters of tundra at just one or two sites. Uncertainties due to generalizing and scaling up are thus significant. The IBP and the ITEX are exceptional examples of how standardized experiments and observations can be implemented throughout the Arctic.

Coverage of species and taxa: Chapin F. and Shaver (1985a) and others have demonstrated the individualistic responses of species to experimental environmental manipulations, including climate, while Dormann and Woodin (2002) have shown the inadequacy of the concept of "plant functional types" in generalizing plant responses to such experiments. An approach has to be developed to measure responses of a relevant range of species to changes in climate, and particularly UV-B radiation levels. Plants studied in the UV-B radiation manipulation experiments were generally at their northernmost distributional limits and well adapted to high UV-B radiation levels characteristic of southern parts of their ranges. Greater responses would be expected from species at their southern distributional limits where increased UV-B radiation would exceed levels in the plants' recent "memory".

Some species and taxonomic groups are particularly difficult to study, or have little socioeconomic value, and so are underrepresented in databases. Examples include mosses, lichens, soil fauna and flora, and microorganisms (section 7.7.1.1).

Nomenclature and concepts

The restricted use of appropriate language often generates uncertainties. The nomenclature of vegetation and plant community types allows changes in the *distribution* of these assemblages of species in a changed climate to be modeled, but constrains understanding of changes in the *structure* of the assemblages that are likely to occur because assemblages of species do not move *en bloc*. This problem limits understanding of novel future communities (Chapin F. and Starfield, 1997) and no-analogue communities of the past, and emphasizes the uncertainties due to the inability of quantitative models to project qualitative changes in systems. Similarly, the concept of "line" to denote the limit of species distributions (e.g., treeline) is inadequate to express the gradient of changes from one zone to another that can occur over tens of kilometers.

The concept of "species" is particularly difficult in the context of microorganisms as discussed previously, and even as applied to flowering plants. The traditional view that there are few rare and endemic arctic plant species is challenged by recent studies of the flora of Wrangel Island and Beringia (Table 7.14) but it is not known to what degree plant taxonomy is problematic (although the Pan Arctic Flora project is addressing this problem). Such problems need to be resolved before the impacts of climate change on biodiversity can be assessed.

7.7.1.2. Uncertainties due to surprises

Perhaps the only certainty in the assessment of impacts of changes in climate and UV radiation levels on terrestrial ecosystems in this chapter is that there will be surprises. By definition, it is difficult to predict surprises. However, the possibility that climate *cooling* will occur because of a change in thermohaline circulation is potentially the most dramatic surprise that could occur.

Regional cooling

The potential for a negative feedback arising from an increased freshwater flux to the Greenland, Icelandic, and Norwegian seas and the Arctic Basin, leading to a partial or complete shut down of the thermohaline circulation of the global oceans, remains an area of considerable uncertainty (sections 6.8.4 and 9.2.3.4). Such an event would be likely to lead to marked and rapid regional cooling in at least northwest Europe. This region at present enjoys an anomalously warm climate given its latitude (50º–72º N), enabling agriculture to be practiced and substantial settlements maintained at far higher latitudes than in any other arctic or subarctic region. Such cooling would be likely to qualitatively alter terrestrial ecosystems (Fossa, 2003), agriculture, and forestry over very large areas of Fennoscandia and Europe.

Mutations

Mutations are projected to occur as a result of increased levels of UV radiation and also as a result of aerosols and volatile chemical mutagens transported to the cool polar atmosphere from the mid- and low latitudes. The direct mutagenic effect is probably not strong, especially if the protecting shielding effects of soil particles and adaptive mechanisms are taken into account. However, possible microbial mutants could lead to epidemic outbreaks that could have profound and unexpected consequences for the Arctic and elsewhere.

Desertification

Several approaches suggest that climate warming will lead to an increase in the productivity of arctic vegetation and long-term net sequestration of CO_2. However, the complex interactions among warming, permafrost dynamics, hydrology, precipitation, and soil type are poorly understood. Desertification is a plausible outcome in some areas where scenarios suggest that permafrost will thaw, drainage will increase, temperatures will increase, and precipitation will *not* increase substantially. In areas of sandy soil and loess deposition, such as parts of eastern Siberia, there is a particular risk of desertification. In the polar deserts, herb barrens, and heaths of northern Greenland, plant productivity is strongly correlated with precipitation and increased evapotranspiration is likely to lead to a similar process (Heide-Jørgensen and Johnsen, 1998). Locally, the impacts of overgrazing and anthropogenic disturbance can accelerate the process. A clear example of the effect of warming and drying on the C balance of Alaskan tundra is provided in section 7.5, and an example of boreal coniferous forest loss in North America is given in section 14.7.3.1. However, the possible wider geographic scale of this process is unknown.

Changes in current distributions of widespread and rare species

Climate change could possibly have counter-intuitive impacts on species distributions. Currently rare arctic plant species, particularly those that are northern outliers of species with more southerly distributions, could possibly expand during initial phases of climate warming. In contrast, currently widespread species, particularly lichens and mosses, could possibly become more restricted in their abundance during warming. It is necessary to reassess the concept of "threatened species" in the context of climate and UV radiation change (see section 7.6 and Chapter 11).

7.7.1.3. Model-related uncertainties

During the IBP period (late 1960s and early 1970s), tundra research was characterized by extensive field observations but a general lack of modeling capability. Currently, a technological revolution has stimulated model generation and remote sensing of ecosystem change. However, in some cases, validation is insufficient. Models that project NPP at a global or circumpolar level are insufficiently validated, as recent measurements of NPP are rare and restricted to a few localities. The lack of inter-comparison between models and existing observations leads to potential projection errors: modeled displacement of the tundra by the boreal forest contradicts current observations of the southward retreat of the treeline in some areas and the expansion of "pseudotundra" in parts of Russia due to permafrost degradation, paludification, and human activities.

The climate models used to provide future climate scenarios for the ACIA were forced with the B2 emissions scenario (section 4.4.1), but projections based on the A2 emissions scenario have been used to a limited extent as a plausible alternative (IPCC, 2001; section 1.4.2). The A2 scenario assumes an emphasis on economic development rather than conservation, while the B2 scenario assumes a greater emphasis on environmental concerns: each has considerable uncertainties (section 4.4.1). In this chapter, projections based mainly on the B2 emissions scenario were used to model changes in vegetation and carbon storage. Projections based on the A2 emissions scenario result in higher temperatures for a particular time period than those based on the B2 emissions scenario. The changes projected by models forced with the A2 emissions scenario for the 2041–2060 and 2071–2090 time slices occur 5 to 10 and 10 to 20 years earlier, respectively, compared with projections based on the B2 scenario. Potential impacts on ecosystems would thus occur faster should emissions follow the A2 scenario.

The major implication for ecosystems of a faster rate of temperature change is an increased mismatch between the rate of habitat change and the rate at which species can relocate to occupy new habitats in appropriate climate envelopes. The overall, generalized, difference between projections based on the B2 and A2 emissions scenarios is likely to be an increased risk of disturbance and disease in species that, under projected conditions based on the A2 scenario, cannot relocate quickly enough. Projections based on the A2 scenario also imply an increased mismatch between initial stimulation of soil respiration and longer-term vegetation feedbacks that would reduce C fluxes to the atmosphere.

7.7.2. Recommendations to reduce uncertainties

7.7.2.1. Thematic recommendations and justification

This section reviews important thematic topics that require particular research. For each topic, the state of knowledge and important gaps are summarized, and recommendations to fill these gaps are suggested (in italic font).

Mechanisms of species responses to changes in climate and UV-B radiation levels. Changes in microbe, animal, and plant populations are triggered by trends in climate and UV radiation levels exceeding thresholds, and by extreme events, particularly during winter. However, information is uneven and dominated by trends in summer climate. *Appropriate scenarios of extreme events are required, as is deployment of long-term experiments simulating extreme events and future winter processes in particular. A better understanding of thresholds relevant to biological processes is also required.*

Biodiversity changes. Some groups of species are very likely to be at risk from climate change impacts, and the biodiversity of particular geographic areas such as Beringia are at particular risk. It is not known if currently threatened species might proliferate under future warming, nor which currently widespread species might decrease in abundance. *The nature of threats to species, including microbes, must be reassessed using long-term climate and UV-B radiation change simulation experiments. There is also a need to identify and monitor currently widespread species that are likely to decline under climate change, and to redefine conservation and protection in the context of climate and UV radiation change.*

Relocation of species. The dominant response of current arctic species to climate change, as in the past, is very likely to be relocation rather than adaptation. Relocation possibilities are very likely to vary according to region and geographic barriers. Some changes are already occurring. However, knowledge of rates of relocation, impact of geographic barriers, and current changes is poor. *There is a need to measure and project rates of species migration by combining paleo-ecological information with observations from indigenous knowledge, environmental and biodiversity monitoring, and experimental manipulations of environment and species.*

Vegetation zone redistribution. Forest is very likely to replace a significant proportion of the tundra and is very likely to have a great effect on species composition. However, several processes (including land use and permafrost dynamics) are expected to modify the modeled response of vegetation redistribution related to warming. *Models of climate, hydrology (permafrost), ecosystems, and land use need to be developed and linked. These models need to be based on improved information about the current boundaries of major vegetation zones, defined and recorded using standardized protocols.*

Carbon sinks and sources in the Arctic. Current models suggest that arctic vegetation and active-layer soils will be a sink for C in the long term because of the northward movement of vegetation zones that are more productive than those they displace. Model output needs to be reconciled with observations that tundra areas that are C sources currently exceed those that are C sinks, although the measurements of circumpolar C balance are very incomplete. To what extent disturbance will reduce the C sink strength of the Arctic is also unknown.

There is a need to establish long-term, annual C monitoring throughout the Arctic; to develop models capable of scaling ecosystem processes from plot experiments to landscapes; to develop observatories, experiments, and models to relate disturbance such as desertification to C dynamics; and to improve the geographic balance of observations by increasing high-arctic measurements. There is also a need to combine estimates of ecosystem carbon flux with estimates of C flux from thawing permafrost and methane hydrates.

Ultraviolet-B radiation and CO_2 impacts. Enhanced CO_2 concentrations and UV-B radiation levels have subtle but long term impacts on ecosystem processes that reduce nutrient cycling and have the potential to decrease productivity. However, these are generalizations from very few plot-scale experiments, and it is difficult to understand impacts that include large herbivores and shrubs. *There is a need for long-term experiments on* CO_2 *and UV-B radiation effects interacting with climate in a range of arctic ecosystems; short-term experiments stimulating repeated episodes of high UV radiation exposure; long-term experiments that determine the consequences of high* CO_2 *concentrations and UV-B radiation levels for herbivores; and short-term screening trials to identify the sensitivity of a wide range of species, including soil microbes, to current and projected UV-B radiation levels.*

Local and regional feedbacks. Displacement of tundra by forest is very likely to lead to a decrease in albedo with a potential for local warming, whereas C sequestration is likely to increase with potential impacts on global concentrations of greenhouse gases. However, the timing of the processes and the balance between the processes are very uncertain. How local factors such as land use, disturbance, tree type, and possible desertification will affect the balance is also uncertain. *There is a need for long-term and annual empirical measurements, analysis of past remotely sensed images, and collection of new images together with the development and application of new models that include land use, disturbance, and permafrost dynamics.*

7.7.2.2. Recommendations for future approaches to research and monitoring

No single research or monitoring approach is adequate, and confidence is increased when results from different approaches converge (section 7.7.1.1). Current approaches should be maintained, and new approaches and even paradigms (e.g., when defining "threatened species" and "protected areas") developed. Some important approaches are highlighted below.

Reducing uncertainty by increasing and extending the use of indigenous knowledge

Arctic indigenous peoples retain strong ties to the land through subsistence economies and they are "active participants" in ecosystems (*sensu* Bielawski, 1997). Unlike a scientist, a hunter is not bound in his observations by a project timeline, budget, seasonality, or logistical constraint (Krupnik, 2000; Riedlinger and Berkes, 2001). Subsistence activities occur on a daily basis, year after year, and throughout the winter period when many scientists are south in home institutions. Indigenous peoples of the Arctic therefore possess a substantial body of knowledge and expertise related to both biological and environmental phenomena. Such local expertise can highlight qualitative changes in the environment and provide pictures of regional variability across the Arctic that are difficult to capture using coarser-scale models.

This chapter presents some of the first efforts at linking western science and indigenous knowledge to expand the range of approaches that inform this assessment. However, the potential is far greater, including, for example, local-scale expertise, information on climate history, generation of research hypotheses, community monitoring, and community adaptation (Riedlinger and Berkes, 2001).

Monitoring

Long-term environmental and biological monitoring have been undervalued but are becoming increasingly necessary to detect change, to validate model projections and results from experiments, and to substantiate measurements made from remote sensing. Present monitoring programs and initiatives are too scarce and are scattered randomly. Data from the Arctic on many topics are often not based on organized monitoring schemes, are geographically biased, and are not long-term enough to detect changes in species ranges, natural habitats, animal population cycles, vegetation distribution, and C balance. More networks of standardized, long-term monitoring sites are required to better represent environmental and ecosystem variability in the Arctic and particularly sensitive habitats. Because there are interactions among many co-varying environmental variables, monitoring programs should be integrated. Observatories should have the ability to facilitate campaigns to validate output from models or ground-truth observations from remote sensing. There should be collaboration with indigenous and other local peoples' monitoring networks where relevant. It would be advantageous to create a decentralized and distributed, ideally web-based, meta-database from the monitoring and campaign results, including relevant indigenous knowledge.

Monitoring also requires institutions, not necessarily sited in the Arctic, to process remotely sensed data. Much information from satellite and aerial photographs exists already on vegetation change, such as treeline displacement, and on disturbances such as reindeer/caribou overgrazing and insect outbreaks. However, relatively little of this information has been extracted and analyzed.

Monitoring C fluxes has gained increased significance since the signing of the Kyoto Protocol. Past temporal and spatial scales of measurement used to directly measure C flux have been a poor match for the larger scale of arctic ecosystem modeling and extrapolation. It remains a challenge to determine if flux measurements and model output are complementary. The technological difficulties in extrapolating many non-linear, complex, interacting factors that comprise fluxes at hundreds to thousands of square kilometers over time, space, and levels of biological and environmental organization in the Arctic have been significant (Oechel et al., 2000b, 1998). Research is needed to better understand how the complex system behaves at the meter scale related to larger spatial scales that can be efficiently modeled and evaluated at the regional and circumpolar scale. To do this, extensive long-term and year-round eddy covariance sites and other long-term flux sites, including repeated aircraft flux measurements and remote sensing (Oechel et al., 2000a), provide the basis for estimating circumpolar net ecosystem CO_2 exchanges. Currently, the circumpolar Arctic is disproportionately covered by current and recent measurements, with Canadian and high-arctic regions particularly poorly represented.

Long-term and year-round approach to observations and experiments

Many observations and experiments are short term (<5 years) and they are biased toward the summer period often because researchers have commitments to institutions outside the Arctic during winter. However, throughout this assessment it has become clear that long-term and year-round measurements and experiments are essential to understand the slow and complex responses of arctic organisms and ecosystems to climate change.

Long-term (>10 years) observations and experiments are required in order to enable transient responses to be separated from possible equilibrium responses; increase the chances that disturbances, extreme events, and significant interannual variation in weather are included in the observations; and allow possible thresholds for responses to be experienced.

Year-round observations are necessary to understand the importance of winter processes in determining the survival of arctic species and the function of arctic ecosystems. Such observations are necessary to recognize the projected amplification of climate warming in winter and to redress the current experimental bias toward summer-only warming. For microbes, it is particularly important to understand changes in winter respiration and nutrient mobilization during freeze–thaw events in spring and late autumn.

It is important to improve the appropriateness of the timing of observations and experiments. For example, current information about the impacts of increased UV-B radiation levels is mainly derived from general summer enhancements or filtration of UV-B radiation, although future increases in UV-B radiation levels are likely to be highest in spring and during specific stratospheric ozone depletion events. The frequency of observations should be fitted to the rate of change of the species or processes of interest, for example, decadal measurements may suffice for some variables such as treeline movement.

Increasing the complexity and scale of environmental and ecosystem manipulation experiments

Single-factor manipulation experiments now have limited applicability because it is clear that there are many interactive effects among co-occurring environmental change variables. There is need for well-designed, large, mutifactorial environmental (e.g., climate, UV-B radiation levels, and CO_2 concentrations) *and* ecosystem (e.g., species removal and addition) manipulation experiments that are long-term and seek to understand annual, seasonal, and event-based impacts of changing environments. The complexity of appropriate treatments and timescales is vast and the spatial scale is also a significant challenge, as it is important to have manipulations that can be related to larger plants (e.g., trees, shrubs) and animals (e.g., reindeer/caribou).

Assessing the impacts of cooling on ecosystems

Scenarios of increased temperature dominate the approaches to projecting responses of ecosystems to future climate. However, cooling in some areas remains a possibility. As the impacts of cooling on terrestrial ecosystems and their services to people are likely to be far more dramatic than the impacts of warming, it is timely to reassess the probabilities of cooling projected by GCMs and the appropriateness of assessing cooling impacts on ecosystems.

Modeling responses of arctic ecosystems to climate and UV-B radiation change and communicating results at appropriate geographic scales

High-resolution models are needed at the landscape scale for a range of landscape types that are projected to experience different future envelopes of climate and UV-B radiation levels. Modeling at the landscape scale will simulate local changes that relate to plot-scale experiments and can be validated by results of experiments and field observations. Visualization of model results presented at the landscape scale will also enhance the understanding of the changes and their implications by local residents and decision-makers. A particular challenge is to provide scenarios for changes in climate and UV-B radiation levels at the scale of tens of meters.

7.7.2.3. Funding requirements

It is inappropriate here to comment on levels of funding required to fulfill the recommendations discussed above. However, it is appropriate to highlight two essential aspects of funding.

First, current short-term funding is inappropriate to support research into long-term processes such as ecosystem responses to climate change and UV-B radiation impacts. *A stable commitment to long-term funding is necessary.*

Second, funding possibilities that are restricted to single nations, or at best a few nations, make it extremely difficult to implement coordinated research that covers the variability in ecosystems and projected climate change throughout the circumpolar north, even though the instruments for coordination exist (e.g., within the International Arctic Sciences Committee, the International Council of Scientific Unions, and the International Geosphere–Biosphere Programme). Limitation of international funding possibilities leads to geographic biases and gaps in important information. *Circumpolar funding is required so that coordinated projects can operate at geographically appropriate sites over the same time periods.*

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Personal communications and unpublished data

Callaghan, T.V. Abisko Scientific Research Station, Sweden.
Clemmensen, K.E. and A. Michelsen, 2004. Institute of Biology, University of Copenhagen.
Flanagan, P.W., 2004. Global Environmental Enterprises, Inc., Chester, Virginia.
Friborg, T., 2005. Institute of Geography, University of Copenhagen, Denmark.
Henttonen, H., 2004. Thule Insitute, University of Oulu, Finland.
Jonasson, S. and A. Michelsen, 2005. Institute of Biology, University of Copenhagen.
Kaplan, J., 2002. Canadian Centre for Climate Modelling and Analysis.
Katenin, A., 2004. Komorov Botanical Institute, St. Petersburg, Russia.
Meltofte, H., 2004. National Environment Research Institute, Denmark.
Nutti, E., 2004. Karesuando, Sweden.
Polozova, T., 2005. Komorov Botanical Institute, St. Petersburg, Russia.
Svoboda, J. Department of Botany, University of Toronto, Canada.
Taulavuori, K., E. Taulavuori and K. Laine, 2004. Thule Institute, University of Oulu, Finland.

References

Aanes, R., B.-E. Sæther and N.A. Øritsland, 2000. Fluctuations of an introduced population of Svalbard reindeer: the effects of density dependence and climatic variation. Ecography, 23:437–443.

Aanes, R., B.-E. Sæther, F.M. Smith, E.J. Cooper, P.A. Wookey and N.A. Øritsland, 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-arctic ecosystem. Ecology Letters, 5:445–453.

Aars, J. and R.A. Ims, 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology, 83:3449–3456.

Abbott, R.J. and C. Brochmann, 2003. History and evolution of the arctic flora: in the footsteps of Eric Hultén. Molecular Ecology, 12:299–313.

Abbott, R.J., H.M. Chapman, R.M.M. Crawford and D.G. Forbes, 1995. Molecular diversity and derivations of populations of *Silene acaulis* and *Saxifraga oppositifolia* from the high Arctic and more southerly latitudes. Molecular Ecology, 4:199–207.

Abbott, R.J., L.C. Smith, R.I. Milne, R.M.M. Crawford, K. Wolff and J. Balfour, 2000. Molecular analysis of plant migration and refugia in the Arctic. Science, 289:1343–1346.

Afonina, O.M. and I.V. Czernyadjeva, 1995. Mosses of the Russian Arctic: check-list and bibliography. Arctoa, 5:99–142.

Agrell, J., E.P. McDonald and R.L. Lindroth, 1999. Responses to defoliation in deciduous trees: effects of CO_2 and light. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:84–95.

Ahmadjian, V., 1970. Adaptations of Antarctic terrestrial plants. In: H.W. Holdgate (ed.). Antarctic Ecology, pp. 801–811. Academic Press.

Aitchinson, C.W., 2001. The effect of snow cover on small animals. In: H.G. Jones, J.W. Pomeroy, D.A. Walker and R.W. Hoham (eds.). Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems, pp. 229–265. Cambridge University Press.

Albon, S.D., A. Stien, R.J. Irvine, R. Langvatn, E. Ropstad and O. Halvorsen, 2002. The role of parasites in the dynamics of a reindeer population. Proceedings of the Royal Society of London B, 269:1625–1632.

Aleksandrova, V.D., 1988. Vegetation of the Soviet Polar Deserts. Cambridge University Press, 228pp.

Alley, R.B., 2000. The Younger Dryas cold interval as viewed from central Greenland. Quaternary Science Reviews, 19:213–226.

Alroy, J., 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. Science, 292:1893–1896.

Anderson, P.M. and L.B. Brubaker, 1993. Holocene vegetation and climate histories of Alaska. In: H.E. Wright Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein (eds.). Global Climates since the Last Glacial Maximum, pp. 386–400. University of Minnesota Press.

Anderson, P.M. and L.B. Brubaker, 1994. Vegetation history of north central Alaska: A mapped summary of late-Quaternary pollen data. Quaternary Science Reviews, 13:71–92.

Andersson, M. and S. Jonasson, 1986. Rodent cycles in relation to food resources on an alpine heath. Oikos, 46:93–106.

Andreev, M.P., Yu.V. Kotlov and I.I. Makarova, 1996. Checklist of lichens and lichenicolous fungi of the Russian Arctic. The Bryologist, 99(2):137–169.

Andrews, J.T., 1987. The late Wisconsin glaciation and deglaciation of the Laurentide ice sheet. In: W.F. Ruddiman and H.E. Wright Jr. (eds.). North America and Adjacent Oceans during the Last Deglaciation, pp. 13–37. The Geological Society of America, Boulder, Colorado.

Angerbjörn, A., M. Tannerfeldt and S. Erlinge, 1999. Predator-prey relationships: arctic foxes and lemmings. Journal of Animal Ecology, 68:34–49.

Angerbjörn, A., M. Tannerfeldt and H. Lundberg, 2001. Geographical and temporal patterns of lemming population dynamics in Fennoscandia. Ecography, 24:298–308.

Arft, A.M., M.D. Walker, J. Gurevitch, J.M. Alatalo, M.S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G.H.R. Henry, M.H. Jones, R.D. Hollister, I.S. Jónsdóttir, K. Laine, E. Lévesque, G.M. Marion, U. Molau, P. Mølgaard, U. Nordenhäll, V. Raszhivin, C.H. Robinson, G. Starr, A. Stenström, M. Stenström, Ø. Totland, P. L. Turner, L.J. Walker, P.J. Webber, J.M. Welker, and P.A. Wookey, 1999. Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. Ecological Monographs, 69:491–511.

Astakhov, V., 1998. The last ice sheet of the Kara Sea: Terrestrial constraints on its age. Quaternary International, 45/46:19–28.

Aurela, M., T. Laurila and J.-P. Tuovinen, 2002. Annual CO_2 balance of a subarctic fen in northern Europe: Importance of the wintertime efflux. Journal of Geophysical Research, 107(D21):4607, doi: 10.1029/2002JD002055.

Aurela M., T. Laurila and J.-P. Tuovinen, 2004. The timing of snow melt controls the annual CO_2 balance in a subarctic fen. Geophysical Research Letters, 31:L16119, doi:10.1029/2004GL020315.

Babenko, A.B. and V.I. Bulavintsev, 1997. Springtails (Collembola) of Eurasian polar deserts. Russian Journal of Zoology, 1(2):177–184.

Back, J., S. Neuvonen and S. Huttunen, 1994. Pine needle growth and fine structure after prolonged acid rain treatment in the subarctic. Plant, Cell and Environment, 17:1009–1021.

Baldocchi, D., F.M. Kelliher, T.A. Black and P.G. Jarvis, 2000. Climate and vegetation controls on boreal zone energy exchange. Global Change Biology, 6(S1):69–83.

Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press, I. Symrnioudis, A.D. Watt and J.B. Whittaker, 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology, 8:1–16.

Barber, D.C., A. Dyke, C. Hillaire-Marcel, A.E. Jennings, J.T. Andrews, M.W. Kerwin, G. Bilodeau, R. McNeely, J. Southon, M.D. Morehead and J.-M. Gagnon, 1999. Forcing of the cold event of 8,200 years ago by catastrophic drainage of Laurentide lakes. Nature, 400:344–348.

Bardgett, R.D., T.C. Streeter, L. Cole and I.R. Hartley, 2002. Linkages between soil biota, nitrogen availability, and plant nitrogen uptake in a mountain ecosystem in the Scottish Highlands. Applied Soil Ecology, 19:121–134.

Barlow, L.K., J.P. Sadler, A.E.J. Ogilvie, P.C. Buckland, T. Amorosi, J.H. Ingimundarson, P. Skidmore, A.J. Dugmore and T.H. McGovern, 1997. Interdisciplinary investigations of the end of the Norse Western Settlement in Greenland. The Holocene, 7(4):489–499.

Barnes, J.D., M.R. Hull and A.W. Davison, 1996. Impacts of air pollutants and elevated carbon dioxide on plants in wintertime. In: M. Iqbal and M. Yunus (eds.). Plant Response to Air Pollution, pp. 135–166. John Wiley & Sons.

Bartlett, K.B. and R.C. Harriss, 1993. Review and assessment of methane emissions from wetlands. Chemosphere, 26:261–320.

Batzli, G.O., 1975. The role of small mammals in arctic ecosystems. In: F.B. Golley, K. Petrusewicz and L. Ryszkowski (eds.). Small Mammals: Their Productivity and Population Dynamics, pp. 243–267. Cambridge University Press.

Batzli, G.O., 1981. Populations and energetics of small mammals in the tundra ecosystem. In: L.C. Bliss, O.W. Heal and J.J. Moore (eds.). Tundra Ecosystems: a Comparative Analysis, pp. 377–396. Cambridge University Press.

Batzli, G.O., 1993. Food selection by lemmings. In: N.C. Stenseth and R.A. Ims (eds.). The Biology of Lemmings, pp. 281–301. Academic Press.

Batzli, G.O., R.G. White, S.F. MacLean Jr., F.A. Pitelka and B.D. Collier, 1980. The herbivore-based trophic system. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 335–410. Dowden, Hutchinson and Ross, Pennsylvania.

Bauert, M.R., 1996. Genetic diversity and ecotypic differentiation in arctic and alpine populations of *Polygonum viviparum*. Arctic and Alpine Research, 28:190–195.

Bayer, R.J., 1991. Allozymic and morphological variation of *Antennaria* (Asteraceae: Inuleae) from the low arctic of northwestern North America. Systematic Botany, 16:492–509.

Beeder, J., R.K. Nilsen, J.T. Rosnes, T. Torsvik and T. Lien, 1994. *Archaeoglobus fulgidus* isolated from hot North Sea oil field waters. Applied and Environmental Microbiology, 60:1227–1231.

Beerling, D.J. and M. Rundgren, 2000. Leaf metabolic and morphological responses of dwarf willow (*Salix herbacea*) in the sub-Arctic to the past 9000 years of global environmental change. New Phytologist, 145:257–269.

Beerling, D.J., A.C. Terry, P.L. Mitchell, T.V. Callaghan, D. Gwynn-Jones and J.A. Lee, 2001. Time to chill: effects of simulated global change on leaf ice nucleation temperatures of subarctic vegetation. American Journal of Botany, 88(4):628–633.

Beijerinck, M.W., 1913. De infusies en de ontdekking der backteriën. In: Jaarboek van de Koninklijke Akademie v. Wetenschappen. Müller, Amsterdam.

Bell, K.L. and L.C. Bliss, 1977. Overwinter phenology of plants in a polar semi-desert. Arctic, 30:118–121.

Bell, K.L. and L.C. Bliss, 1980. Plant reproduction in a high arctic environment. Arctic and Alpine Research, 12:1–10.

Bennike, O., 1999. Colonisation of Greenland by plants and animals after the last ice age: a review. Polar Record, 35:323–336.

Berendse, F. and S. Jonasson, 1992. Nutrient use and nutrient cycling in northern ecosystems. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 337–356. Academic Press.

Bergman, G., 1982. Why are wings of *Larus fuscus* so dark? Ornis Fennica, 59:77–83.

Beringer, J., A.H. Lynch, F.S. Chapin III, M. Mack and G.B. Bonan, 2001a. The representation of Arctic soils in the Land Surface Model: the importance of mosses. Journal of Climate, 14:3324–3335.

Beringer, J., N.J. Tapper, I. McHugh, F.S. Chapin III, A.H. Lynch, M.C. Serreze and A. Slater, 2001b. Impact of Arctic treeline on synoptic climate. Geophysical Research Letters, 28:4247–4250.

Berkes, F. and H. Fast, 1996. Aboriginal peoples: the basis for policy-making towards sustainable development. In: A. Dale and J.B. Robinson (eds.). Achieving Sustainable Development, pp. 204–264. University of British Columbia Press.

Bernatchez, L., A. Chouinard and G. Lu, 1999. Integrating molecular genetics and ecology in studies of adaptive radiation: whitefish, *Coregonus* sp., as a case study. Biological Journal of the Linnean Society, 68(1–2):173–194.

Betts, A.K. and J.H. Ball, 1997. Albedo over the boreal forest. Journal of Geophysical Research, 102(D24):28901–28909.

Betts, R.A., 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. Nature, 408:187–190.

Betts, R.A., 2001. The boreal forest and surface albedo change. In: Proceedings of the International Conference on Arctic Feedbacks to Global Change, Rovaniemi, Finland, 25–26 October 2001, pp. 15–19. Arctic Centre, University of Lapland, Rovaniemi.

Bety, J., G. Gauthier, E. Korpimäki and J.F. Giroux, 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. Journal of Animal Ecology, 71:88–98.

Bianchi, G.G. and I.N. McCave, 1999. Holocene periodicity in North Atlantic climate and deep-ocean flow south of Iceland. Nature, 397:515–517.

Bielawski, E., 1997. Aboriginal participation in global change research in the Northwest Territories of Canada. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 475–483. Springer-Verlag.

Bigelow, N.H., L.B. Brubaker, M.E. Edwards, S.P. Harrison, I.C. Prentice, P.M. Anderson, A.A. Andreev, P.J. Bartlein, T.R. Christensen, W. Cramer, J.O. Kaplan, A.V. Lozhkin, N.V. Matveyeva, D.F. Murray, A.D. McGuire, V.Y. Razzhivin, J.C. Ritchie, B. Smith, D.A. Walker, K. Gajewski, V. Wolf, B.H. Holmqvist, Y. Igarashi, K. Kremenetskii, A. Paus, M.F.J. Pisaric and V.S. Volkova, 2003. Climate change and Arctic ecosystems: 1. Vegetation changes north of 55°N between the last glacial maximum, mid-Holocene, and present. Journal of Geophysical Research, 108(D19):8170, doi:10.1029/2002JD002558.

Billings, W.D., 1973. Arctic and Alpine vegetations: similarities, differences, and susceptibility to disturbance. Bioscience, 23:697–704.

Billings, W.D., 1987. Carbon balance of Alaskan tundra and taiga ecosystems: Past, present, and future. Quaternary Science Reviews, 6:165–177.

Billings, W.D., 1992. Phytogeographic and evolutionary potential for the Arctic flora and vegetation in a changing climate. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 91–109. Academic Press.

Billings, W.D. and L.C. Bliss, 1959. An alpine snowbank environment and its effects on vegetation, plant development and productivity. Ecology, 40(3):388–397.

Billings, W.D. and H.A. Mooney, 1968. The ecology of Arctic and Alpine plants. Biological Reviews, 43:481–529.

Billings, W.D., J.O. Luken, D.A. Mortensen and K.M. Peterson, 1982. Arctic tundra: a source or sink for atmospheric carbon dioxide in a changing environment? Oecologia, 53:7–11.

Billings, W.D., K.M. Peterson, J.O. Luken and D.A. Mortensen, 1984. Interaction of increasing atmospheric carbon dioxide and soil nitrogen on the carbon balance of tundra microcosms. Oecologia, 65:26–29.

BirdLife International, 2001. Threatened Birds of Asia: The BirdLife International Red Data Book. N.J. Collar, A.V. Andreev, S. Chan, M.J. Crosby, S. Subramanya and J.A. Tobias (eds.). BirdLife International, Cambridge, UK, 3038pp.

Birkemoe, T. and H.P. Leinaas, 2000. Effects of temperature on the development of an arctic Collembola (*Hypogastrura tullbergi*). Functional Ecology, 14:693–700.

Birkemoe, T. and L. Sømme, 1998. Population dynamics of two collembolan species in an Arctic tundra. Pedobiologia, 42:131–145.

Björck, S., M.J.C. Walker, L.C. Cwynar, S. Johnsen, K.-L. Knudsen, J.J. Lowe and B. Wohlfarth, 1998. An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. Journal of Quaternary Science, 13(4):283–292.

Björn, L.O., 2002. Effects of UV-B radiation on terrestrial organisms and ecosystems with special reference to the Arctic. In: D.O. Hessen (ed.). UV Radiation and Arctic Ecosystems. Ecological Studies, 153:93–121.

Bliss, L.C., 1971. Arctic and alpine plant life cycles. Annual Review of Ecology and Systematics, 2:405–438.

Bliss, L.C. and N.V. Matveyeva, 1992. Circumpolar Arctic vegetation. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 59–89. Academic Press.

Bliss, L.C., O.W. Heal and J.J. Moore (eds.), 1981. Tundra Ecosystems: A Comparative Analysis. Cambridge University Press, 813pp.

Blum, O.B., 1974. Water relations. In: V. Ahmadjian and M.E. Hale (eds.). The Lichens, pp. 381–400. Academic Press.

Bonan, G.B., D. Pollard and S.L. Thompson, 1992. Effects of boreal forest vegetation on global climate. Nature, 359:716–718.

Bonan, G.B., F.S. Chapin III and S.L. Thompson, 1995. Boreal forest and tundra ecosystems as components of the climate system. Climatic Change, 29:145–167.

Borgen, T., S.A. Elborne and H. Knudsen. A Checklist of the Greenland Basidiomycota. Meddelelser om Grønland, Bioscience (in press.).

Boudreau, L.D. and W.R. Rouse, 1995. The role of individual terrain units in the water balance of wetland tundra. Climate Research, 5:31–47.

Bovis, M.J. and R.G. Barry, 1974. A climatological analysis of north polar desert areas. In: T.L. Smiley and J.H. Zumberge (eds.). Polar Deserts and Modern Man, pp. 23–31. University of Arizona Press.

Braga, G.U.L., S.D. Flint, C.D. Miller, A.J. Anderson and D.W. Roberts, 2001a. Variability in response to UV-B among species and strains of *Metarhizium* isolated from sites at latitudes from 61° N to 54° S. Journal of Invertebrate Pathology, 78:98–108.

Braga, G.U.L., S.D. Flint, C.L. Messias, A.J. Anderson and D.W. Roberts, 2001b. Effects of UVB irradiance on conidia and germinants of the entomopathogenic hyphomycete *Metarhizium anisopliae*: A study of reciprocity and recovery. Photochemistry and Photobiology, 73:140–146.

Braga, G.U.L., S.D. Flint, C.D. Miller, A.J. Anderson and D.W. Roberts, 2001c. Both solar UVA and UVB radiation impair conidial culturability and delay germination in the entomopathogenic fungus *Metarhizium anisopliae*. Photochemistry and Photobiology, 74:734–739.

Bret-Harte, M.S., G.R. Shaver, J.P. Zoerner, J.F. Johnstone, J.L. Wagner, A.S. Chavez, R.F. Gunkelman, S.C. Lippert and J.A. Laundre, 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. Ecology, 82:18–32.

Bret-Harte, M.S., G.R. Shaver and F.S. Chapin III, 2002. Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. Journal of Ecology, 90:251–267.

Brochmann, C. and S.W. Steen, 1999. Sex and genes in the flora of Svalbard – implications for conservation biology and climate change. In: I. Nordal and V.Y. Razzhivin (eds.). The Species Concept in the High North - a Panarctic Flora Initiative. Det Norske Videnskaps – Akademi. I. Matematisk Naturvitenskapelig Klasse, Skrifter, Ny serie 38:33–72. Novus Forlag, Oslo.

Brochmann, C., T.M. Gabrielsen, I. Nordal, J.Y. Landvik and R. Elven, 2003. Glacial survivial or *tabula rasa*? The history of North Atlantic biota revisited. Taxon, 52:417–450.

Brockmann-Jerosch, H., 1919. Baumgrenze und Klimacharakter. Pflanzengeographische Kommission der Schweiz Naturforschenden Gesellschaft, Beiträge zur geobotanischen Landesaufnahmne, Vol 6. Rascher, Zürich.

Brooker, R. and T.V. Callaghan, 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos, 81:196–207.

Brooker, R., T.V. Callaghan and S. Jonasson, 1999. Nitrogen uptake by rhizomes of the clonal sedge *Carex bigelowii*: a previously overlooked nutritional benefit of rhizomatous growth. New Phytologist, 142:35–48.

Brooker, R.W., B.Å. Carlsson and T.V. Callaghan, 2001. *Carex bigelowii* Torrey ex Schweinitz (*C. rigida* Good., non Schrank; *C. hyperborea* Drejer). Journal of Ecology, 89:1072–1095.

Brooks, P.D., M.W. Williams and S.K. Schmidt, 1998. Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. Biogeochemistry, 43:1–15.

Brown, J., K.R. Everett, P.J. Webber, S.F. MacLean Jr. and D.F. Murray, 1980. The coastal tundra at Barrow. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 1–29. Dowden, Hutchinson and Ross, Pennsylvania.

Brown, J., K.M. Hinkel and F.E. Nelson, 2000. The Circumpolar Active Layer Monitoring (CALM) Program: research designs and initial results. Polar Geography, 24(3):165–258.

Brunner, P.C., M.R. Douglas, A. Osinov, C.C. Wilson and L. Bernatchez, 2001. Holarctic phylogeography of Arctic char (*Salvelinus alpinus L.*) inferred from mitochondrial DNA sequences. Evolution, 55(3):573–586.

Bryant, J.P., F.S. Chapin III and D.R. Klein, 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos, 40:357–368.

Bryson, R.A., 1966. Air masses, streamlines, and the boreal forest. Geographical Bulletin, 8:228–269.

Bubier, J.L. and T.R. Moore, 1994. An ecological perspective on methane emissions from northern wetlands. Trends in Ecology and Evolution, 9:460–464.

Buck, N.D., 1999. The direct and indirect effects of enhanced UV-B on larvae of the moth *Epirrita autumnata*. Ph.D Thesis, University of Sheffield, 206pp.

Buck, N.D. and T.V. Callaghan, 1999. The direct and indirect effects of enhanced UV-B on the moth caterpillar *Epirrita autumnata*. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:68–76.

Buckland, P.C., T. Amorosi, L.K. Barlow, A.J. Dugmore, P.A. Mayewski, T.H. McGovern, A.E.J. Ogilvie, J.P. Sadler and P. Skidmore, 1996. Bioarchaeological and climatological evidence for the fate of Norse farmers in medieval Greenland. Antiquity, 70(267):88–96.

Buffoni Hall, R.S., J.F. Bornman and L.O. Björn, 2002. UV-induced changes in pigment content and light penetration in the fruticose lichen *Cladonia arbuscula* ssp. mitis. Journal of Photochemistry and Photobiology B: Biology, 66:13–20.

Buffoni Hall, R.S., M. Paulsson, K. Duncan, A.K. Tobin, S. Widell and J.F. Bornman, 2003. Water- and temperature-dependence of DNA damage and repair in the fruticose lichen *Cladonia arbuscula* ssp. *mitis* exposed to UV-B radiation. Physiologia Plantarum, 118:371–379.

Bunnell, F., O.K. Miller, P.W. Flanagan and R.E. Benoit, 1980. The microflora: composition, biomass and environmental relations. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 255–290. Dowden, Hutchinson and Ross, Pennsylvania..

Burn, C.R., 1997. Cryostratigraphy, paleogeography, and climate change during the early Holocene warm interval, western Arctic coast, Canada. Canadian Journal of Earth Sciences, 34:912–925.

Bylund, H., 1999. Climate and the population dynamics of two insect outbreak species in the north. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:54–62.

CAFF, 2001. Arctic Flora and Fauna: Status and Conservation. Conservation of Arctic Flora and Fauna, Edita, Helsinki, 272pp.

Callaghan, T.V., 1974. Intraspecific variation in *Phleum alpinum* L. with special reference to polar regions. Arctic and Alpine Research, 6:361–401.

Callaghan, T.V. and B.A. Carlsson, 1997. Impacts of climate change on demographic processes and population dynamics in Arctic plants. In: W.C. Oechel, T.V. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 129–152. Springer Verlag.

Callaghan, T.V. and U. Emanuelsson, 1985. Population structure and processes of tundra plants and vegetation. In: J. White (ed.). The Population Structure of Vegetation, pp. 399–439. Junk, Dordrecht.

Callaghan, T.V. and S. Jonasson, 1995. Arctic terrestrial ecosystems and environmental change. Philosophical Transactions of the Royal Society of London A, 352:259–276.

Callaghan, T.V., A.D. Headley and J.A. Lee, 1991. Root function related to the morphology, life history and ecology of tundra plants. In: D. Atkinson (ed.). Plant Root Growth: An Ecological Perspective, pp. 311–340. Blackwell.

Callaghan, T.V., B.A. Carlsson, M. Sonesson and A. Temesvary, 1997. Between-year variation in climate-related growth of circumarctic populations of the moss *Hylocomium splendens*. Functional Ecology, 11:157–165.

Callaghan, T.V., M.C. Press, J.A. Lee, D.L. Robinson and C.W. Anderson, 1999. Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. Polar Research, 18(2):191–197.

Callaghan, T.V., R.M.M. Crawford, M. Eronen, A. Hofgaard, S. Payette, W.G. Rees, O. Skre, B. Sveinbjörnsson, T.K. Vlassova and B.R. Werkman, 2002a. The dynamics of the tundra-taiga boundary: An overview and suggested coordinated and integrated approach to research. Ambio Special Report, 12:3–5.

Callaghan, T.V., B.R. Werkman and R.M.M. Crawford, 2002b. The tundra-taiga interface and its dynamics: concepts and applications. Ambio Special Report, 12:6–14.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas, D. Kikodze and B.J. Cook, 2002. Positive interactions among alpine plants increase with stress. Nature, 417:844–848.

Caporn, S.J.M., M. Risager and J.A. Lee, 1994. Effect of nitrogen supply on frost hardiness in *Calluna vulgaris* (L.) Hull. New Phytologist, 128:461–468.

Carlsson, B.A. and T.V. Callaghan, 1991. Positive plant interactions in tundra vegetation and the importance of shelter. Journal of Ecology, 79:973–983.

Carlsson, B.A. and T.V. Callaghan, 1994. Impact of climate change factors on the clonal sedge *Carex bigelowii*: implications for population growth and vegetative spread. Ecography, 17:321–330.

Chapin, D.M. and C.S. Bledsoe, 1992. Nitrogen fixation in arctic plant communities. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 301–319. Academic Press.

Chapin, F.S. III, 1974. Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. Ecology, 55:1180–1198.

Chapin, F.S. III, 1983. Direct and indirect effects of temperature on Arctic plants. Polar Biology, 2:47–52.

Chapin, F.S. III and A.J. Bloom, 1976. Phosphate absorption: adaptation of tundra graminoids to a low temperature, low phosphorus environment. Oikos, 26:111–121.

Chapin, F.S. III and G.R. Shaver, 1985a. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology, 66:564–576.

Chapin, F.S. III and G.R. Shaver, 1985b. Arctic. In: B.F. Chabot and H.A. Mooney (eds.). Physiological Ecology of North American Plant Communities, pp. 16–40. Chapman and Hall.

Chapin, F.S. III and A.M. Starfield, 1997. Time lags and novel ecosystems in response to transient climatic change in Arctic Alaska. Climatic Change, 35:449–461.

Chapin, F.S. III, P.C. Miller, W.D. Billings and P.I. Coyne, 1980. Carbon and nutrient budgets and their control in coastal tundra. In: J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 458–482. Dowden, Hutchinson and Ross, Pennsylvania.

Chapin, F.S. III, L. Moilanen and K. Kielland, 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal Arctic sedge. Nature, 361:150–153.

Chapin, F.S. III, L.R. Walker, C.L. Fastie and L.C. Sharman, 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs, 64:149–175.

Chapin, F.S. III, G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer and J.A. Laundre, 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology, 76:694–711.

Chapin, F.S. III, M.S. Bret-Harte, S.E. Hobbie and H. Zhong, 1996. Plant functional types as predictors of transient responses of Arctic vegetation to global change. Journal of Vegetation Science, 7:347–358.

Chapin, F.S. III, W. Eugster, J.P. McFadden, A.H. Lynch and D.A. Walker, 2000a. Summer differences among Arctic ecosystems in regional climate forcing. Journal of Climate, 13:2002–2010.

Chapin, F.S. III, A.D. McGuire, J. Randerson, R. Pielke Sr., D. Baldocchi, S.E. Hobbie, N. Roulet, W. Eugster, E. Kasischke, E.B. Rastetter, S.A. Zimov and S.W. Running, 2000b. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biology, 6(S1):211–223.

Chapman, W.L. and J.E. Walsh, 1993. Recent variations of sea ice and air temperatures in high latitudes. Bulletin of the American Meteorological Society, 74(1):33–47.

Cheng, W. and R.A. Virginia, 1993. Measurement of microbial biomass in arctic tundra soils using fumigation-extraction and substrate-induced respiration procedures. Soil Biology and Biochemistry, 25:135–141.

Chernov, Y.I., 1985. Synecological analysis of yeasts in the Taimyr tundra. Ekologiya, 1:54–60.

Chernov, Y.I., 1989. Heat conditions and Arctic biota. Ekologiya, 2:49–57. (In Russian)

Chernov, Y.I., 1995. Diversity of the Arctic terrestrial fauna. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies, 113:81–95.

Chernov, Y.I., 2002. Arctic biota: taxonomic diversity. Zoologicheski Zhurnal, 81(12):1411–1431. (In Russian with English summary)

Chernov, Y.I. and N.V. Matveyeva, 1997. Arctic ecosystems in Russia. In: F.E. Wielgolaski (ed.). Polar and Alpine Tundra. Ecosystems of the World, 3:361–507. Elsevier.

Christensen, S. and B.T. Christensen, 1991. Organic matter available for denitrification in different soil fractions: Effect of freeze/thaw cycles and straw disposal. Journal of Soil Science, 42:637–647.

Christensen, T.R., 1993. Methane emission from Arctic tundra. Biogeochemistry, 21(2):117–139.

Christensen, T.R. and P. Cox, 1995. Response of methane emission from Arctic tundra to climatic change: results from a model simulation. Tellus B:47:301–309.

Christensen, T.R. and M. Keller, 2003. Element interactions and trace gas exchange. In: J.M. Melillo, C.B. Field and B. Moldan (eds.). Interactions of the Major Biogeochemical Cycles: Global Changes and Human Impacts. SCOPE 61, pp. 247–258. Island Press.

Christensen, T.R., S. Jonasson, T.V. Callaghan and M. Havström, 1995. Spatial variation in high-latitude methane flux along a transect across Siberian and European tundra environments. Journal of Geophysical Research, 100(D10):21035–21046.

Christensen, T.R., I.C. Prentice, J. Kaplan, A. Haxeltine and S. Sitch, 1996. Methane flux from northern wetlands and tundra: an ecosystem source modelling approach. Tellus B:48:652–661.

Christensen, T.R., S. Jonasson, A. Michelsen, T.V. Callaghan and M. Havström, 1998. Environmental controls on soil respiration in the Eurasian and Greenlandic Arctic. Journal of Geophysical Research, 103(D22):29015–29021.

Christensen, T.R., A. Michelsen and S. Jonasson, 1999a. Exchange of CH_4 and N_2O in a subarctic heath soil: effects of inorganic N and P and amino acid addition. Soil Biology and Biochemistry, 31:637–641.

Christensen, T.R., S. Jonasson, T.V. Callaghan and M. Havström, 1999b. On the potential CO_2 releases from tundra soils in a changing climate. Applied Soil Ecology, 11:127–134.

Christensen, T.R., T. Friborg, M. Sommerkorn, J. Kaplan, L. Illeris, H. Søgaard, C. Nordstrøm and S. Jonasson, 2000. Trace gas exchange in a high-arctic valley. 1: Variations in CO_2 and CH_4 flux between tundra vegetation types. Global Biogeochemical Cycles, 14:701–714.

Christensen, T.R., N. Panikov, M. Mastepanov, A. Joabsson, A. Stewart, M. Oquist, M. Sommerkorn, S. Reynaud and B. Svensson, 2003a. Biotic controls on CO_2 and CH_4 exchange in wetlands - a closed environment study. Biogeochemistry, 64:337–354.

Christensen, T.R., A. Ekberg, L. Ström, M. Mastepanov, N. Panikov, M. Öquist, B.H. Svensson, H. Nykänen, P.J. Martikainen and H. Oskarsson, 2003b. Factors controlling large scale variations in methane emissions from wetlands. Geophysical Research Letters, 30(7):1414, doi:10.1029/2002GL016848.

Christensen, T.R, T. Johansson, H.J. Åkerman, M. Mastepanov, N. Malmer, T. Friborg, P. Crill and B. Svensson, 2004. Thawing sub-arctic permafrost: effects on vegetation and methane emissions. Geophysical Research Letters, 31(4):L04501, doi:10.1029/2003GL018680.

Clein, J.S. and J.P. Schimel, 1995. Microbial activity of tundra and taiga soils at sub-zero temperatures. Soil Biology and Biochemistry, 27:1231–1234.

Clein, J.S., B.L. Kwiatkowski, A.D. McGuire, J.E. Hobbie, E.B. Rastetter, J.M. Melillo and D.W. Kicklighter, 2000. Modelling carbon responses of tundra ecosystems to historical and projected climate: A comparison of a plot- and a global-scale ecosystem model to identify process-based uncertainties. Global Change Biology, 6(S1):127–140.

Clymo, R.S. and E.J.F. Reddaway, 1971. Productivity of *Sphagnum* (bog-moss) and peat accumulation. Hydrobiologia, 12:181–192.

Cole, J.J., N.F. Caraco, G.W. Kling and T.K. Kratz, 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science, 265:1568–1570.

Coley, P.D., J.P. Bryant and F.S. Chapin III, 1985. Resource availability and plant antiherbivore defense. Science, 230:895–899.

Conrad, R., 1996. Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). Microbiological Reviews, 60(4):609–640.

Convey, P., 2000. How does cold constrain life cycles of terrestrial plants and animals? CryoLetters, 21:73–82.

Cooper, E.J., 1996. An ecophysiological investigation of some species of Arctic temperature *Ranunculus L.* with respect to climate warming. Responses of above- and below-ground growth and carbon dioxide exchange to season and temperature. Ph.D Thesis, University of Bradford.

Cornelissen, J.H.C., N. Perez-Harguineguy, S. Diaz, J. Grime, B. Marazano, M. Cabido, F. Vendramini and B. Cerabolini, 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytologist, 143:191–200.

Cornelissen, J.H.C., T.V. Callaghan, J.M. Alatalo, A. Michelsen, E. Graglia, A.E. Hartley, D.S. Hik, S.E. Hobbie, M.C. Press, C.H. Robinson, G.H.R. Henry, G.R. Shaver, G.K. Phoenix, D. Gwynn-Jones, S. Jonasson, F.S. Chapin III, U. Molau, J.A. Lee, J.M. Melillo, B. Sveinbjornsson and R. Aerts, 2001. Global change and Arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of Ecology, 89:984–994.

Corner, R.W.M. and R.I.L. Smith, 1973. Botanical evidence of ice recession in the Argentine Islands. British Antarctic Survey Bulletin, 35:83–86.

Coulson, S.J., I.D. Hodkinson, A.T. Strathdee, W. Block, N.R. Webb, J.S. Bale and M.R. Worland, 1995. Thermal environments of Arctic soil organisms during the winter. Arctic and Alpine Research, 27:364–370.

Coulson, S.J., I.D. Hodkinson, N.R. Webb, W. Block, J.S. Bale, A.T. Strathdee, M.R. Worland and C. Wooley, 1996. Effects of experimental temperature elevation on high-arctic soil microarthropod populations. Polar Biology, 16:147–153.

Coulson, S.J., H.P. Leinaas, R.A. Ims and G. Søvik, 2000. Experimental manipulation of winter surface ice layer: The effects on a High Arctic soil microarthropod community. Ecography, 23:299–306.

Coyne, P.I. and J.J. Kelley, 1971. Release of carbon dioxide from frozen soil to the Arctic atmosphere. Nature, 234:407–408.

Crawford, R.M.M., 1989. Studies in Plant Survival. Blackwell.

Crawford, R.M.M., 1997a. Habitat fragility as an aid to long-term survival in Arctic vegetation. In: S.J. Woodin and M. Marquiss (eds.). Ecology of Arctic Environments, pp. 113–136. Blackwell Scientific Ltd.

Crawford, R.M.M. (ed.), 1997b. Disturbance and Recovery in Arctic Lands: An Ecological Perspective. Kluwer Academic Publishers, 621pp.

Crawford, R.M.M. and L.C. Smith, 1997. Responses of some high Arctic shore plants to variable lengths of growing season. Opera Botanica, 132:201–214.

Crawford, R.M.M., H.M. Chapman and H. Hodge, 1994. Anoxia tolerance in high Arctic vegetation. Arctic and Alpine Research, 26:308–312.

Crawford, R.M.M., C.E. Jeffree and W.G. Rees, 2003. Paludification and forest retreat in northern oceanic environments. Annals of Botany, 91:213–226.

Crill, P., K.B. Bartlett and N.T. Roulet, 1992. Methane flux from boreal peatlands. Suo, 43:173–182.

Cronberg, N., U. Molau and M. Sonesson, 1997. Genetic variation in the clonal bryophyte *Hylocomium splendens* at hierarchical geographical scales in Scandinavia. Heredity, 78:293–301.

Curl, H. Jr., J.T. Hardy and R. Ellermeier, 1972. Spectral absorption of solar radiation in alpine snowfields. Ecology, 53:1189–1194.

Dalén, L., E. Fuglei, P. Hersteinsson, C. Kapel, J. Roth, G. Samelius, M. Tannerfeldt and A. Angerbjörn, 2005. Population history and genetic structure of a circumpolar species: the Arctic fox. Biological Journal of the Linnean Society, 84:79–89.

Dankers, R., 2002. Sub-arctic Hydrology and Climate Change. A Case Study of the Tana River Basin in Northern Fennoscandia. Netherlands Geographical Studies, 304. Royal Dutch Geographical Society/ Faculteit Ruimtelijke Wetenschappen Universiteit Utrecht, 240pp.

Danks, H.V., 1999. Life cycles in polar arthropods – flexible or programmed? European Journal of Entomology, 96:83–102.

Dansgaard, W., J.W.C. White and S.J. Johnsen, 1989. The abrupt termination of the Younger Dryas climate event. Nature, 339:532–534.

Davidson, E.A. and J.P. Schimel, 1995. Microbial processes of production and consumption of nitric oxide, nitrous oxide and methane. In: P.A. Matson and R.C. Harriss (eds.). Biogenic Trace Gases: Measuring Emissions from Soil and Water, pp. 327–357. Blackwell Science.

Davidson, N.C., K.B. Strann, N.J. Crockford, P.R. Evans, J. Richardson, L.J. Standen, D.J. Townshend, J.D. Uttley, J.R. Wilson and A.G. Wood, 1986. The origins of Knots *Calidris canutus* in arctic Norway in Spring. Ornis Scandinavica, 17(2):175–179.

de Vernal, A. and C. Hillaire-Marcel, 2000. Sea-ice cover, sea-surface salinity and halo/thermocline structure of the northwest North Atlantic: modern versus full glacial conditions. Quaternary Science Reviews, 19(1–5):65–85.

de Vernal, A., C. Hillaire-Marcel, J.-L. Turon and J. Matthiessen, 2000. Reconstruction of sea-surface temperature, salinity, and sea-ice cover in the northern North Atlantic during the last glacial maximum based on dinocyst assemblages. Canadian Journal of Earth Sciences, 37(5):725–750.

Dedysh, S.N., N.S. Panikov, W. Liesack, R. Grosskopf, J. Zhou and J.M. Tiedje, 1998. Isolation of acidophilic methane-oxidizing bacteria from northern peat wetlands. Science, 282:281–284.

Dedysh, S.N., W. Liesack, V.N. Khmelenina, N.E. Suzina, Y.A. Trotsenko, J.D. Semrau, A.M. Bares, N.S. Panikov and J.M. Tiedje, 2000. *Methylocella palustris* gen. nov., sp. nov., a new methane-oxidizing acidophilic bacterium from peat bogs, representing a novel subtype of serine-pathway methanotrophs. International Journal of Systematic and Evolutionary Microbiology, 50:955–969.

Derda, G.S. and R. Wyatt, 1999. Levels of genetic variation and its partitioning in the wide-ranging moss *Polytrichum commune*. Systematic Botany, 24:512–528.

Dimmer, C.H., P.G. Simmonds, G. Nickless and M.R. Bassford, 2001. Biogenic fluxes of halomethanes from Irish peatland ecosystems. Atmospheric Environment, 35:321–330.

Dixon, E.J., 2001. Human colonization of the Americas: timing, technology and process. Quaternary Science Reviews, 20:277–299.

Dorland, S. and E.G. Beauchamp, 1991. Denitrification and ammonification at low soil temperatures. Canadian Journal of Soil Science, 71:293–303.

Dormann, C.F. and S.J. Woodin, 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. Functional Ecology, 16:4–17.

Dunican, L.K. and T. Rosswall, 1974 Taxonomy and physiology of tundra bacteria in relationship to site characteristics. In: A.J. Holding, O.W. Heal, S.F. MacLean Jr. and P.W. Flanagan (eds.). Soil Organisms and Decomposition in Tundra, pp. 79–92. International Biological Programme Tundra Biome Steering Committee, Stockholm.

Dunne, J.A., J. Harte and K.J. Taylor, 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. Ecological Monographs, 73:69–86.

Dunning, C.A., L. Chalker-Scott and J.D. Scott, 1994. Exposure to ultraviolet-B radiation increases cold hardiness in *Rhododendron*. Physiologia Plantarum, 92:516–520.

Dye, D.G., 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. Hydrological Processes, 16:3065–3077.

Edlund, S.A. and B.T. Alt, 1989. Regional congruence of vegetation and summer climate patterns in the Queen Elizabeth Islands, Northwest Territories, Canada. Arctic, 42:3–23.

Ehrich, D., V.B. Fedorov, N.C. Stenseth, C.J. Krebs and A. Kenney, 2000. Phylogeography and mitochondrial DNA (mtDNA) diversity in North American collared lemmings (*Dicrostonyx groenlandicus*). Molecular Ecology, 9(3):329–337.

Elster, J., 2002. Ecological classification of terrestrial algal communities in polar environments. In: L. Beyer and M. Bolter (eds.). Geoecology of Antarctic Ice-free Coastal Landscapes. Ecological Studies 154:303–326.

Elster, J. and E.E. Benson, 2004. Life in the polar terrestrial environment: a focus on algae. In: B. Fuller, N. Lane and E.E. Benson (eds.). Life in the Frozen State, pp. 111–150. CRC Press.

Elster, J. and J. Svoboda, 1995. *In situ* simulation and manipulation of a glacial stream ecosystem in the Canadian High Arctic. In: A. Jenkins, R.C. Ferrier and C. Kirby (eds.). Ecosystem Manipulation Experiments: Scientific Approaches, Experimental Design and Relevant Results. Ecosystem Research Report 20, pp. 254–263. Commission of the European Communities, Brussels.

Elster, J. and J. Svoboda, 1996. Algal diversity, seasonality and abundance in, and along glacial stream in Sverdrup Pass 79º N, Central Ellesmere Island, Canada. Memoirs of National Institute of Polar Research, Special Issue 51:99–118.

Elster, J., J. Svoboda, J. Komárek and P. Marvan, 1997. Algal and cyanoprocaryote communities in a glacial stream, Sverdrup Pass, 79º N, Central Ellesmere Island, Canada. Archiv fuer Hydrobiologie. Supplementband. Algological Studies, 85:57–93.

Elster, J., A. Lukesova, J. Svoboda, J. Kopecky and H. Kanda, 1999. Diversity and abundance of soil algae in the polar desert, Sverdrup Pass, central Ellesmere Island. Polar Record, 35(194):231–254.

Elster, J., J. Svoboda and H. Kanda, 2001. Controlled environment platform used in temperature manipulation study of a stream periphyton in the Ny-Ålesund, Svalbard. In: J. Elster, J. Seckbach, W.F. Vincent and O. Lhotsky (eds.). Algae and Extreme Environments – Ecology and Physiology. Nova Hedvigia Beihefte, 123:63–75.

Elster, J., J. Svoboda, S. Ohtani and H. Kanda, 2002. Feasibility studies on future phycological research in polar regions. Polar Bioscience, 15:114–122.

Elton, C.S., 1924. Periodic fluctuations in the number of animals: their causes and effects. British Journal of Experimental Biology, 2:119–163.

Elton, C.S., 1925. The dispersal of insects to Spitsbergen. Transactions of the Entomological Society of London 1925, 73:289–299.

Elton, C. and M. Nicholson, 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology, 11:215–244.

Emanuelsson, U., 1987. Human influence on vegetation in the Torneträsk area during the last three centuries. In: M. Sonesson (ed.). Research in Arctic Life and Earth Sciences: Present Knowledge and Future Perspectives. Ecological Bulletin, 38:95–111.

Engstrom, R.N., A.S. Hope, D.A. Stow and H. Kwon, 2002. Characteristics of the spatial distribution of surface moisture in an eddy flux tower footprint in Arctic Coastal Plain ecosystems. EOS, Transactions of the American Geophysical Union, 83(2002 Fall Meeting Supplement): Abstract #H61B-0764.

Erlinge, S., K. Danell, P. Frodin, D. Hasselquist, P. Nilsson, E.-B. Olofsson and M. Svensson, 1999. Asynchronous population dynamics of Siberian lemmings across the Palaearctic tundra. Oecologia, 119:493–500.

Eugster, W., W.R. Rouse, R.A. Pielke, J.P. McFadden, D.D. Baldocchi, T.G.F. Kittel, F.S. Chapin III, G.E. Liston, P.L. Vidale, E. Vaganov and S. Chambers, 2000. Land-atmosphere energy exchange in Arctic tundra and boreal forest: available data and feedbacks to climate. Global Change Biology, 6(S1):84–115.

Eugster, W., G. Kling, T. Jonas, J.P. McFadden, A. Wust, S. MacIntyre and F.S. Chapin III. 2003. CO_2 exchange between air and water in an Arctic Alaskan and midlatitude Swiss lake: Importance of convective mixing. Journal of Geophysical Research, 108(D12):4362, doi:10.1029/2002JD002653.

Evans, P.R., 1997. Migratory birds and climate change. In: B. Huntley, W. Cramer, A.V. Morgan, H.C. Prentice and J.R.M. Allen (eds.). Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota, pp. 227–238. Springer Verlag.

Fahnestock, J.T., M.H. Jones and J.M. Welker, 1999. Wintertime CO_2 efflux from Arctic soils: Implications for annual carbon budgets. Global Biogeochemical Cycles, 13:775–780.

Fahnestock, J.T., K.L. Povirk and J.M. Welker, 2000. Ecological significance of litter redistribution by wind and snow in arctic landscapes. Ecography, 23:623–631.

Fairbanks, R.G., 1989. A 17,000-year glacio-eustatic sea level record: Influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature, 342:637–642.

Fajer, E.D., M.D. Bowers and F.A. Bazzaz, 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. Science, 243:1198–1200.

FAUNMAP Working Group, 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science, 272:1601–1606.

Fedorov, V.B. and A.V. Goropashnaya, 1999. The importance of ice ages in diversification of Arctic collared lemmings (*Dicrostonyx*): evidence from the mitochondrial cytochrome b region. Hereditas, 130(3):301–307.

Fedorov, V.B., K. Fredga and G.H. Jarrell, 1999a. Mitochondrial DNA variation and the evolutionary history of chromosome races of collared lemmings (*Dicrostonyx*) in the Eurasian Arctic. Journal of Evolutionary Biology, 12(1):134–145.

Fedorov, V., A. Goropashnaya, G.H. Jarrell and K. Fredga, 1999b. Phylogeographic structure and mitochondrial DNA variation in true lemmings (*Lemmus*) from the Eurasian Arctic. Biological Journal of the Linnean Society, 66(3):357–371.

Fetcher, N., 1985. Effects of removal of neighboring species on growth, nutrients, and microclimate of *Eriophorum vaginatum*. Arctic and Alpine Research, 17:7–17.

Finegold, L., 1996. Molecular and biophysical aspects of adaptation of life to temperatures below the freezing point. Advances in Space Research, 18(12):87–95.

Fioletov, V.E., J.B. Kerr, D.I. Wardle, J. Davies, E.W. Hare, C.T. McElroy and D.W. Tarasick, 1997. Long-term ozone decline over the Canadian Arctic to early 1997 from ground-based and balloon observations. Geophysical Research Letters, 24(22):2705–2708.

Flagstad, Ø. and K.H. Røed, 2003. Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. Evolution, 57:658–670.

Flanagan, P.W. and F.L. Bunnell, 1980. Microfloral activities and decomposition. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 291–335. Dowden, Hutchinson, and Ross, Pennsylvania.

Flanagan, P.W. and W. Scarborough, 1974. Physiological groups of decomposer fungi in tundra plant remains. In: A.J. Holding, O.W. Heal, S.F. MacLean Jr. and P.W. Flanagan (eds.). Soil Organisms and Decomposition in Tundra, pp. 159–181. International Biological Programme Tundra Biome Steering Committee, Stockholm.

Fogg, G.E., 1998. The Biology of Polar Habitats. Oxford University Press, 274pp.

Foley, J.A., J.E. Kutzbach, M.T. Coe and S. Levis, 1994. Feedbacks between climate and boreal forests during the Holocene epoch. Nature, 371:52–54.

Forbes, B.C., J.J. Ebersole and B. Strandberg, 2001. Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conservation Biology, 15(4):954–969.

Forchhammer, M.C. and D.M. Boertmann, 1993. The muskoxen *Ovibos moschatus* in north and northeast Greenland: population trends and the influence of abiotic parameters on population dynamics. Ecography, 16:299–308.

Fossa, A.M., 2003. Mountain vegetation in the Faroe Islands in a climate change perspective. Ph.D Thesis, University of Lund, 119pp.

Fox, S., 2002. These are things that are really happening: Inuit perspectives on the evidence and impacts of climate change in Nunavut. In: I. Krupnik and D. Jolly (eds.). The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change, pp. 12–53. Arctic Research Consortium of the United States, Fairbanks, Alaska.

Friborg, T., T.R. Christensen, B.U. Hansen, C. Nordstrøm and H. Søgaard, 2000. Trace gas exchange in a high arctic valley 2: Landscape CH_4 fluxes measured and modeled using eddy correlation data. Global Biogeochemical Cycles, 14:715–724.

Friborg, T., H. Soegaard, T.R. Christensen, C.R. Lloyd and N.S. Panikov, 2003. Siberian wetlands: Where a sink is a source. Geophysical Research Letters, 30(21):2129, doi:10.1029/2003GL017797.

Friend, A.D., A.K. Stevens, R.G. Knox and M.G.R. Cannell, 1997. A process-based, terrestrial biosphere model of ecosystem dynamics. (Hybrid v3.0). Ecological Modelling, 95:249–287.

Fuchigami, L.H., C.J. Weiser, K. Kobayshi, R. Timmis and L.V. Gusta, 1982. A degree growth stage (°GS) model and cold acclimation in temperate woody plants. In: P.H. Li and A. Sakai (eds.). Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications, Vol. 2, pp. 93–116. Academic Press.

Fuglei, E. and N.A. Øritsland, 1999. Seasonal trends in body mass, food intake and resting metabolic rate, and induction of metabolic depression in arctic foxes (Alopex lagopus) at Svalbard. Journal of Comparative Physiology B, 169:361–369.

Fulthorpe, R.R., A.N. Rhodes and J.M. Tiedje, 1998. High levels of endemicity of 3-chlorobenzoate-degrading soil bacteria. Applied and Environmental Microbiology, 64:1620–1627.

Funder, S., C. Hjort, J.Y. Landvik, S.-I. Nam, N. Reeh and R. Stein, 1998. History of a stable ice margin - East Greenland during the Middle and Upper Pleistocene. Quaternary Science Reviews, 17(1–3):77–123.

Fung, I., 1997. A greener north. Nature, 386:659–660.

Fung, I., J. John, J. Lerner, E. Matthews, M. Prather, L.P. Steele and P.J. Fraser, 1991. Three-dimensional model synthesis of the global methane cycle. Journal of Geophysical Research, 96:13033–13065.

Furness, R.W., 1990. Evolutionary and ecological constraints on the breeding distributions and behaviour of skuas. In: R. van den Elzen, K.-L. Schuchmann and K. Schmidt-Koenig (eds.). Current Topics in Avian Biology. Proceedings of the International Centennial Meeting of the Deutsche Ornithologen-Gesellschaft, pp. 153–158. Bonn.

Gabrielsen, T.M. and C. Brochmann, 1998. Sex after all: high levels of diversity detected in the arctic clonal plant *Saxifraga cernua* using RAPD markers. Molecular Ecology, 7:1701–1708.

Garcia-Pichel, F., L. Prufert-Bebout and G. Muyzer, 1996. Phenotypic and phylogenetic analyses show *Microcoleus chthonoplastes* to be a cosmopolitan cyanobacterium. Applied and Environmental Microbiology, 62:3284–3291.

Galand, P.E., S. Saarnio, H. Fritze and K. Yrjala, 2002. Depth related diversity of methanogen Archaea in Finnish oligotrophic fen. FEMS Microbiology Ecology, 42:441–449.

Gauslaa, Y., 1984. Heat resistance and energy budget in different Scandinavian plants. Holarctic Ecology, 7:1–78.

Gauslaa, Y. and E.M. Ustvedt, 2003. Is parietin a UV-B or a blue-light screening pigment in the lichen *Xanthoria parietina*? Photochemical and Photobiological Sciences, 2:424–432.

Gehrke, C., U. Johanson, T.V. Callaghan, D. Chadwick and C.H. Robinson, 1995. The impact of enhanced ultraviolet-B radiation on litter quality and decomposition processes in *Vaccinium* leaves from the Subarctic. Oikos, 72:213–222.

Geiges, O., 1996. Microbial processes in frozen food. Advances in Space Research, 18(12):109–118.

Giblin, A.E., K.J. Nadelhoffer, G.R. Shaver, J.A. Laundre and A.J. McKerrow, 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecological Monographs, 61:415–435.

Gilg, O., 2002. The summer decline of the collared lemming, *Dicrostonyx groenlandicus*, in high Arctic Greenland. Oikos, 99:499–510.

Gilg, O., I. Hanski and B. Sittler, 2003. Cyclic dynamics in a simple vertebrate predator-prey community. Science, 302:866–868.

Gilichinsky, D. (ed.), 1994. Viable Microorganisms in Permafrost. Russian Academy of Science, Pushchino Scientific Centre, 115pp.

Gilichinsky, D., 2002. Permafrost as a microbial habitat. In: G. Bitton (ed.). Encyclopedia of Environmental Microbiology, Vol 6, pp. 932–956. Wiley.

Gjærevoll, O., 1956. The plant communities of the Scandinavian alpine snowbeds. Det Kongelige Norske Videnskabernes Selskabs Skrifter, 1956(1):1–405.

Gold, W.G. and L.C. Bliss, 1995. The nature of water limitations for plants in a high arctic polar desert. In: T.V. Callaghan, W.C. Oechel, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau, B. Sveinbjornsson and M.J. Tyson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 149–155. Ecosystems Research Report 10. European Commission, Brussels.

Gough, L., G.R. Shaver, J. Carroll, D.L. Royer and J.A. Laundre, 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. Journal of Ecology, 88:54–66.

Graglia, E., S. Jonasson, A. Michelsen and I.K. Schmidt, 1997. Effects of shading, nutrient application and warming on leaf growth and shoot densities of dwarf shrubs in two arctic-alpine plant communities. Ecoscience, 4:191–198.

Graglia, E., S. Jonasson, A. Michelsen, I.K. Schmidt, M. Havström and L. Gustavsson, 2001a. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. Ecography, 24:5–12.

Graglia, E., R. Julkunen-Tiitto, G. Shaver, I.K. Schmidt, S. Jonasson and A. Michelsen, 2001b. Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. New Phytologist, 151:227–236.

Granberg, G., M. Ottosson-Lofvenius, H. Grip, I. Sundh and M. Nilsson, 2001. Effect of climatic variability from 1980 to 1997 on simulated methane emission from a boreal mixed mire in northern Sweden. Global Biogeochemical Cycles, 15(4):977–991.

Grogan, P. and S. Jonasson, 2003. Controls on annual nitrogen cycling in the understory of a subarctic birch forest. Ecology, 84(1):202–218.

Grogan, P., L. Illeris, A. Michelsen and S. Jonasson, 2001. Respiration of recently-fixed plant carbon dominates mid-winter ecosystem CO_2 production in sub-arctic heath tundra. Climatic Change, 50:129–142.

Grootes, P.M., M. Stuiver, J.W.C. White, S. Johnsen and J. Jouzel, 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. Nature, 366:552–554.

Grosswald, M.G., 1988. An Antarctic-style ice sheet in the Northern Hemisphere: Toward a new global glacial theory. Polar Geography and Geology, 12:239–267.

Grosswald, M.G., 1998. Late-Weichselian ice sheets in Arctic and Pacific Siberia. Quaternary International, 45/46:3–18.

Grulke, N., G.H. Riechers, W.C. Oechel, U. Hjelm and C. Jaeger, 1990. Carbon balance in tussock tundra under ambient and elevated atmospheric CO_2. Oecologia, 83:485–494.

Guenther, A., P. Zimmerman and M. Wildermuth, 1993. Natural volatile organic compound emission rate estimates for U.S. woodland landscapes. Atmospheric Environment, 28:1197–1210.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quaternary Science Reviews, 20:549–574.

Gwynn-Jones, D., 1999. Enhanced UV-B radiation and herbivory. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin, 47:77–83.

Gwynn-Jones, D., L.O. Björn, T.V. Callaghan, C. Gehrke, U. Johanson, J.A. Lee and M. Sonesson, 1996. Effects of enhanced UV-B radiation and elevated concentrations of CO_2 on a subarctic heathland. In: C. Korner and F.A. Bazzaz (eds.). Carbon Dioxide, Populations and Communities, pp. 197–207. Academic Press.

Gwynn-Jones, D., J.A. Lee and T.V. Callaghan, 1997. Effects of enhanced UV-B radiation and elevated carbon dioxide concentrations on a sub-Arctic forest heath ecosystem. Plant Ecology, 128:243–249.

Gwynn-Jones, D., U. Johanson, G.K. Phoenix, C. Gehrke, T.V. Callaghan, L.O. Björn, M. Sonesson and J.A. Lee, 1999. UV-B impacts and interactions with other co-occurring variables of environmental change: an Arctic perspective. In: J. Rozema (ed.). Stratospheric Ozone Depletion: The Effects of Enhanced UV-B Radiation on Terrestrial Ecosystems, pp. 187–201. Backhuys Publishers.

Hales, B.A., C. Edwards, D.A. Ritchie, G. Hall, R.W. Pickup and J.R. Saunders, 1996. Isolation and identification of methanogen-specific DNA from blanket bog peat by PCR amplification and sequence analysis. Applied and Environmental Microbiology, 62:668–675.

Hamrick, J.L. and M.J.W. Godt, 1990. Allozyme diversity in plant species. In: A.H.D. Brown, M.T. Clegg, A.L. Kahler and B.S. Weir (eds.). Plant Population Genetics, Breeding, and Genetic Resources, pp. 43–63. Sinauer Associates Inc.

Hansell, R.I.C., J.R. Malcom, H. Welch, R.L. Jefferies and P.A. Scott, 1998. Atmospheric change and biodiversity in the Arctic. Environmental Monitoring and Assessment, 49:303–325.

Hanski, I. and H. Henttonen, 1996. Predation on competing rodent species: a simple explanation of complex patterns. Journal of Animal Ecology, 65:220–232.

Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen and P. Turchin, 2001. Small-rodent dynamics and predation. Ecology, 82:1505–1520.

Hansson, L. and H. Henttonen, 1988. Rodent dynamics as community processes. Trends in Evolution and Ecology, 3:195–200.

Harazono, Y., M. Mano, A. Miyata, R.C. Zulueta and W.C. Oechel, 2003. Inter-annual carbon dioxide uptake of a wet sedge tundra ecosystem in the Arctic. Tellus B, 55:215–231.

Harding, R., P. Kuhry, T.R. Christensen, M.T. Sykes, R. Dankers and S. van der Linden, 2002. Climate feedbacks at the tundra-taiga interface. Ambio Special Report, 12:47–55.

Harriss, R., K. Bartlett, S. Frolking and P. Crill, 1993. Methane emissions from northern high-latitude wetlands. In: R.S. Oremland (ed.). Biogeochemistry of Global Change: Radiatively Active Trace Gases, pp. 449–486. Chapman & Hall.

Hartley, A.E., C. Neill, J.M. Melillo, R. Crabtree and F.P. Bowles, 1999. Plant performance and soil nitrogen mineralization in response to simulated climate change in subarctic dwarf shrub heath. Oikos, 86:331–343.

Hastings, S.J., S.A. Luchessa, W.C. Oechel and J.D. Tenhunen, 1989. Standing biomass and production in water drainages of the foothills of the Philip Smith Mountains, Alaska. Holarctic Ecology, 12:304–311.

Haukioja, E., 1980. On the role of plant defences in the fluctuation of herbivore populations. Oikos, 35:202–213.

Haukioja, E., 1991. Induction of defenses in trees. Annual Review of Entomology, 36:25–42.

Haukioja, E. and S. Neuvonen, 1987. Insect population dynamics and induction of plant resistance: the testing of hypotheses. In: P. Barbosa and J.C. Schultz (eds.). Insect Outbreaks: Ecological and Evolutionary Perspectives, pp. 411–432. Academic Press.

Haukioja, E., V. Ossipov, J. Koricheva, T. Honkanen, S. Larsson and K. Lempa, 1998. Biosynthetic origin of carbon-based secondary compounds: cause of variable responses of woody plants to fertilization? Chemoecology, 8:133–139.

Haukisalmi, V. and H. Henttonen, 1990. The impact of climatic factors and host density on the long-term population dynamics of vole helminths. Oecologia, 83:309–315.

Haukisalmi, V., L.M. Wickström, H. Henttonen, J. Hantula and A. Gubányi, 2004. Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Hermann, 1783) (Cestoda: Anoplocephalidae) in Microtus-voles (Arvicolinae). Zoologica Scripta, 33(3):277–290.

Havas, P., 1971. The water economy of the bilberry (*Vaccinium myrtillus*) under winter conditions. Reports from the Kevo Subarctic Research Station, 8:41–52.

Havas, P., 1985. Winter and the boreal forests. Aquilo Series Botanica, 23:9–16.

Havström, M., T.V. Callaghan and S. Jonasson, 1993. Differential growth responses of *Cassiope tetragona*, an arctic dwarf shrub, to environmental perturbations among three contrasting high- and subarctic sites. Oikos, 66:389–402.

Havström, M., T.V. Callaghan and S. Jonasson, 1995a. Effects of simulated climate change on the sexual reproductive effort of *Cassiope tetragona*. In: T.V. Callaghan, W.C. Oechel, T. Gilmanov, U. Molau, B. Maxwell, M. Tyson, B. Sveinbjörnsson and J.I. Holten (eds.). Global change and Arctic terrestrial ecosystems, pp 109–114. Proceedings of papers contributed to the international conference, 21–26 August 1993, Oppdal, Norway. European Commission Ecosystems research report 10.

Havström, M., T.V. Callaghan, S. Jonasson and J. Svoboda, 1995b. Little ice age temperature estimated by growth and flowering differences between sub fossil and extant shoots of *Cassiope tetragona*, an arctic heather. Functional Ecology, 9:650–654.

Hawkins, B.A., 1990. Global patterns of parasitoid assemblage size. Journal of Animal Ecology, 59:57–72.

Hawksworth, D.L., 1991. The fungal dimension of biodiversity: magnitude, significance, and conservation. Mycological Research, 95:641–655.

Haxeltine, A. and I.C. Prentice, 1996. BIOME3: An equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. Global Biogeochemical Cycles, 10:693–710.

Heal, O.W., P.W. Flanagan, D.D. French and S.F. MacLean Jr., 1981. Decomposition and accumulation of organic matter in tundra. In: L.C. Bliss, O.W. Heal and J.J. Moore (eds.). Tundra Ecosystems: A Comparative Analysis, pp. 587–634. Cambridge University Press.

Heide, O.M., R.K.M. Hay and H. Baugerod, 1985. Specific daylength effects on leaf growth and dry-matter production in high-latitude grasses. Annals of Botany, 55:579–586.

Heide-Jørgensen, H.S. and I. Johnsen, 1998. Ecosystem vulnerability to climate change in Greenland and the Faroe Islands. Miljønyt, 33:1–266.

Heikkinen, J.E.P., T. Virtanen, J.T. Huttunen, V. Elsakov and P.J. Martikainen, 2004. Carbon balance in East European tundra. Global Biogeochemical Cycles, 18(1), GB1023, doi:10.1029/2003GB002054.

Hein, R., P.J. Crutzen and M. Heimann, 1997. An inverse modeling approach to investigate the global atmospheric methane cycle. Global Biogeochemical Cycles, 11:43–76.

Helander, E., 2002. Global change – climate change observations among the Sami. Proceedings of the Snowchange Conference, February 21–24, 2002, Tampere, Finland.

Henry, G.H.R. and U. Molau, 1997. Tundra plants and climate change: the International Tundra Experiment (ITEX). Global Change Biology, 3(S1):1–9.

Henttonen, H., 2000. Long-term dynamics of the bank vole *Clethrionomys glareolus* at Pallasjarvi, northern Finnish taiga. In: G. Bujalska and L. Hansson (eds.). Bank Vole Biology: Recent Advances in the Population Biology of a Model Species. Polish Journal of Ecology, 48(Suppl.):87–96.

Henttonen, H. and K.A. Burek, 2001. Parasitism: an underestimated stressor of arctic fauna? In: Arctic Flora and Fauna: Status and Conservation, p. 145. Conservation of Arctic Flora and Fauna, Helsinki.

Henttonen, H. and A. Kaikusalo, 1993. Lemming movements. In: N.C. Stenseth and R.A. Ims (eds.). The Biology of Lemmings, pp. 157–186. Academic Press.

Henttonen, H. and H. Wallgren, 2001. Rodent dynamics and communities in the birch forest zone of northern Fennoscandia. In: F.E. Wielgolaski (ed.). Nordic Mountain Forest Ecosystems. Man and the Biosphere Series 27:261–278. UNESCO, Paris and Parthenon Publishing Group.

Henttonen, H., T. Oksanen, A. Jortikka and V. Haukisalmi, 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? Oikos, 50:353–365.

Hershey, A.E., W.B. Bowden, L.A. Deegan, J.E. Hobbie, B.J. Peterson, G.W. Kipphut, G.W. Kling, M.A. Lock, R.W. Merritt, M.C. Miller, J.R. Vestal and J.A. Schuldt, 1997. The Kuparuk River: A long-term study of biological and chemical processes in an arctic river. In: A.M. Milner and M.W. Oswood (eds.). Freshwaters of Alaska: Ecological Syntheses. Ecological Studies 119:107–130. Springer-Verlag.

Hersteinsson, P. and D.W. MacDonald, 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos, 64:505–515.

Hertzberg, K., N.G. Yoccoz, R.A. Ims and H.P. Leinaas, 2000. The effects of spatial habitat configuration on recruitment, growth and population structure in arctic Collembola. Oecologia, 124:381–390.

Heske, E.J., R.A. Ims and H. Steen, 1993. Four experiments on a Norwegian subalpine microtine rodent assemblage during a summer decline. In: N.C. Stenseth and R.A. Ims (eds.). The Biology of Lemmings, pp. 411–424. Academic Press.

Hill, J.K., C.D. Thomas and B. Huntley, 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proceedings of the Royal Society of London: Biological Sciences, 266:1197–1206.

Hill, J.K., C.D. Thomas and B. Huntley, 2003. Modelling present and potential future ranges of European butterflies using climate response surfaces. In: C.L. Boggs, W.B. Watt and P.R. Ehrlich (eds.). Butterflies: Ecology and Evolution Taking Flight, pp. 149–167. University of Chicago Press.

Hinzman, L.D., D.J. Goering, S. Li and T.C. Kinney, 1997. Numeric simulation of thermokarst formation during disturbance. In: R.M.M. Crawford (ed.). Disturbance and Recovery in Arctic Lands: An Ecological Perspective, pp. 199–212. Kluwer Academic Publishers.

Hinzman, L.D., M. Fukuda, D.V. Sandberg, F.S. Chapin III and D. Dash, 2003. FROSTFIRE: An experimental approach to predicting the climate feedbacks from the changing boreal fire regime. Journal of Geophysical Research, 108(D1):8153, doi:10.1029/2001JD000415.

Hobbie, S.E., 1995. Direct and indirect species effects on biogeochemical processes in arctic ecosystems. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes, and Ecosystem Consequences. Ecological Studies, 113:213–224. Springer-Verlag.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs, 66:503–522.

Hobbie, S.E. and F.S. Chapin III, 1996. Winter regulation of tundra litter carbon and nitrogen dynamics. Biogeochemistry, 35:327–338.

Hobbie, S.E. and F.S. Chapin III, 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO$_2$ flux to experimental warming. Ecology, 79:1526–1544.

Hobbie, S.E., J.P. Schimel, S.E. Trumbore and J.R. Randerson, 2000. Controls over carbon storage and turnover in high-latitude soils. Global Change Biology, 6(S1):196–210.

Hoberg, E.P., S.J. Kutz, K.E. Galbreath and J. Cook, 2003. Arctic biodiversity: from discovery to faunal baselines – revealing the history of a dynamic ecosystem. Journal of Parasitology, 89: S84–S95.

Hodkinson, I.D. and J. Bird, 1998. Host-specific insect herbivores as sensors of climate change in arctic and alpine environments. Arctic and Alpine Research, 30(1):78–83.

Hodkinson, I.D., S.J. Coulson, N.R. Webb, W. Block, A.T. Strathdee and J.S. Bale, 1994. Feeding studies on Onychiurus arcticus (Tullberg) Collembola: Onychiuridae on West Spitsbergen. Polar Biology, 14:17–19.

Hodkinson, I.D., N.R. Webb, J.S. Bale, W. Block, S.J. Coulson and A.T. Strathdee, 1998. Global change and high arctic ecosystems: conclusions and predictions from experiments with terrestrial invertebrates on Spitsbergen. Arctic and Alpine Research, 30(3):306–313.

Hodkinson, I.D., N.R. Webb, J.S. Bale and W. Block, 1999. Hydrology, water availability and tundra ecosystem function in a changing climate: the need for a closer integration of ideas? Global Change Biology, 5:359–369.

Høgda, K.A., S.R. Karlsen and I. Solheim, 2001. Climate change impact on growing season in Fennoscandia studied by a time series of NOAA AVHRR NDVI data. Geoscience and Remote Sensing Symposium, 2001. IGARSS '01, 2001 IEEE International, 3:1338–1340.

Høgda, K.A., S.R. Karlsen, I. Solheim, H. Tommervik and H. Ramfjord, 2002. The start dates of birch pollen seasons in Fennoscandia studied by NOAA AVHRR NDVI data. Geoscience and Remote Sensing Symposium, 2002. IGARSS '02, 2002 IEEE International, 6:3299–3301.

Hollister, R.D. and P.J. Webber, 2000. Biotic validation of small open-top chambers in a tundra ecosystem. Global Change Biology, 6:835–842.

Holt, J.G., N.R. Krieg, P.H.A. Sneath, J.T. Staley and S.T. Williams (eds.), 1994. Bergey's Manual of Determinative Bacteriology, 9th Edition. Williams and Wilkins, 787pp.

Hultén, E., 1964. The Circumpolar Plants. 1, Vascular Cryptogams, Conifers, Monocotyledons. Almqvist & Wiksell, 275pp.

Huntley, B., 1988. Glacial and Holocene vegetation history: Europe. In: B. Huntley and T. Webb III (ed.). Vegetation History. Handbook of Vegetation Science, 7:341–383. Kluwer Academic Publishers.

Huntley, B., 1997. The responses of vegetation to past and future climate changes. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 290–311. Springer-Verlag.

Huntley, B. and H.J.B. Birks, 1983. An Atlas of Past and Present Pollen Maps for Europe: 0–13000 Years Ago. Cambridge University Press, 667pp.

Huntley, B. and R. Bradshaw, 1999. Palaeoecological evidence and opportunities in determining environmental change and ecological responses. In: M. Turunen, J. Hukkinen, O.W. Heal, J.I. Holten and N.R. Saelthun (eds.). A Terrestrial Transect for Scandinavia/Northern Europe: Proceedings of the International SCANTRAN Conference. Ecosystems Research Report 31:153–157. European Commission, Brussels.

Huntley, B., P.M. Berry, W. Cramer and A.P. McDonald, 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography, 22:967–1001.

Huntley, B., M. Baillie, J.M. Grove, C.U. Hammer, S.P. Harrison, S. Jacomet, E. Jansen, W. Karlen, N. Koc, J. Luterbacher, J. Negendank and J. Schibler, 2002. Holocene paleoenvironmental changes in north-west Europe: Climatic implications and the human dimension. In: G. Wefer, W.H. Berger, K.-E. Behre, and E. Jansen (eds.). Climate Development and History of the North Atlantic Realm, pp. 259–298. Springer-Verlag.

Huntley, B., M.J. Alfano, J.R.M. Allen, D. Pollard, P.C. Tzedakis, J.-L. de Beaulieu, E. Gruger and B. Watts, 2003. European vegetation during Marine Oxygen Isotope Stage-3. Quaternary Research, 59(2):195–212.

Hustich, I., 1983. Tree-line and tree growth studies during 50 years: some subjective observations. Collection Nordicana, 47:181–188.

Iason, G.R. and A.J. Hester, 1993. The response of heather (*Calluna vulgaris*) to shade and nutrients - predictions of the carbon-nutrient balance hypothesis. Journal of Ecology, 81:75–80.

IISD and the community of Sachs Harbour, 2000. Sila Alangotok: Inuit Observations on Climate Change. Video production. International Institute for Sustainable Development, Winnipeg.

Illeris, L., A. Michelsen and S. Jonasson. 2003. Soil plus root respiration and microbial biomass following water, nitrogen, and phosphorus application at a high arctic semi desert. Biogeochemistry, 65:15–29.

Ims, R.A. and H.P. Andreassen, 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature, 408:194–196.

Ims, R.A. and H. Steen, 1990. Geographical synchrony in cyclic microtine populations: a theoretical evaluation of the role of nomadic avian predators. Oikos, 57:381–387.

Ims, R.A., H.P. Leinaas and S. Coulson, 2004. Spatial and temporal variation in patch occupancy and population density in a model system of an arctic Collembola species assemblage. Oikos, 105:89–100.

Ingham, R.E., J.A. Trofymow, E.R. Ingham and D.C. Coleman, 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecological Monographs, 55:119–140.

IPCC, 1990. Climate Change: The IPCC Scientific Assessment. J.T. Houghton, G.J. Jenkins and J.J. Ephraums (eds.). Intergovernmental Panel on Climate Change, World Meteorological Organization/United Nations Environment Programme. Cambridge University Press, 364pp.

IPCC, 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell and C.A. Johnson (eds.). Cambridge University Press, 881pp.

Irvine, R.J., A. Stien, O. Halvorsen, R. Langvatn and S.D. Albon, 2000. Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Parasitology, 120:297–311.

Isidorov, V.A. and M. Jdanova, 2002. Volatile organic compounds from leaves litter. Chemosphere, 48(9):975–979.

Isidorov, V.A, I.G. Zenkevich and B.V. Ioffe, 1983. Methods and results of gas chromatographic-mass spectrometric determination of volatile organic substances in an urban atmosphere. Atmospheric Environment, 17(7):1347–1353.

IUCN, 2003. The 2003 IUCN Red List of Threatened Species. World Conservation Union, Species Survival Commission, Gland, Switzerland. http://www.iucnredlist.org/

Jaeger, C.H., R.K. Monson, M.C. Fisk and S.K. Schmidt, 1999. Seasonal partitioning of nitrogen by plants and soil microorganisms in an alpine ecosystem. Ecology, 80:1883–1891.

Jean, D. and L. Lapointe, 2001. Limited carbohydrate availability as a potential cause of fruit abortion in *Rubus chamaemorus*. Physiologia Plantarum, 112(3):379–387.

Jefferies, R.L. and L.D. Gottlieb, 1983. Genetic variation within and between populations of the asexual plant Puccinellia x phryganodes. Canadian Journal of Botany, 61:774–779.

Jefferies, R.L., D.R. Klein and G.R. Shaver, 1994. Herbivores and northern plant communities: Reciprocal influences and responses. Oikos, 71:193–206.

Jefferies, R.L., F.L. Gadallah, D.S. Srivastava and D.J. Wilson, 1995. Desertification and trophic cascades in arctic coastal ecosystems: a potential climatic change scenario? In: T.V. Callaghan, W.C. Oechel, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau, B. Sveinbjornsson and M.J. Tyson, (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 201–206. Ecosystems Research Report 10. European Commission, Brussels.

Joabsson, A. and T.R. Christensen, 2001. Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. Global Change Biology, 7:919–932.

Joabsson, A., T.R. Christensen and B. Wallén, 1999. Vascular plant controls on methane emissions from northern peatforming wetlands. Trends in Ecology and Evolution, 14:385–388.

Johanson, U., C. Gehrke, L.O. Bjorn and T.V. Callaghan, 1995. The effects of enhanced UV-B radiation on the growth of dwarf shrubs in a subarctic heathland. Functional Ecology, 9:713–719.

Johnson, D., C.D. Campbell, J.A. Lee, T.V. Callaghan and D. Gwynn-Jones, 2002. Arctic soil microorganisms respond more to elevated UV-B radiation than CO_2. Nature, 416:82–83.

Jonasson, S., 1992. Plant responses to fertilization and species removal in tundra related to community structure and clonality. Oikos, 63:420–429.

Jonasson, S. and T.V. Callaghan, 1992. Root mechanical properties related to disturbed and stressed habitats in the Arctic. New Phytologist, 122:179–186.

Jonasson, S. and F.S. Chapin III, 1985. Significance of sequential leaf develop¬ment for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. Oecologia, 67:511–518.

Jonasson, S., J.P. Bryant, F.S. Chapin III and M. Andersson, 1986. Plant phenols and nutrients in relation to variations in climate and rodent grazing. American Naturalist, 128:394–408.

Jonasson, S., A. Michelsen, I.K. Schmidt, E.V. Nielsen and T.V. Callaghan, 1996. Microbial biomass C, N, and P in two arctic soils and responses to addition of NPK fertilizer and sugar: Implications for plant nutrient uptake. Oecologia, 106:507–515.

Jonasson, S., A. Michelsen and I.K. Schmidt, 1999a. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. Applied Soil Ecology, 11:135–146.

Jonasson, S., A. Michelsen, I.K. Schmidt and E.V. Nielsen, 1999b. Responses in microbes and plants to changed temperature, nutrient and light regimes in the Arctic. Ecology, 80:1828–1843.

Jonasson, S., T.V. Callaghan, G.R. Shaver and L.A. Nielsen, 2000. Arctic Terrestrial ecosystems and ecosystem function. In: M. Nuttall and T.V. Callaghan (eds.). The Arctic: Environment, People, Policy, pp. 275–313. Harwood Academic Publishers.

Jonasson, S., F.S. Chapin III and G.R. Shaver, 2001. Biogeochemistry in the Arctic: patterns, processes and controls. In: E.-D. Schulze, M. Heimann, S.P. Harrison, E.A. Holland, J.J. Lloyd, I.C. Prentice and D. Schimel (eds.). Global Biogeochemical Cycles in the Climate System, pp. 139–150. Academic Press.

Jones, M.H., J.T. Fahnestock, D.A Walker, M.D. Walker and J.M. Welker, 1998. Carbon dioxide fluxes in moist and dry arctic tundra during the snow-free season: Responses to increases in summer temperature and winter snow accumulation. Arctic and Alpine Research, 30:373–380.

Jónsdóttir, I.S., T.V. Callaghan and J.A. Lee, 1995. Fate of added nitrogen in a moss-sedge Arctic community and effects of increased nitrogen deposition. Science of the Total Environment, 161:677–685.

Jónsdóttir, I.S., M. Augner, T. Fagerström, H. Persson and A. Stenström, 2000. Genet age in marginal populations of two clonal *Carex* species in the Siberian Arctic. Ecography, 23:402–412.

Jonsson, B.O., I.S. Jonsdottir and N. Cronberg, 1996. Clonal diversity and allozyme variation in populations of the arctic sedge *Carex bigelowii* (Cyperaceae). Journal of Ecology, 84:449–459.

Kalela, O., 1961. Seasonal change of the habitat in the Norwegian lemming, *Lemmus lemmus*. Annales Academiae Scientiarium Fennicae (A, IV), 55:1–72.

Källen, E., V. Kattsov, J. Walsh and E. Weatherhead, 2001. Report from the Arctic Climate Impact Assessment Modeling and Scenarios Workshop. January 29–31, 2001, Stockholm. Available from: ACIA Secretariat, P.O. Box 757740, Fairbanks, Alaska 99775 USA or www.acia.uaf.edu, 28pp.

Kallio, P. and J. Lehtonen, 1973. Birch forest damage caused by *Oporinia autumnata* (Bkh.) in 1965–66, in Utsjoki, N Finland. Reports from the Kevo Subarctic Research Station, 10:55–69.

Kane, D.L., K.M. Hinkel, D.J. Goering, L.D. Hinzman and S.I. Outcalt, 2001. Non-conductive heat transfer associated with frozen soils. Global and Planetary Change, 29:275–292.

Kaplan, J.O., 2001. Geophysical applications of vegetation modelling. Ph.D. Thesis, Lund University.

Kaplan, J.O., N.H. Bigelow, I.C. Prentice, S.P. Harrison, P.J. Bartlein, T.R. Christensen, W. Cramer, N.V. Matveyeva, A.D. McGuire, D.F. Murray, V.Y. Razzhivin, B. Smith, D.A. Walker, P.M. Anderson, A.A. Andreev, L.B. Brubaker, M.E. Edwards and A.V. Lozhkin, 2003. Climate change and Arctic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. Journal of Geophysical Research, 108(D19):8171, doi:10.1029/2002JD002559.

Kappen, L., 1974. Response to extreme environments. In: V. Ahmadjian and M.E. Hale (eds.). The Lichens, pp. 311–380. Academic Press.

Kappen, L., 1993. Lichens in the Antarctic region. In: E.I. Friedmann (ed.). Antarctic Microbiology, pp. 433–490. Wiley-Liss, Inc.

Kappen, L., B. Schroeter, C. Scheidegger, M. Sommerkorn and G. Hestmark, 1996. Cold resistance and metabolic activity of lichens below 0 °C. Advances in Space Research, 18(12):119–128.

Karatygin, I.V., E.L. Nezdoiminogo, Y.K. Novozhilov and M.P. Zhurbenko, 1999. Russian Arctic Fungi: A Checklist. St. Petersburg. 212pp.

Kattenberg, A., F. Giorgi, H. Grassl, G.A. Meehl, J.F.B. Mitchell, R.J. Stouffer, T. Tokioka, A.J. Weaver and T.M.L. Wigley, 1996. Climate models - projections of future climate. In: J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell (eds.). Climate Change 1995. The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change, pp. 285–357. Cambridge University Press.

Kaye, J.P. and S.C. Hart, 1997. Competition for nitrogen between plants and soil microorganisms. Trends in Ecology and Evolution, 12:139–143.

Kelliher, F.M., R. Leuning, M.R. Raupach and E.-D. Schulze, 1995. Maximum conductances for evaporation from global vegetation types. Agricultural and Forest Meteorology, 73:1–16.

Kershaw, K.A., 1983. The thermal operating environment of a lichen. The Lichenologist, 15:191–207.

Keyser, A.R., J.S. Kimball, R.R. Nemani and S.W. Running, 2000. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. Global Change Biology, 6(S1):185–195.

Kienel, U., C. Siegert and J. Hahne, 1999. Late Quaternary palaeoenvironmental reconstructions from a permafrost sequence (North Siberian Lowland, SE Taymyr Peninsula) - a multidisciplinary case study. Boreas, 28(1):181–193.

Killick, H.J. and S.J. Warden, 1991. Ultraviolet penetration of pine trees and insect virus survival. Entomophaga, 36:87–94.

Klein, D.R., 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management, 32:350–367.

Klein, D.R., 1996. Arctic ungulates at the northern edge of terrestrial life. Rangifer, 16:51–56.

Klein, D.R., 1999. The roles of climate and insularity in establishment and persistence of *Rangifer tarandus* populations in the high Arctic. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:96–104.

Kling, G.W., G.W. Kipphut and M.C. Miller. 1991. Arctic lakes and streams as gas conduits to the atmosphere: Implications for tundra carbon budgets. Science, 251:298–301.

Kling, G.W., G.W. Kipphut and M.C. Miller, 1992. The flux of CO_2 and CH_4 from lakes and rivers in arctic Alaska. Hydrobiologia, 240:23–36.

Kling, G.W., G.W. Kipphut, M.C. Miller and W.J. O'Brien, 2000. Integration of lakes and streams in a landscape perspective: the importance of material processing on spatial patterns and temporal coherence. Freshwater Biology, 43:477–497.

Klinger, L.F., P.R. Zimmerman, J.P. Greenberg, L.E. Heidt and A.B. Guenther, 1994. Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. Journal of Geophysical Research, 99(D1):1469–1494.

Koç, N., E. Jansen, M. Hald and L. Labeyrie, 1996. Late glacial–Holocene sea surface temperatures and gradients between the North Atlantic and the Norwegian Sea: implications for the nordic heat pump. In: J.T. Andrews, W.E.N. Austin, H.E. Bergsten and A.E. Jennings (eds.). Late Quaternary Palaeoceanography of the North Atlantic Margins. Geological Society Special Publication 111:177–185.

Koerner, R.M., 1980. The problem of lichen-free zones in Arctic Canada. Arctic and Alpine Research, 12:87–94.

Kofinas, G. with the communities of Aklavik, Arctic Village, Old Crow and Fort McPherson, 2002. Community contributions to ecological monitoring: knowledge co-production in the U.S.-Canada arctic borderlands. In: I. Krupnik and D. Jolly (eds.). The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change, pp. 54–91. Arctic Research Consortium of the United States, Fairbanks, Alaska.

Konstantinova, N.A. and A.D. Potemkin, 1996. Liverworts of the Russian Arctic: an annotated check-list and bibliography. Arctoa, 6:125–150.

Köppen, W., 1931. Grundriss der Klimakunde. Walter de Gruyter & Co., 388pp. (In German)

Körner, C.H., 1995. Alpine plant diversity: A global survey and functional interpretations. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies, 113:45–62.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia, 115:445–459.

Körner, C., 1999. Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems. Springer, 338pp.

Korpelainen, H., 1994. Sex ratios and resource allocation among sexually reproducing plants of *Rubus chamaemorus*. Annals of Botany, 74(6):627–632.

Koskina, T.V., 1961. New data on the nutrition of Norwegian lemming (*Lemmus lemmus*). Bulletin of the Moscow Society of Naturalists, 66:15–32.

Kouki, J., P. Niemel and M. Viitasaari, 1994. Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). Annales Zoologici Fennici, 31:83–88.

Koval, T.M., 1988. Enhanced recovery from ionizing radiation damage in a lepidopteran insect cell line. Radiation Research, 115:413–420.

Kozhevnikov, Y.P., 2000. Is the Arctic getting warmer or cooler? In: B.S. Ebbinge, Y.L. Mazourov and P.S. Tomkovich (eds.). Heritage of the Russian Arctic: Research, Conservation and International Cooperation, pp.145–157. Ecopros.

Kraaijeveld, K. and E.N. Nieboer, 2000. Late Quaternary paleogeography and evolution of Arctic breeding waders. Ardea, 88(2):193–205.

Krebs, C.J., K. Danell, A. Angerbjorn, J. Agrell, D. Berteaux, K.A. Bråthen, O. Danell, S. Erlinge, V. Fedorov, K. Fredga, J. Hjältén, G. Högstedt, I.S. Jónsdóttir, A.J. Kenney, N. Kjellén, T. Nordin, H. Roininen, M. Svensson, M. Tannerfeldt and C. Wiklund, 2003. Terrestrial trophic dynamics in the Canadian Arctic. Canadian Journal of Zoology, 81:827–843.

Krupnik, I., 2000. Native perspectives on climate and sea-ice changes. In: H.P. Huntington (ed.). Impacts of Changes in Sea Ice and other Environmental Parameters in the Arctic. Final Report of the Marine Mammal Commission Workshop, Girdwood, Alaska, 15–17 February 2000, pp. 35–52. Marine Mammal Commission, Maryland.

Kubeckova, K., J. Elster and H. Kanda, 2001. Periphyton ecology of glacial and snowmelt streams, Ny-Ålesund, Svalbard: presence of mineral particles in water and their erosive activity. In: J. Elster, J. Seckbach, W. Vincent and O. Lhotsky (eds.). Algae and Extreme Environments. Nova Hedwigia Beihefte, Beiheft 123:141–172.

Kudo, G., 1991. Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. Arctic and Alpine Research, 23:436–443.

Kudo, G., 1993. Relationship between flowering time and fruit set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. American Journal of Botany, 80:1300–1304.

Kullman, L., 1979. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915–1975. Acta Phytogeographica Suecica, 65:1–121.

Kumpula, J., P. Parikka and M. Nieminen, 2000. Occurrence of certain microfungi on reindeer pastures in northern Finland during winter 1996–97. Rangifer, 20:3–8.

Kushner, D., 1981. Extreme environments: Are there any limits to life? In: C. Ponnamperuma (ed.). Comets and the Origin of Life, pp. 241–248. D. Reidel.

Kutz, S.J., E.P. Hoberg, J. Nishi and L. Polley, 2002. Development of the muskox lungworm *Umingmakstrongylus pallikuukensis* (Protostrongylidae), in gastropods in the Arctic. Canadian Journal of Zoology, 80:1977–1985.

Lafleur, P.M., W.R. Rouse and D.W. Carlson, 1992. Energy balance differences and hydrologic impacts across the northern treeline. International Journal of Climatology, 12:193–203.

Laine, K., 1988. Long-term variations in plant quality and quantity in relation to cyclic microtine rodents at Kilpisjärvi, Finnish Lapland. Acta Universitasis Ouluenis Series A, 198. 33pp.

Laine, K. and H. Henttonen, 1983. The role of plant production in microtine cycles in northern Fennoscandia. Oikos, 40:407–418.

Laine, K. and H. Henttonen, 1987. Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. Oikos, 50:389–395.

Lal, R., J.M. Kimble and B.A. Stewart (eds.), 2000. Global Climate Change and Cold Regions Ecosystems. Lewis Publishers, 265pp.

Lamb, H.F., 1980. Late Quaternary vegetational history of southeastern Labrador. Arctic and Alpine Research, 12:117–135.

Lamb, H.F. and M.E. Edwards, 1988. Glacial and Holocene vegetation history: the Arctic. In: B. Huntley and T. Webb III (eds.). Vegetation History. Handbook of Vegetation Science, 7:519–555.

Lamb, H.H., 1982. Climate, History and the Modern World. Methuen, 387pp.

Lambeck, K., 1995. Constraints on the Late Weichselian ice sheet over the Barents Sea from observations of raised shorelines. Quaternary Science Reviews, 14:1–16.

Lange, O.L., 1953. Hitze- und Trockenresistenz der Flechten in Beziehung zu ihrer Verbreitung. Flora, 140:39–97.

Lange, O.L., 1954. Einige Messungen zum Warmehaushalt poikilohydrer Flechten und Moose. Archiv fur Meteorologie, Geophysik und Bioklimatologie, Serie B: Allgemeine und Biologische Klimatologie, 5:182–190.

Lange, O.L. and H. Metzner, 1965. Lichtabhängiger Kohlenstoff-Einbau in Flechten bei tiefen Temperaturen. Naturwissenschaften, 52:191–192.

Larcher, W., 1995. Physiological Plant Ecology. 3rd Edition. Springer Verlag, 506pp.

Larkin, J.M. and J.L. Stokes, 1968. Growth of psychrophilic microorganisms at subzero temperatures. Canadian Journal of Microbiology, 14:97–101.

Larsen, K.S., S. Jonasson and A. Michelsen, 2002. Repeated freeze–thaw cycles and their effects on biological processes in two arctic ecosystem types. Applied Soil Ecology, 21:187–195.

Laurila, T., H. Soegaard, C.R. Lloyd, M. Aurela, J.-P. Tuovinen and C. Nordström, 2001. Seasonal variations of net CO_2 exchange in European Arctic ecosystems. Theoretical and Applied Climatology, 70:183–201.

Lavola, A., R. Julkunen-Tiitto, P. Aphalo, T. de la Rosa and T. Lehto, 1997. The effect of UV-B radiation on UV-absorbing secondary metabolites in birch seedlings grown under simulated forest soil conditions. New Phytologist, 137:617–621.

Lavola, A., R. Julkunen-Tiitto, H. Roininen and P. Aphalo, 1998. Host-plant preference of an insect herbivore mediated by UV–B and CO_2 in relation to plant secondary metabolites. Biochemical Systematics and Ecology, 26:1–12.

Lebedeva, E., 1998. Waders in agricultural habitats of European Russia. In: H. Hotker, E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud and R.B. West (eds.). Migration and International Conservation of Waders: Research and Conservation on North Asian, African and European Flyways. International Wader Studies, 10:315–324.

Lee, S.E., M.C. Press and J.A. Lee, 2000. Observed climate variations during the last 100 years in Lapland, Northern Finland. International Journal of Climatology, 20:329–346.

Legrand, M., 1995. Atmospheric chemistry changes versus past climate inferred from polar ice cores. In: R.J. Charlson and J. Heintzenberg (eds.). Aerosol Forcing of Climate, pp. 123–151, Wiley.

Lehtonen, J. and R.K. Heikkinen, 1995. On the recovery of mountain birch after *Epirrita* damage in Finnish Lapland, with a particular emphasis on reindeer grazing. Ecoscience, 2:349–356.

Leinaas, H.P., 2002. UV tolerance, pigmentation and life forms in high Arctic collembola. In: D. Hessen (ed.). UV Radiation and Arctic Ecosystems. Ecological Studies, 153:123–134.

Lennihan, R., D.M. Chapin and L.G. Dickson, 1994. Nitrogen fixation and photosynthesis in high arctic forms of Nostoc commune. Canadian Journal of Botany, 72:940–945.

Li, S., M. Paulsson and L.O. Björn, 2002a. Temperature-dependent formation and photorepair of DNA damage induced by UV-B radiation in suspension-cultured tobacco cells. Journal of Photochemistry and Photobiology B:66(1):67–72.

Li, S., Y. Wang and L.O. Björn, 2002b. Temperature effects on the formation of DNA damage in *Nicotiana tabacum* leaf discs induced by UV-B irradiation. Ecologic Science, 21:115–117.

Linderholm, H.W., B.Ö. Solberg and M. Lindholm, 2003. Tree-ring records from central Fennoscandia: the relationship between tree growth and climate along a west-east transect. The Holocene, 13:887–895.

Lindström, Å. and J. Agrell, 1999. Global change and possible effects on the migration and reproduction of arctic-breeding waders. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:145–159.

Lipson, D.A., S.K. Schmidt and R.K. Monson, 1999. Links between microbial population dynamics and nitrogen availability in an alpine ecosystem. Ecology, 80:1623–1631.

Lister, A. and P. Bahn, 1995. Mammoths. Boxtree, London, 168pp.

Lloyd, A.H., T.S. Rupp, C.L. Fastie and A.M. Starfield, 2003. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. Journal of Geophysical Research, 108(D2):8161, doi:10.1029/2001JD000852.

Lloyd, C.R., 2001. The measurement and modelling of the carbon dioxide exchange at a high Arctic site in Svalbard. Global Change Biology, 7:405–426.

Lugert, J. and C. Zockler, 2001. The bird fauna of the Yakut horse pastures in northeast Siberia. In: B. Gerken and M. Görner (eds.). Neue Modelle zu Maßnahmen der Landschaftsentwicklung mit großen Pflanzenfressern -Praktische Erfahrungen bei der Umsetzung. Natur- und Kulturlandschaft, 4:458–461.

Lundelius, E.L. Jr., R.W. Graham, E. Anderson, J. Guilday, J.A. Holman, D.W. Steadman, and D.S. Webb, 1983. Terrestrial vertebrate faunas. In: S.C. Porter (ed.). Late Quaternary Environments of the United States. Vol 1: The Late Pleistocene, pp. 311–353. University of Minnesota Press.

Luo, Y., S. Wan, D. Hui and L.L. Wallace, 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature, 413:622–625.

MacDonald, G.M., A.A. Velichko, C.V. Kremenetski, O.K. Borisova, A.A. Goleva, A.A. Andreev, L.C. Cwynar, R.T. Riding, S.L. Forman, T.W.D. Edwards, R. Aravena, D. Hammarlund, J.M. Szeicz and V.N. Gattaulin, 2000. Holocene treeline history and climate change across northern Eurasia. Quaternary Research, 53(3):302–311.

MacKenzie, T.D.B, M. Krol, N.P.A. Huner and D.A. Campbell, 2002. Seasonal changes in chlorophyll fluorescence quenching and the induction and capacity of the photoprotective xanthophyll cycle in Lobaria pulmonaria. Canadian Journal of Botany, 80:255–261.

MacLean, S.F., B.M. Fitzgerald and F.A. Pitelka, 1974. Population cycles in arctic lemmings: winter reproduction and predation by weasels. Arctic and Alpine Research, 6:1–12.

Madsen, J., G. Cracknell and A.D. Fox (eds.), 1999. Goose Populations of the Western Paleoartic: A Review of Status and Distribution. Wetlands International Publications 48. National Environment Research Institute, Ronde, Denmark, 344pp.

Malhi, S.S., W.B. McGill and M. Nyborg, 1990. Nitrate losses in soils: effect of temperature, moisture and substrate concentration. Soil Biology and Biochemistry, 22:733–737.

Marion, G.M. and W.C. Oechel, 1993. Mid- to late-Holocene carbon balance in Arctic Alaska and its implications for future global warming. The Holocene, 3:193–200.

Marks, T.C., 1978. The carbon economy of *Rubus chamaemorus* L. II. Respiration. Annals of Botany, 42:181–190.

Marks, T.C. and K. Taylor, 1978. The carbon economy of *Rubus chamaemorus* L. I. Photosynthesis. Annals of Botany, 42:165–179.

Matveyeva, N.V., 1998. Zonation in Plant Cover of the Arctic. Proceedings of the Komarov Botanical Institute, 21. Russian Academy of Sciences, Moscow, 219pp. (In Russian)

Matveyeva, N. and Y. Chernov, 2000. Biodiversity of terrestrial ecosystems. In: M. Nuttall and T.V. Callaghan (eds.). The Arctic: Environment, People, Policy, pp. 233–274. Harwood Academic Publishers.

Max, K.N., S.K. Mouchaty and K.E. Schwaegerle, 1999. Allozyme and morphological variation in two subspecies of *Dryas octopetala* (Rosaceae) in Alaska. American Journal of Botany, 86:1637–1644.

Maxwell, B., 1997. Recent climate patterns in the Arctic. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 21–46. Springer-Verlag.

Mayr, E., 1998. Two empires or three? Proceedings of the National Academy of Sciences, 95:9720–9723.

Mazur, P., 1980. Limits to life at low temperatures and at reduced water contents and water activities. Origins of Life, 10:137–159.

McDonald, I.R., M. Upton, G. Hall, R.W. Pickup, C. Edwards, J.R. Saunders, D.A. Ritchie and J.C. Murrel, 1999. Molecular ecological analysis of methanogens and methanotrophs in blanket bog peat. Microbial Ecology, 38:225–233.

McFadden, J.P., F.S. Chapin III and D.Y. Hollinger, 1998. Subgrid-scale variability in the surface energy balance of Arctic tundra. Journal of Geophysical Research, 103(D22):28947–28961.

McFadden, J.P., G.E. Liston, M. Sturm, R.A. Pielke Sr. and F.S. Chapin III, 2001. Interactions of shrubs and snow in arctic tundra: Measurements and models. In: A.J. Dolman, A.J. Hall, M.L. Kavvas, T. Oki and J.W. Pomeroy (eds.). Soil-Vegetation-Atmosphere Transfer Schemes and Large-Scale Hydrological Models. IAHS Publication 270:317–325. International Association of Hydrological Sciences, UK.

McFadden, J.P., W. Eugster and F.S. Chapin III, 2003. A regional study of the controls on water vapor and CO_2 exchange in Arctic tundra. Ecology, 84:2762–2776.

McGraw, J.B., 1995. Patterns and causes of genetic diversity in arctic plants. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies, 113:33–43.

McGraw, J.B. and J. Antonovics, 1983. Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life-cycle stages of selection. Journal of Ecology, 71:879–897.

McGuire, A.D., J.M. Melillo, D.W. Kicklighter, Y. Pan, X. Xiao, J. Helfrich, B.M. Moore III, C.J. Vorosmarty and A.L. Schloss, 1997. Equilibrium responses of global net primary production and carbon storage to doubled atmospheric carbon dioxide: sensitivity to changes in vegetation nitrogen concentration. Global Biogeochemical Cycles, 11:173–189.

McGuire, A.D., J.S. Clein, J.M. Melillo, D.W. Kicklighter, R.A. Meier, C.J. Vorosmarty and M.C. Serreze, 2000. Modeling carbon responses of tundra ecosystems to historical and projected climate: sensitivity of pan-arctic carbon storage to temporal and spatial variation in climate. Global Change Biology, 6(S1):141–159.

McGuire, A.D., C. Wirth, M. Apps, J. Beringer, J. Clein, H. Epstein, D.W. Kicklighter, J. Bhatti, F.S. Chapin III, B. de Groot, D. Efremov, W. Eugster, M. Fukuda, T. Gower, L.D. Hinzman, B. Huntley, G.J. Jia, E.S. Kasischke, J. Melillo, V.E. Romanovsky, A. Shvidenko, E. Vaganov and D.A. Walker, 2002. Environmental variation, vegetation distribution, carbon dynamics, and water/energy exchange in high latitudes. Journal of Vegetation Science, 13:301–314.

McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre and F.S. Chapin III, 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. Ecology, 78:1170–1187.

McKane, R.B., L.C. Johnson, G.R. Shaver, K.J. Nadelhoffer, E.B. Rastetter, B. Fry, A.E. Giblin, K. Kielland, B.L. Kwiatkowski, J.A. Laundre and G. Murray, 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature, 415:68–71.

Mehlum, F., 1999. Adaptation in arctic organisms to a short summer season. In: S.-A. Bengtsson, F. Mehlum and T. Severinsen (eds.). The Ecology of the Tundra in Svalbard. Norsk Polarinstitutt, Meddeleser, 150:161–169.

Meltofte, H., 1985. Populations and breeding schedules of waders, *Charadrii*, in high Arctic Greenland. Meddelelser om Gronland Bioscience, 16:1–43.

Meltofte, H., 2000. Birds. In: K. Caning and M. Rasch (eds.). Zackenberg Ecological Research Operations, ZERO, 5th Annual Report, 1999, pp. 32–39. Danish Polar Center, Ministry of Research and Information Technology.

Merilä, J., M. Pahkala and U. Johanson, 2000. Increased ultraviolet-B radiation, climate change and latitudinal adaptation - a frog perspective. Annales Zoologici Fennici, 37:129–134.

Michaelson, G.J., C.-L. Ping and J.M. Kimble, 1996. Carbon storage and distribution in tundra soils in Arctic Alaska, U.S.A. Arctic and Alpine Research, 28:414–424.

Michelsen, A., I.K. Schmidt, S. Jonasson, J. Dighton, H.E. Jones and T.V. Callaghan, 1995. Inhibition of growth, and effects on nutrient uptake on Arctic graminoids by leaf extracts – allelopathy or resource competition between plants and microbes? Oecologia, 103:407–418.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby and D. Sleep, 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia, 105:53–63.

Michelsen, A., C. Quarmby, D. Sleep and S. Jonasson, 1998. Vascular plant 15N abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. Oecologia, 115:406–418.

Michelsen, A., E. Graglia, I.K. Schmidt, S. Jonasson, D. Sleep and C. Quarmby, 1999. Differential responses of grass and a dwarf shrub to long-term changes in soil microbial biomass C, N and P following factorial addition of NPK fertilizer, fungicide and labile carbon to a heath. New Phytologist, 143:523–538.

Miller, O.K. and D.F. Farr, 1975. Index of the Common Fungi of North America, Synonymy and Common Names. Bibliotheca Mycologia, 44:206–230. J. Cramer, Vaduz.

Mirchink, T.G., 1988. Soil Mycology. Moscow University Publishers.

Molau, U., 1996. Climatic impacts on flowering, growth, and vigour in an arctic-alpine cushion plant, Diapensia lapponica, under different snow cover regimes. In: P.S. Karlsson and T.V. Callaghan (eds.). Plant Ecology in the Sub-Arctic Swedish Lapland. Ecological Bulletin 45:210–219.

Molau, U., 2001. Tundra plant responses to experimental and natural temperature changes. Memoirs of National Institute of Polar Research, Special Issue 54:445–466.

Molau, U. and J.M. Alatalo, 1998. Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. Ambio, 27:322–329.

Molau, U. and E.-L. Larsson, 2000. Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. Canadian Journal of Botany, 78:728–747.

Molau, U. and G.R. Shaver, 1997. Controls on seed production and seed germinability in *Eriophorum vaginatum*. Global Change Biology, 3(S1):80–88.

Mølgaard, P., 1982. Temperature observations in high Arctic plants in relation to microclimate in the vegetation of Peary Land, North Greenland. Arctic and Alpine Research, 14:105–115.

Moody, S.A., K.K. Newsham, P.G. Ayres and N.D. Paul, 1999. Variation in the responses of litter and phylloplane fungi to UV-B radiation (290–315 nm). Mycological Research, 103(11):1469–1477.

Moody, S.A., N.D. Paul, L.O. Björn, T.V. Callaghan, J.A. Lee, Y. Manetas, J. Rozema, D. Gwynn-Jones, U. Johanson, A. Kyparissis and A.M.C. Oudejans, 2001. The direct effects of UV-B radiation on *Betula pubescens* litter decomposing at four European field sites. Plant Ecology, 154:27–36.

Mooney, H.A. and W.D. Billings, 1961. Comparative physiological ecology of Arctic and Alpine populations of *Oxyria digyna*. Ecological Monographs, 31:1–29.

Moran, P.A.P., 1953. The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. Australian Journal of Zoology, 1:291–298.

Morneau, C. and S. Payette, 2000. Long-term fluctuations of a caribou population revealed by tree-ring data. Canadian Journal of Zoology, 78:1784–1790.

Morozov, V.V., 1998. Distribution of breeding waders in the north-east European Russian tundras. In: H. Hotker, E. Lebedeva, P.S. Tomkovich, J. Gromadzka, N.C. Davidson, J. Evans, D.A. Stroud and R.B. West (eds.). Migration and International Conservation of Waders: Research and Conservation on North Asian, African and European Flyways. International Wader Studies, 10:186–194.

Morrison, R.I.G., Y. Aubry, R.W. Butler, G.W. Beyersbergen, C. Downes, G.M. Donaldson, C.L. Gratto-Trevor, P.W. Hicklin, V.H. Johnston and R.K. Ross, 2001. Declines in North American shorebird populations. Wader Study Group Bulletin, 94:34–38.

Morrissey, L.A and G.P. Livingston, 1992. Methane emissions from Alaska arctic tundra: An assessment of local spatial variability. Journal of Geophysical Research, 97(D15):16661–16670.

Murray, D.F., 1995. Causes of Arctic plant diversity: origin and evolution. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies, 113:21–32.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar and R.R. Nemani, 1997. Increased plant growth in the northern high latitudes from 1981–1991. Nature, 386:698–702.

Myneni, R.B., J. Dong, C.J. Tucker, R.K. Kaufmann, P.E. Kauppi, J. Liski, L. Zhou, V. Alexeyev and M.K. Hughes, 2001. A large carbon sink in the woody biomass of northern forests. Proceedings of the National Academy of Sciences, 98:14784–14789.

Myrberget, S., 1973. Geographic synchronism of cycles of small rodent in Norway. Oikos, 24:220–224.

Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver and J.A. Laundre, 1991. Effects of temperature and substrate quality on element mineralization in six Arctic soils. Ecology, 72:242–253.

Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver and A.E. Linkins, 1992. Microbial processes and plant nutrient availability in arctic soils. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate. An Ecophysiological Perspective, pp. 281–300. Academic Press.

Nadelhoffer, K.J., G. Shaver, B. Fry, A.E. Giblin, L. Johnson and R. McKane, 1996. 15N natural abundances and N use by tundra plants. Oecologia, 107:386–394.

Neilson, P.R. and R.J. Drapek, 1998. Potentially complex biosphere responses to transient global warming. Global Change Biology, 4:505–521.

Nellemann, C., L. Kullerud, I. Vistnes, B.C. Forbes, E. Husby, G.P. Kofinas, B.P. Kaltenborn, J. Rouaud, M. Magomedova, R. Bobiwash, C. Lambrechts, P.J. Schei, S. Tveitdal, O. Gron and T.S. Larsen, 2001. GLOBIO. Global Methodology for Mapping Human Impacts on the Biosphere. UNEP/DEWA/TR.01-3. United Nations Environment Programme, 47pp.

Neuvonen, S., P. Niemela and T. Virtanen, 1999. Climatic change and insect outbreaks in boreal forests: the role of winter temperatures. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:63–67.

New, M., M. Hulme and P.D. Jones, 1999. Representing twentieth-century space-time climate variability. Part 1: development of a 1961–90 mean monthly terrestrial climatology. Journal of Climate, 12:829–856.

Niemi, R., P.J. Martikainen, J. Silvola, A. Wulff, S. Turtola and T. Holopainen, 2002. Elevated UV-B radiation alters fluxes of methane and carbon dioxide in peatland microcosms. Global Change Biology, 8:361–371.

Nojd, P. and P. Hari, 2001. The effect of temperature on the radial growth of Scots pine in northernmost Fennoscandia. Forest Ecology and Management, 142:65–77.

Nordström, C., H. Soegaard, T.R. Christensen, T. Friborg and B.U. Hansen, 2001. Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. Theoretical and Applied Climatology, 70(1–4):149–166.

Oberbauer, S.F., N. Sionit, S.J. Hastings and W.C. Oechel, 1986. Effects of CO_2 enrichment and nutrition on growth, photosynthesis, and nutrient concentration of Alaskan tundra plant species. Canadian Journal of Botany, 64:2993–2998.

Oberbauer, S.F., J.D. Tenhunen and J.F. Reynolds, 1991. Environmental effects on CO_2 efflux from water track and tussock tundra in arctic Alaska, U.S.A. Arctic and Alpine Research, 23(2):162–169.

Oberbauer, S.F., C.T. Gillespie, W. Cheng, A. Sala, R. Gebauer and J.D. Tenhunen, 1996. Diurnal and seasonal patterns of ecosystem CO_2 efflux from upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.. Arctic and Alpine Research, 28(3):328–338.

Odasz, A.M. and O. Savolainen, 1996. Genetic variation in populations of the arctic perennial *Pedicularis dasyantha* (Scrophulariaceae), on Svalbard, Norway. American Journal of Botany, 83:1379–1385.

Oechel, W.C. and W.D. Billings, 1992. Effects of global change on the carbon balance of Arctic plants and ecosystems. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 139–168. Academic Press.

Oechel, W.C., S.J. Hastings, G.L. Vourlitis, M. Jenkins, G. Riechers and N. Grulke, 1993. Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature, 361:520–523.

Oechel, W.C., S. Cowles, N. Grulke, S.J. Hastings, B. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue and G. Vourlitis, 1994. Transient nature of CO_2 fertilization in Arctic tundra. Nature, 371:500–503.

Oechel, W.C., G.L. Vourlitis, S.J. Hastings and S.A. Bochkarev, 1995. Change in Arctic CO_2 flux-over two decades: Effects of climate change at Barrow, Alaska. Ecological Applications, 5:846–855.

Oechel, W.C., G. Vourlitis and S.J. Hastings, 1997. Cold season CO_2 emission from Arctic soils. Global Biogeochemical Cycles, 11:163–172.

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, R.P. Ault Jr. and P. Bryant, 1998. The effects of water table manipulation and elevated temperature on the net CO_2 flux of wet sedge tundra ecosystems. Global Change Biology, 4:77–90.

Oechel, W.C., G.L. Vourlitis, J. Verfaillie Jr., T. Crawford, S. Brooks, E. Dumas, A. Hope, D. Stow, B. Boynton, V. Nosov and R. Zulueta, 2000a. A scaling approach for quantifying the net CO_2 flux of the Kuparuk River Basin, Alaska. Global Change Biology, 6(S1):160–173.

Oechel, W.C., G.L. Vourlitis, S.J. Hastings, R.C. Zulueta, L. Hinzman and D. Kane, 2000b. Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. Nature, 406:978–981.

Ogilvie, A.E.J., 1984. The past climate and sea-ice record from Iceland. Part 1: Data to A.D. 1780. Climatic Change, 6:131–152.

Ogilvie, A.E.J., 1991. Climatic changes in Iceland A.D. c.865 to 1598. In: G.F. Bigelow (ed.). The Norse of the North Atlantic. Acta Archaelogica, 61:233–251.

Ogilvie, A.E.J. and I. Jonsdottir, 2000. Sea ice, climate, and Icelandic fisheries in the eighteenth and nineteenth centuries. Arctic, 53:383–394.

Ogilvie, A.E.J. and T. Jonsson, 2001. 'Little Ice Age' research: A perspective from Iceland. Climatic Change, 48:9–52.

Ögren, E., 1996. Premature dehardening in *Vaccinium myrtillus* during a mild winter: a cause for winter dieback? Functional Ecology, 10:724–732.

Ögren, E., 1997. Relationship between temperature, respiratory loss of sugar and premature dehardening in dormant Scots pine seedlings. Tree Physiology, 17:724–732.

Ögren, E., T. Nilsson and L.-G. Sundblad, 1997. Relationship between respiratory depletion of sugars and loss of cold hardiness in coniferous seedlings over-wintering at raised temperatures: indications of different sensitivities of spruce and pine. Plant, Cell and Environment, 20:247–253.

Oksanen, L., S.D. Fretwell, J. Arruda and P. Niemela, 1981. Exploitation ecosystems in a gradient of primary productivity. American Naturalist, 118:240–261.

Oksanen, L., M. Aunapuu, T. Oksanen, M. Schneider, P. Ekerholm, P.A. Lundberg, T. Amulik, V. Aruaja and L. Bondestad, 1997. Outlines of food webs in a low arctic tundra landscape in relation to three theories on trophic dynamics. In: A.C. Gange and V.K. Brown (eds.). Multitrophic Interactions in Terrestrial Ecosystems, pp. 425–437. Blackwell Scientific.

Öquist, M.G. and B.H. Svensson, 2002. Vascular plants as regulators of methane emissions from a subarctic mire ecosystem. Journal of Geophysical Research, 107(D21):4580.

Osterkamp, T.E and V.E. Romanovsky, 1999. Evidence for warming and thawing of discontinuous permafrost in Alaska. Permafrost and Periglacial Processes, 10:17–37.

Ostler, W.K., K.T. Harper, K.B. McKnight and D.C. Anderson, 1982. The effects of increasing snowpack on a subalpine meadow in the Uinta Mountains, Utah, USA. Arctic and Alpine Research, 14:203–214.

Overpeck, J., K. Hughen, D. Hardy, R. Bradley, R. Case, M. Douglas, B. Finney, K. Gajewski, G. Jacoby, A. Jennings, S. Lamoureux, A. Lasca, G. MacDonald, J. Moore, M. Retelle, S. Smith, A. Wolfe and G. Zielinski, 1997. Arctic environmental change of the last four centuries. Science, 278:1251–1256.

Paetkau, D., S.C. Amstrup, E.W. Born, W. Calvert, A.E. Derocher, G.W. Garner, F. Messier, I. Stirling, M.K. Taylor, Ø. Wiig and C. Strobeck, 1999. Genetic structure of the world's polar bear populations. Molecular Ecology, 8(10):1571–1584.

Pahkala, M., A. Laurila and J. Merilä, 2002. Effects of ultraviolet-B radiation on common frog Rana temporaria embryos from along a latitudinal gradient. Oecologia, 133:458–465.

Palmqvist K., L. Dahlman, F. Valladares, A. Tehler, L.G. Sancho and J.-E. Mattsson, 2002. CO_2 exchange and thallus nitrogen across 75 contrasting lichen associations from different climate zones. Oecologia, 133:295–306.

Panikov, N.S., 1994. Response of soil microbial community to global warming: simulation of seasonal dynamics and multiyear succession exemplified by typical tundra. Microbiology (Russia) - English Translation, 63(3):389–404.

Panikov, N.S., 1995. Microbial Growth Kinetics. Chapman & Hall, 378pp.

Panikov, N.S., 1997. A kinetic approach to microbial ecology in arctic and boreal ecosystems in relation to global change. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 171–189. Springer-Verlag.

Panikov, N.S., 1999. Fluxes of CO_2 and CH_4 in high latitude wetlands: measuring, modelling and predicting response to climate change. Polar Research, 18(2):237–244.

Panikov, N.S. and S.N. Dedysh, 2000. Cold season CH_4 and CO_2 emission from boreal peat bogs (West Siberia): Winter fluxes and thaw activation dynamics. Global Biogeochemical Cycles, 14(4):1071–1080.

Panikov, N.S., M.V. Sizova, V.V. Zelenev, G.A. Machov, A.V. Naumov and I.M. Gadzhiev, 1995. Methane and carbon dioxide emission from several Vasyugan wetlands: spatial and temporal flux variations. Ecological Chemistry, 4:13–23.

Panikov, N.S., S.N. Dedysh, O.M. Kolesnikov, A.I. Mardini and M.V. Sizova, 2001. Metabolic and environmental control on methane emission from soils: mechanistic studies of mesotrophic fen in West Siberia. Water, Air, and Soil Pollution, Focus, 1(5–6):415–428.

Papen, H. and K. Butterbach-Bahl, 1999. A 3-year continuous record of nitrogen trace gas fluxes from untreated and limed soil of a N-saturated spruce and beech forest ecosystem in Germany. Part 1: N_2O emissions. Journal of Geophysical Research, 104(D15):18487–18503.

Parmesan, C. and G. Yohe, 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421:37–42.

Parmesan, C., N. Ryrholm, C. Stefanescu, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W.J. Tennent, J.A. Thomas and M. Warren, 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature, 399:579–583.

Parsons, A.N., J.M. Welker, P.A. Wookey, M.C. Press, T.V. Callaghan and J.A. Lee, 1994. Growth responses of four sub–Arctic dwarf shrubs to simulated environmental change. Journal of Ecology, 82:307–318.

Paulsson, M.,2003. Temperature Effects on UV-B Induced DNA Damage and Repair in Plants and a Lichen. Ph.D Thesis, University of Lund, 49pp.

Pavlov, P., J.I. Svendsen and S. Indrelid, 2001. Human presence in the European Arctic nearly 40,000 years ago. Nature, 413:64–67.

Payette, S., M. Eronen and J.J.P. Jasinski, 2002. The circumboreal tundra-taiga interface: Late Pleistocene and Holocene changes. Ambio Special Report, 12:15–22.

Perfect, E., R.D. Miller and B. Burton, 1988. Frost upheaval of overwintering plants: a quantitative field study of the displacement process. Arctic and Alpine Research, 20:70–75.

Peteet, D.M. (ed.), 1993. Global Younger Dryas? Quaternary Science Reviews, 12(5):277–356.

Peteet, D.M. (ed.), 1995. Global Younger Dryas Vol. 2, Quaternary Science Reviews, 14(9):811–958.

Peterson, B.J., T.L. Corliss, K. Kriet and J.E. Hobbie, 1992. Nitrogen and phosphorus concentrations and export for the Upper Kuparuk River on the North Slope of Alaska in 1980. Hydrobiologia, 240:61–69.

Philipp, M., 1997. Genetic diversity, breeding system, and population structure in *Silene acaulis* (Caryophyllaceae) in West Greenland. Opera Botanica, 132:89–100.

Philipp, M., 1998. Genetic variation in four species of *Pedicularis* (Scrophulariaceae) within a limited area in West Greenland. Arctic and Alpine Research, 30:396–399.

Phoenix, G.K., 2000. Effects of ultraviolet radiation on sub-Arctic heathland vegetation. Ph.D Thesis, University of Sheffield, 129pp.

Phoenix, G.K., D. Gwynn-Jones, J.A. Lee and T.V. Callaghan, 2000. The impacts of UV-B radiation on the regeneration of a sub-Arctic heath community. Plant Ecology, 146:67–75.

Phoenix, G.K., D. Gwynn-Jones, T.V. Callaghan, D. Sleep and J.A. Lee, 2001. Effects of global change on a sub-Arctic heath: effects of enhanced UV-B radiation and increased summer precipitation. Journal of Ecology, 89:256–267.

Pielke, R.A. and P.L. Vidale, 1995. The boreal forest and the polar front. Journal of Geophysical Research, 100(D12):25755–25758.

Piersma, T., 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? Oikos, 80:623–631.

Pop, E.W., S.F. Oberbauer and G. Starr, 2000. Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana.* Oecologia, 124:176–184.

Porsild, A.E., 1951. Plant life in the Arctic. Canadian Geographical Journal, 42:120–145.

Post, E., R.O. Peterson, N.C. Stenseth and B.E. McLaren, 1999. Ecosystem consequences of wolf behavioural response to climate. Nature, 401:905–907.

Potter, J.A., M.C. Press, T.V. Callaghan and J.A. Lee, 1995. Growth responses of *Polytrichum commune* (Hedw.) and *Hylocomium splendens* (Hedw.) Br. Eur. to simulated environmental change in the subarctic. New Phytologist, 131:533–541.

Predavec, M., C.J. Krebs, K. Danell and R. Hyndman, 2001. Cycles and synchrony in the collared lemming (*Dicrostonyx groenlandicus*) in Arctic North America. Oecologia, 126:216–224

Prentice, I.C., W.P. Cramer, S.P. Harrisson, R. Leemans, R.A. Monserud and A.M. Solomon, 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19:117–134.

Press, M.C., T.V. Callaghan and J.A. Lee, 1998a. How will European Arctic ecosystems respond to projected global environmental change? Ambio, 27:306–311.

Press, M.C., J.A. Potter, M.J.W. Burke, T.V. Callaghan and J.A. Lee, 1998b. Responses of a subarctic dwarf shrub heath community to simulated environmental change. Journal of Ecology, 86:315–327.

Prestrud, P. and K. Nilssen, 1992. Fat deposition and seasonal variation in body composition of arctic foxes in Svalbard. Journal of Wildlife Management, 56:221–233.

Price, P.W., T.P. Craig and H. Roininen, 1995. Working toward a theory on galling sawfly population dynamics. In: N. Cappuccino and P.W. Price (eds.). Population Dynamics: New Approaches and Synthesis, pp. 321–338. Academic Press.

Prock, S. and C. Körner, 1996. A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in arctic and temperate zone herbaceous plants from contrasting altitudes. In: P.S. Karlsson and T.V. Callaghan (eds.). Plant Ecology in the Sub-Arctic Swedish Lapland. Ecological Bulletin 45:93–103.

Pruitt, W.O., 1957. Observations on the bioclimate of some taiga mammals. Arctic, 10:131–138.

Putkonen, J. and G. Roe, 2003. Rain-on-snow events impact on soil temperatures and affect ungulate survival. Geophysical Research Letters, 30(4):1188, doi:10.1029/2002GL016326.

Quested, H.M., M.C. Press, T.V. Callaghan and J.H.C. Cornelissen, 2002. The hemiparasitic angiosperm Bartsia alpina has the potential to accelerate decomposition in sub-Arctic communities. Oecologia, 130:88–95.

Quested, H.M., J.H.C. Cornelissen, M.C. Press, T.V. Callaghan, R. Aerts, F. Trosien, P. Riemann, D. Gwynn-Jones, A. Kondratchuk and S.E. Jonasson, 2003. Decomposition of sub-arctic plants with differing nitrogen economies: A functional role for hemiparasites. Ecology, 84:3209–3221.

Radajewsky, S., P. Ineson, N.R. Parekh and J.C. Murrell, 2000. Stable-isotope probing as a tool in microbial ecology. Nature, 403:646–649.

Rannie, W.F., 1986. Summer air temperature and number of vascular species in Arctic Canada. Arctic, 39:133–137.

Ranta, E., J. Lindstrom, V. Kaitala, H. Kokko, H. Linden and E. Helle, 1997. Solar activity and hare dynamics: A cross-continental comparison. American Naturalist, 149:765–775.

Rapp, A., 1996. Photo documentation of landscape change in Northern Swedish mountains. In: P.S. Karlsson and T.V. Callaghan (eds.). Plant Ecology in the Sub-Arctic Swedish Lapland. Ecological Bulletin 45:170–179.

Rastetter, E.B., R.B. McKane, G.R. Shaver, K.J. Nadelhoffer and A.E. Giblin, 1997. Analysis of CO$_2$, temperature, and moisture effects on carbon storage in Alaskan arctic tundra using a general ecosystem model. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau and B. Sveinbjornsson (eds.). Global Change and Arctic Terrestrial Ecosystems, pp. 437–451. Springer-Verlag.

Read, D.J., J.R. Leake and A.R. Langdale, 1989. The nitrogen nutrition of mycorrhizal fungi and their host plants. In: L. Boddy, R. Marchant and D.J. Read (eds.). Nitrogen, Phosphorus and Sulphur Utilisation by Fungi. British Mycological Society Symposia, 15:181–204. Cambridge University Press.

Réale, D., A.G. McAdam, S. Boutin and D. Berteaux, 2003. Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society of London: Biological Sciences, 270:591–596.

Reid, D.G., C.J. Krebs and A. Kenney, 1995. Limitation of collared lemming population growth at low densities by predation mortality. Oikos, 73:387–398.

Reierth, E. and K.-A. Stokkan, 1998. Activity rhythm in High Arctic Svalbard ptarmigan (Lagopus mutus hyperboreus). Canadian Journal of Zoology, 76:2031–2039.

Reimers, E., 1982. Winter mortality and population trends of reindeer on Svalbard, Norway. Arctic and Alpine Research, 14:295–300.

Renssen, H., H. Goosse, T. Fichefet and J.-M. Campin, 2001. The 8.2 kyr BP event simulated by a global atmosphere-sea-ice-ocean model. Geophysical Research Letters, 28(8):1567–1570.

Richardson, S.J., 2000. Response of a Sub-arctic Dwarf Shrub Heath Community to Nutrient Addition and Warming. Ph.D Thesis, University of Sheffield, 159pp.

Riedlinger, D., 2001. Community-based assessments of change: contributions of Inuvialuit knowledge to understanding climate change in the Canadian Arctic. MSc. Thesis. University of Manitoba.

Riedlinger, D. and F. Berkes, 2001. Contributions of traditional knowledge to understanding climate change in the Canadian Arctic. Polar Record, 37(203):315–328.

Ries, G., W. Heller, H. Puchta, H. Sandermann, H.K. Seidlitz and B. Hohn, 2000. Elevated UV-B radiation reduces genome stability in plants. Nature, 406:98–101.

Ritchie, J.C., 1987. Postglacial Vegetation of Canada. Cambridge University Press, 178pp.

Ritchie, J.C. and G.M. MacDonald, 1986. The patterns of post-glacial spread of white spruce. Journal of Biogeography, 13:527–540.

Rivkina, E.M., E.I. Friedmann, C.P. McKay and D.A. Gilichinsky, 2000. Metabolic activity of permafrost bacteria below the freezing point. Applied and Environmental Microbiology, 66:3230–3233.

Robberecht, R., M.M. Caldwell and W.D. Billings, 1980. Leaf ultraviolet optical properties along a latitudinal gradient in the Arctic-Alpine life zone. Ecology, 61(3):612–619.

Robinson, C.H., O.B. Borisova, T.V. Callaghan and J.A. Lee, 1996. Fungal hyphal length in litter of *Dryas octopetala* in a high-Arctic polar semi-desert, Svalbard. Polar Biology, 16:71–74.

Robinson, C.H., A. Michelsen, J.A. Lee, S.J. Whitehead, T.V. Callaghan, M.C Press and S. Jonasson, 1997. Elevated atmospheric CO$_2$ affects decomposition of *Festuca vivipara* (L.) Sm. litter and roots in experiments simulating environmental change in two contrasting Arctic ecosystems. Global Change Biology, 3:37–49.

Robinson, C.H., P.A. Wookey, J.A. Lee, T.V. Callaghan and M.C. Press, 1998. Plant community responses to simulated environmental change at a high Arctic polar semi-desert. Ecology, 79:856–866.

Roff, D.A., 1997. Evolutionary Quantitative Genetics. Chapman & Hall, 493pp.

Roulet, N.T., T. Moore, J. Bubier and P. Lafleur, 1992. Northern fens: methane flux and climatic change. Tellus B, 44:100–105.

Roulet, N.T., A. Jano, C.A. Kelly, L.F. Klinger, T.R. Moore, R. Protz, J.A. Ritter and W.R. Rouse, 1994. Role of the Hudson Bay lowland as a source of atmospheric methane. Journal of Geophysical Research, 99(D1):1439–1454.

Rouse, W.R., 2000. The energy and water balance of high-latitude wetlands: controls and extrapolation. Global Change Biology, 6(S1):59–68.

Rovansek, R.J., L.D. Hinzman and D.L. Kane, 1996. Hydrology of a tundra wetland complex on the Alaskan Arctic Coastal Plain. Arctic and Alpine Research, 28(3):311–317.

Rozema, J., B. van Geel, L.O. Björn, J. Lean and S. Madronich, 2002. Toward solving the UV puzzle. Science, 296:1621–1622.

Ruess, L., A. Michelsen, I.K. Schmidt and S. Jonasson, 1999a. Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. Plant and Soil, 212:63–73.

Ruess, L., A. Michelsen and S. Jonasson, 1999b. Simulated climate change in subarctic soils: responses in nematode species composition and dominance structure. Nematology, 1:513–526.

Rundgren, M. and O. Ingolfsson, 1999. Plant survival in Iceland during periods of glaciation? Journal of Biogeography, 26(2):387–396.

Ruohomäki, K., M. Tanhuanpää, M.P. Ayres, P. Kaitaniemi, T. Tammaru and E. Haukioja, 2000. Causes of cyclicity of *Epirrita autumnata* (Lepidoptera, Geometridae): grandiose theory and tedious practice. Population Ecology, 42:211–223.

Russell, N.J., 1990. Cold adaptation of microorganisms. Philosophical Transactions of the Royal Society of London Series B, 326:595–611.

Russell, R.S., 1940. Physiological and ecological studies on Arctic vegetation. II. The development of vegetation in relation to nitrogen supply and soil micro-organisms on Jan Mayen Island. Journal of Ecology, 28:269–288.

Sakai, A. and W. Larcher, 1987. Frost Survival of Plants: Responses and Adaptation to Freezing Stress. Ecological Studies 62. Springer-Verlag, 321pp.

Sala, O.E. and T. Chapin, 2000. Scenarios of global biodiversity. Global Change Newsletter, 43:7–11, 19. International Geosphere-Biosphere Programme, Stockholm.

Savile, D.B.O., 1971. Arctic Adaptations in Plants. Agriculture Canada Research Branch, Monograph 6, 81pp.

Schimel, J.P., 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry, 28:183–200.

Schimel, J.P. and F.S. Chapin III, 1996. Tundra plant uptake of amino acid and NH$_4^+$ nitrogen in situ: plants compete well for amino acid N. Ecology, 77:2142–2147.

Schimel, J.P. and J.S. Clein, 1996. Microbial response to freeze–thaw cycles in tundra and taiga soils. Soil Biology and Biochemistry, 28:1061–1066.

Schipperges, B. and C. Gehrke, 1996. Photosynthetic characteristics of subarctic mosses and lichens. In: P.S. Karlsson and T.V. Callaghan (eds.). Plant Ecology in the Sub-Arctic Swedish Lapland. Ecological Bulletin 45:121–126.

Schmidt, I.K., S. Jonasson and A. Michelsen, 1999. Mineralization and microbial immobilization of N and P in arctic soils in relation to season, temperature and nutrient amendment. Applied Soil Ecology, 11:147–160.

Schmidt, I.K., L. Ruess, E. Bååth, A. Michelsen, F. Ekelund and S. Jonasson, 2000. Long term manipulation of the microbes and microfauna of two subarctic heaths by addition of fungicide, bactericide, carbon and fertilizer. Soil Biology and Biochemistry, 32:707–720.

Schmidt, I.K., S. Jonasson, G.R. Shaver, A. Michelsen and A. Nordin, 2002. Mineralization and distribution of nutrients in plants and microbes in four arctic ecosystems: responses to warming. Plant and Soil, 242:93–106.

Schmidt-Nielsen, K., 1979. Animal Physiology: Adaptation and Environment. Cambridge University Press, 560pp.

Scholander, P.F., V. Walters, R. Hock and L. Irving, 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biological Bulletin, 99:259–271.

Schroeter, B., T.G.A. Green, L. Kappen and R.D. Seppelt, 1994. Carbon dioxide exchange at subzero temperatures: field measurements on *Umbilicaria aprina* in Antarctica. Cryptogamic Botany, 4:233–241.

Schultz, A.M., 1969. A study of an ecosystem: the arctic tundra. In: G.M. Van Dyne (ed.). The Ecosystem Concept in Natural Management, pp. 77–93. Academic Press.

Schulze, E.-D., F.M. Kelliher, C. Körner, J. Lloyd and R. Leuning, 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. Annual Review of Ecology and Systematics, 25:629–662.

Scott, D.A., 1998. Global Overview of the Conservation of Migratory Arctic Breeding Birds outside the Arctic. CAFF Technical Report 4. Conservation of Arctic Flora and Fauna, 134pp.

Searles, P.S., S.D. Flint, S.B. Diaz, M.C. Rousseaux, C.L. Ballaré and M.M. Caldwell, 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. Global Change Biology, 5:225–234.

Searles, P.S., S.D. Flint and M.M. Caldwell, 2001. A meta-analysis of plant field studies simulating stratospheric ozone depletion. Oecologia, 127:1–10.

Sekretareva, N.A., 1999. The Vascular Plants of the Russian Arctic and Adjacent Territories. Sofia, Moscow, 160pp.

Seldal, T., K.J. Andersen and G. Högstedt, 1994. Grazing-induced proteinase inhibitors: a possible cause for lemming population cycles. Oikos, 70:3–11.

Semerdjieva, S.I., E. Sheffield, G.K. Phoenix, D. Gwynn-Jones, T.V. Callaghan and G.N. Johnson, 2003. Contrasting strategies for UV-B screening in sub-Arctic dwarf shrubs. Plant, Cell and Environment, 26:957–964.

Semikhatova, O.A., T.V. Gerasimenko and T.I. Ivanova, 1992. Photosynthesis, respiration, and growth of plants in the Soviet Arctic. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver and J. Svoboda (eds.). Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective, pp. 169–192. Academic Press.

Serreze, M.C., J.E. Walsh, F.S. Chapin III, T. Osterkamp, M. Dyurgerov, V. Romanovsky, W.C. Oechel, J. Morison, T. Zhang and R.G. Barry, 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change, 46:159–207.

Shaver, G.R. and W.D. Billings, 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. Ecology, 56:401–409.

Shaver, G.R. and F.S. Chapin III, 1991. Production: biomass relationships and element cycling in contrasting Arctic vegetation types. Ecological Monographs, 61:1–31.

Shaver, G.R and J.C. Cutler, 1979. The vertical distribution of live vascular phytomass in cottongrass tussock tundra. Arctic and Alpine Research, 11:335–342.

Shaver, G.R. and S. Jonasson, 2000. Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. Polar Research, 18:245–252.

Shaver, G.R., F.S. Chapin III and W.D. Billings, 1979. Ecotypic differentiation in *Carex aquatilis* on ice-wedge polygons in the Alaskan coastal tundra. Journal of Ecology, 67:1025–1046.

Shaver, G.R., N. Fetcher and F.S. Chapin III, 1986. Growth and flowering in *Eriophorum vaginatum*: Annual and latitudinal variation. Ecology, 67:1524–1535.

Shaver, G.R., W.D. Billings, F.S. Chapin III, A.E. Giblin, K.J. Nadelhoffer, W.C. Oechel and E.B. Rastetter, 1992. Global change and the carbon balance of arctic ecosystems. Bioscience, 42:433–441.

Shaver, G.R., J.A. Laundre, A.E. Giblin and K.J. Nadelhoffer, 1996. Changes in live plant biomass, primary production, and species composition along a riverside toposequence in arctic Alaska, U.S.A. Arctic and Alpine Research, 28:363–379.

Shaver, G.R., L.C. Johnson, D.H. Cades, G. Murray, J.A. Laundre, E.B. Rastetter, K.J. Nadelhoffer and A.E. Giblin, 1998. Biomass and CO_2 flux in wet sedge tundras: responses to nutrients, temperature, and light. Ecological Monographs, 68:75–97.

Shaver, G.R., J. Canadell, F.S. Chapin III, J. Gurevitch, J. Harte, G. Henry, P. Ineson, S. Jonasson, J. Melillo, L. Pitelka and L. Rustad, 2000. Global warming and terrestrial ecosystems: A conceptual framework for analysis. Bioscience, 50:871–882.

Shaver, G.R., M.S. Bret-Harte, M.H. Jones, J. Johnstone, L. Gough, J. Laundre and F.S. Chapin III, 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology, 82:3163–3181.

Sher, A., 1997. Late-Quaternary extinction of large mammals in northern Eurasia: A new look at the Siberian contribution. In: B. Huntley, W. Cramer, A.V. Morgan, H.C. Prentice and J.R.M. Allen (eds.). Past and Future Rapid Environmental Changes: The Spatial and Evolutionary Responses of Terrestrial Biota, pp. 319–339. Springer-Verlag.

Shevtsova, A., A. Ojala, S. Neuvonen, M. Vieno and E. Haukioja, 1995. Growth and reproduction of dwarf shrubs in a subarctic plant community: annual variation and above-ground interactions with neighbours. Journal of Ecology, 83:263–275.

Shevtsova, A., E. Haukioja and A. Ojala, 1997. Growth response of subarctic dwarf shrubs, *Empetrum nigrum* and *Vaccinium vitis-ideae*, to manipulated environmental conditions and species removal. Oikos, 78:440–458.

Siegert, M.J., J.A. Dowdeswell and M. Melles, 1999. Late Weichselian glaciation of the Russian High Arctic. Quaternary Research, 52(3):273–285.

Silapaswan, C.S., D. Verbyla and A.D. McGuire, 2001. Land cover change on the Seward Peninsula: The use of remote sensing to evaluate the potential influences of climate change on historical vegetation dynamics. Canadian Journal of Remote Sensing, 27(5):542–554.

Sinclair, A.R.E., J.M. Gosline, G. Holdsworth, C.J. Krebs, S. Boutin, J.N.M. Smith, R. Boonstra and M. Dale, 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. American Naturalist, 141:173–198.

Sitch, S., B. Smith, I.C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J.O. Kaplan, S. Levis, W. Lucht, M.T. Sykes, K. Thonicke and S. Venevsky, 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology, 9:161–185.

Sitch, S., A.D. McGuire, J. Kimball, N. Gedney, J. Gamon, R. Engstrom, A. Wolf, Q. Zhuang, and J. Clein, submitted. Assessing the circumpolar carbon balance of arctic tundra with remote sensing and process-based modeling approaches. Ecological Applications.

Sizova, M.V., N.S. Panikov, T.P. Tourova and P.W. Flanagan, 2003. Isolation and characterization of oligotrophic acido-tolerant methanogenic consortia from a *Sphagnum* peat bog. FEMS Microbiology Ecology, 45:301–315.

Sjögersten, S. and P.A. Wookey, 2002. Spatio-temporal variability and environmental controls of methane fluxes at the forest-tundra ecotone in the Fennoscandian mountains. Global Change Biology, 8:885–895.

Skinner, L.J., 2002. The Role of *Exobasidium* in the Ecology of its Dwarf Shrub Hosts. Ph.D Thesis, University of Sheffield, 174pp.

Skinner, W.R., R.L. Jefferies, T.J. Carleton, R.F. Rockwell and K.F. Abraham, 1998. Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Change Biology, 4:3–16.

Skotnicki, M.L., P.M. Selkirk and C. Beard, 1998. RAPD profiling of genetic diversity in two populations of the moss *Ceratodon purpureus* in Victoria Island, Antarctica. Polar Biology, 19:172–176.

Skotnicki, M.L., P.M. Selkirk and J.A. Ninham, 1999. RAPD analysis of genetic variation and dispersal of the moss *Bryum argenteum* in Ross Island and Victoria Land, Antarctica. Polar Biology, 21:417–422.

Skre, O., R. Baxter, R.M.M. Crawford, T.V. Callaghan and A. Fedorkov, 2002. How will the tundra-taiga interface respond to climate change? Ambio Special Report, 12:37–46.

Smaglik, P., 2002. A climate of uncertainty. Nature, 415:Naturejobs p. 6.

Smith, P.A., J.A. Schaefer and B.R. Patterson, 2002. Variation at high latitudes: the geography of body size and cranial morphology of the muskox, *Ovibos moschatus*. Journal of Biogeography, 29:1089–1094.

Smith, R.I.L., 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. British Antarctic Survey Scientific Report 68, 124pp.

Sniegowski, P.D., P.J. Gerrish, and R.E. Lenski, 1997. Evolution of high mutation rates in experimental populations of *E. coli.* Nature, 387:703–705.

Søgaard, H., C. Nordstrøm, T. Friborg, B.U. Hansen, T.R. Christensen and C. Bay, 2000. Trace gas exchange in a high-arctic valley. 3: Integrating and scaling CO_2 fluxes from canopy to landscape using flux data, footprint modeling, and remote sensing. Global Biogeochemical Cycles, 14:725–744.

Solberg, E.J., P. Jorhøy, O. Strand, R. Aanes, A. Loison, B.-E. Sæther and J.D.C. Linnell, 2001. Effects of density-dependence and climate on the dynamics of a Svalbard reindeer population. Ecography, 24:441–451.

Solheim, B., U. Johanson, T.V. Callaghan, J.A. Lee, D. Gwynn-Jones and L.O. Björn, 2002. The nitrogen fixation potential of arctic cryptogam species is influenced by enhanced UV-B radiation. Oecologia, 133:90–93.

Soloviev, M.Y., P.S. Tomkovich and N. Davidson, 1998. An international breeding condition survey of arctic waterfowl: progress report. Wader Study Group Bulletin, 87:43–47.

Sommerfeld, R.A., A.R. Mosier and R.C. Musselman, 1993. CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. Nature, 361:140–142.

Sonesson, M. and J. Hoogesteger, 1983. Recent tree-line dynamics (Betula pubescens Ehrh. ssp. tortuosa [Ledeb.] Nyman) in northern Sweden. Nordicana, 47:47–54.

Sonesson, M., C. Gehrke and M. Tjus, 1992. CO_2 environment, microclimate and photosynthesis characteristics of the moss *Hylocomium splendens* in a subarctic habitat. Oecologia, 92:23–29.

Sonesson, M., T.V. Callaghan and L.O. Bjorn, 1995. Short term effects of enhanced UV-B and CO_2 on lichens at different latitudes. The Lichenologist, 27:547–557.

Sonesson, M., T.V. Callaghan and B.A. Carlsson, 1996. Effects of enhanced ultraviolet radiation and carbon dioxide concentration on the moss Hylocomium splendens. Global Change Biology, 2:101–107.

Sonesson, M., B.A. Carlsson, T.V. Callaghan, S. Halling, L.O. Björn, M. Bertgren and U. Johanson, 2002. Growth of two peat-forming mosses in subarctic mires: species interactions and effects of simulated climate change. Oikos, 99:151–160.

Sørensen, T., 1941. Temperature relations and phenology of the northeast Greenland flowering plants. Meddelelser om Grönland, 125:1–305.

Srivastava, D.S. and R.L. Jefferies, 1996. A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. Journal of Ecology, 84:31–42.

Staley, J.T., 1997. Biodiversity: Are microbial species threatened? Current Opinion in Biotechnology, 8:340–345.

Staley, J.T. and J.J. Gosink, 1999. Poles apart: biodiversity and biogeography of sea ice bacteria. Annual Review of Microbiology, 53:189–215.

Staley J.T. and A. Konopka, 1985. Measurement of in situ activities of nonphotosynthetic microorganisms in aquatic and terrestrial habitats. Annual Review of Microbiology, 39:321–346.

Steen, H., N.G. Yoccoz and R.A. Ims, 1990. Predators and small rodent cycles: An analysis of a 79-year time series of small rodent population fluctuations. Oikos, 59:115–120.

Stehlik, I., J.J. Schneller and K. Bachmann, 2001. Resistance or emigration: response of the high-alpine plant *Eritrichium nanum* (L.) Gaudin to the ice age within the Central Alps. Molecular Ecology, 10(2):357–370.

Steiglitz, M., A. Giblin, J. Hobbie, M. Williams and G. Kling, 2000. Simulating the effects of climate change and climate variability on carbon dynamics in Arctic tundra. Global Biogeochemical Cycles, 14:1123–1136.

Stenseth, N.C. and R.A. Ims, 1993. The Biology of Lemmings. Academic Press, UK, 683pp.

Stenström, A., B.O. Jonsson, I.S. Jónsdóttir, T. Fagerström and M. Augner, 2001. Genetic variation and clonal diversity in four clonal sedges (*Carex*) along the Arctic coast of Eurasia. Molecular Ecology, 10:497–513.

Stenström, A., I.S. Jónsdóttir and M. Augner, 2002. Genetic and environmental effects on morphology in clonal sedges in the Eurasian Arctic. American Journal of Botany, 89:1410–1421.

Stetter, K.O., R. Huber, E. Blochl, M. Kurr, R.D. Eden, M. Fielder, H. Cash and I. Vance, 1993. *Hyperthermophilic archaea* are thriving in deep North Sea and Alaskan oil reservoirs. Nature, 365:743–745.

Strann, K.-B., N.G. Yoccoz and R.A. Ims, 2002. Is the heart of the Fennoscandian rodent cycle still beating? A 14-year study of small mammals and Tengmalm's owls in northern Norway. Ecography, 25:81–87.

Strathdee, A.T. and J.S. Bale, 1998. Life on the edge: insect ecology in Arctic environments. Annual Review of Entomology, 43:85–106.

Strathdee, A.T., J.S. Bale, W.C. Block, S.J. Coulson, I.D. Hodkinson and N.R. Webb, 1993. Effects of temperature elevation on a field population of *Acyrthosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. Oecologia, 96:457–465.

Strathdee, A.T., J.S. Bale, F.C. Strathdee, W. Block, S.J. Coulson, I.D. Hodkinson and N.R. Webb, 1995. Climatic severety and responses to warming of Arctic aphids. Global Change Biology, 1:23–28.

Ström, L., A. Ekberg and T.R. Christensen, 2003. The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland. Global Change Biology, 9:1185–1192.

Stuart, A.J., 1982. Pleistocene Vertebrates in the British Isles. Longman, 212pp.

Stuart, A.J., L.D. Sulerzhitsky, L.A. Orlova, Y.V. Kuzmin and A.M. Lister, 2002. The latest woolly mammoths (*Mammuthus primigenius* Blumenbach) in Europe and Asia: a review of the current evidence. Quaternary Science Reviews, 21:1559–1569.

Stuiver, M., P.M. Grootes and T.F. Braziunas, 1995. The GISP2 ‰18O climate record of the past 16,500 years and the role of the sun, ocean, and volcanoes. Quaternary Research, 44:341–354.

Sturm, M., J.P. McFadden, G.E. Liston, F.S. Chapin III, C.H. Racine and J. Holmgren, 2001a. Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. Journal of Climate, 14:336–344.

Sturm, M., C. Racine and K. Tape, 2001b. Climate change: Increasing shrub abundance in the Arctic. Nature, 411:546–547.

Summers, R.W. and L.G. Underhill, 1987. Factors relating to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. Bird Study, 34:161–171.

Sutherland, W.J., 1988. Predation may link the cycles of lemmings and birds. Trends in Ecology and Evolution, 3:29–30.

Sveinbjarnardóttir, G., 1992. Farm Abandonment in Medieval and Post-Medieval Iceland: An Interdisciplinary Study. Oxbow Monograph 17. Oxbow Books, 192pp.

Sveinbjörnsson, B., A. Hofgaard and A. Lloyd, 2002. Natural causes of the tundra-taiga boundary. Ambio Special Report, 12:23–29.

Svensson, B.H., 1980. Carbon dioxide and methane fluxes from the ombrotrophic parts of a subarctic mire. In: M. Sonesson (ed.). Ecology of a Subarctic Mire. Ecological Bulletin, 30:235–250. Swedish Natural Science Research Council, Stockholm.

Svensson, B.H., T.R. Christensen, E. Johansson and M. Öquist, 1999. Interdecadal changes in CO_2 and CH_4 fluxes of a subarctic mire: Stordalen revisited after 20 years. Oikos, 85:22–30.

Svoboda, J. and B. Freedman (eds.), 1994. Ecology of a Polar Oasis. Alexandra Fiord, Ellesmere Island, Canada. Captus Press, 268pp.

Syroechovski, E.E. and A.G. Kuprianov, 1995. Wild reindeer of the arctic Eurasia: geographical distribution, numbers and population structure. In: E. Grønlund and O. Melander (eds.). Swedish-Russian Tundra Ecology – Expedition 94: A Cruise Report, pp. 175–180. Swedish Polar Research Secretariat, Stockholm.

Taalas, P., J. Kaurola, A. Kylling, D. Shindell, R. Sausen, M. Dameris, V. Grewe, J. Herman, J. Damski and B. Steil, 2000. The impact of greenhouse gases and halogenated species on future solar UV radiation doses. Geophysical Research Letters, 27(8):1127–1130.

Talbot, S.S. and D.F. Murray (eds.), 2001. Proceedings of the First International Conservation of Arctic Flora and Fauna (CAFF) Flora Group Workshop. CAFF Technical Report 10. 65pp.

Talbot, S.S., B.A. Yurtsev, D.F. Murray, G.W. Argus, C. Bay and A. Elvebakk, 1999. Atlas of Rare Endemic Vascular Plants of the Arctic. CAFF Technical Report 3. Conservation of Arctic Flora and Fauna. 73pp.

Tanhuanpää, M., K. Ruohomaki and E. Uusipaikka, 2001. High larval predation rate in non-outbreaking populations of a geometrid moth. Ecology, 82:281–289.

Tannerfeldt, M. and A. Angerbjörn, 1998. Fluctuating resources and the evolution of litter size in the arctic fox. Oikos, 83:545–559.

Tast, J. and O. Kalela, 1971. Comparisons between rodent cycles and plant production in Finnish Lapland. Annales Academiae Scientiarum Fennicae, 186:1–14.

Taulavuori, E., K. Taulavuori, K. Laine, T. Pakonen and E. Saari, 1997. Winter hardening and glutathione status in the bilberry (*Vaccinium myrtillus L.*) in response to trace gases (CO_2, O3) and nitrogen fertilization. Physiologia Plantarum, 101:192–198.

Taulavuori, K., A. Niinimaa, K. Laine, E. Taulavuori and P. Lähdesmäki, 1997a. Modelling frost resistance of Scots pine seedlings using temperature, daylength and pH of cell effusate. Plant Ecology, 133:181–189.

Taulavuori, K., K. Laine, E. Taulavuori, T. Pakonen and E. Saari, 1997b. Accelerated dehardening in bilberry (*Vaccinium myrtillus L.*) induced by a small elevation in air temperature. Environmental Pollution, 98:91–95.

Taulavuori, K., E. Taulavuori, T. Sarjala, E.-M. Savonen, P. Pietiläinen, P. Lähdesmäki and K. Laine, 2000. In vivo chlorophyll fluorescence is not always a good indicator of cold hardiness. Journal of Plant Physiology, 157:227–229.

Taulavuori, K., E. Taulavuori, A. Niinimaa and K. Laine, 2001. Acceleration of frost hardening in *Vaccinium vitis-idaea* (L.) by nitrogen fertilization. Oecologia, 127:321–323.

Tenow, O., 1972. The outbreaks of *Oporinia autumnata* Bkh. and Operophtera spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862–1968. Zoologiska Bidrag från Uppsala, Supplement 2:1–107.

Tenow, O., 1996. Hazards to a mountain birch forest - Abisko in perspective. In: P.S. Karlsson and T.V. Callaghan (eds.). Plant Ecology in the Sub-Arctic Swedish Lapland. Ecological Bulletin 45:104–114.

Tenow, O. and H. Bylund, 2000. Recovery of a *Betula pubescens* forest in northern Sweden after severe defoliation by *Epirrita autumnata*. Journal of Vegetation Science, 11:855–862.

Tenow, O. and A. Nilssen, 1990. Egg cold hardiness and topoclimatic limitations to outbreaks of *Epirrita autumnata* in Northern Fennoscandia. Journal of Applied Ecology, 27:723–734.

Thomas, G. and P.R. Rowntree, 1992. The boreal forests and climate. Quarterly Journal of the Royal Meteorological Society, 118:469–497.

Thommessen, T., 1996. The early settlement of northern Norway. In: L. Larsson (ed.). The Earliest Settlement of Scandinavia and its Relationship with Neighbouring Areas. Acta Archaeologica Lundensia, Series in 8°, 24:235–240. Almquist and Wiksell International.

Thorpe, N., 2000. Contributions of Inuit Ecological Knowledge to Understanding the Impacts of Climate Change to Bathurst Caribou Herd in the Kitikmeot Region, Nunavut. MSc Thesis, Simon Fraser University, Vancouver.

Thorpe, N., N. Hakongak, S. Eyegetok and the Kitikmeot Elders, 2001. Thunder on the Tundra: Inuit Qaujimajatuqangit of the Bathurst Caribou. Tuktuk and Nogak Project, Ikaluktuuthak, Nunavut, 240pp.

Thorpe, N., S. Eyegetok, N. Hakongak and the Kitikmeot Elders, 2002. Nowadays it is not the same: Inuit Qaujimajatuqangit, climate and caribou in the Kitikmeot region of Nunavut, Canada. In: I. Krupnik and D. Jolly (eds.). The Earth is Faster Now: Indigenous Observations of Arctic Environmental Change, pp. 198–239. Arctic Research Consortium of the United States, Fairbanks, Alaska.

Tissue, D.T. and W.C. Oechel, 1987. Response of *Eriophorum vaginatum* to elevated CO_2 and temperature in the Alaskan tussock tundra. Ecology, 68:401–410.

Torn, M.S. and F.S. Chapin III, 1993. Environmental and biotic controls over methane flux from Arctic tundra. Chemosphere, 26:357–368.

Torsvik, V., L. Øvreås and T. Frede Thingstad, 2002. Prokaryotic diversity – magnitude, dynamics, and controlling factors. Science, 296:1064–1066.

Tremblay, N.O. and D.J. Schoen, 1999. Molecular phylogeography of *Dryas integrifolia*: glacial refugia and postglacial recolonization. Molecular Ecology, 8(7):1187–1198.

Tsapin, A.I., G.D. McDonald, M. Andrews, R. Bhartia, S. Douglas and D. Gilichinsky, 1999. Microorganisms from permafrost viable and detectable by 16SRNA analysis: a model for Mars. The Fifth International Conference on Mars, July 19–23, 1999, Pasadena, California. Abstract 6104.

Turchin, P. and G.O. Batzli, 2001. Availability of food and the population dynamics of arvicoline rodents. Ecology, 82:1521–1534.

Turchin, P. and I. Hanski, 1997. An empirically based model for latitudinal gradients in vole population dynamics. American Naturalist, 149:842–874.

Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen and H. Henttonen, 2000. Are lemmings prey or predators? Nature, 405:562–565.

Tyler, N.J.C. and N.A. Øritsland, 1989. Why don't Svalbard reindeer migrate? Holarctic Ecology, 12:369–379.

Väisänen, R.A, E. Lammi and P. Koskimies, 1998. Muuttuva Pesimälinnusto. Otava, Helsinki, 567pp.

van Herk, C.M., A. Aptroot and H.F. van Dobben, 2002. Long-term monitoring in the Netherlands suggests that lichens respond to global warming. The Lichenologist, 34(2):141–154.

Van Wijk, M.T., K.E. Clemmensen, G.R. Shaver, M. Williams, T.V. Callaghan, F.S. Chapin III, J.H.C. Cornelissen, L. Gough, S.E. Hobbie, S. Jonasson, J.A. Lee, A. Michelsen, M.C. Press, S.J. Richardson and H. Rueth, 2004. Long term ecosystem level experiments at Toolik Lake, Alaska and at Abisko, Northern Sweden: generalisations and differences in ecosystem and plant type responses to global change. Global Change Biology, 10:105–123.

Vardy, S.R., B.G. Warner and R. Aravena, 1997. Holocene climate effects on the development of a peatland on the Tuktoyaktuk Peninsula, Northwest Territories. Quaternary Research, 47(1):90–104.

Vartanyan, S.L., V.E. Garutt and A.V. Sher, 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. Nature, 362:337–340.

Velichko, A.A., 1995. The Pleistocene termination in Northern Eurasia. Quaternary International, 28:105–111.

Virtanen, T. and S. Neuvonen, 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. Oecologia, 120:92–101.

Vlassova, T.K., 2002. Human impacts on the tundra-taiga zone dynamics: the case of the Russian lesotundra. Ambio Special Report, 12:30–36.

Vourlitis, G.L. and W.C. Oechel, 1997. Landscape-scale CO_2, H2O vapor, and energy flux of moist-wet coastal tundra ecosystems over two growing seasons. Journal of Ecology, 85:575–590.

Vourlitis, G.L. and W.C. Oechel, 1999. Eddy covariance measurements of CO_2 and energy fluxes of an Alaskan tussock tundra ecosystem. Ecology, 80:686–701.

Vourlitis, G.L., W.C. Oechel, S.J. Hastings and M.A. Jenkins, 1993. The effect of soil moisture and thaw depth on CH_4 flux from wet coastal tundra ecosystems on the North slope of Alaska. Chemosphere, 26(1–4):329–337.

Wager, H.G., 1938. Growth and survival of plants in the Arctic. Journal of Ecology, 26:390–410.

Wagner, D., S. Kobabe, E.-M. Pfeiffer and H.-W. Hubberten, 2003. Microbial controls on methane fluxes from a polygonal tundra of the Lena Delta, Siberia. Permafrost and Periglacial Processes, 14:173–185.

Walbot, V., 1999. UV-B damage amplified by transposons in maize. Nature, 397:398–399.

Walker, D.A., 2000. Hierarchical subdivision of Arctic tundra based on vegetation response to climate, parent material and topography. Global Change Biology, 6(S1):19–34.

Walker, D.A. and M.D. Walker, 1991. History and pattern of disturbance in Alaskan Arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. Journal of Applied Ecology, 28:244–276.

Walker, D.A., E. Binnian, B.M. Evans, N.D. Lederer, E. Nordstrand and P.J. Webber, 1989. Terrain, vegetation, and landscape evolution of the R4D research site, Brooks Range foothills, Alaska. Holarctic Ecology, 12:238–261.

Walker, D.A., N.A. Auerbach, J.G. Bockheim, F.S. Chapin III, W. Eugster, J.Y. King, J.P. McFadden, G.J. Michaelson, F.E. Nelson, W.C. Oechel, C.-L. Ping, W.S. Reeburgh, S. Regli, N.I. Shiklomanov and G.L. Vourlitis, 1998. Energy and trace-gas fluxes across a soil pH boundary in the Arctic. Nature, 394:469–472.

Walker, D.A., J.G. Bockheim, F.S. Chapin III, W. Eugster, F.E. Nelson and C.L. Ping, 2001. Calcium-rich tundra, wildlife, and the 'Mammoth Steppe'. Quaternary Science Reviews, 20:149–163.

Walker, D.A., W.A. Gould, H.A. Maier and M.K. Raynolds, 2002. The Circumpolar Arctic Vegetation Map: AVHRR-derived base maps, environmental controls, and integrated mapping procedures. International Journal of Remote Sensing, 23:4551–4570.

Walker, M.D., 1995. Patterns of arctic plant community diversity. In: F.S. Chapin III and C. Körner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies, 113:1–18.

Walker, M.D., D.A. Walker and K.R. Everett, 1989. Wetland Soils and Vegetation, Arctic Foothills, Alaska. U.S. Fish and Wildlife Service Biological Report 89(7), 89pp.

Walker, M.D., D.A. Walker, K.R. Everett and S.K. Short, 1991. Steppe vegetation on south-facing slopes of pingos, central arctic coastal-plain, Alaska, USA. Arctic and Alpine Research 23(2):170–188.

Walker, M.D., D.A. Walker and N.A. Auerbach, 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. Journal of Vegetation Science, 5:843–866.

Walker, M.D., D.A. Walker, J.M. Welker, A.M. Arft, T. Bardsley, P.D. Brooks, J.T. Fahnestock, M.H. Jones, M. Losleben, A.N. Parsons, T.R. Seastedt and P.L. Turner, 1999. Long-term experimental manipulation of winter snow regime and summer temperature in Arctic and alpine tundra. Hydrological Processes, 13:2315–2330.

Walker, M.J.C., 1995. Climatic changes in Europe during the last glacial/interglacial transition. Quaternary International, 28:63–76.

Wallenius, T.H., 1999. Yield variations of some common wild berries in Finland in 1956 – 1996. Annales Botanici Fennici, 36(4):299–314.

Walter, B.P. and M. Heimann, 2000. A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate. Global Biogeochemical Cycles, 14:745–766.

Warren, M.S., J.K. Hill, J.A. Thomas, J. Asher, R. Fox, B. Huntley, D.B. Roy, M.G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S.G. Willis, J.N. Greatorex-Davies, D. Moss and C.D. Thomas, 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature, 414:65–69.

Wayne, L.G., D.J. Brenner, R.R. Colwell, P.A.D. Grimont, O. Kandler, M.I. Krichevsky, L.H. Moore, W.E.C. Moore, R.G.E. Murray, E. Stackebrandt, M.P. Starr and H.G. Truper, 1987. Report of the ad hoc committee on reconcilation of approaches to bacterial systematics. International Journal of Systematic Bacteriology, 37(4):463–464.

Webber, P.J., P.C. Miller, F.S. Chapin III and B.H. McCown, 1980. The vegetation: pattern and succession. In: J. Brown, P.C. Miller, L.L. Tieszen and F.L. Bunnell (eds.). An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska, pp. 186–218. Dowden, Hutchinson and Ross, Pennsylvania.

Weider, L.J. and A. Hobaek, 2000. Phylogeography and Arctic biodiversity: a review. Annales Zoologici Fennici, 37(4):217–231.

Welker, J.M., U. Molau, A.N. Parsons, C.H. Robinson and P.A. Wookey, 1997. Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. Global Change Biology, 3(S1):61–73.

Welker, J.M., J.T. Fahnestock and M.H. Jones, 2000. Annual CO_2 flux in dry and moist Arctic tundra: field responses to increases in summer temperatures and winter snow depth. Climatic Change, 44:139–150.

Weller, G., 2000. The weather and climate of the Arctic. In: M. Nuttall and T.V. Callaghan (eds.). The Arctic: Environment, People, Policy, pp. 143–160. Harwood Academic Publishers.

Wennerberg, L., 2001. Breeding origin and migration pattern of dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. Molecular Ecology, 10(5):1111–1120.

West, R.G., 2000. Plant Life of the Quaternary Cold Stages: Evidence from the British Isles. Cambridge University Press, 332pp.

Whalen, S.C. and W.S. Reeburgh, 1990. A methane flux transect along the Trans-Alaska Pipeline Haul Road. Tellus B: 42:237–249.

Whalen, S.C. and W.S. Reeburgh, 1992. Interannual variations in tundra methane emission: a 4-year time series at fixed sites. Global Biogeochemical Cycles, 6:139–159.

Whalen, S.C. and W.S. Reeburgh, 2001. Carbon monoxide consumption in upland boreal forest soils. Soil Biology and Biogeochemistry, 33:1329–1338.

White, A., M.G.R. Cannell and A.D. Friend, 2000. The high-latitude terrestrial carbon sink: a model analysis. Global Change Biology, 6:227–245.

Wickström, L.M., V. Haukisalmi, S. Varis, J. Hantula, V.B. Fedorov and H. Henttonen, 2003. Phylogeography of the circumpolar *Paranoplocephala arctica* species complex (Cestoda: Anoplocephalidae) parasitizing collared lemmings (*Dicrostonyx* spp.). Molecular Ecology, 12:3359–3371.

Wickström, L.M., V. Haukisalmi, S. Varis, J. Hantula and H. Henttonen, in press. A molecular phylogeny of anoplocephaline cestodes in rodents and lagomorphs. Systematic Parasitology.

Wielgolaski, F.E., S. Kjelvik and P. Kallio, 1975. Mineral content of tundra and forest tundra plants in Fennoscandia. In: F.E. Wielgolaski, P. Kallio and T. Rosswall (eds.). Fennoscandian Tundra Ecosystems: Plants and Microorganisms. Ecological Studies, 16:316–332.

Wielgolaski, F.E., L.C. Bliss, J. Svoboda and G. Doyle, 1981. Primary production of tundra. In: L.C. Bliss, O.W. Heal and J.J. Moore (eds.). Tundra Ecosystems: A Comparative Analysis, pp. 187–225. Cambridge University Press.

Wijk, S., 1986. Performance of *Salix herbacea* in an alpine snow-bed gradient. Journal of Ecology, 74:675–684.

Wiklund, C.G., A. Angerbjorn, E. Isakson, N. Kjellen and M. Tannerfeldt, 1999. Lemming predators on the Siberian tundra. Ambio, 28:281–286.

Wilke, C.O., J.L. Wang, C. Ofria, R.E. Lenski and C. Adami, 2001. Evolution of digital organisms at high mutation rates leads to survival of the flattest. Nature, 412:331–333.

Williams, M. and E.B. Rastetter, 1999. Vegetation characteristics and primary productivity along an arctic transect: implications for scaling up. Journal of Ecology, 87:885–898.

Williams, M., W. Eugster, E.B. Rastetter, J.P. McFadden and F.S. Chapin III, 2000. The controls on net ecosystem productivity along an Arctic transect: a model comparison with flux measurements. Global Change Biology, 6(S1):116–126.

Williams, M., E.B. Rastetter, G.R. Shaver, J.E. Hobbie, E. Carpino and B.L. Kwiatkowski, 2001. Primary production of an arctic watershed: an uncertainty analysis. Ecological Applications, 11:1800–1816.

Wilson, D.J., C.J. Krebs and T. Sinclair, 1999. Limitation of collared lemming populations during a population cycle. Oikos, 87:382–398.

Wilson, E.O., 1992. The Diversity of Life. Belknap Press.

Wookey, P.A., A.N. Parsons, J.M. Welker, J.A. Potter, T.V. Callaghan, J.A. Lee and M.C. Press, 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high Arctic plants. Oikos, 67:490–502.

Wookey, P.A., C.H. Robinson, A.N. Parsons, J.M. Welker, M.C. Press, T.V. Callaghan and J.A. Lee, 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high arctic polar semi-desert, Svalbard. Oecologia, 102:478–489.

Yoccoz, N.G. and R.A. Ims, 1999. Demography of small mammals in cold regions: The importance of environmental variability. In: A. Hofgaard, J.P. Ball, K. Danell and T.V. Callaghan (eds.). Animal Responses to Global Change in the North. Ecological Bulletin 47:137–144.

Young, S.B., 1971. The vascular flora of St. Lawrence Island with special reference to floristic zonation in the Arctic regions. Contributions from the Gray Herbarium, 201:11–115.

Yurtsev, B.A., 2001. The Pleistocene 'Tundra-Steppe' and the productivity paradox: the landscape approach. Quaternary Science Reviews, 20:165–174.

Zackrisson, O. and M.-C. Nilsson, 1992. Allelopathic effects by *Empetrum hermaphroditum* on seed germination of two boreal tree species. Canadian Journal of Forest Research, 22:1310–1319.

Zepp, R.G., T.V. Callaghan and D.J. Erikson III, 2003. Interactive effects of ozone depletion and climate change on biogeochemical cycles. Photochemical and Photobiological Sciences, 2(1):51–61.

Zimov, S.A., G.M. Zimova, S.P. Davidov, A.I. Davidova, Y.V. Voropaev, Z.V. Voropaeva, S.F. Prosiannikov, O.V. Prosiannikova, I.V. Semiletova and I.P. Semiletov, 1993. Winter biotic activity and production of CO_2 in Siberian soils: A factor in the greenhouse effect. Journal of Geophysical Research, 98:5017–5023.

Zöckler, C., 1998. Patterns in Biodiversity in Arctic Birds. WCMC Biodiversity Bulletin 3. World Conservation Monitoring Centre, Cambridge, 15pp.

Zöckler, C., 2002. A comparison between tundra and wet grassland breeding waders with special reference to the Ruff (*Philomachus pugnax*). Schriftenreihe für Landschaftspflege und Naturschutz 74. Federal Agency for Nature Conservation, Bonn, 115pp.

Zöckler, C. and I. Lysenko, 2000. Water Birds on the Edge: First Circumpolar Assessment of Climate Change Impact on Arctic Breeding Water Birds. WCMC Biodiversity Series No. 11. World Conservation Monitoring Centre, Cambridge, 20pp. plus Annex.

Zöckler, C., J.H. Mooij, I.O. Kostin, K. Günther and R. Bräsecke, 1997. Notes on the distribution of some bird species on the Taimyr Peninsula. Vogelwelt, 118:329–338.

Zöckler, C., S. Delany and W. Hagemeijer, 2003. Wader populations are declining – how will we elucidate the reasons? Wader Study Group Bulletin, 100:202-211.